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Associations among Fish Length, Dam Passage History, and Survival to Adulthood in Two At-Risk Species of Pacific Salmon

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Abstract

Threatened or endangered salmon and steelhead originating in the Snake River basin must pass through a series of eight major hydroelectric dams during their seaward migration. Understanding the effects of specific dam passage routes on lifetime survival for these stocks is essential for successful management. Juvenile fish may pass these dams via three primary routes: (1) spillways, (2) turbines, or (3) juvenile bypass systems, which divert fish away from turbines and route them downstream. Bypass systems may expose fish to trauma, increased stress, or disease. However, numerous studies have indicated that direct survival through bypass systems is comparable to and often higher than that through spillways. Some researchers have suggested that the route of dam passage affects mortality in the estuary or ocean, but this is complicated by studies finding that fish size affects the route of passage. We tested whether passage through bypass systems was associated with the probability of adult return after accounting for fish length and other covariates for two species of concern. We also investigated the association between fish length and the probability of bypass at dams and how this relationship could lead to spurious conclusions regarding effects of bypass systems on survival if length is ignored. We found that (1) larger fish had lower bypass probabilities at six of seven dams; (2) larger fish had a higher probability of surviving to adulthood; (3) bypass history had little association with adult return after accounting for fish length; and (4) simulations indicated that spurious effects of bypass on survival may arise when no true bypass effect exists, especially in models without length. Our results suggest that after fish leave the hydropower system, bypass passage history has little effect on mortality. Our findings underscore the importance of accounting for fish size in studies of dam passage or survival.

Four evolutionarily significant units from the Snake River basin that are listed for protection under the U.S. Endangered Species Act—spring/summer Chinook Salmon *Oncorhynchus tshawytscha*, fall Chinook Salmon, Sockeye

Salmon *O. nerka*, and steelhead *O. mykiss*—must pass a series of eight large hydroelectric dams, part of the Federal Columbia River Power System (hereafter, “hydropower system”), on their migrations to the Pacific

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Ocean as smolts and upon their return as adults. A question central to the management of these populations is whether the set of passage routes taken by juvenile salmon as they migrate through dams impacts their survival after they have completed their downstream migration.

Providing safe and effective downstream passage for juvenile salmon through the hydropower system has proven to be more problematic than providing adult upstream passage, which is achieved through the use of fish ladders. Juveniles have several possible routes by which to pass a dam (Figure 1). They can pass through spill, which is water passed directly through spill gates or through spillway weirs. Alternatively, juveniles can pass through the powerhouse, where the hydroelectric turbines are located. However, at seven of eight dams the majority of fish entering the powerhouse are diverted into a juvenile bypass system (hereafter, "bypass system"). Bypass systems are designed to divert fish in powerhouses away from turbine passage by using screens and a system of pipes that lead to a fish sampling and collection facility. From this facility, the fish can be directed into the dam tailrace or (at four of the dams) loaded onto barges or trucks in a transportation program designed to avoid passage through downstream dams.

Numerous studies have been conducted with tagged fish to estimate survival through these various passage routes. Estimates of direct survival (to a short distance below the dam) from recent studies for yearling Chinook Salmon and steelhead ranged from 90% to 100% across eight dams, with a mean of 97% (Axel et al. 2008; Beeman et al. 2008; Ploskey et al. 2011, 2012; Skalski et al. 2013a, 2013b; Weiland et al. 2013, 2015). Differences between estimates of direct survival through the spillway and bypass system (i.e., spill – bypass) from these studies were relatively small, ranging from –5.4 to 5.0 percentage points (mean = –0.8 percentage points) for Chinook Salmon and ranging from –3.9 to 3.0 percentage points (mean = –0.9 percentage points) for steelhead, indicating slightly higher survival on average through bypass systems. Estimated probabilities of bypass system passage from the previously mentioned studies ranged from 6.3% to 31.0% (mean = 18.1%) for yearling Chinook Salmon and from 5.9% to 41.9% (mean = 22.1%) for steelhead, while estimated probabilities of turbine passage at dams with a single powerhouse were much lower, ranging from 3.2% to 8.7% (mean = 5.4%) for yearling Chinook Salmon and from 1.8% to 5.8% (mean = 3.2%) for steelhead.

Although direct passage survival through bypass systems is relatively high, there is concern that delayed or long-term negative effects of bypass system passage are not detected by studies of direct survival. Sandford and Smith (2002) found that smolt-to-adult return probabilities (hereafter, "return probabilities") were frequently lower for fish that passed through a bypass system one or more

times than for fish that were never bypassed. This and other studies at the time led to the concept of delayed or latent mortality, which refers to mortality that occurs in the ocean or estuary based on stress, injury, or diminished condition experienced during downstream migration through the hydropower system. This idea was proposed by Schaller et al. (1999) and Deriso et al. (2001) in terms of the effect of dam passage in general. A review by Budy et al. (2002) suggested that the cumulative stress of passing through turbine or bypass systems might result in an increased mortality risk downstream. Petrosky and Schaller (2010) and Schaller et al. (2014) also attempted to incorporate the effects of the specific route of passage in their analyses. They found that ocean survival in Chinook Salmon was negatively correlated with an index of the expected number of times a group of fish passed through turbine or bypass system routes and with longer travel times through the hydropower system. Haeseker et al. (2012) used an index of spill proportion experienced by groups of fish as a surrogate for individual routes of passage and found that it was positively correlated with ocean survival. Buchanan et al. (2011) found that multiple bypass events for individual fish were associated with lower return probability in hatchery yearling Chinook Salmon and steelhead from the Snake River basin, but the timing and location of mortality could not be estimated.

Another possible explanation for reduced return probabilities of bypassed fish is that smaller fish and those in poorer condition tend to enter bypass systems with a higher probability (Zabel et al. 2005; Hostetter et al. 2015), and smaller fish and fish in poorer condition also have a lower return probability (Ward and Slaney 1988; Zabel and Williams 2002; Evans et al. 2014). This suggests that the apparent effects of bypass on return probability could be at least partly due to a correlation between bypass probability and fish size and condition and not due to bypass passage itself.

Even though numerous authors have demonstrated a difference in return probability between fish that experienced one or more bypasses compared to fish that were never bypassed, success in demonstrating a cause-and-effect relationship has been limited. One obvious causal mechanism is that impaired function due to injury or stress caused by bypass system passage could make smolts more susceptible to predation. Hostetter et al. (2012) found that steelhead with injuries or disease were more likely to be preyed upon by piscivorous birds in the Columbia River estuary. Although Budy et al. (2002) and other authors have discussed the potential for injury in fish passing through the pipes and over the screens of the bypass system, recent descaling and injury rates in bypass systems on the Snake and Columbia rivers are reportedly minimal (Ferguson et al. 2005) and much lower than those observed in the 1970s and early 1980s (Williams and

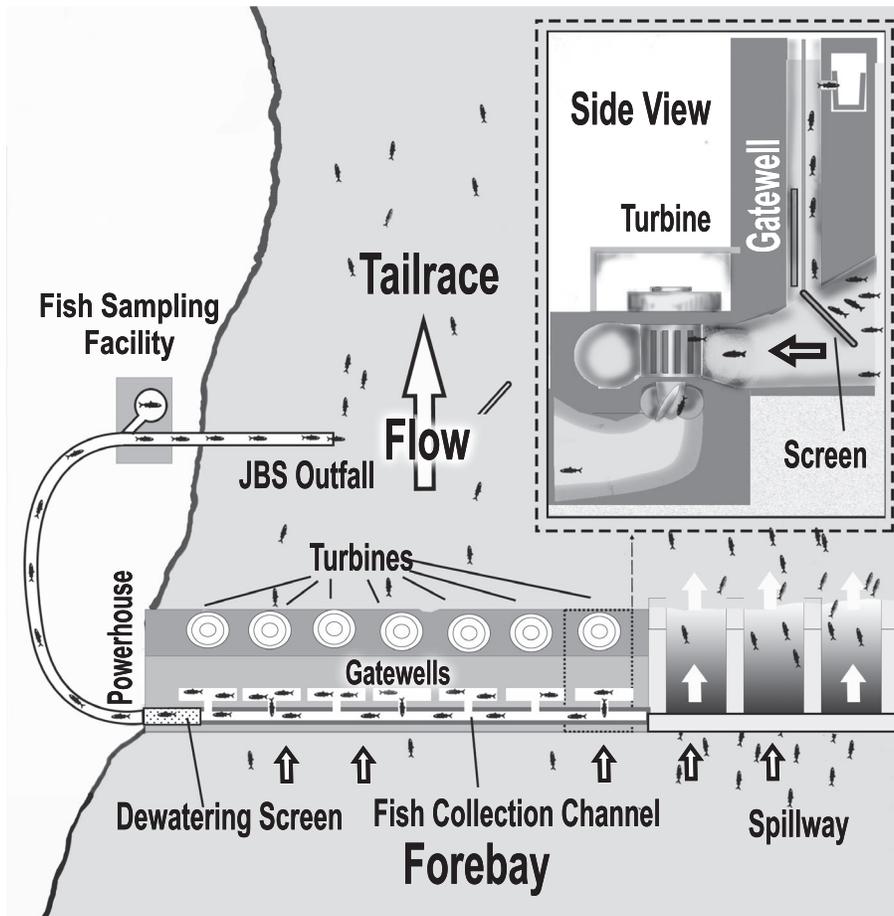


FIGURE 1. Overhead view of a hydroelectric dam with a powerhouse and juvenile bypass system (JBS) on the left and a spillway on the right. Inset shows a turbine intake with a bypass screen and entry into a gatewell and the collection channel for the bypass system.

