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UNITED STATES DISTRICT COURT
DISTRICT OF OREGON

NATIONAL WILDLIFE FEDERATION, *et al.*	Civil No. 01-640-RE
Plaintiffs,	
v.	2008 DECLARATION OF RICHARD W. ZABEL, Ph.D.
NATIONAL MARINE FISHERIES SERVICE, *et al.*	
Defendants.	

Background

1. I am a mathematical statistician for the Fish Ecology Division in the Northwest Fisheries Science Center of the National Marine Fisheries Service, an agency of the National Oceanic and Atmospheric Administration (hereafter "NOAA Fisheries"). I serve as the head of the Quantitative Ecology Team, which includes 11 researchers (7 of whom have Ph.D.s). Our research is focused on developing statistical analyses and models to support management of threatened and endangered salmon populations. My group works on a broad range of topics, including survival analyses, population viability analyses, climate and climate change modeling, growth modeling, stream ecology, and evolutionary ecology.

2. I have worked at NOAA Fisheries for the past nine years. Previous to that I worked at the University of Washington as a Research Scientist and a post-doctoral Research Associate. I received a B.S. (with honors and distinction) and M.S. from the University of Michigan, Ann Arbor and a Ph.D. (in 1994) from the University of Washington, in the Quantitative Ecology and Resource Management program. I have published 28 peer-reviewed papers on salmon ecology and modeling. My curriculum vitae is attached as Exhibit 1 listing these publications.

3. I led the development of the Comprehensive Passage (COMPASS) model. This was a collaborative effort lasting more than two years that involved not only several researchers from my team, but also scientists from throughout the Northwest, including scientists from state, federal, and tribal agencies. I coordinated dozens of team meetings during the model development process. I also gave several presentations to the Independent Scientific Advisory Board (ISAB) for purposes of model review.

4. In preparing this declaration, I have reviewed the following documents: FCRPS biological opinion, the manual for the COMPASS model(NOAA AR B.367[1]), the ISAB's Review of latent mortality (ISAB 2007, NOAA AR B.210[2]), the latest ISAB review of COMPASS (ISAB 2008[3]), and the declarations filed on behalf of the plaintiffs' motions for summary judgment by Frederick Olney and Edward Bowles.

5. I will begin by providing a detailed description of the COMPASS model. I will then describe how COMPASS was used to produce model results for the 2008 FCRPS Biological Opinion. Finally, I will respond to concerns raised in the Bowles and Olney depositions and clarify some misrepresentations.

COMPASS Model

Background

6. COMPASS simulates the migration of cohorts of juvenile salmonids through the hydropower system (from the forebay of Lower Granite Dam to the tailrace of Bonneville Dam) and return rate of juveniles from below Bonneville Dam to adults at Lower Granite Dam. The primary management purpose for COMPASS is to compare the effects of alternative hydropower operations on salmon survival through the hydropower system and adult return.

7. The foundation of the model is based on estimates of survival and travel time within the hydropower system derived from hundreds of thousands of juvenile fish PIT-tagged (tagged with Passive Integrated Transponder tags) between 1997 and 2007, thousands of radio-

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[1] NMFS. 2008. Comprehensive Passage (COMASS) Model - version 1.1. Review draft February 2008. NMFS, Northwest Fisheries Science Center, Seattle, Washington, 2/1/2008.

[2] ISAB (Independent Scientific Advisory Board). 2007. Latent mortality report: review of hypotheses and causative factors contributing to latent mortality and their likely relevance to the "Below Bonneville" component of the COMPASS model. ISAB, Report 2007-1, Portland, Oregon, 4/6/2007.

[3] ISAB (Independent Scientific Advisory Board). 2008. Review of the Comprehensive Passage (COMPASS) model – version 1.1. ISAB, Report 2008-3, Portland, Oregon, 6/2/2008.

tagged fish from dozens of telemetry studies at the dams, and 4-5 years of adult return data from fish PIT tagged earlier as juveniles. In fact, the FCRPS is one of the most data-rich ecological systems in the world. The fundamental principle of the model is that every algorithm that enters into it is based on empirical data. As such, model complexity is determined by data availability. The one drawback to this approach is that in some cases, the modeling team was required to choose simpler algorithms to simulate processes we knew were more complex. We believe, though, that this parsimonious approach produces a much more objective model than one where complexity surpasses the data.

8. COMPASS is supported by extensive documentation (NOAA AR B.367[4]). We documented every model algorithm and the data supporting it. In addition, we provided an unprecedented amount of documentation of model diagnostics and sensitivity analyses. To account for alternative points of view, COMPASS was developed to accommodate multiple hypotheses. For instance, reservoir survival can be modeled using several alternative relationships, one of which was developed by CRITFC. Also, the post-Bonneville component represents several alternative hypotheses, each of which was proposed by separate parties (IDFG, USFWS, BPA, and NOAA). Because many different opinions existed on how to develop the model, we sought extensive external review. The ISAB reviewed various aspects of the model four times (ISAB 2006 (NOAA AR B.208),[5] ISAB 2006 (NOAA AR B.209),[6] ISAB 2007

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[4] NMFS. 2008. Comprehensive Passage (COMASS) Model - version 1.1. Review draft February 2008. NMFS, Northwest Fisheries Science Center, Seattle, Washington, 2/1/2008.

[5] ISAB (Independent Scientific Advisory Board). 2006. Review of the COMPASS mode. ISAB, Report 2006-2, Portland, Oregon, 3/15/2006.

[6] ISAB (Independent Scientific Advisory Board). 2006. December 2006 review of the COMPASS model, version 1.0. ISAB, Report 2006-7, Portland, Oregon, 12/15/2006.

(NOAA AR B.210),[7] and ISAB 2008[8]), and the iterative approach greatly enhanced the quality of the model. In addition, COMPASS has favorably undergone the peer-review process, with a paper addressing the model recently published in the journal *Hydrobiologia* (Zabel et al. 2008: NOAA AR B.548)[9].

9. As new data become available, the modeling team will continue to develop the model to provide new functionality and to support new algorithms. Currently we are actively involved in improving several components of the model – hydrological modeling, model uncertainty, user's interface – and we are expanding the model to represent the Upper Columbia River. Approximately 25 scientists from state, federal and tribal agencies are taking part in this new phase of development, demonstrating strong support throughout the region for the model.

10. COMPASS is clearly the best available model to assess the effects of alternative hydropower system operations on salmon survival. Dozens of scientists in the region have contributed to its development, and it has received rigorous review by the ISAB and other peer reviewers. It represents survival during downstream migration through the hydropower system and through adult return. It is supported by an extraordinary amount of data and fits well to those data. Finally, it has demonstrated predictive capabilities.

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[7] ISAB (Independent Scientific Advisory Board). 2007. Latent mortality report: review of hypotheses and causative factors contributing to latent mortality and their likely relevance to the "Below Bonneville" component of the COMPASS model. ISAB, Report 2007-1, Portland, Oregon, 4/6/2007.

[8] ISAB (Independent Scientific Advisory Board). 2008. Review of the Comprehensive Passage (COMPASS) model – version 1.1. ISAB, Report 2008-3, Portland, Oregon, 6/2/2008.

[9] Zabel, R.W., J. Faulkner, S.G. Smith, et al. 2008. Comprehensive Passage (COMPASS) Model: a model of downstream migration and survival of juvenile salmonids through a hydropower system. Hydrobiolgia 609:289–300. A prepublication "accepted for publication" draft of this paper was available prior to issuance of the FCRPS Biop on May 5, 2008. The final published paper is attached to this Declaration as Exhibit 2.

Downstream passage

11. Downstream passage operates on a daily time step and is represented by four modules: reservoir survival, travel time, dam passage, and hydrological processes. The reservoir survival module relates survival to flow, water temperature, spill, travel time and travel distance. We used model selection routines with PIT-tag survival estimates to choose the best fitting relationships among a suite of alternative models. This method removes subjectivity from the choice of reservoir survival relationships. The travel time module moves fish downstream and spreads out cohorts through time. Travel time relationships were fit to PIT-tag data in a manner similar to the survival relationships. We also incorporated the proportion of fish passing through the spillway as a factor in the travel time relationships, which had the effect of moving fish downstream more quickly as more fish pass through the spillway. We provided dozens of plots demonstrating survival and travel time fits to PIT-tag data (COMPASS documentation; NOAA AR B.367).

12. The dam passage module represents the proportion of fish passing through each possible passage route through a dam (bypass, spillway, turbines, etc.) and the estimated survival through each route. Fish collected in bypass systems can be routed onto barges for transport according to transportation schedule. We based dam survival estimates on radio-telemetry studies. Passage route algorithms were based on a combination of PIT-tag data and radio telemetry data. The collaborative modeling team recently put substantial effort into improving this module, which greatly improved our ability to predict the proportion of fish transported, a key model output.

13. The hydrological component simulates daily flows, temperatures and spill at each project. Based on river geometry, river flow is translated to water velocity, an important factor for fish travel time. Input data are derived from two sources. We used historical data during

1997-2008 when we compared model outputs to PIT-tag data. In this mode of model operation, we attempted to simulate historical conditions as closely as possible. When we ran the model in a prospective manner (e.g., during comparisons of alternative scenarios for the BiOp), we used HYDSIM (hydrological model run by BPA) output for the seventy-year water record (1929-1998). In this mode, we attempted to represent the suite of possible water conditions the fish may encounter in future years. HYDSIM also represents alternative scenarios of storage reservoir drafting and alternative spill scenarios (COMPASS manual, Appendix 8-3; NOAA AR B.367).

14. We recently proposed new algorithms for representing uncertainty in model predictions of survival. These algorithms were favorably reviewed by the ISAB, and we are now implementing them into COMPASS. In the near future, we will produce confidence intervals with all survival predictions.

15. In their most recent review, the ISAB stated, "COMPASS is a welcome addition to the analytical tools available to both scientists and managers." Due to critiques that COMPASS was too complex, we asked the ISAB specifically whether the level of complexity was appropriate. They replied:

> There is always a tradeoff between the need to provide enough detail to capture the nuances of the real situation and the need to keep the model as simple as possible. The ISAB's sense is that this latest version (1.1) of the COMPASS model strikes a healthy balance between simplicity and realism. This modeling tool has to serve myriad purposes, and we find ourselves calling for more detail at various points, while constantly reminding the team to "keep it as simple as possible."

Regarding the model fit to the data, the ISAB stated:

> The model allows for variability in prediction, based on variability in the input parameters. And, at least where the requisite empirical data exist, the model does a credible job of reflecting a dynamic reality. The requisite data are sometimes in short

> supply, however, and both the COMPASS team and the ISAB recommend that more data of the necessary types be gathered. The value of testing the performance of the model against the real world cannot be overestimated.

Our model predictions for 2008 (described below) relate directly to the last sentence above. In our first test against “the real world” the results were quite successful, as explained in the following section.

Model predictions for 2008

16. The ultimate test of a model’s predictive capabilities is to predict independent data. By independent, we mean data that were not used to calibrate model parameters. To conduct this type of test, we used COMPASS, calibrated with data from 1997-2007, to predict season-wide survival for 2008 for wild Snake River spring/summer Chinook and steelhead. Predicted survival was well within the 95% confidence intervals for Snake River spring/summer Chinook and steelhead for both the upper reaches (Lower Granite to McNary dams) and lower reaches (McNary to Bonneville Dams) (Figure 1). This exercise demonstrates COMPASS’ capability as a predictive tool.

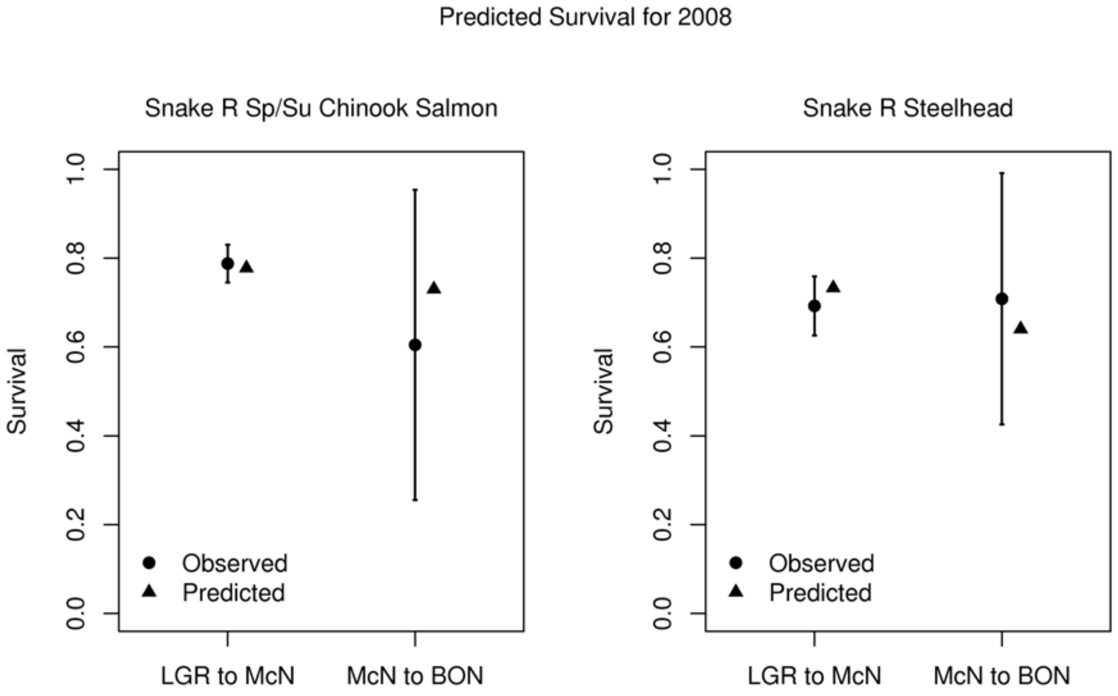

Figure 1. Predicted survival (triangles) versus observed survival (circles with 95 % confidence intervals) through the hydropower system in 2008 for Snake River spring/summer Chinook salmon and steelhead. The prediction for 2008 is an independent prediction, meaning no 2008 data were used in model calibration.

Post-Bonneville survival

17. The post-Bonneville module estimates return rates of fish from when they pass Bonneville Dam as juveniles to their detection at Lower Granite Dam as adults. In their review of post-Bonneville survival, the ISAB stated:

> The ISAB concludes that the hydrosystem causes some fish to experience latent mortality, but strongly advises against continuing to try to measure absolute latent mortality. Latent mortality relative to a damless reference is not measurable. Instead, the focus should be on the total mortality of in-river migrants and transported fish, which is the critical issue for recovery of listed salmonids. Efforts would be better expended on estimation of processes, such as in-river versus transport mortality that can be measured directly.
>
> Estimates based on limited time series have a high degree of uncertainty, and ocean conditions that affect survival will vary on several time/space scales. Thus there will be considerable uncertainty in estimates of post-Bonneville survival, and the ISAB recommends that this uncertainty be accounted for as efforts to reduce it continue. Estimates of the uncertainty should be bounded and incorporated in simulation models and annual management planning processes.
>
> The ISAB also recommends that a logit modeling approach be investigated as a potential alternative framework for future modeling of post-Bonneville mortality.

18. The Scheuerell and Zabel methodology (Scheuerell and Zabel 2007, NOAA AR B.455), which was utilized in prospective modeling for the FCRPS Biological Opinion, incorporates all these suggestions. Further, the logit modeling approach, which treats fish individually, provides a much more powerful method than previous methods, which grouped fish into cohorts, to discern differences across the season and between transported fish and in-river migrants. The COMPASS manual (Appendix 8-2; NOAA AR B.367), demonstrates how we treated uncertainty within relationships, among alternative model formulations, and among years. This uncertainty was carried through to show variability about differences between predicted adult return rates associated with alternative management actions.

19. We note that the intention of the COMPASS post-Bonneville module, as modeled in the FCRPS BiOp, is not to try to predict overall return rate in a particular year. Much of the year to year variability in return rate is determined by ocean conditions, and we do not have enough years of data to relate ocean conditions to water years. Instead, we estimate average (across years) return rate as a function of when fish (transported and in-river migrants) arrive below Bonneville Dam. Typically, fish that arrive earlier return at greater rate with the

exception that fish transported early in the season perform relatively poorly. Thus actions, such as spill and flow, that lead to earlier arrival time for in-river migrants translate into higher return rates for the in-river portion of the population. Overall return rate is determined by the return rates of in-river migrants and of transported fish, and the proportion of each population arriving below Bonneville. Thus the overall goal is to estimate changes in smolt to adult survival when comparing alternative hydropower system operations.

20. In their latest review (ISAB 2008), the ISAB, referring to the implementation of the post-Bonneville survival in the COMPASS BiOp model runs stated:

> The models are also informative as to the likely effects of transportation. Different hydro-system scenarios are modeled, and the results suggest that COMPASS will be very useful for this sort of scenario evaluation.

Response to Bowles Declaration (paragraphs 80-103)

Steelhead survival in 2007

21. Bowles points out that COMPASS underestimated survival for Snake River steelhead migrating from Lower Granite Dam to McNary Dam in 2007. He further states that the reason for this is that COMPASS was "calibrated to a preponderance of years when in-river passage conditions were different from 2006-7," (that is, 2006 and 2007 were characterized by greater levels spill than in previous years). Although we agree that COMPASS underestimated survival of steelhead migrating from Lower Granite Dam to McNary Dam in 2007, we disagree with Mr. Bowles regarding the reason for this. He is implying that COMPASS does not fit the data in years of high spill and thus underestimates the benefits of spill. On the contrary, model fits for Snake River spring/summer Chinook salmon in 2006-7 and steelhead predictions for

2006 are well within 95% confidence intervals for cohorts migrating from Lower Granite to McNary Dams, and the same applies for both species migrating from McNary to Bonneville Dam in both 2006 and 2007. In addition, for 2008, when passage conditions were similar to those in 2006-7, COMPASS accurately predicted seasonal average survival using an independent approach described above. In general the model fits data quite well, particularly in the upper reaches, and the ISAB concurs with this. Thus, Mr. Bowles is pointing out an exceptional case, and, in fact, we would be surprised if such cases didn't exist because of the inherent variability present in natural systems.

22. Nonetheless, as Bowles points out, 2001 and 2007 are two years when the COMPASS-predicted survival for steelhead in the Snake River fell outside of the 95% intervals of the data. We believe this highlights that factors beyond river conditions contribute to observed survival through the hydropower system. In particular, as described in the 2007 Survival Studies annual report[10] (Figures 11-13 and Table 47), juvenile survival is strongly related to avian predation rate (as measured by percentage of PIT tags recovered on bird colonies) in the river segments between Lower Monumental and McNary Dams, where juveniles are susceptible to predation by birds from Crescent Island and other islands upstream of McNary Dam. This is particularly the case for steelhead, which are more susceptible to avian predation than Chinook. In 2001, when COMPASS over-predicted survival from Lower Granite to McNary Dam, over 21 per cent of the PIT-tagged fish detected at Lower Monumental Dam were subsequently detected at a bird colony. In 2007, when COMPASS under-predicted survival, less than 4 per cent of PIT-tagged fish detected at Lower Monumental Dam were subsequently

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[10] Faulkner, J.R., S.G. Smith, W.D. Muir, D.M. Marsh, and J.G. Williams. 2008. Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia river dams and reservoirs, 2007. Report to the Bonneville Power Administration, Contract DE-AI79-93BP10891. A copy is attached as Exhibit 3 to this Declaration.

detected at a bird colony. These differences in avian predation rate among years can easily explain the discrepancy between predictions and observations. Although strong retrospective evidence exists for the role of avian predation in survival, we do not believe sufficient data currently exist to include predator-prey dynamics into COMPASS to predict future survival. We are currently exploring this phenomenon, and we plan to incorporate it into COMPASS in the future when more data become available.

Model fit in the lower Columbia River

23. Bowles points out the poor fit of reservoir survival models to survival data in the lower Columbia River (McNary Dam to Bonneville Dam). We believe this a data quality issue (relatively large standard errors about the survival estimate) and not a model issue. Thus any analysis incorporating these data will encounter the same problem. The ISAB concurred a critical need exists for improved precision of survival estimates in the lower Columbia River. Furthermore, COMPASS survival predictions in the lower Columbia River generally fall within the middle of the 95% confidence intervals of the data. Therefore, the model does a reasonable job of predicting yearly mean survival through the lower Columbia, which is about all the data support. Nonetheless, the relative simple model implemented in the lower Columbia River does respond to river conditions (see COMPASS Manual, NOAA AR B.367, Appendix 9).