Matthews 1995). Indeed, Sandford et al. (2012) found no significant difference in survival between bypassed and non-bypassed fish in seawater challenge experiments conducted on fish surviving passage through the hydropower system, suggesting that there was no bypass effect on subsequent survival.

Our main objective for this study was to investigate potential delayed effects of bypass passage on post-hydropower-system survival. We used an extensive data set on juvenile Chinook Salmon and steelhead tagged at or upstream of Lower Granite Dam, the first dam encountered during downstream migration. We attempted to isolate the delayed effects of bypass by only using fish that were known to have survived to downstream of the final dam in the hydropower system (Bonneville Dam). However, we also recognized the need to account for fish size in our investigations, given established associations between fish size and (1) the probability of bypass and (2) the probability of adult return. In this paper, we first investigate the relationship between fish size at tagging and the probability of passage through a juvenile bypass

system. We then investigate the association between fish length and return probability. We found that fish with more bypass events tended to have a lower return probability, but evidence of a causal effect of bypass passage was greatly diminished or disappeared when fish length was accounted for. Using simulated data, we also found that associations between bypass probability and fish length could lead to erroneous estimates of the negative effects of bypass passage on return probability when length was not accounted for.

METHODS

Data.— We used data on tagging and detection history for spring/summer Chinook Salmon and steelhead originating in the Snake River basin and implanted with PIT tags (Prentice et al. 1990a) as juveniles. Passive integrated transponder tags allow unique identification of individual fish from juvenile through adult life stages and are used extensively in salmon research. We downloaded the PIT tag data from the PTAGIS database (PSMFC 2017).

Tagging data included locations and times of tagging and release, rearing type (hatchery or wild), and information about the researcher and study associated with each individual fish. We restricted the data to include only those fish with FL (mm) recorded at the time of tagging. Detection data included the location and time of detection of individual fish at any site with PIT tag detection systems (Prentice et al. 1990b), providing information from both juvenile and adult life stages.

Detection of PIT-tagged juveniles is possible at seven of the eight hydroelectric dams on the lower Snake River and lower Columbia River (Figure 2). The Dalles Dam (river kilometer [rkm] 308; rkm 0=Columbia River mouth) is the only one of these dams without juvenile detection. Lower Granite Dam (rkm 695) is the furthest upstream dam and Bonneville Dam (rkm 234) is the furthest downstream in the hydropower system. The seven dams with tag detection have detectors installed in the bypass systems, but Bonneville Dam has additional detection in a sluiceway known as the “corner collector.” The corner collector is located next to one of the two powerhouses and is designed to pass fish via water collected from the surface and directed through a gently sloping flume for several-hundred feet to the tailrace. The final detection site for juveniles is in the Columbia River estuary: a detection array towed behind a pair of boats near rkm 50 (Ledgerwood et al. 2004). We will refer to this detection site as the “estuary towed array.” The main sites of adult detection during our study were the fish ladders at Bonneville Dam, McNary Dam (rkm 470), Ice Harbor Dam (rkm 538), and Lower Granite Dam.

Lower Granite Dam is the first dam encountered by fish migrating from upstream, and large numbers of fish are tagged at the dam each year for research studies, with a large proportion of those also measured at tagging. Although many fish that are tagged upstream of Lower Granite Dam are measured at tagging, tagging can occur from weeks to several months before those fish enter the hydropower system. Substantial growth can occur between tagging and entering the hydropower system. We therefore restricted our analyses to include fish that were tagged at Lower Granite Dam and those that were released at sites close enough upstream of Lower Granite Dam to reach the dam in less than 3 weeks on average. We used average travel times from each release location to Lower Granite Dam for fish in our data sets to determine which sites met this criterion. We further restricted the date of tagging to be between March 18 and June 30 and the date of release to be between April 1 and June 30. This restricted the set of fish to spring migrants and reduced the expected amount of growth before passing Lower Granite Dam. Juvenile bypass systems are turned off in the winter months and are typically turned back on around April 1. Restricting the release date to April 1 or later ensured that

all fish had an opportunity for detection. The Snake River trap (rkm 747), Clearwater River trap (rkm 756), and Grande Ronde River trap (rkm 795) were the only tagging and release sites upstream of Lower Granite Dam that met the combination of date and travel time restrictions.

We performed two different main analyses: one investigating the association between fish length and the probability of bypass; and the other investigating the associations of fish length and bypass history with the probability of returning as an adult. Additionally, we investigated the association between fish length and detection in the corner collector in comparison to the bypass system at Bonneville Dam. For all analyses, we used only fish that were detected either at Bonneville Dam or the estuary towed array as juveniles and therefore were known to be alive while in the hydropower system. Any mortality experienced by these fish thus occurred after passage through all of the dams.

For comparisons between fish length and the number of bypass events, we used fish that were detected as juveniles at Bonneville Dam or the estuary towed array during the years 2000–2014. This set of years was chosen to be consistent with those used for adult return models (see below) but allowed for a few additional years to increase sample sizes. Juvenile detections were not possible at Ice Harbor Dam until 2005, so data for those models were restricted to 2005–2014. Juvenile detection was not possible in the corner collector at Bonneville Dam until 2006, so all fish that were detected as juveniles at Bonneville Dam prior to that year passed through the bypass system at Bonneville Dam. For specific comparisons between bypass and corner collector passage at Bonneville Dam, we used data from the years 2006–2014.

For return probability modeling, we used fish detected as juveniles at Bonneville Dam or the estuary towed array in 2004–2014. We excluded years prior to 2004 because equipment for PIT tag detection of adults at Bonneville Dam was not consistent with modern configurations and because sample sizes in some years were low. The cutoff of 2014 allowed nearly complete returns at the time of data acquisition in early 2017. Any fish that was detected in a fish ladder (adult fishway) at one or more dams in any year after its juvenile migration year was known to be alive at Bonneville Dam and was recorded as an adult return. Therefore, we defined return probability as survival from the site of the last juvenile detection (Bonneville Dam or the estuary towed array) to Bonneville Dam as an adult. We excluded fish returning in less than 1 year (mini-jacks) from the return probability data because they may never reach the ocean and they experience different conditions than fish returning after one or more years in the ocean.

For all data sets, we excluded fish that were tagged with acoustic or radio tags and those that were known to