Multiply bypassed fish

24. Bowles states that only fish that were bypassed 0 times are appropriate as controls to describe in-river migrants in the post-Bonneville survival. An issue with the use of C_0 (non-bypassed) versus C_1 (bypassed 1-3 times) individuals is the uncertainty regarding the mechanisms that lead to their relative differences in performance (measured in terms of smolt-to-adult return rate or SAR). Two hypotheses, which are not mutually exclusive, have been

proposed to explain the observation that C_0 fish return at a greater rate than C_1 fish. The first, proposed by Budy et al. (2002; NOAA AR B.52)[11] is that passage by juvenile fish though bypass systems leads to latent mortality effects, most likely due to stress, that are not expressed until after fish exit the hydrosystem. The second, proposed by Williams et al. (2005; NOAA AR B.538)[12], notes that bypassed juveniles tend to be smaller (Zabel et al. 2005)[13], and smaller fish tend to return at lower rates than larger ones (Zabel and Williams 2002)[14]. Thus, by extension, bypassed (smaller) fish would be expected to return at lower rates. Realistic combinations of selection coefficients (for return rate versus fish length) and slope coefficients (for bypass detection rate versus fish length) can recreate the observed patterns (see Williams et al. 2005, p. 117; NOAA AR B.538). We note that we have found size selectivity for fish detected in the bypass system at Little Goose and Lower Monumental Dams but not at Lower Granite Dam. Additionally, bypass systems may also select for sick and weak fish, because like smaller fish, they cannot resist the currents leading into bypass systems. We believe that both the hypotheses mentioned above are plausible and, in fact, may both operate to a certain degree. However, the implications of the two hypotheses for transportation studies (and other assessments of alternative management strategies) are important: the selectivity hypothesis suggests that the quality of fish entering the hydrosystem determines, to a certain extent, their subsequent return rate; the latent mortality hypothesis suggests that hydrosystem experience determines return rate. Under the selectivity hypothesis, shuffling fish among passage routes would have less of effect on overall return rate compared to the latent mortality hypothesis.

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[11] Budy, P., G. P. Thiede, N. Bouwes, et al. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35-51, 1/1/2002.

[12] Williams, J.G., S.G. Smith, R.W. Zabel, et al. 2005. Effects of the Federal Columbia River Power System on salmonid populations, U. S. Dept. of Commerce, NOAA Tech. Memo., NMFS-NWFSC-63., 2/1/2005.

[13] A copy of which is attached to this declaration as Exhibit 4.

[14] A copy of which is attached to this declaration as Exhibit 5.

25. Even if one fully accepts the latent mortality hypothesis, C_0 individuals do not represent in-river fish when transportation is not occurring. When transportation is not occurring, bypassed fish are returned to the river, and thus C_0 fish typically represent a (usually small) portion of run-of-the-river fish. In fact, during times of no-transport, the population of in-river fish behave identically to the PIT-tag population. Thus the entire population of PIT-tagged fish (C_0 and C_1 fish) is the appropriate set of fish to model adult return rates under periods of no transportation. This was the set of fish used for the BiOp runs.

Should project better returns for 2006, 2007 fish

26. Bowles contends that we should project improved returns for fish migrating in 2006 and 2007 because they encountered better in-river conditions (more spill) than in previous years. As stated in the COMPASS model description, we based all model algorithms on available data. Bowles suggests we abandon this approach and enter the realm of speculation. In response, we have repeatedly stated that when fish return from the 2006 and 2007 out-migrations, we will incorporate the new data into the model and revise results if necessary. This is consistent with an adaptive management approach.

SAR related to WTT and spill

27. Bowles cites studies that demonstrate relationships between smolt-to-adult return rate (SAR) and the factors water travel time and spill. In response, we note that COMPASS already contains these relationships. Increased spill and decreased water travel time both result in fish arriving to below Bonneville earlier in the season. Based on the Scheuerell and Zabel post-Bonneville algorithm, early arriving fish return at greater rates.

Response to Olney (paragraphs 51-59, 110-120)

28. First off, we note that Olney was not a part of COMPASS development, and the many misconceptions in his declaration demonstrate his lack of familiarity with the model. Further, several of the comments made by Olney reiterated those in the Bowles declaration. Nonetheless, we respond here to the statements made by Olney.

29. Olney states that COMPASS only used the Scheuerell and Zabel Hypothesis, but the ISAB recommended a composite hypothesis using multiple data sets. First, we note that although the ISAB recommended using multiple data sets, they provided little guidance on how to do so. Further, in the same review, they recommended against using the spawner-recruit data for post-Bonneville modeling, and this was the only data set other than PIT-tag data used in the suite of alternative hypotheses. Analyses based on using PIT-tag SARs from Lower Granite (juveniles) to Lower Granite (adults) provided essentially the same temporal patterns as analyses based on SARs from Bonneville (juveniles) to Lower Granite (adults). We chose the latter data set because it allowed us to reflect changes in hydropower system operations in adult return rates. The SARs from Lower Granite reflected the specific operations that occurred each year of the dataset. Finally, as stated above, the Scheuerell and Zabel methodology was the only one that met the requirements of the ISAB review.

30. Olney states that the ISAB recommended that uncertainty of post-Bonneville relationship should be characterized. This was done in the COMPASS manual (Appendix 8-2; NOAA AR B.367). In addition, Olney notes that ISAB recommended against estimating overall latent mortality. The algorithms utilized by COMPASS in the prospective modeling for the Biop do not do this. However, an alternative hypothesis (as formulated by IDFG and USFWS) contained in COMPASS allows the model user to specify overall latent mortality. We again note this alternative hypothesis was not used in Biop runs based on ISAB recommendations.

31. Olney notes that previous studies did not convincingly demonstrate transportation benefits. The previous studies cited only considered season-wide SAR estimates for transported fish and in-river migrants. It is clear that the benefits of transport show strong seasonality, with minimal to no benefits early and benefits increasing substantially later in the season (Compass manual Appendix 8-2; NOAA AR B.367). Thus studies that do not consider this seasonality may not detect the benefits.

32. Olney states that implementing the Scheuerell and Zabel methodology required using fish from all transportation sites and all migration histories (i.e., number of times bypassed) to increase sample sizes. In fact, all fish were used so effects of transportation site and bypass history could be tested directly. The analysis detected transportation site effects for steelhead and bypass effects for spring/summer Chinook salmon.

33. Regarding incorporating transportation site effects into COMPASS model runs, we note that for the comparison of prospective model alternatives, the primary concern would be if the alternative operations resulted in shifts in proportions of fish transported from each site. We don't believe this is the case as the base case and proposed action both result in the majority of fish transported from Lower Granite. Thus incorporating site effects would have little effect on relative return rate between scenarios, which is the measure used in the Biop. Also, we addressed the issue of incorporating bypass effects into COMPASS modeling above.

34. Olney states, "Because COMPASS model must use specific assumptions about transportation, its outputs cannot reflect this flexibility or the spill and transportation options that will be implemented under the 2008 BiOp." This statement is absolutely false and reflects a lack of understanding of how COMPASS operates. In fact, COMPASS was designed to accommodate any spill or transportation scenario. Similarly, the statement that "[COMPASS] is

not currently designed to simulate actual hydrosystem management or provide the basis for selecting the detailed management scenarios that resulted in tradeoffs between survival of Snake River spring/summer Chinook and steelhead" is also inaccurate. COMPASS was designed specifically to conduct this type of analysis. This lack of understanding of how the model operates calls into question Olney's ability to critique COMPASS.

35. As stated above, COMPASS simplifies some of the finer details of dam passage due to data limitations. However, the model produces responses to all management actions considered, including decreased delay and increased survival as a result of increased spill, seasonal responses to transportation scheduling, increased survival due to dam improvements, and responses of survival and travel time to increased flow. The generally strong model fits to survival data, passage-timing data, and transportation proportion demonstrate the capability of the model to accurately capture these responses.

36. Olney cites critiques by the USFWS and States and Tribes. Regarding the USFWS critique, we addressed this specifically in an internal memorandum from John Ferguson (NWFSC) to Bruce Suzumoto of February 1, 2007. See NOAA AR C.409. This critique contained many misconceptions on how the model operates. In particular, the USFWS was confused as to how the survival predictions in COMPASS are generated, how the model was fit to data, and the level of complexity of the model. Both the USFWS and States and Tribes critique mention the issue of model complexity. We were also concerned with this issue, so we specifically asked the ISAB for guidance on this issue. They repeatedly stated that the level of model complexity was appropriate. Regarding the ISAB comment about the model's ability to model future scenarios, we believe the independent model predictions of the 2008 data (see above) demonstrate the model's capabilities. Regarding Olney's issues with the 2007 data point

and the role of avian predation, we addressed these issues above in response to Bowles similar concerns.

I declare under penalty of perjury that the foregoing is true and correct.

Executed on October 23, 2008, in Seattle, Washington.

Richard W. Zabel

Richard W. Zabel

EXHIBIT 1

DECLARATION OF RICHARD W. ZABEL

CURRICULUM VITAE

Richard William Zabel
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Education

B.S. (with honors and distinction), in Botany, The University of Michigan, Ann Arbor, 1983.

M.S., in Plant Biology, The University of Michigan, Ann Arbor, 1988.

Ph.D., in Quantitative Ecology and Resource Management, University of Washington, Seattle, 1994.

Research Interests

Growth and Bioenergetics. Developing models of growth and bioenergetics in response to varying habitat conditions.

Response of populations to climate. Impacts of climate variability and climate change on natural populations.

Migrational Behavior. Models of dispersal patterns in natural populations. Variability of migration-related life history traits among closely-related taxa.

Survival and Selection Processes in Natural Populations. Patterns of population survival and selection related to individually-varying phenotypic traits

Population Dynamics and Life Cycle Modeling. Using demographic population viability analyses to assess impacts to populations. Detecting density dependence in natural populations.

Ecosystem-Based Management. Impacts of fishing on marine communities.

Research experience and Employment

June 2005 to present: Supervisory Mathematical Statistician, Fish Ecology Division, Northwest Fisheries Science Center, National marine Fisheries Service. Team Leader of the Quantitative Ecology Team.

September 1999 to June 2005: Mathematical Statistician, Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service. Research on survival and behavior of threatened and endangered salmonid species including developing models of population dynamics and spatial patterns, and conducting survival studies. Other areas of research include Population Viability Analysis and Ecosystem modeling.

July 1997 to September 1999: Research Consultant, Columbia Basin Research, School of Fisheries, University of Washington. Research on salmon survival issues including participation in the Plan for Analyzing Testable Hypotheses (PATH) process, a multiple agency research effort to recommend measures to recover endangered stocks of salmon.

January 1995 to June 1997: Post Doctoral Research Associate, School of Fisheries, University of Washington. Worked with Professor James Anderson developing and calibrating models of salmonid migration.

March 1994 to December 1994: Research Consultant, Center for Quantitative Science, University of Washington.

September 1988 to February 1994: Research Assistant, Quantitative Ecology and Resource Management Graduate Program, University of Washington.

January 1985 - June 1988: Graduate student and Teaching Assisitant, Department of Biology, University of Michigan. Research on the systematics, genetics and ecology of plant populations.

Publications

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1995. Aquaculture Research Institute, University of Idaho.

Zabel, R. W. 1994. Spatial and Temporal Models of Migrating Juvenile Salmon with Applications. Ph.D. dissertation, University of Washington, Seattle.

Teaching experience

1994 and 1995: Lecturer, University of Washington. Taught Statistical Inference in Applied Research.

January 1985 to June 1988: Teaching Assistant, University of Michigan. Taught the following courses: Introductory Biology, Writing for Biologists, Plant Systematics, Biology of World Hunger, Plant Biology, General Ecology, and Genetics.

Talks delivered at Annual Meetings

Fisheries and the Environment (2007)

European Inland Fisheries Advisory Commission (2006).

American Society of Limnology and Oceanography, 2005 (Invited speaker).

Western Society of Naturalists, 2004, 2005 (Invited Symposium Speaker).

Society for Conservation Biology, 2001.

International Fish Biology Congress, 2000, 2002.

Biometrical Society, Western North American Region, 1999 (Invited speaker).

Ecological Society of America, 1993, 1995, and 2004 (presider).

Resource Modeling Association, 1990 and 1998.

Honors, Fellowships, Awards

College Honors Program, 1979-1981, University of Michigan.

Honors Concentration Program, 1983, University of Michigan.

Mellon Foundation Fellowship to attend the Naturalist-Ecologist Training Program, University of Michigan Biological Station, 1985.

Special Act Award, 2005, Northwest Fisheries Science Center.

Service

Guest Subject Matter Editor: Ecological Applications.

Reviewer for the following peer-reviewed journals: Proceedings of the National Academy of Science, Proceedings of the Royal Society of London *B*, Ecology, Ecological Applications, Ecology Letters, Journal of Applied Ecology, Journal of Animal Ecology, Frontiers in Ecology and the Environment, Oikos, Canadian Journal of Fisheries and Aquatic Sciences, Transactions of the American Fisheries Society, North American Journal of Fisheries Management, Fisheries, Amercian Fisheries Society Symposium, Journal of Experimental Marine Biology and Ecology, Environmental Modelling and Software, Hydrobiologia.

Reviewer for the Millennium Ecosystem Assessment

Scientific Review Committee (SRC) for the Cooperative Monitoring and Research Committee, established by the Washington State Board of Natural Resources

Reviewed reports and proposals for: NSF, CALFED, Bonneville Power Administration, Chelan County PUD, ODFW, NOAA Northwest Regional Office, University of Washington

Oversight Committee: Acoustic tag design and development team, Chelan County PUD
Committee member: Computer committee, Northwest Fisheries Science Center
Reviewer for NWFSC internal grants program

Advising/Mentoring

Master's Thesis Committee: Erica Alston, Clark University, Atlanta (graduated 2004).
National Research Council (NRC) Postdoctoral adviser for Lisa Crozier (2004-2007).
Oak Ridge Institute for Science and Education Mentor for Kerri Haught (2005-2006).
Dissertation Supervisory Committee: Eli Gurarie (graduated 2008), University of Washington.
Master's Supervisory Committee: Kara Cromwell (2006 – present), University of Idaho
Master's Supervisory Committee: Jessica Beetz (2007 – present), University of Washington

EXHIBIT 2

DECLARATION OF RICHARD W. ZABEL

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EIFAC 2006: DAMS, WEIRS AND FISH

Comprehensive passage (COMPASS) model: a model of downstream migration and survival of juvenile salmonids through a hydropower system

Richard W. Zabel · James Faulkner · Steven G. Smith · James J. Anderson · Chris Van Holmes · Nicholas Beer · Susannah Iltis · Jared Krinke · Gary Fredricks · Blane Bellerud · Jason Sweet · Albert Giorgi

Abstract Migratory fish populations are impacted worldwide by river impoundments. Efforts to restore populations will benefit from a clear understanding of survival and migration process over a wide-range of river conditions. We developed a model that estimates travel time and survival of migrating juvenile salmonids (*Oncorhynchus* spp.) through the impounded Snake and Columbia rivers in the northwestern United States. The model allows users to examine the effects of river management scenarios, such as manipulations of river flow and spill, on salmonid survival. It has four major components: dam passage and survival, reservoir survival, fish travel time, and hydrological processes. The probability that fish pass through specific routes at a dam and route-specific survival probabilities were based on hydroacoustic, radio telemetry, PIT tag, and acoustic tag data. We related reservoir mortality rate (per day and per km) to river flow, water temperature, and percentage of fish passing through spillways and then fit the relationships to PIT-tag survival data. We related fish migration rate to water velocity, percentage of fish passing through spillways, and date in the season. We applied the model to two threatened "Evolutionarily Significant Units" (as defined under the US Endangered Species Act): Snake River spring/summer Chinook salmon (*O. tshawytscha* Walbaum) and Snake River steelhead (*O. mykiss* Walbaum). A sensitivity analysis demonstrated that for both species survival through the hydropower system was responsive to water temperature, river flow, and spill proportion. The two species, however, exhibited different patterns in their response. Such information is crucial for managers to effectively restore migratory fish populations in regulated rivers.

Keywords Ecological modeling · Salmon · Migration · Survival · Hydropower

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Hydropower, Flood Control and Water Abstraction: Implications for Fish and Fisheries

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Introduction

How do migratory fish populations respond to varying river conditions? This question is particularly relevant in regulated rivers because river impoundments have impacted migratory populations worldwide (McCully, 2001) and because management operations can have substantial effects on population survival and migration timing. Thus, efforts to restore migratory fish populations in regulated rivers will benefit greatly from a clear understanding of survival and migration processes over a wide-range of river conditions and dam operations.

In the Columbia River basin in northwestern United States (Fig. 1), this issue is critical because 13 "Evolutionarily Significant Units" (ESUs) of Pacific salmon (*Oncorhynchus* spp.) that spawn within the basin are listed as threatened or endangered under the US Endangered Species Act. Further, the basin provides irrigation for millions of acres of farmland and has traditionally supported sport, commercial, and tribal fisheries for salmon and steelhead. In addition, the Columbia River and its tributaries is one of the most hydroelectrically developed river system in the world (capacity of approximately 20,000 megawatts), and dams allow for river navigation and provide flood control. Consequently, actions to mitigate effects on fish can cost tens of millions of US dollars per year.

The social and economic importance of these conflicting interests has led to an effort to develop a model to describe juvenile salmon passage through the Columbia River and Snake River (the largest tributary to the Columbia). Scientists from throughout the northwestern United States have developed the Comprehensive Passage (COMPASS) model to predict the effects of alternative hydropower operations on salmon survival rates.

The model has a variety of applications, including developing management plans for the highly regulated Columbia and Snake rivers and monitoring intra seasonal progress of migrating populations to determine if timely adjustments to river operations are required. The model simulates several types of management actions: spill scheduling (for many dams, the spillway is the safest and quickest passage route for juvenile salmon), timing of water releases from storage reservoirs (which can alter water velocity and temperature downstream), transportation timing (many juvenile salmon are collected at upstream dams and transported in barges and trucks

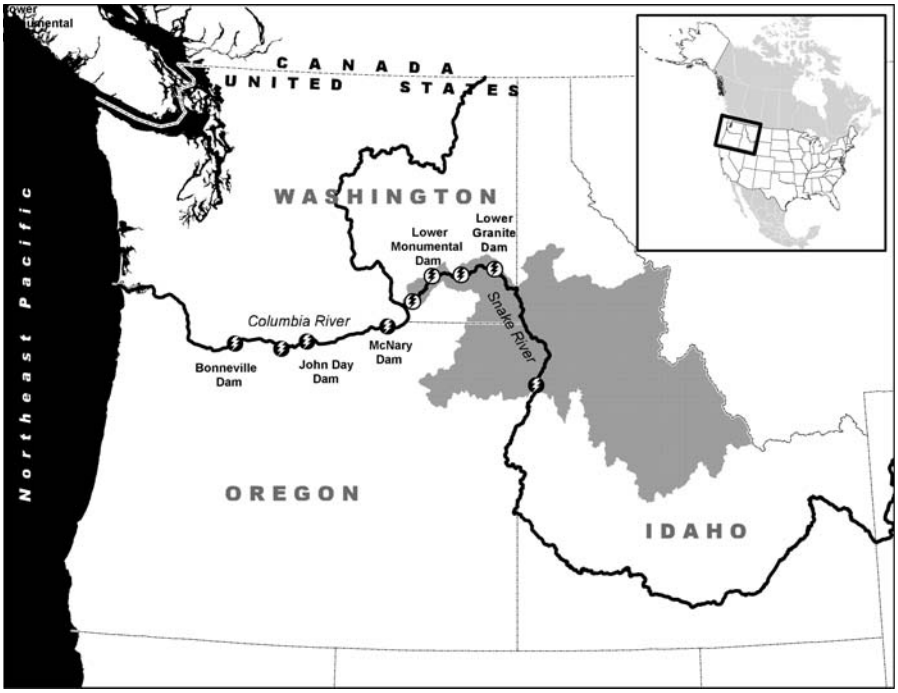

Fig. 1 Columbia and Snake Rivers, with major dams on the Snake and lower Columbia rivers identified with lightning bolts. The Snake River basin is highlighted in grey

and released below the hydropower system). In the future, we may also use the model to address more dramatic actions, such as reservoir drawdown and dam removal.

This article focuses on the dynamics of the seaward migration of juvenile anadromous salmonids. We present overviews of the model components, data to support the model, and range of predictions produced by the model. Due to space limitations, we cannot provide all model details, but more details are available upon request to the lead author. This article presents results for two ESUs: Snake River spring/summer Chinook salmon (*O. tshawytscha* Walbaum) and Snake River steelhead (*O. mykiss* Walbaum).

Model description

The downstream passage component of COMPASS is written in the C programming language and was derived from CRiSP (Anderson et al., 2000), a previous salmon passage model. The model is composed of four submodels: dam passage, reservoir survival, travel time, and hydrological processes.