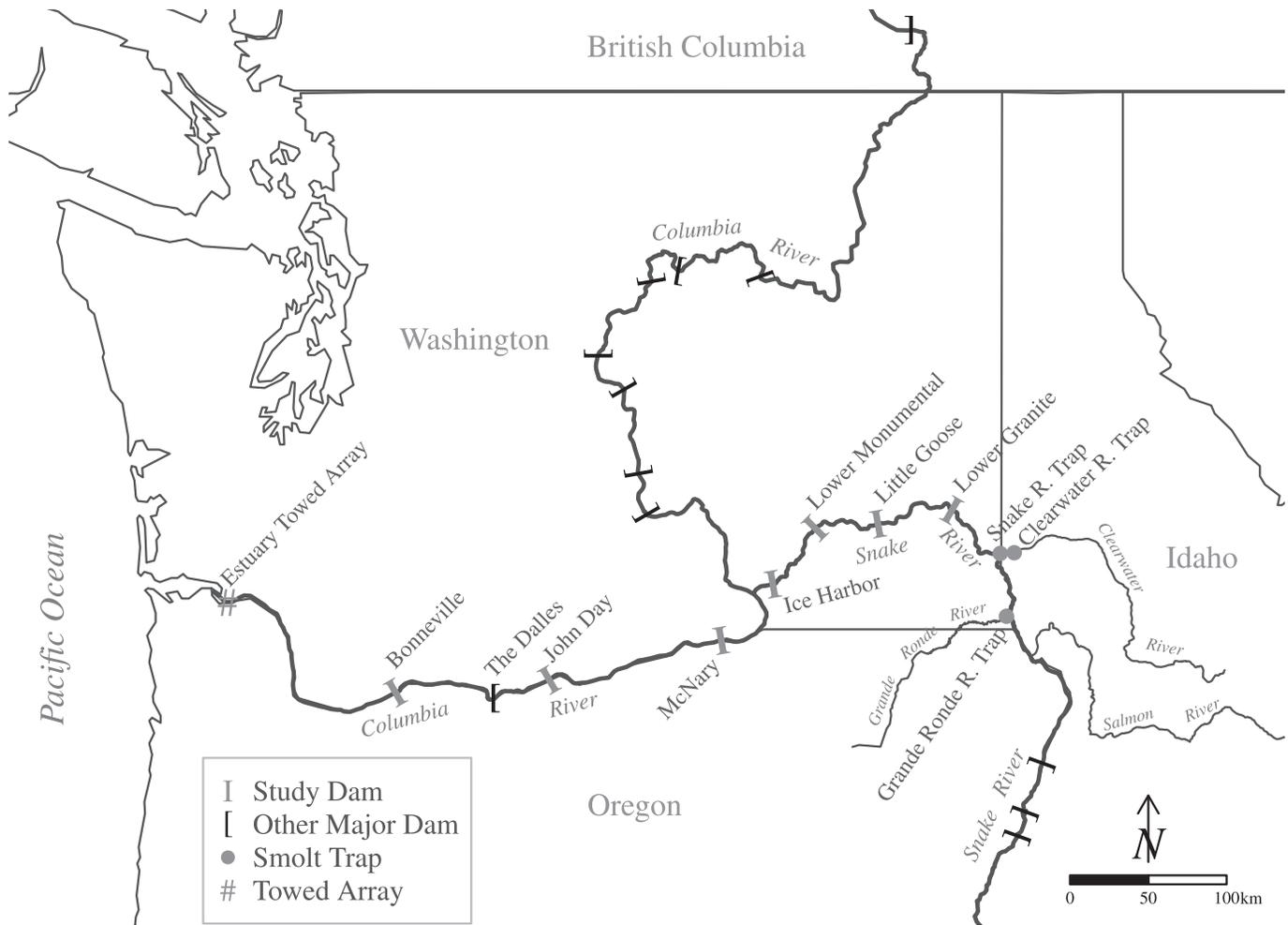


FIGURE 2. Map of the Snake River–Columbia River study area, showing locations of rivers, dams, the estuary towed array, and smolt traps used as tagging and release sites upstream of Lower Granite Dam. Study dams are those dams on the Snake River or lower Columbia River with PIT tag detection.

have been part of experiments involving multiple handling events or anesthetizations. We also excluded fish that were transported on barges since those fish are known to have different survival and have fewer opportunities for detection than fish that remain in the river. Some summaries of the data are provided in Supplemental Tables S1 and S2 available in the online version of this article.

Modeling of bypass probability.—Our objective was to describe relationships between fish length and the probability of passage through a bypass system after accounting for other sources of variation. We used all fish with FL measured at the time of tagging (with the restrictions described previously), where the site of tagging was either Lower Granite Dam or sites upstream. The length variable was standardized across rearing types and tagging locations and separately by species. We fitted separate models for each of the following dams: Lower Granite,

Little Goose (rkm 635), Lower Monumental (rkm 589), Ice Harbor, McNary, John Day (rkm 347), and Bonneville dams. We used fish that were tagged upstream of Lower Granite Dam for modeling the bypass probability at Lower Granite Dam. We used fish that were detected at the estuary towed array for modeling the bypass probability at Bonneville Dam. For all other dams, we used the combined set of fish tagged at or upstream of Lower Granite Dam.

We modeled bypass probability with binary logistic regression, where a fish was given a 1 for bypass system passage (bypassed) or a 0 for passage through another route (not bypassed). We used two classes of model, which were distinguished by their representation of time in the season. The first model class used standardized day of passage at Lower Granite Dam (*pday*) and was used for dams on the Snake River (Lower Granite, Little Goose, Lower

Monumental, and Ice Harbor dams). The second model class used standardized day of detection (*dday*) at Bonneville Dam or the estuary towed array, where days of passage or detection were measured continuously to account for the time of detection or passage. This model class was only used for dams on the Columbia River (McNary, John Day, and Bonneville dams). For fish tagged upstream of Lower Granite Dam, *pday* was (1) the day and time of last detection at Lower Granite Dam if a fish went through the bypass system or (2) the release day and time plus the predicted travel time to Lower Granite Dam for the particular release site, release day, and year if the fish was not detected at Lower Granite Dam. Predicted travel times were generated from linear models fitted to observed travel times (see Supplemental Materials for details). For fish tagged at Lower Granite Dam, *pday* was the day and time of release. The variable *pday* was therefore a mixture of observed and estimated days of passage at Lower Granite Dam for the fish tagged upstream of Lower Granite Dam. For the fullest possible models of each class, the probability (p_i) of being bypassed at a dam for individual fish i was assumed to be a logit-linear function of the day variables, release site (*rsite*), an indicator variable for wild rearing type (*wild*), and standardized length at tagging (*length*) with random intercepts by year and random slopes for date variables by year:

$$\begin{aligned} \text{logit}(p_i) = & (\beta_0 + b_{0,j}) + \beta_1 \text{length}_i + \beta_2 \text{wild}_i + \beta_{3,h} \text{rsite}_{hi} \\ & + (\beta_4 + b_{4,j}) \text{pday}_i + (\beta_5 + b_{5,j}) \text{pday}_i^2, \end{aligned} \quad (1)$$

$$\begin{aligned} \text{logit}(p_i) = & (\beta_0 + b_{0,j}) + \beta_1 \text{length}_i + \beta_2 \text{wild}_i + \beta_{3,h} \text{rsite}_{hi} \\ & + (\beta_6 + b_{6,j}) \text{dday}_i + (\beta_7 + b_{7,j}) \text{dday}_i^2, \end{aligned} \quad (2)$$

where β_0 is the fixed intercept; and β_1 , β_2 , and $\beta_{3,h}$ are the fixed effects of *length*, *wild*, and the h th level of *rsite*, respectively. The fixed effects for the continuous *pday*, *pday*², *dday*, and *dday*² are represented by β_4 through β_7 , respectively. The coefficients $b_{0,j}$ and $b_{4,j}$ through $b_{7,j}$ are random effects for the migration year j in which fish i migrated. The sum of $\beta_0 + b_{0,j}$ amounts to a separate intercept for each year, and the sum of slope coefficients such as $\beta_4 + b_{4,j}$ allows the slopes to vary by year. The random effects were assumed to be independent and normally distributed with mean of zero and a separate constant variance for each variable. The year and day effects and their combinations allowed us to account for variation in detectability at the dams due to river conditions and dam operations that vary with time but are difficult to measure and summarize for individual fish that are not detected. Models were constructed separately for each species and dam. Each model contained year, length, rearing type,

and release site and differed only in the inclusion of the various combinations of the fixed and random day variables, which resulted in six possible models per dam and species (see Supplemental Table S3).

We performed additional analyses for Bonneville Dam that involved a comparison between bypass system and corner collector passage only, which excluded spill and turbine routes. For these models, we were able to use all fish that were detected in the bypass system or corner collector at Bonneville Dam whether or not they were detected at the estuary towed array. The purpose of these models was to test whether the probability of passing through the bypass system relative to the corner collector was dependent on fish size. The response variable was 1 for fish entering the bypass system and 0 for fish entering the corner collector. We used the same set of explanatory variables as was used in the main analyses of bypass probability for Bonneville Dam.

We should note that we originally modeled bypass probabilities separately for each rearing type. We found that relationships between length and bypass probability were very similar between the rearing types, so in the interest of simplifying the analyses we decided to combine the data and include an indicator variable for rearing type without interactions. This improved the power to estimate a length relationship while still allowing the rearing types to differ in their bypass probabilities.

Modeling of adult return probability.—Our objective was to test for associations between the probability of returning as an adult and bypass history after accounting for fish length and other factors that account for variation in return probability over time. We investigated three alternative variables to describe bypass system passage (bypass) history: (1) a binary variable for detection in any bypass system (yes or no); (2) a categorical variable with categories for 0, 1, 2, 3, or 4 or more bypass events; and (3) a continuous variable for the number of bypass events. The first bypass variable allowed us to assess whether one or more bypass events had a different effect than zero events. The second bypass variable allowed each number of events to have a different effect, which could capture nonlinear or threshold effects of the number of bypass events. The third bypass variable targeted linear effects of the number of bypass events. Data were from fish detected as juveniles at Bonneville Dam or the estuary towed array, and potential covariates included a categorical indicator variable for detection at the estuary towed array. Fish detected at both Bonneville Dam and the estuary towed array were included only once in the data set, and the date at the estuary towed array was used as the detection date covariate for those fish. The time variables were a categorical variable for juvenile migration year and a continuous variable for day of year at either Bonneville Dam or the estuary towed array, which were standardized separately for each location. Hatchery and wild fish were modeled

together using an indicator variable for wild fish. Models were fitted separately for each species.

We also fitted separate models for fish that were tagged at Lower Granite Dam and those that were tagged upstream of Lower Granite Dam. All fish that were tagged at Lower Granite Dam go through the bypass system, but no non-bypassed fish are tagged or measured at Lower Granite Dam. This causes the data to be unbalanced due to the large number of fish tagged at Lower Granite Dam and makes bypass effects related to bypass at Lower Granite Dam almost completely confounded with effects related to fish tagged at Lower Granite Dam if data from all tagging sites are combined. Fitting separate models by tagging site thus allowed us to avoid potential bias due to confounding between bypass effects and potential effects associated with fish tagged at Lower Granite Dam (e.g., population of origin, tagging effects, tag loss, and fish condition). For models with fish tagged upstream of Lower Granite Dam, we included a categorical variable for tagging site. Fish tagged upstream of Lower Granite Dam had a maximum of seven possible bypass events, and those tagged at Lower Granite Dam had six; the exception was in 2004, when there were six and five possible bypass events, respectively, due to no detection at Ice Harbor Dam. We combined data from the Clearwater River trap with that from the Snake River trap due to small sample sizes at the Clearwater River trap and the close proximity of the two traps (10 km apart). The length variable was standardized separately by species and main tagging location (upstream of or at Lower Granite Dam), across rearing types, and across smolt trapping locations (for fish tagged upstream of Lower Granite Dam).