The model is initiated with a simulated release of fish at a particular release site, with the timing of this release typically corresponding to the migration of wild populations. Releases may be distributed across days with varying numbers of fish per day. All fish in a release group share common travel time, survival, and dam passage behaviors. The model moves fish in half-daily time increments through river segments and dams following a sequence of steps (Fig. 2). Step 1 releases all fish into a reservoir on a given day and Step 2 distributes their exit time at the bottom of the reservoir according to the travel time model, described below. Step 3 applies a reservoir survival function to the fish before they move to the dam passage algorithm. At the dam, arriving fish are distributed across passage routes according to specified passage probabilities (Step 4). Step 5 applies route-specific survival probabilities. Step 6 recombines fish that passed through the various passage routes. Fish that enter the bypass system in collector dams may be transported, according to transportation schedules (Step 7); the remaining fish are released to the next downstream reservoir (Step 8). Note that because travel time and dam passage algorithms disperse fish, the daily groups exiting a dam are composed of fish from different release groups within or at the top of the reservoir. Fish move through the system until they pass the lowermost dam and enter the estuary.

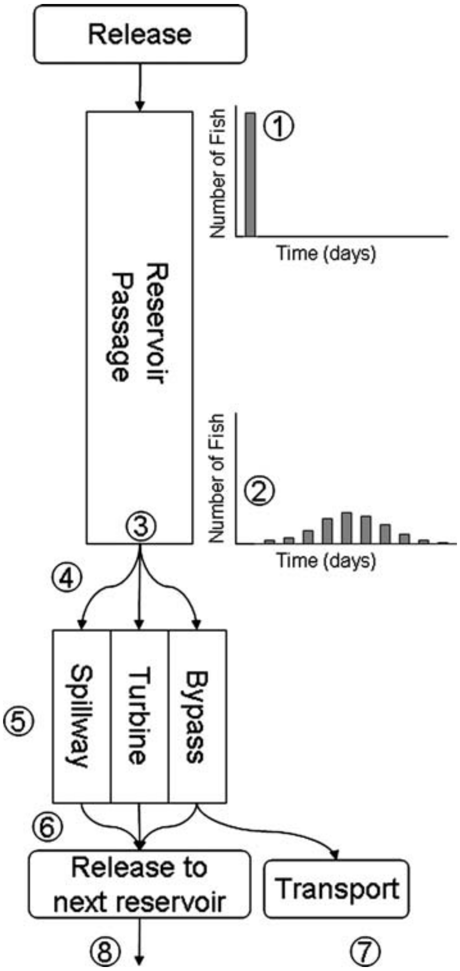

Fig. 2 Passage model algorithm, features the steps taken to move a daily release of fish through a project. See text for description

Dam passage

Fish pass from the reservoir module to the dam module on half-daily time steps corresponding to a daytime and nighttime period. Dam passage is represented as a sequence of passage probabilities which are derived from dam passage studies using radio and acoustic tagged fish (e.g., Skalski et al., 2002). First, the typically nonlinear spill efficiency relationship between the portion of fish passing through a spillway and the proportion of river flow passing through the spillway (e.g., Wilson et al., 1991) determines a portion of the fish are diverted to spillway passage (Fig. 3). Each dam and species has a unique spill efficiency relationship.

Fish that do not pass via the spillway enter the turbine intakes at the powerhouse. At most dams, turbine intake screens divert a large proportion of the fish to a juvenile bypass system, with this proportion defined as Fish Guidance Efficiency (FGE). FGE can be specified separately for day and night at each dam, if sufficient data exist. At some dams, fish can pass via sluiceways or alternate surface bypass routes not associated with turbine intakes or the spillways. These passage routes also have specified passage probabilities.

Reservoir survival

The primary data for calibrating model survival are PIT-tag (Prentice et al., 1990) data. Most dams in the lower Columbia and Snake rivers have automatic PIT-tag detectors in their juvenile bypass systems. PIT-tagged fish are also detected downstream from Bonneville Dam in the Columbia River estuary. Using standard mark-recapture methods (Burnham et al., 1987) we estimated survival and standard errors through four river segments delineated by dams (Fig. 1): Lower Granite (release site) to Lower Monumental; Lower Monumental to McNary; McNary to John Day; and John Day to Bonneville.

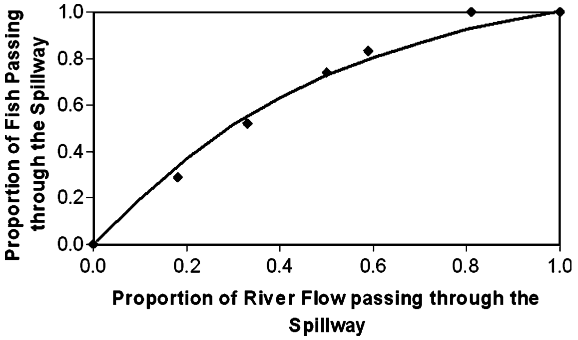

Fig. 3 Sample spill efficiency curve (see text for definition) fit to data (points). The data are based on radio-tagged Snake River spring/summer Chinook salmon passing Lower Granite Dam in 2002 and 2003

Reservoir survival estimates were based on fish PIT-tagged from 1995 through 2005. Juvenile wild Snake River spring/summer Chinook salmon and steelhead were captured, PIT tagged, and released at Lower Granite Dam or upstream from the dam. Tagged fish were placed into weekly release groups based on either day of release or day of passage at Lower Granite Dam. Because groups of fish spread out as they migrate downstream, we formed new weekly cohorts (of Snake River origin) at McNary Dam based on when fish were detected there for survival estimation through the lower Columbia River.

PIT-tag survival estimates represent survival through an entire "project" (reservoir and dam), or two such projects in some cases (e.g., Lower Monumental Dam to McNary Dam, which includes Ice Harbor Dam (Fig. 1)):

$$S_{\mathrm{PROJECT}} = S_{\mathrm{RESERVOIR}} \cdot S_{\mathrm{DAM}} \tag{1}$$

In order to estimate the components of survival, we used independent data, primarily radio telemetry data, to estimate dam survival, as described above. We divided this out of project survival and then treated the remaining survival as reservoir survival. We related this remaining survival to river conditions in the reservoir. Therefore, some of the variability in our model fits described below reflects variability in dam survival in addition to variability in reservoir survival.

A standard form for survival functions is

$$S(t) = \exp(-r \cdot t) \tag{2}$$

where $S(t)$ is the probability of surviving through t units of time and r is the mortality rate, with units time^{-1} (Hosmer & Lemeshow, 1999). The parameter r is interpreted as the instantaneous probability that an individual will die in the next time increment given that the individual has survived to the current time (Ross, 1993). Thus, as r increases, survival across a time period decreases (Fig. 4).

However, a strict exposure time model is not consistent with the PIT-tag survival data (Smith et al., 2002). Both observations (Muir et al., 2001) and theory (Anderson et al., 2005) indicate that survival is also related to distance travelled. As the exposure, in this case, is to distance traveled, we modified the exposure model accordingly:

$$S(d) = \exp(-r \cdot d) \tag{3}$$

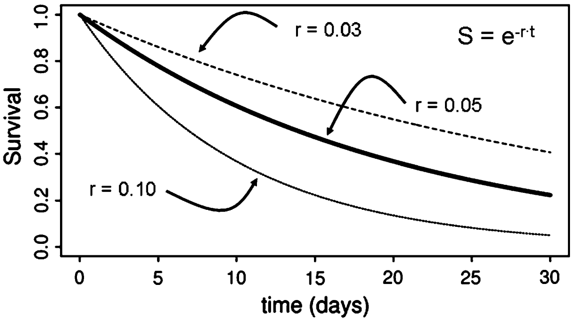

Fig. 4 Exponential survival relationships as a function of exposure time for various values of the parameter *r* (instantaneous mortality). As *r* increases, survival decreases at a greater rate

To accommodate both survival processes, we implemented a hybrid model where survival is a function of travel time and distance traveled:

$$S(t,d) = \exp(-(r_t \cdot t + r_d \cdot d)) \tag{4}$$

In order to relate reservoir survival to river conditions we modeled the instantaneous mortality rates, r_t and r_d, as a function of predictor variables and assumed that predation is the primary cause of mortality in the reservoir. Since predator activity has a nonlinear response to temperature (e.g., Vigg & Burley, 1991), we expressed the predation rates as quadratic functions of temperature. Evidence exists to support the hypothesis that predation rate is negatively related to river flow, perhaps through turbidity, which could decrease the predators–prey encounter rate (Gregory & Levings, 1998, Anderson et al., 2005). Finally, we included proportion of fish passing a spillway as a potential variable, based on the assumption that increased spill leads to increased reservoir survival due to a quicker and safer dam passage. Including these covariates in both the distance and time mortality rates and taking the log transform of Eq. 4 yields a simple linear model (Hosmer & Lemeshow 1999):

$$\begin{aligned} -\log(S_{g,s}) = {} & (\alpha_0 + \alpha_1 \cdot \text{Flow} + \alpha_2 \cdot \text{Temp} \\ & + \alpha_3 \cdot \text{Temp}^2 + \alpha_4 \cdot \text{Spill}) \cdot d \\ & + (\beta_0 + \beta_1 \cdot \text{Flow} + \beta_2 \cdot \text{Temp} \\ & + \beta_3 \cdot \text{Temp}^2 + \beta_4 \cdot \text{Spill}) \cdot t + \varepsilon_{g,s} \end{aligned} \tag{5}$$

where survival and the error term are referenced to a particular release group (*g*) and river segment (*s*), *Spill* is the proportion of fish passing the spillway at the upstream dam, *Flow* and Temperature (*Temp*) are the mean across the time the fish were in the reservoir, *t* is the average reservoir travel time of the release group, *d* is the reservoir length, and ε is a normally distributed error term with zero mean. Note that this is just one possible form of the survival relationship. COMPASS accommodates alternative hypotheses of reservoir survival.

Equation (5) parameters were estimated by fitting the COMPASS model to the 1995–2005 PIT-tag survival data using a maximum likelihood optimization routine that drew on the historical hydrosystem and river conditions for each year. We removed insignificant parameters based on their Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). Since the Snake and Columbia rivers are physically different, we developed separate reservoir survival relationships for each river. Further, because the survival estimates varied considerably in precision, we weighted the estimates by their inverse "relative" variance (coefficient-of-variation squared) because the variance of log(S) is equal to relative variance (Burnham et al., 1987).

We imposed the following constraints on model selection: (1) a quadratic term must include its corresponding linear term; (2) a time intercept (β_0) must be included with time-exposure variables; (3) a distance intercept (α_0) must be included with distance-exposure variables. Also, to protect against overfitting, we rejected models with coefficients whose signs were inconsistent with the mechanisms outlined above. For example, we rejected models with negative flow coefficients, based on the hypothesis that survival is positively related to flow. We calculated a weighted R^2 for each model fit.