We assumed that the binary variable for adult return followed a binomial distribution where the probability of return was a logit-linear function of the explanatory variables. For the fullest possible model, the logit of the probability of returning as an adult (s_i) for individual fish i was

$$\begin{aligned} \text{logit}(s_i) = & (\beta_0 + b_{0,j}) + (\beta_1 + b_{1,j})day_i + (\beta_2 + b_{2,j})day_i^2 \\ & + \beta_3wild_i + \beta_4ETA_i + \beta_{5,h_i}rsite_{h_i} + \beta_6length_i \\ & + \beta_7bypass_i, \end{aligned}$$

where β_0 is the fixed intercept; and β_1 through β_6 are the fixed effects of standardized day at Bonneville Dam or the estuary towed array (day), associated day squared (day^2), indicator for wild rearing type ($wild$), indicator for last detection at the estuary towed array (ETA), h th level of release site ($rsite$), length at tagging ($length$), and bypass history ($bypass$), respectively. The bypass variable here is generic for one of the three possible bypass variables (binary, categorical, or continuous) and would have one level for either the binary or continuous version and four levels for the categorical version. The random effects $b_{0,j}$, $b_{1,j}$,

and $b_{2,j}$ are associated with the migration year j for fish i for the intercept, day , and day^2 variables, respectively. Similar to the models for bypass probability, the random effects allow separate values of the coefficients for the intercept, day , and day^2 variables by year. The random effects were assumed to be independent and normally distributed with a mean of zero and a separate constant variance for each variable.

We used Akaike's information criterion (AIC; Akaike 1973; Burnham and Anderson 2002) as a measure of the relative predictive ability of a set of competing models. For the bypass probability analysis, we fitted a set of six models for each dam and species, where each model contained the variable for length (see Supplemental Materials for the set of models). For the return probability analyses, we first constructed a set of models based on possible combinations of the fixed covariates and random effects that did not include the fish length or bypass variables (we will refer to these as "covariate models"). For each species, there were 12 possible covariate models for fish tagged upstream of Lower Granite Dam and 12 possible covariate models for fish tagged at Lower Granite Dam (see Supplemental Materials for the model sets). For both the bypass probability and return probability analyses, we selected the best model within each set based on AIC, where lower AIC values indicate better performance. For the return probability analysis, we then added the variables of interest (length and/or bypass) to the best covariate models. In all cases, we recorded AIC and the P -values associated with the length and/or bypass variables. Our objectives were to test whether the parameter estimates for the variables of interest were different from zero and to assess whether the variables of interest improved the predictive ability of the models. We interpreted the strength of evidence in favor of particular models or variables by using a combination of the size of differences in AIC between models, associated Akaike weights (Burnham and Anderson 2002), and the degree of P -values of individual effects. We used 95% CIs to express uncertainty in parameter estimates.

We used the R computing environment (R Core Team 2017) for all aspects of the analyses; we specifically used the R package lme4 (Bates et al. 2015) for fitting the generalized linear mixed models. The data and R code used in the analyses for this paper are available online at <https://github.com/jrfaulkner/bypass-length-sar>.

Simulations.—The association between fish length and the probability of entering bypass systems makes it difficult to separate the individual effects of these variables on the probability of returning as an adult. If length truly did have an association with return probability but the number of bypass events did not, we wanted to know whether the number of bypass events would still come up as a significant predictor in return probability models due to its

correlation with fish length. One way to address this question is by simulating data with both the number of bypasses and the return probability associated with length—but with no independent effect of the number of bypass events on return probability. If the number of bypass events then appeared as a significant predictor in models fitted to such simulated data, where fitted models did not include length, this would suggest that an apparent bypass effect on return probability in real data could actually be explained by the association with fish length alone. Conversely, if the bypass effect was not significant in return probability models fitted to the simulated data but was significant in models fitted to real data, this would suggest (1) an effect of bypass passage that was separate from length or (2) an association between bypass and some other unmeasured variable that was also associated with return probability.

To address these questions, we used simulations to assess the chance of detecting a bypass effect on return probability if one did not actually exist. We did this by generating data from the best return probability models of observed data that contained length and other covariates but no bypass effects; we then fitted models with a term for the number of bypasses to those simulated data and recorded the results. For each species and tagging location, we generated 1,000 simulated data sets. We fixed the data for the observed number of bypasses, length, and other measured covariates and only simulated the adult return data for each fish. By fixing these covariates, the observed association between length and the number of bypasses was preserved.

We simulated data by first drawing a set of model parameter values from a multivariate normal distribution for which the mean was the vector of parameter estimates (both fixed and conditional random effects) from the best model with length and covariates (but no bypass effect) fitted to the real data and the covariance matrix was the estimated joint covariance of the associated model parameters (see Supplemental Materials for details). Using the random draw of model parameters and the static covariate data, we then calculated predicted probabilities of adult return for each fish. Adult return data (0 or 1) were simulated for each fish by drawing from Bernoulli distributions given the set of predicted adult return probabilities. This process was replicated for a second set of simulations in which the data-generating model was the best covariate-only model within each species and tagging location. This second set of simulations was used for testing the effect of the number of bypass events when there was no true association between return probability and bypass or return probability and length.

For each simulated data set, we fitted three models. The null model (M0) contained just the fixed and

random covariate terms. The second model (M1) added the term for number of bypass events, and the third model (M2) added the length variable to M1. A fourth model (M3), which was M0 with length added, was also fitted for comparison. For each model, we recorded the parameter estimate for the number of bypasses and associated *P*-values and the model AIC values. For M1 and M2, we recorded the proportion of simulations in which the parameter estimate for the number of bypasses was negative and had a *P*-value less than 0.05. For the model with number of bypasses and no length, we also recorded the proportion of simulations in which the parameter estimate for the number of bypasses was negative and the AIC was lower than that of the null model. We also calculated the mean and 0.025 and 0.975 quantiles of the parameter estimates for the number of bypasses across simulations.

If there was no association between the number of bypasses and the return probability, then we would expect the bypass variable to have a negative estimate approximately 50% of the time and we would expect it to be both negative and significant at the 0.05 level (two-sided test) approximately 2.5% of the time when models including the bypass variable were fitted to return probability data simulated using a length effect but no bypass effect. These percentages are those expected by chance alone when there is no bypass effect on return probability. We would also expect that any apparent effect of bypass would be diminished when length was also included in the fitted model.

RESULTS

Bypass Probability

For both Chinook Salmon and steelhead at most dams, we found strong evidence that the probability of entering the bypass system at a dam was negatively associated with fish length after accounting for the other variables (Table 1; Figure 3). The addition of the length variable to these models greatly reduced the model AIC (and, equivalently, resulted in small *P*-values for length) for each species at most dams (Table 1). For Chinook Salmon at Lower Granite Dam, there was only weak to moderate evidence for an association with length ($P=0.07$; AIC dropped by 1.2). There was no evidence for an association with length for either species at Bonneville Dam when bypass system passage was compared to all other routes. However, when bypass system passage was compared to only the corner collector route at Bonneville Dam, there was strong evidence that the probability of entering the bypass system was negatively associated with length for each species (Table 1; Figure 3). The strongest associations between bypass probability and length (based on

TABLE 1. Estimated slope parameters and associated 95% CIs, change in Akaike's information criterion (AIC; dAIC), and *P*-values for standardized length variables from models for bypass probability by species and dam (see text for definitions). Parameter values represent the estimated change in log odds of bypass at a dam associated with a 1-SD increase in standardized length after accounting for other variables in the models. Estimates are from the best models with length selected by AIC. Here, dAIC represents the change in AIC associated with adding the length variable to the corresponding model without length for each dam. The sample size (*n*) is also shown for each data set. Dams are Lower Granite Dam (LGD), Little Goose Dam (LGSD), Lower Monumental Dam (LMD), Ice Harbor Dam (IHD), McNary Dam (MCD), John Day Dam (JDD), and Bonneville Dam (BVD); BVCC represents BVD when non-bypassed fish are from the corner collector only.

Dam	<i>n</i>	Estimate	95% CI	dAIC	<i>P</i> -value
Chinook Salmon					
LGD	8,231	-0.066	-0.138, +0.006	-1.2	0.0729
LGSD	88,393	-0.210	-0.237, -0.184	-249.6	<0.0001
LMD	88,393	-0.179	-0.209, -0.149	-138.0	<0.0001
IHD	76,604	-0.221	-0.263, -0.179	-107.2	<0.0001
MCD	88,393	-0.226	-0.250, -0.202	-343.6	<0.0001
JDD	88,393	-0.329	-0.361, -0.297	-413.2	<0.0001
BVD	14,729	0.015	-0.078, +0.107	1.9	0.7548
BVCC	62,970	-0.230	-0.257, -0.203	-282.7	<0.0001
Steelhead					
LGD	11,036	-0.112	-0.175, -0.049	-10.3	0.0005
LGSD	52,409	-0.161	-0.186, -0.136	-162.4	<0.0001
LMD	52,409	-0.174	-0.202, -0.146	-148.6	<0.0001
IHD	37,075	-0.203	-0.250, -0.157	-72.0	<0.0001
MCD	52,409	-0.260	-0.292, -0.229	-268.3	<0.0001
JDD	52,409	-0.293	-0.326, -0.259	-293.9	<0.0001
BVD	8,437	-0.057	-0.179, +0.065	1.2	0.3617
BVCC	31,220	-0.069	-0.105, -0.033	-12.1	0.0002

magnitude of the parameter for length) occurred at McNary and John Day dams for both species. For each species, the form of the best model for bypass probability varied by dam, but most included random slopes for the effects of *day* and *day*² (see Supplemental Table S4).

Return Probability

For Chinook Salmon that were tagged upstream of Lower Granite Dam, the best return probability model without length or bypass effects included fixed effects for rearing type, release site, site of last detection, and day of year and included random year effects for the intercept (Supplemental Table S6). Adding the length variable resulted in a decrease in AIC of 4.6 and a *P*-value of 0.005, thus providing moderate to strong evidence of an association between length and return probability (Table 2). When length was not included in the model, adding the binary bypass variable increased AIC, adding the categorical bypass variable decreased AIC by 1.5 with an associated *P*-value of 0.039, and adding the continuous number of bypasses decreased AIC by 2.5 with a *P*-value of 0.036. This suggests moderate evidence of an association between return probability and the number of bypass events when length was not in the model. When length was included in the model, adding the binary bypass

variable resulted in an increase in AIC, adding the categorical bypass variable reduced AIC by 1.1 with a *P*-value of 0.060, and adding the continuous variable for number of bypasses reduced AIC by 1.3 with a *P*-value of 0.074. This suggests weak to moderate evidence of an association with the number of bypasses after accounting for length. For the model with length and a continuous number of bypasses, the odds of adult return increased by an estimated multiplicative factor of 1.35 for every 1-SD increase in length (16.1 mm; 95% CI = 1.07–1.70) and the odds of return decreased by a multiplicative factor of 0.85 for each additional bypass event (95% CI = 0.71–1.02; Figure 4).

For Chinook Salmon tagged at Lower Granite Dam, the best model for just the covariates included fixed effects for rearing type and day and random year effects for the intercept and the slope of day. Adding length to this model reduced AIC by 20.8 with *P* < 0.0001, indicating strong evidence of an association between length and return probability. In contrast, when length was not in the model, adding the binary bypass variable increased AIC, while adding the categorical bypass variable decreased AIC by 1.2 with an associated *P*-value of 0.056 and adding the continuous number of bypasses decreased AIC by 1.7 with a *P*-value of 0.053. These results indicate weak to

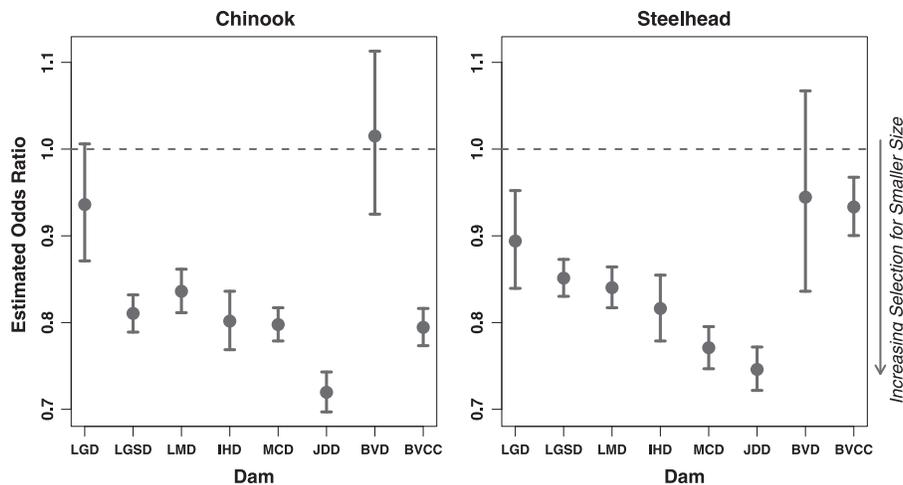


FIGURE 3. Parameter estimates (with associated 95% CIs) for multiplicative effect of a 1-unit increase in standardized length on the odds of entering the bypass system at a dam. Results are shown for each dam and each species (Chinook Salmon and steelhead). The horizontal line at 1.0 is used as a reference to assess difference of the estimates from 1.0. An odds ratio less than 1.0 indicates that smaller fish are more likely to pass through a bypass system than through other routes. Dams are Lower Granite Dam (LGD), Little Goose Dam (LGSD), Lower Monumental Dam (LMD), Ice Harbor Dam (IHD), McNary Dam (MCD), John Day Dam (JDD), and Bonneville Dam (BVD); BVCC represents BVD where bypass is compared to the corner collector only.

moderate evidence of an association between bypass history and return probability when not accounting for length. After length was included in the model, adding either the binary variable ($P=0.329$) or the categorical variable ($P=0.111$) for bypass did not improve AIC but adding the continuous variable for the number of bypasses decreased AIC by 0.1 with a P -value of 0.147. These results suggest that any association between a bypass variable and return probability could potentially be explained by length, but there is still weak evidence for a bypass effect beyond that due to length. For the model with length and a continuous number of bypasses, the odds of adult return increased by an estimated multiplicative factor of 1.30 for every 1-SD increase in length (15.3 mm; 95% CI = 1.17–1.45) and the odds of return decreased by a multiplicative factor of 0.94 for each additional bypass event (95% CI = 0.87–1.02; Figure 4).

For steelhead that were tagged upstream of Lower Granite Dam, the best model built from only the covariates included fixed effects for rearing type, tagging site, the site of last detection, *day*, and *day*² and a random year effect for the intercept. Adding length to the model resulted in a decrease in AIC of 14.4 and $P < 0.0001$, thereby providing strong evidence that return probability was associated with length. Adding any of the bypass variables resulted in increases in AIC whether or not length was included in the model ($P > 0.40$ for each bypass variable), suggesting no evidence that return probability for steelhead was associated with bypass history. For the model with length and a continuous number of bypasses, the odds of adult return increased by an estimated

multiplicative factor of 1.38 for every 1-SD increase in length (27.6 mm; 95% CI = 1.18–1.61) and the odds of return increased by a multiplicative factor of 1.00 for each additional bypass event (95% CI = 0.89–1.13; Figure 4).

For steelhead tagged at Lower Granite Dam, the best covariate model included fixed effects for rearing type and day of year and included random year effects for the intercept and slope on day of year. Adding length to this model resulted in a reduction in AIC of 116.5 and $P < 0.0001$, thus presenting very strong evidence for an association between length and return probability. When length was not included in the model, adding the binary bypass variable decreased AIC by 3.6 with an associated P -value of 0.017, adding the categorical bypass variable decreased AIC by 1.6 with a P -value of 0.048, and adding the continuous number of bypasses decreased AIC by 3.5 with a P -value of 0.019. These results suggest moderate to strong evidence for an association between bypass history and return probability when not accounting for length. However, when length was incorporated into the model, adding the binary bypass variable decreased AIC by 0.1 with a P -value of 0.144, adding the categorical bypass variable increased AIC by 2.1 with a P -value of 0.207, and adding the continuous number of bypasses increased AIC by 0.8 with a P -value of 0.271. This indicates that after accounting for length, there was weak to no evidence remaining for an association between bypass history and return probability. For the model with length and a continuous number of bypasses, the odds of adult return increased by an estimated multiplicative factor of 1.64 for every 1-SD increase in length (30.7 mm; 95% CI = 1.50–1.79) and the

TABLE 2. Results for return probability models by species and tag site, where tag sites are Lower Granite Dam (LGD) or sites upstream of LGD (ULGD). Also shown are the number of individuals (smolts) and number of adult returns for each data set used for model fitting. Each row gives the terms in the model and the number of parameters (np), the difference in Akaike's information criterion (AIC; Δ AIC) compared to the model with lowest AIC, the model Akaike weight (w), and P -values associated with respective length (len) or bypass variables in the model. Each model had a set of covariates ($covs$; described in the text) that were common to all models within a particular species and tag site. The bypass variables are the binary bypass indicator (byp), the categorical number of bypasses ($byp.cat$), and the number of bypasses ($n.byp$).