Although no consensus exists on how to calculate R^2 in cases of no intercept, we applied the following calculation:

$$R^2 = \frac{\sum_{i=1}^{N} w_i \cdot d_i^2}{\sum_{i=1}^{N} w_i \cdot (S_i - \bar{S})^2} \tag{6}$$

where *i* indexes each group/river segment survival, *N* is total number of group/river segment combinations, *w* is the weight (inverse relative variance), *d* is the deviance between observed and predicted survival, *S* is the observed survival, and $\bar{S}$ is the mean of the observed survivals.

Travel time

Fish reservoir travel time is based on a model developed by Zabel & Anderson (1997) and is governed by two parameters: fish velocity, v, and population spread rate, σ. The predicted travel time distribution is right-skewed, which is consistent with the data (Fig. 5).

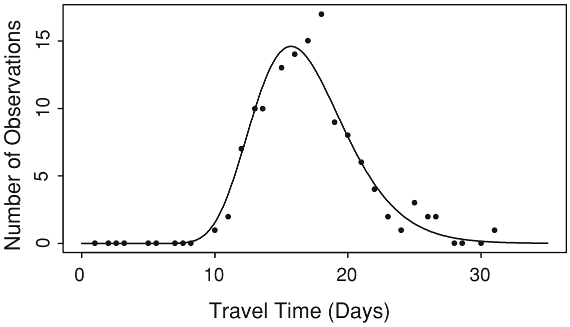

Fig. 5 Examples of the fish travel time model fit to PIT-tag data for Snake River spring/summer Chinook salmon migrating from Lower Granite Dam to McNary Dam, 225 km downstream. Points represent data; solid line is model fit

Zabel et al. (1998) determined that fish velocity is related to river velocity and date in the season. In the current version of the model, fish velocity is also related to percentage of fish passing through the spillway. This accounts for the fact that spilled fish pass over dams more quickly than nonspilled fish (or, spilled fish experience less delay than nonspilled fish). For COMPASS we modified the Zabel et al. model to include spill effects. The resulting fish velocity (km day^{-1}) is:

$$v_i = \beta_0 + \beta_1 \cdot \text{velocity}_i + \beta_2 \cdot \text{date}_i + \beta_3 \cdot \text{velocity}_i \cdot \text{date}_i + \beta_4 \cdot \text{spill}_i + \beta_5 + \varepsilon_i \tag{7}$$

where v_i is the fish velocity of the ith cohort, *velocity*$_i$ is mean water velocity over the migration period, spill is the percentage of fish passing the spillway and is measured on the day the fish pass the upstream dam, *date*$_i$ is the date the cohort enters a reservoir, and ε_i, is a normally distributed error term. As with the reservoir survival modeling, we began with the "full" model above and selected the best fit model based on AIC. We compared model-predicted fish

Table 1 Regression results for −log (survival) versus environmental covariates, distance and travel time

Coefficient	Variables	Value	s.e.	t-value	P-value
Chinook Salmon/Upper River		*N = 236 AIC = −326.52 R^2 = 0.882*			
α_0	Distance	0.0167	0.00166	10.02	<0.00001
α_1	Distance · flow	−0.0000117	0.0000026	−4.45	0.00001
α_2	Distance · temp	−0.00284	0.000289	−9.84	<0.00001
α_3	Distance · temp^2	0.000140	0.0000128	10.90	<0.00001
α_4	Distance · spill	−0.00195	0.000574	−3.39	0.00082
Chinook Salmon/Lower River		*N = 126 AIC = 61.06 R^2 = 0.627*			
α_0	Distance	0.0105	0.00414	2.53	0.01271
α_2	Distance · temp	−0.00184	0.000650	−2.83	0.0055
α_3	Distance · temp^2	0.0000812	0.0000257	3.17	0.00196
β_0	Time	0.0118	0.00363	3.26	0.00145
Steelhead/Upper River		*N = 225 AIC = −53.83 R^2 = 0.756*			
α_0	Distance	−0.00317	0.00108	−2.95	0.00354
α_2	Distance · temp	0.000956	0.0000865	11.05	<0.00001
β_0	Time	0.0476	0.00397	11.98	<0.00001
β_1	Time · flow	−0.00105	0.0000811	−12.94	<0.00001
Steelhead/Lower River		*N = 104 AIC = 145.30 R^2 = 0.749*			
β_0	Time	0.0179	0.0352	0.51	0.61218
β_1	Time · flow	−0.000358	0.0000586	−6.10	<0.00001
β_2	Time · temp	0.00793	0.00206	3.86	0.00021

See text (Eq. 5) for definitions of coefficients. Abbreviations: temp = temperature; s.e. = standard error; N = sample size (number of cohorts) velocities to PIT-tag data. As with the reservoir survival modeling, we developed separate relationships for the Snake and Columbia rivers. Also, model fits were weighted by the inverse variance of the fish velocity and, the spread parameter, σ, was set to its (analytical) maximum likelihood values (see Zabel & Anderson, 1997).

Hydrological processes

Daily river flow, water velocity, and water temperature are represented through a detailed hydrological submodel, which we briefly describe. Flow and temperature, specified at system headwaters, are propagated downstream according to water velocity, which is determined by river flow and reservoir geometry. Flow and temperature are adjusted at downstream sites to be consistent with monitoring sites, which reflect evaporative loss, irrigation withdrawals, tributary flows, and heating and cooling.

Implementing the model

We used parameters from the best fit survival and travel time models (presented in *Results*) to run COMPASS in a prospective, predictive mode. In this mode, we used the current dam passage parameters to predict hydropower system survival under current conditions. In order to characterize model sensitivity we varied river flow, water temperature, and spill proportion and modeled expected survival and travel time through the entire hydrosystem, and survival through the dams (removing reservoir survival). We only used combinations of river conditions that were observed during 1995–2005; the period over which the model was fit.

Results

The model-predicted survival relationships for Chinook salmon and steelhead from Lower Granite Dam to McNary Dam and from McNary Dam to

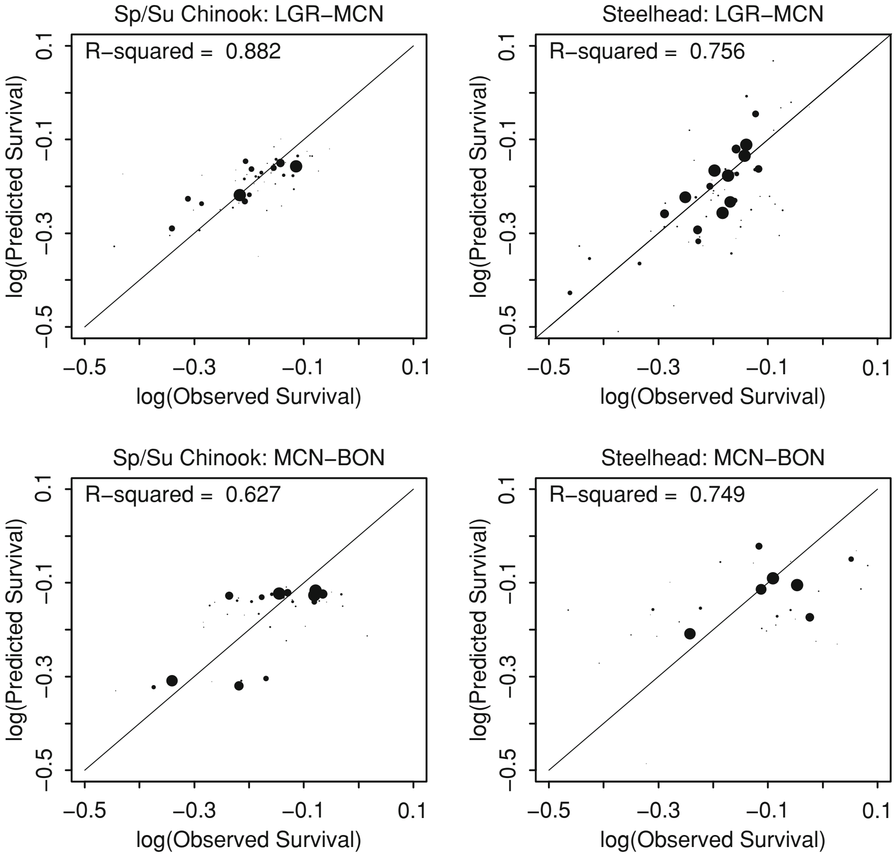

Fig. 6 Predicted log (survival) versus observed log (survival) for cohorts of Chinook and Steelhead migrating through the upper (Lower Granite (LGR) Dam to McNary (MCN) Dam) and lower (McNary Dam to Bonneville (BON) Dam) river reaches. The size of the point represents its weight, with maximum size set equal to 2/3 of the greatest weight

Table 2 Regression results for fish velocity versus environmental covariates and date in the season

Coefficient	Factors	Value	s.e.	*t*-value	*P*-value
Chinook Salmon/Upper River		*N = 383 AIC = 948.80* R^2 *= 0.704*			
β_0	Intercept	−3.545	0.0601	−59.00	<0.00001
β_1	Velocity	0.403	0.0219	18.43	<0.00001
β_2	Date	0.0309	0.00014	226.41	<0.00001
β_3	Date · velocity	−0.00043	0.00018	−2.32	0.02082
Chinook Salmon/Lower River		*N = 148 AIC = 639.02* R^2 *= 0.869*			
β_0	Intercept	14.171	0.813	17.43	<0.00001
β_1	Velocity	−2.287	0.0690	−33.14	<0.00001
β_2	Date	−0.117	0.00491	−23.82	<0.00001
β_3	Date · velocity	0.0222	0.00061	36.15	<0.00001
β_4	Spill	7.593	0.759	10.01	<0.00001
Steelhead/Upper River		*N 371 AIC = 992.12* R^2 *= 0.739*			
β_0	Intercept	−2.797	0.0249	−112.41	<0.00001
β_1	Velocity	0.403	0.0331	12.19	<0.00001
β_2	Date	0.0197	0.00131	15.03	<0.00001
β_3	Date · velocity	0.000577	0.00024	2.41	0.01667
Steelhead/Lower River		*N = 147 AIC = 643.36* R^2 *= 0.742*			
β_0	Intercept	−2.850	0.159	−17.91	<0.00001
β_1	Velocity	0.756	0.0365	20.73	<0.00001
β_4	Spill	4.919	1.0315	4.77	<0.00001

See text (Eq. 7) for definitions of coefficients. Abbreviations: s.e. = standard error; *N* = sample size (number of cohorts). “Velocity” refers to river velocity

Bonneville Dam conformed well with the PIT-tag survival data (weighted R^2 ranged from 0.627 to 0.882, Table 1, Fig. 6). In all cases, the “best fit” model was reduced (at most five parameters) from the full ten parameter model. The upper river models included more parameters, probably because of larger sample sizes and greater precision of survival estimates. Both distance traveled and travel time were important factors, which justifies including both in the model. Temperature appeared in all four models, and flow appeared in three out of four; flow was not significant for survival of Chinook through the lower river. Spill was important for Chinook (upper river) but not for steelhead.