Species	Tag site	Smolts	Returns	Model	np	Δ AIC	w	P -value	
								Length	Bypass
Chinook Salmon	ULGD	6,348	100	$covs$	6	5.9	0.02		
				$covs + len$	7	1.2	0.18	0.005	
				$covs + byp$	7	7.1	0.01		0.349
				$covs + byp.cat$	10	3.9	0.05		0.039
				$covs + n.byp$	7	3.5	0.06		0.036
				$covs + byp + len$	8	2.8	0.08	0.006	0.527
				$covs + byp.cat + len$	11	0.1	0.30	0.010	0.060
				$covs + n.byp + len$	8	0.0	0.32	0.011	0.074
Chinook Salmon	LGD	71,171	638	$covs$	6	20.9	0.00		
				$covs + len$	7	0.1	0.29	<0.001	
				$covs + byp$	7	21.3	0.00		0.192
				$covs + byp.cat$	10	19.7	0.00		0.056
				$covs + n.byp$	7	19.2	0.00		0.053
				$covs + byp + len$	8	1.2	0.17	<0.001	0.329
				$covs + byp.cat + len$	11	0.6	0.23	<0.001	0.111
				$covs + n.byp + len$	8	0.0	0.31	<0.001	0.147
Steelhead	ULGD	8,572	295	$covs$	7	14.4	0.00		
				$covs + len$	8	0.0	0.52	<0.001	
				$covs + byp$	8	16.1	0.00		0.537
				$covs + byp.cat$	11	20.8	0.00		0.800
				$covs + n.byp$	8	16.3	0.00		0.738
				$covs + byp + len$	9	1.3	0.27	<0.001	0.400
				$covs + byp.cat + len$	12	6.5	0.02	<0.001	0.827
				$covs + n.byp + len$	9	2.0	0.19	<0.001	0.980
Steelhead	LGD	29,077	659	$covs$	6	116.4	0.00		
				$covs + len$	7	0.1	0.33	<0.001	
				$covs + byp$	7	112.9	0.00		0.017
				$covs + byp.cat$	10	114.9	0.00		0.048
				$covs + n.byp$	7	112.9	0.00		0.019
				$covs + byp + len$	8	0.0	0.34	<0.001	0.144
				$covs + byp.cat + len$	11	2.2	0.11	<0.001	0.207
				$covs + n.byp + len$	8	0.9	0.22	<0.001	0.271

odds of return decreased by a multiplicative factor of 0.95 for each additional bypass event (95% CI = 0.88–1.04; Figure 4).

We note that rearing type was important for both species in all of the models that included length, where wild fish had a higher probability of return than hatchery fish. Since hatchery fish are longer on average than wild fish, the effect of rearing type was masked and seemingly unimportant in some models without length. However, retaining rearing type in the models with length helped to more accurately estimate the length effect.

Simulations

Our simulations showed that a spurious bypass effect could arise more frequently than by chance, whether fish length was accounted for in the fitted model or not (Table 3). When the covariate-only model (M0) was the data-generating model, there were more negative estimates and more significant negative estimates than expected, with larger differences from expected occurring for the groups tagged upstream of Lower Granite Dam. This effect was likely induced by a combination of small sample sizes for groups with multiple bypass events and low overall return probabilities.

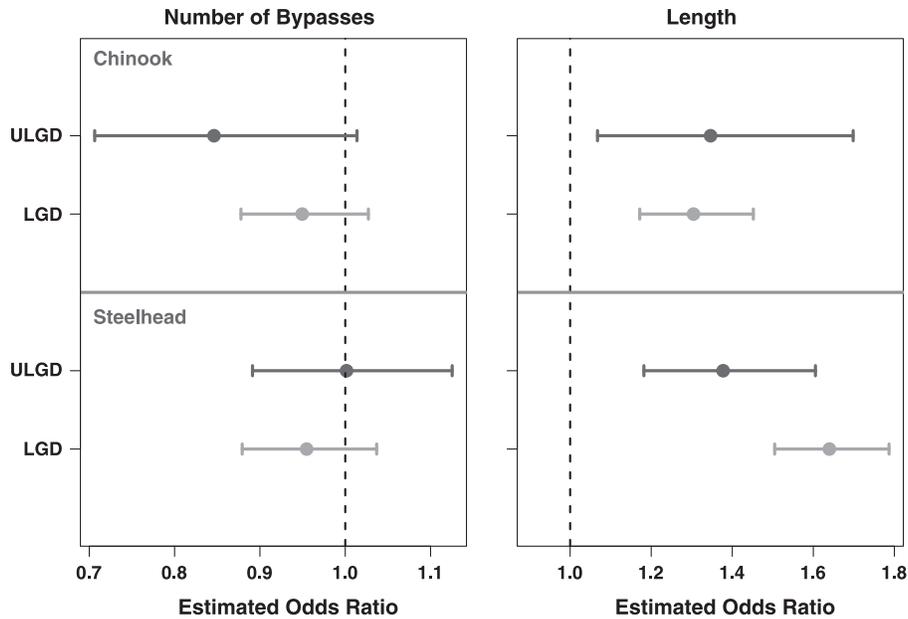


FIGURE 4. Parameter estimates (with associated 95% CIs) for the multiplicative effects of the number of bypass events and standardized length on the odds of adult return. Estimates are from models that included both the number of bypass events and fish length. Results are shown by species (Chinook Salmon and steelhead) and tagging location (at Lower Granite Dam [LGD] or upstream of LGD [ULGD]). The vertical lines at 1.0 are used as a reference to assess difference of the estimates from 1.0. A parameter estimate less than 1.0 for the number of bypasses indicates that fish with more bypass events are less likely to return as adults, and a parameter estimate greater than 1.0 for length indicates that larger fish are more likely to return.

TABLE 3. Simulation results, showing the percentage of simulations with indicated outcome by species and tagging location. Tagging locations are Lower Granite Dam (LGD) or sites upstream of LGD (ULGD). Models are as follows: M0 = covariates (*covs*); M1 = *covs* + number of bypass events (*n.byp*); M2 = *covs* + *n.byp* + fish length (*len*); and M3 = *covs* + *len*. Data models are those used to generate the simulated data, and fitted models are those fitted to the simulated data. Outcomes include a negative parameter estimate for the effect of *n.byp* (*n.byp*(-)) and whether the associated *P*-value was also less than 0.05 or whether Akaike's information criterion (AIC) for the specified fitted model was less than that from the corresponding model without *n.byp* fitted to the same data. Shown for comparison is the expected percentage of times each outcome would be true given the data-generating model and no association between length and *n.byp*.

Data model	Fitted model	Outcome	Expected (%)	Chinook Salmon		Steelhead	
				ULGD (%)	LGD (%)	ULGD (%)	LGD (%)
M0	M1	<i>n.byp</i> (-)	50.0	60.9	57.2	63.5	58.6
		<i>n.byp</i> (-) and <i>P</i> < 0.05	2.5	4.9	3.5	5.8	3.1
		<i>n.byp</i> (-) and lower AIC vs. M0	7.8	13.0	9.8	14.3	12.0
M3	M1	<i>n.byp</i> (-)	50.0	74.8	76.3	74.4	93.8
		<i>n.byp</i> (-) and <i>P</i> < 0.05	2.5	10.1	10.1	9.1	34.8
		<i>n.byp</i> (-) and lower AIC vs. M0	7.8	24.1	24.8	22.3	55.3
M3	M2	<i>n.byp</i> (-)	50.0	59.5	75.4	59.8	60.0
		<i>n.byp</i> (-) and <i>P</i> < 0.05	2.5	3.7	9.9	6.0	5.5
		<i>n.byp</i> (-) and lower AIC vs. M3	7.8	11.8	24.6	12.7	14.8

When the model with covariates and fish length (M3) was the data-generating model, spurious bypass effects occurred more frequently than by chance, especially when length was not accounted for in the fitted model. For the fitted model that did not include length (M1), a negative parameter estimate for the effect of the number of

bypasses occurred in greater than 74% of the simulations for each species and tagging location when no bypass effect actually existed; a significant and negative parameter estimate occurred in at least 9% of simulations for each species and tagging location. Additionally, M1 had a lower AIC than M0 when there was also a negative

estimate for a bypass effect in greater than 21% of simulations for each species and tagging location. After accounting for length in the fitted model (M2), the proportion of negative estimates and the proportion of negative and significant estimates declined but were still greater than those expected by chance. The simulation results were similar for Chinook Salmon at both tagging locations and for steelhead tagged upstream of Lower Granite Dam. The results for steelhead tagged at Lower Granite Dam indicated that when length was not accounted for, a significant negative estimate of bypass effect was much more likely in comparison with the results for Chinook Salmon and for steelhead tagged upstream of Lower Granite Dam.

Mean parameter estimates across simulations were similar to parameter estimates from models fitted to the observed data for all species and tagging locations except for Chinook Salmon tagged upstream of Lower Granite Dam (Supplemental Figure S2). The estimated effect of bypass from the model fitted to observed data for Chinook Salmon from upstream of Lower Granite Dam was much more negative than the mean of parameter estimates from the simulated data. This suggests that the association between fish length and the number of bypass events does not completely explain the apparent effect of the number of bypass events on return probability seen in the observed data.

DISCUSSION

We investigated associations between fish length and the probability of entering juvenile bypass systems at dams; furthermore, we investigated associations among fish length, bypass history, and the probability of returning as an adult for fish known to have survived through a system of hydropower dams. Our main findings were as follows: (1) there was strong evidence for a negative association between fish length and the probability of bypass at most dams, (2) there was strong evidence for a positive association between fish length and return probability, and (3) there was moderate to weak evidence for a negative association between bypass history and return probability, which weakened further when fish length was included in the models.