In all cases, model-predicted fish velocity was significantly influenced by water velocity (Table 2), with significant water velocity/date interactions in three out of four cases. The proportion of fish passing through spillways was important in the lower river but not in the upper river. Date was important in three of the models, and combined with the water velocity interaction, fish velocity generally increased through the season. Overall, model fits were strong with weighted R^2 ranging from 0.704 to 0.869 (Table 2, Fig. 7).

Chinook salmon hydropower system survival was much more sensitive to water temperature than river flow (Fig. 8). The survival and temperature relationship was notably nonlinear, with the highest survival occurring at approximately 11°C. Chinook salmon hydropower system survival was also sensitive to percentage of river passing spillways, particularly when spill increased from 0 to 25% of the river flow. Survival through the dams was also sensitive to spill proportion; increasing approximately 10% when spill increased from 0 to 50%. Chinook salmon hydropower system travel time had a strong inverse relation to river flow, decreasing by over 30 d in high flow compared to low flow conditions. Increased spill also decreased travel time by 5–10 d at lower flows.

Steelhead hydropower system survival was much more sensitive to river flow than was that for Chinook salmon (Fig. 9). Survival decreased consistently with

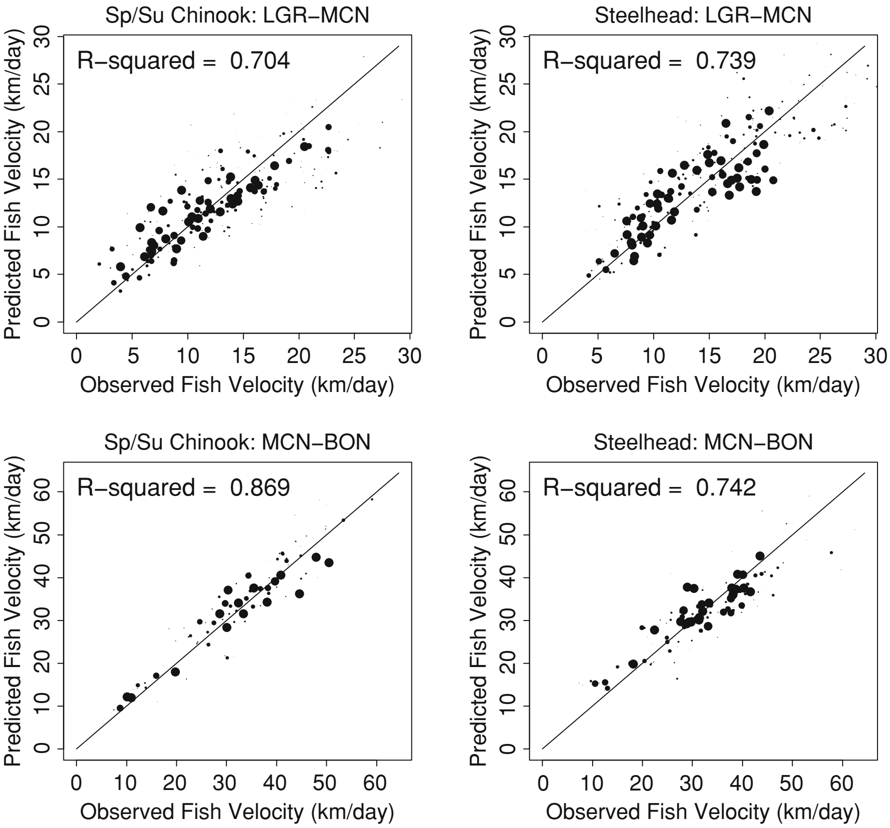

Fig. 7 Predicted migration rate versus observed migration rate for cohorts of Chinook and Steelhead migrating through the upper (Lower Granite (LGR) Dam to McNary (MCN) Dam) and lower (McNary Dam to Bonneville (BON) Dam) river reaches. The size of the point represents its weight, with maximum size set equal to 1/3 of the greatest weight

increasing water temperature, in contrast to the pattern observed with Chinook salmon. The sensitivity of steelhead survival through the dams to spill proportion was similar to that of Chinook salmon, but steelhead survival through dams was approximately 2–3% greater. Finally, the sensitivity of steelhead travel time through the hydropower system to river flow and spill was similar to that of Chinook salmon.

Discussion

Since management actions on regulated rivers are often large-scale, constricted by operating restrictions, and expensive, it is difficult to determine the benefits of various actions through manipulative experiments. Thus, models based on a sufficient understanding of the mechanisms and comprehensive data can be valuable tools for assessing the impacts of river conditions on fish populations. Recent developments in fish tagging technology (e.g., PIT tags and acoustic tags) and a strong commitment to conduct multiyear studies has provided the data on which to develop such a model. The COMPASS model described here appears to realistically portray the available data, primarily PIT-tag data, and thus can potentially serve as important tool in the management of the Columbia River hydropower system. Model results suggest that salmonid populations are responsive to river conditions and thus will respond to river manipulations. However, the results also suggest that different species will respond differentially, and thus multi-species approaches are desirable.

In any ecological modeling exercise, a tradeoff exists between increasing model complexity, with its added realism, and model simplicity, which guards against over parameterization (Johnson & Omland, 2004). We strove for a level of complexity in COMPASS appropriate to the available data. Due to the large PIT-tag data set, we were able to develop travel time and survival algorithms using standard model selection criteria. However, we do not have sufficient data to fully characterize the temporal component of dam passage, which is complex (e.g.,

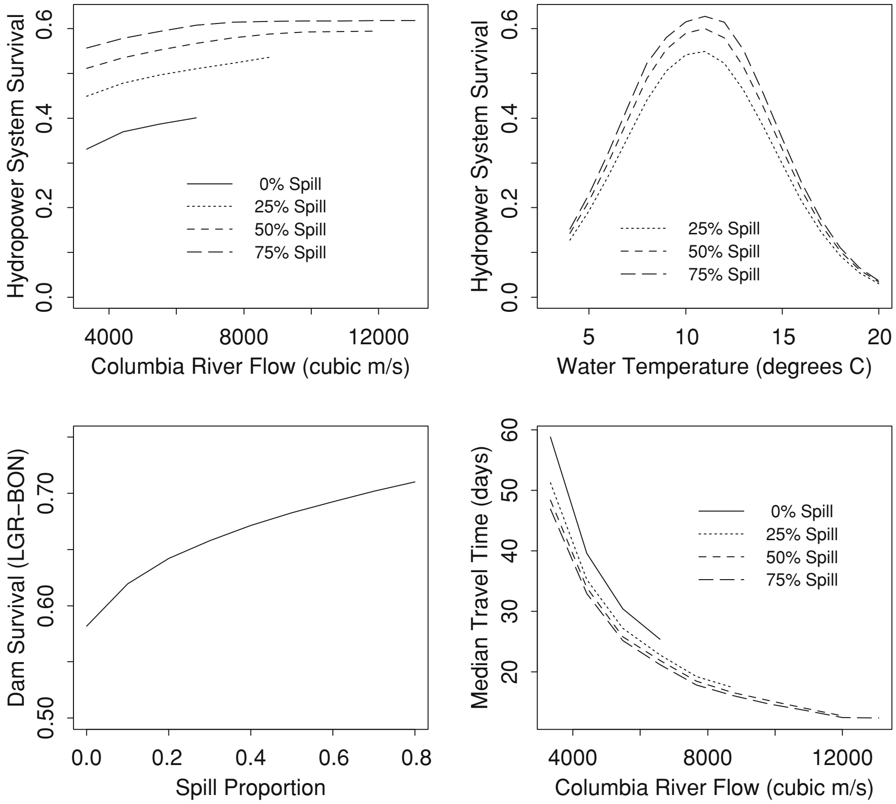

Fig. 8 Sensitivity analysis for spring/summer Chinook salmon. See text for details

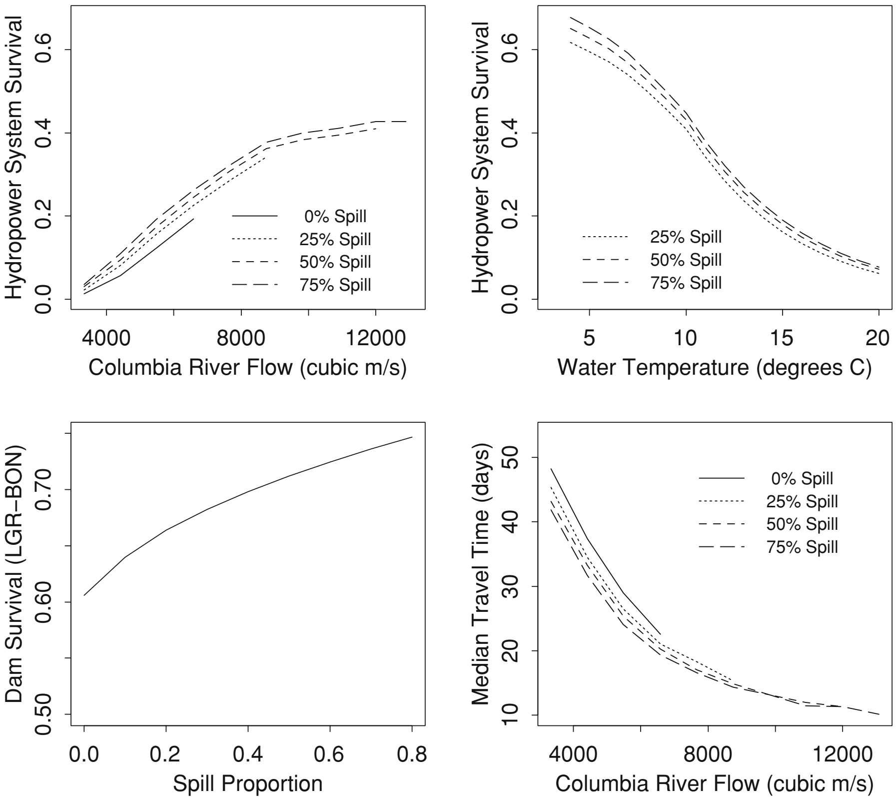

Fig. 9 Sensitivity analysis for steelhead. See text for details

Beeman & Maule, 2001, Castros-Santos and Haro, 2003). However, by relating migration rate to percentage of fish passing through the spillway, we captured an important feature: fish spillway passage is faster than powerhouse passage. We encourage more detailed studies so that we can explore the significance of dam passage behavior on fish survival. Indeed, reducing dam passage time may be a cost-effective way to improve total hydropower system survival.