We found strong evidence for a negative association between the length of fish at tagging and bypass probability for both steelhead and Chinook Salmon at six of the seven study dams, with smaller fish being more likely to enter a bypass system. There was a negative association with length at Lower Granite Dam for both species, but the evidence was not strong for Chinook Salmon. At Bonneville Dam, there was no evidence for an association with fish length when the bypass system was compared to all other routes combined, but there was strong evidence

that the bypass system was more likely to pass smaller fish in comparison to the corner collector alone (see discussion below). One caveat is that Lower Granite and Bonneville dams had much smaller sample sizes, so the statistical power to detect length relationships was diminished for those data sets. The general layout of Bonneville Dam is also very different from the layouts of the other dams in the hydropower system. Each of the other six study dams comprises a continuous structure that spans the river with a powerhouse at one end and a spillway at the other. Bonneville Dam consists of two powerhouses and a spillway, which are separated by natural islands so that each is essentially in its own channel, with no direct route between powerhouses or the spillway. Bonneville Dam also has the corner collector, which collects water and fish from the surface and diverts them away from the second powerhouse. These differences in dam structure can be expected to produce different fish passage behaviors that could depend on size. Finally, it should also be noted that experimental structures designed to guide fish away from the powerhouses were in periodic use at both Lower Granite Dam (2000, 2002, and 2006) and Bonneville Dam (2008–2010), which could have affected bypass size selectivity at those sites during those years.

Our results confirm those of Zabel et al. (2005) and Hostetter et al. (2015), who found that length was an important predictor of bypass probability for Snake River Chinook Salmon and steelhead at Snake River dams, with smaller fish being more likely to enter a bypass system. Brown et al. (2013) also found that the bypass probability of yearling Chinook Salmon released from Lower Granite Dam decreased with increasing FL on average across multiple dams. Buchanan et al. (2011) investigated associations between bypass passage and fish length, but they found mixed results, with significant size selectivity evident in some release groups but not in others. Similar to our study, Buchanan et al. (2011) found no relationship between size and bypass probability at Lower Granite Dam or Bonneville Dam. Buchanan et al. (2011) did not restrict release sites to those closest to Lower Granite Dam, however, and they did not account for time since tagging in their analyses. This likely resulted in a large number of measured lengths that were not representative of true lengths once fish entered the hydropower system.

Two general mechanisms that could explain size selection in bypass systems are the vertical distribution of fish as they approach a dam and the physical ability of fish to escape the bypass screens. The horizontal distribution of fish as they approach a dam will also affect their route of passage depending on whether they approach on the spillway side or the powerhouse side; however, to the best of our knowledge this distribution is likely not dependent on fish size. The depth at which fish are swimming as they approach a dam will affect their route of passage (Li et al.

2015, 2018). Surface collection structures, such as spillway weirs, sluiceways, or the corner collector, collect fish from the first few meters of the surface of the river. Entrances to standard spillways are 10–15 m below the surface, while the upper ceilings of entrances to turbine intake bays are 15–25 m below the surface for dams on the Snake and Columbia rivers. Bypass diversion screens extend approximately 6–12 m below the declining turbine intake ceilings and are designed to collect the fish orienting along the ceiling as they enter the intake. This means that fish must reach depths of approximately 20–35 m to escape the screens and enter the turbines. Li et al. (2015) found that (1) yearling Chinook Salmon and steelhead that passed through juvenile bypass systems approached dams significantly deeper than those that passed through spillways and (2) fish that passed through turbines approached deeper than those that passed through bypass systems. If swim depth is related to fish size, then this could explain size differences by passage route.

Li et al. (2015, 2018) did not investigate relationships between length and swim depth but did find that subyearling Chinook Salmon, which are smaller than yearlings, traveled deeper than yearling Chinook Salmon; however, they noted that this could have been due to higher water temperatures occurring when subyearling Chinook Salmon migrated in late spring and summer. Fish size and level of smoltification have been documented to affect buoyancy (Saunders 1965; Pinder and Eales 1969), with larger and more smolted fish being more buoyant and more likely to migrate higher in the water column. This suggests that the larger, more smolted fish are more likely to pass through spill and surface routes than through bypasses or turbines. This is consistent with our findings that smaller fish were more likely to enter bypass systems compared to other routes, especially given that the probability of entering turbines is low at most dams. Our results for bypass system passage in comparison with the corner collector at Bonneville Dam further support this idea, where larger fish were more likely to pass through the corner collector, which is a surface route. The reason we did not find an effect of length on bypass system passage at Bonneville Dam when comparing to all other routes could be related to the higher turbine passage at Bonneville Dam. The probability of turbine passage is approximately 20–30% for both species at Bonneville Dam (Ploskey et al. 2012), which is much higher than at the other dams and results from having two powerhouses and a relatively low probability of being guided by the bypass screens. If fish passing through turbines at Bonneville Dam are generally smaller and those passing via spill and the corner collector are larger, then the combination of these groups would have a wide range of lengths, which could explain the results for bypass system passage versus the other routes combined.

The second possible mechanism of size selection by bypass systems is the ability of a fish to escape when it senses the change in water velocity created by the bypass screens and gatewells (Zabel et al. 2005; Enders et al. 2012). Larger and more physically fit fish have greater strength and swim speed, allowing them a better chance to escape the bypass screens. This suggests that among fish entering the powerhouse, those that are guided into the bypass system would be smaller and in poorer condition, on average, than those that pass via turbines. However, it provides no information regarding differences in size or condition between fish that enter the powerhouse and those that pass via spill.

It was not possible in our study to distinguish whether the association between length and bypass probability was due to differential passage between the powerhouse and the spillway or whether it was driven by selection between bypass and turbine passage given entry to the powerhouse. This distinction can only be made if the exact route of passage is known for each fish, and we only had information on whether a fish passed through a bypass system or not. Further research using data from dam passage studies that employ radiotelemetry or acoustic tags, which allow accurate determination of each passage route, should focus on associations between length, spatial distribution, and route of passage.

Our second major finding was the strong evidence for an association between fish length and return probability for both species, with larger fish having a higher probability of returning as adults. Size has been found to be a significant factor in survival during the first ocean year for seven species of Pacific salmon *Oncorhynchus* spp. (Holtby et al. 1990; Koenings et al. 1993; Miyakoshi et al. 2001; Farley et al. 2007; Cross et al. 2009) as well as other related anadromous salmonids, such as Atlantic Salmon *Salmo salar* (Saloniemi et al. 2004), Brown Trout *Salmo trutta*, and Arctic Char *Salvelinus alpinus* (Jensen et al. 2017). A mass review of marine survival studies focused on anadromous salmonids spanning a range of species and tag types found that fish length was one of the most frequent significant predictors of fish survival (Drenner et al. 2012).

Within the Columbia River basin, Tipping (2011) found that size at tagging had a significant effect on adult return probabilities for Chinook Salmon in 7 of 10 release groups. Releases of hatchery fish in the Deschutes River (a tributary that enters the Columbia River upstream of two dams in the hydropower system) also showed length to be a strong predictor of adult return (Beckman et al. 1999). Evans et al. (2014) found that juvenile length and condition were strong predictors of adult survival in steelhead from the Columbia and Snake rivers. In a study of Chinook Salmon from the Willamette River (a tributary of the Columbia River that enters downstream of the

hydropower system) based on scale analysis, Claiborne et al. (2011) found a significant effect of ocean entry size on adult survival in 3 of 4 years examined. However, Romer et al. (2013) did not find a significant effect of fish length on adult survival and return in two coastal groups of steelhead tagged in 2009. Zabel and Williams (2002) found that larger yearling Chinook Salmon were more likely to return as adults, and Zabel et al. (2005) and Passolt and Anderson (2013) reported a size-dependent survival pattern in the hydropower system.

Three mechanisms controlling size-selective mortality in teleost fish were suggested by Sogard (1997): differences in vulnerability to predation, susceptibility to starvation, and tolerance of environmental extremes. Currently, the two primary hypotheses explaining observations of higher survival by larger smolts are the critical size hypothesis (Beamish and Mahnken 2001; Farley et al. 2007) and size-related susceptibility to predation (Holtby et al. 1990; Henderson and Cass 1991; Saloniemi et al. 2004; Cross et al. 2009). The critical size hypothesis suggests that juvenile salmonids must reach some minimum critical size to survive their first winter at sea. This may be related to energy reserves or other factors involved in surviving the winter. Smaller smolts grow more slowly (Ruggerone et al. 2009) and thus are less likely to reach this critical size in time, especially during years with poor ocean productivity (Holtby et al. 1990; Saloniemi et al. 2004). This hypothesis also explains the differing strength of size-dependent survival between years. In studies of Atlantic Salmon, Coho Salmon *O. kisutch*, Pink Salmon *O. gorbuscha*, and Sockeye Salmon, size was identified as a good predictor of survival within years but the strength of the relationship varied between years (Holtby et al. 1990; Henderson and Cass 1991; Saloniemi et al. 2004; Cross et al. 2009).

Size-specific consumption by predators can be due to limitations of mouth gape size, behavioral selection, or size-dependent escape ability of the prey. Size-selective predation on juvenile salmonids has been documented in the early phase of ocean residence (Parker 1971; Healy 1982; Hargreaves and LeBrasseur 1986; Holtby et al. 1990). Since predation risk is generally assumed to decrease with increasing size, size-specific survival patterns due to predation seem likely to vary between years for the same reasons as the critical size hypothesis. Regardless of the specific mechanism or combination of mechanisms, at least in some years there are strong indications that larger juvenile salmon survive at higher rates during their first year of ocean residence.

As predators themselves, larger salmon smolts have a wider selection of prey available due to their larger gape sizes and faster swim speeds, allowing faster growth in the ocean and a lower probability of starvation. Larger salmon also mature faster and return at earlier ages (Scheuerell 2005; Tattam et al. 2015), which means that

they have a shorter duration of exposure to mortality risks in the ocean.

Our third major finding was the moderate to weak evidence for a negative association between bypass history and return probability when length was not accounted for, whereas evidence for that association weakened or disappeared when length was taken into account. For Chinook Salmon tagged at Lower Granite Dam and steelhead tagged at or upstream of Lower Granite Dam, bypass variables were nonsignificant before accounting for length or they became nonsignificant when length was also included in the model. Only for Chinook Salmon tagged upstream of Lower Granite Dam was the number of bypass events marginally significant after accounting for length.

The negative association between fish length and bypass probability was the most likely explanation for the cases where evidence for a bypass effect on return probability diminished or disappeared after accounting for fish length. Smaller fish were more likely to experience multiple bypasses, so the number of bypasses essentially functioned as a surrogate for length in the model. It is clear from our models of bypass passage that smaller fish have a higher probability of bypass passage at most dams when compared to larger fish, which translates into a higher expected number of bypass events during migration. If length is not explicitly accounted for in a model of adult return, inclusion of a variable for the number of bypass events (or even for the number of spillway passage events) in the model could act as a surrogate for fish length. If the bypass variable does not contain additional explanatory power beyond that offered by the correlation with length, then one would expect the apparent effect of the bypass variable on return probability to disappear when length is included in the same model. We saw this phenomenon occur for all steelhead and for Chinook Salmon tagged at Lower Granite Dam. Our simulations further indicated that a false signal for the number of bypasses could be detected as significant more often than by chance when there is no true association with return probability due to the association between fish length and the probability of entering bypass systems.

When evidence for a negative effect of bypass on return probability remains after accounting for length and other confounding variables, it suggests that there could be delayed or long-term effects of multiple bypass events on fish. Our results for Chinook Salmon tagged upstream of Lower Granite Dam provide some support for this possibility. Passage through bypass systems at multiple dams could be causing an accumulation of trauma and stress that results in impaired condition, reduced energy reserves, and increased susceptibility to predation in the estuary and ocean, as has been suggested by others (e.g., Budy et al. 2002; Schaller et al. 2014). Although this seems like

a biologically reasonable assumption, the available direct empirical evidence in support of it is mixed.

Maule et al. (1988) reported that blood measures of stress increased cumulatively as fish passed through points in the bypass system at McNary Dam, and several studies summarized by Ferguson et al. (2005) showed increased indices of stress in bypass systems at other dams, but indices returned to pre-stress levels in a relatively short time. Barton et al. (1986) found that multiple handling events of juvenile Chinook Salmon resulted in cumulative physiological stress. Barton and Schreck (1987) identified a relationship between multiple stress events and increased metabolic rate in juvenile steelhead, suggesting that multiple stress events (e.g., multiple bypasses) could result in decreased energy reserves. Mesa (1994) exposed juvenile Chinook Salmon to multiple stressors and found preferential predation by Northern Pikeminnow *Ptychocheilus oregonensis*, an important predator of salmonids in the hydropower system (Rieman et al. 1991), on the stressed individuals compared to controls in a short period, but there were no differences in predation after 1 h of recovery. Sandford et al. (2012) investigated the delayed effect of bypass passage on post-hydropower-system survival by collecting juvenile Chinook Salmon at Bonneville Dam and holding them in seawater tanks; those authors found no effect of bypass history on survival, but they could not account for predation or factors that only occur in the natural environment.

The proportion of yearling Chinook Salmon and steelhead experiencing some level of descaling due to bypass system passage ranged from 1.5% to 9.6% in studies of bypass passage at individual dams in the hydropower system (Ferguson et al. 2005). Multiple bypass events would certainly increase the probability that a fish experiences some level of descaling or trauma. Evans et al. (2014) found that steelhead with general bodily injuries had higher susceptibility to avian predation but that the level of descaling was not influential. Gadomski et al. (1994) reported that experimentally descaled juvenile Chinook Salmon had short-term physiological stress responses but were not more susceptible to predation than controls. Descaled juvenile salmon can suffer high mortality due to an impaired ability to osmoregulate when exposed to seawater within 1 d of the descaling event, but they can recover and survive at normal levels if allowed to remain in freshwater for a few days (Bouck and Smith 1979; Zydlewski et al. 2010). Juveniles migrating through the hydropower system would have sufficient time to recover before reaching the estuary.

It is difficult to explain why multiple bypass events would affect return probability more for Chinook Salmon tagged upstream than for those tagged at Lower Granite Dam and why they would affect Chinook Salmon but not steelhead, especially when we consider that Chinook

Salmon from upstream of Lower Granite Dam had the smallest sample size and the lowest number of returning adults compared to the other groups. We cannot rule out the possibility that the results for Chinook Salmon from upstream of Lower Granite Dam reflected a spurious relationship driven by small sample sizes. The direction of the bypass effect for Chinook Salmon tagged upstream of Lower Granite Dam was not consistent from year to year, based on the direct return probability estimates for each number of bypass events (see Supplemental Materials). We were also unable to account for all of the confounding variables that are associated with both bypass probability and adult return, such as fish condition and disease status, which may have differed among the tagging locations. Given these uncertainties, the evidence for a causal relationship between the number of bypass events and return probability for Chinook Salmon tagged upstream of Lower Granite Dam is still questionable.

Another important point is that the probability of experiencing a particular number of bypass events decreases rapidly for each additional number of events greater than two (Supplemental Table S2). This means that the proportion of the migrating populations of yearling Chinook Salmon and steelhead experiencing more than three bypass events is low. Our results indicated that return probability for fish with zero to two or three bypass events tended to be similar (Supplemental Figures S3–S6). Therefore, the overall return probabilities for these migrating populations would not be affected much by any delayed mortality experienced by fish that undergo multiple bypass events.

We were only able to investigate the effects of passing through bypass systems and were not able to investigate the effects of passing through turbines or other routes due to a lack of PIT tag detection in those routes. Turbine passage can result in rapid pressure changes and strikes with blades and other structures in the turbine housing. Multiple passage events through turbines would be expected to lead to accumulated trauma and stress and increased susceptibility to predation. Ferguson et al. (2007) found that juvenile salmon had significant delayed mortality between 15 and 46 km downstream after passing through turbines at McNary Dam; those authors concluded that the likely cause was impaired sensory systems, leading to increased vulnerability to predation. Studies on the delayed effects of turbine passage or other routes of passage on survival beyond the hydropower system are needed but are lacking, mostly due to limitations in tagging and detection technologies.

Others have attempted to estimate the effect of passage through either bypass systems or turbines on survival to adulthood by creating an index of powerhouse passage for release groups of fish (Petrosky and Schaller 2010; Schaller et al. 2014; McCann et al. 2017). There are different ways of calculating these indices based on various assumptions

about passage route probabilities, but the resulting group-level metric is an estimate of the expected number of powerhouse passage events experienced by each fish across the set of dams passed during the migration. These methods do not account for the known bypass events of individual fish, and there is no way to know which fish actually went through turbines. There is also no way of knowing whether the individual fish that actually went through turbines or bypass systems had a lower probability of return. The authors of those studies found negative associations between survival to adulthood and indices of the number of powerhouse passages, but they did not account for fish size or condition in their models. Even if they would have included fish characteristics, modeling approaches that use temporal or spatial aggregations of fish as observational units can only account for individual fish characteristics as group-level summary statistics, which results in the loss of important information. There is a need to be able to account for individual fish characteristics as well as individual passage route histories in our modeling of survival to adulthood, but doing so directly is not possible given current data limitations.

Ideally, tag detection would be present in every route of passage, and we could then explicitly link the actual route of passage to the fate of individual fish. Monitoring of PIT tags in this way is costly and not a viable option in the near future. Active (radio or acoustic) tags allow for determination of the passage route with fairly high precision, but the current life of those tags is short and they cannot be used to obtain data on adult returns. Application of both PIT tags and active tags to fish could provide a solution, but such tagging efforts are costly and burdensome on the fish, resulting in small sample sizes and results that are potentially not representative of the population at large. A secondary solution could be to develop more sophisticated models that would take advantage of all available tagging data and would account for the unknown passage routes (spill or turbine) of individual fish by using probabilistic relationships that depend on fish length and other covariates, such as in a Bayesian framework. Such models may offer more accurate predictions of the effects of specific passage routes on adult returns than are currently available. This is an area of our current research.

In conclusion, based on our results and those of others, it is imperative that researchers investigating return probability or bypass probability include the length of individual fish in their models. If other data related to measures of individual fish health exist (e.g., condition factor, disease status, etc.), then those data should also be included. Neglecting these important sources of information could lead to spurious modeling results, which could misinform management decisions and lead to misallocation of limited resources.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.