We are expanding the model in several areas. First, some effects of fish passage through a hydrosystem are potentially expressed outside the hydrosystem as latent mortality due to stress, injury, and disrupted migration timing. Accordingly, to further characterize the impacts of a hydrosystem on migratory fish, we are developing algorithms that represent alternative latent mortality hypotheses. On a related note, because the most important measures of mitigation actions are population viability measures, such as population abundance or probability of quasi-extinction, the COMPASS model will be linked with a population viability model (Zabel et al., 2006) to assess the impacts of hydropower system improvements on population viability. Further, to effectively use model predictions, managers require, not only direct survival estimates, but also uncertainty about the estimates. Consequently, we are developing methods to characterize prediction uncertainty, primarily due to fitting the model to data. Finally, because one goal of our model development is to produce a management tool that is transparent and easy to use by a broad range of users, we are developing a graphical user interface that allows users to simulate management actions and predict the response of migrating fish populations.

Although COMPASS has been formulated for the Columbia and Snake rivers, it is based on a flexible geographic mapping algorithm that can be configured to any river system. Further, our general approach of developing simulation models to explore alternative management scenarios is applicable to a wide-range of river systems.

Acknowledgments Scientists throughout the northwestern United States have contributed to the COMPASS model: Ron Boyce, Dave Clugston, Brad Eppard, Kim Fodrea, Steve Grabowski, Steve Haeseker, Fred Higginbotham, Dave Hurson, Rick Kruger, Mike Langeslay, Tom Lorz, Jerry McCann, Paul Ocker, Charlie Paulsen, Charlie Petrosky, Kris Ryding, Mark Scheuerell, Ann Setter, Marvin Shutters, Earl Weber, Tim Wik, John Williams, and Paul Wilson. Valuable reviews by the Independent Scientific Advisory Board (ISAB) and two anonymous reviewers greatly improved the model and this article.

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EXHIBIT 3

DECLARATION OF RICHARD W. ZABEL

Survival Estimates for the Passage of Spring-Migrating Juvenile Salmonids through Snake and Columbia River Dams and Reservoirs, 2007

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and John G. Williams

Report of research by

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Northwest Fisheries Science Center
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for

U.S. Department of Energy
Bonneville Power Administration
Division of Fish and Wildlife
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Project 199302900

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EXECUTIVE SUMMARY

In 2007, the National Marine Fisheries Service completed the fifteenth year of a study to estimate survival and travel time of juvenile salmonids *Oncorhynchus* spp. passing through dams and reservoirs on the Snake and Columbia Rivers. All estimates were derived from detections of fish tagged with passive integrated transponder (PIT) tags. We PIT tagged and released a total of 19,352 hatchery steelhead *O. mykiss*, 11,286 wild steelhead, and 14,576 wild yearling Chinook salmon *O. tshawytscha* at Lower Granite Dam in the Snake River.

In addition, we utilized fish PIT tagged by other agencies at traps and hatcheries upstream from the hydropower system and at sites within the hydropower system in both the Snake and Columbia Rivers. These included 55,074 yearling Chinook salmon tagged at Lower Granite Dam for evaluation of “extra” or “latent” mortality related to passage through Snake River dams. PIT-tagged smolts were detected at interrogation facilities at Lower Granite, Little Goose, Lower Monumental, Ice Harbor, McNary, John Day, and Bonneville Dams and in the PIT-tag detector trawl operated in the Columbia River estuary. Survival estimates were calculated using a statistical model for tag-recapture data from single release groups (the “single-release model”).

Primary research objectives in 2007 were to:

1) estimate reach survival and travel time in the Snake and Columbia Rivers throughout the migration period of yearling Chinook salmon and steelhead,
2) evaluate relationships between survival estimates and migration conditions, and
3) evaluate the survival estimation models under prevailing conditions.

This report provides reach survival and travel time estimates for 2007 for PIT-tagged yearling Chinook salmon (hatchery and wild), hatchery sockeye salmon *O. nerka*, hatchery coho salmon *O. kisutch*, and steelhead (hatchery and wild) in the Snake and Columbia Rivers. Additional details on the methodology and statistical models used are provided in previous reports cited here.

Survival and detection probabilities were estimated precisely for most of the 2007 yearling Chinook salmon and steelhead migrations. Hatchery and wild fish were combined in some of the analyses. For yearling Chinook salmon, overall percentages for combined release groups used in survival analyses in the Snake River were 84% hatchery-reared and 16% wild. For steelhead, the overall percentages were 64% hatchery-reared and 36% wild.

Estimated survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam averaged 0.938 for yearling Chinook salmon and 0.887 for steelhead. Respective average survival estimates for yearling Chinook salmon and steelhead through the following reaches were 0.957 and 0.911 from Little Goose Dam tailrace to Lower Monumental Dam tailrace, 0.876 and 0.852 from Lower Monumental Dam tailrace to McNary Dam tailrace (including passage through Ice Harbor Dam), 0.920 and 0.988 from McNary Dam tailrace to John Day Dam tailrace, and 0.824 and 0.579 from John Day Dam tailrace to Bonneville Dam tailrace (including passage through The Dalles Dam).

Combining average estimates from the Snake River smolt trap to Lower Granite Dam, from Lower Granite Dam to McNary Dam, and from McNary Dam to Bonneville Dam, estimated average survival through the entire hydropower system from the head of Lower Granite reservoir to the tailrace of Bonneville Dam (eight projects) was 0.563 (s.e. 0.037) for Snake River yearling Chinook salmon and 0.369 (s.e. 0.047) for steelhead during 2007.

For yearling spring Chinook salmon released in the Upper Columbia River, estimated survival from point of release to McNary Dam tailrace ranged from 0.659 (s.e. 0.028) for East Bank Hatchery fish released from Chiwawa Pond to 0.260 (s.e. 0.068) for fish released from Wells Hatchery.

For steelhead released in the Upper Columbia River, estimated survival from point of release to McNary Dam tailrace ranged from 0.659 (s.e. 0.046) for fish from Turtle Rock Hatchery released in the Wenatchee River to 0.179 (s.e. 0.017) for fish from Cassimer Bar Hatchery released in the Okanagon River. Survival of sockeye salmon released to the Wenatchee River from East Bank Hatchery through this reach was 0.299 (s.e. 0.013).

During 2007, flows were relatively low, especially when compared to flows during the 2006 migration year. The index for flow calculated for steelhead was the lowest measured in the last six years, very near the flow index of 2001.

Yearling Chinook salmon hydropower system survival (Snake River trap to Bonneville Dam tailrace) in 2007 was the second highest estimated in the last 15 years. The highest estimated was in 2006. Steelhead hydropower system survival was also lower compared to 2006 survival, but was higher than in 2001 through 2003 (survival could not be estimated through the entire hydropower system in 2004 and 2005). High survival was estimated despite the low flows experienced during 2007.

This was likely a result of a larger number of steelhead migrating below Lower Monumental Dam than occurred in previous years under low-flow conditions. This larger number of fish resulted from a combination of factors: high spill levels in 2007 compared to other recent low flow years (2001 and 2004), the addition of a surface spill device (removable spillway weir) at Lower Granite Dam, and a delayed start to barge transport operations. As a result, survival estimates were higher through the Snake River in 2007, in part due to lower predation rates on PIT-tagged smolts by avian predators near the confluence of the Snake and Columbia Rivers.

Yearling Chinook salmon and steelhead travel times through the hydropower system were relatively fast considering the low flows experienced during 2007, likely a result of spill and use of surface collectors at several projects.

CONTENTS

INTRODUCTION

Accurate and precise survival estimates are needed for depressed stocks of juvenile Chinook *Oncorhynchus tshawytscha*, sockeye salmon *O. nerka*, and steelhead *O. mykiss* that migrate through reservoirs, hydroelectric projects, and free-flowing sections of the Snake and Columbia Rivers. To develop recovery strategies that will optimize smolt survival during migration, knowledge of the magnitude, locations, and causes of smolt mortality is needed. Such knowledge is necessary for strategies applied under present passage conditions as well as under conditions projected for the future (Williams and Matthews 1995; Williams et al. 2001).

From 1993 through 2006, the National Marine Fisheries Service (NMFS) developed survival estimates for these stocks using detections of PIT-tagged (Prentice et al. 1990a) juvenile salmonids passing through Snake River dams and reservoirs (Iwamoto et al. 1994; Muir et al. 1995, 1996, 2001a,b, 2003; Smith et al. 1998, 2000a,b, 2003, 2005, 2006; Hockersmith et al. 1999; Zabel et al. 2001, 2002; Faulkner et al. 2007). In 2007, NMFS completed the fifteenth year of the study.

Research objectives in 2007 were to:

1) estimate reach survival and travel time in the Snake and Columbia Rivers throughout the yearling Chinook salmon and steelhead migrations,
2) evaluate relationships between survival estimates and migration conditions, and
3) evaluate the performance of the survival-estimation models under prevailing operational and environmental conditions.

Additionally, as adult return information becomes available, we will evaluate relationships between juvenile survival and subsequent adult returns for fish with different juvenile migration histories. This task was recently completed for adult returns to date, and the results were reported by Williams et al. (2005).

METHODS

Experimental Design

The single-release (SR) model was used to estimate survival for groups of PIT-tagged yearling Chinook salmon, sockeye salmon, and steelhead (Cormack 1964; Jolly 1965; Seber 1965; Skalski 1998; Skalski et al. 1998; Muir et al. 2001a). Iwamoto et al. (1994) presented background information and underlying statistical theory pertaining to the SR model. In 2007, PIT-tagged fish used for survival estimates were released from hatcheries, traps, and Lower Granite Dam in the Snake River Basin, and from hatcheries and dams in the Upper Columbia River.

During the 2007 migration season, automatic PIT-tag detectors (Prentice et al. 1990a,b,c) were operational in the juvenile bypass systems at the following seven dams: Lower Granite (rkm 695), Little Goose (rkm 635), Lower Monumental (rkm 589), Ice Harbor (rkm 538), McNary (rkm 470), John Day (rkm 347), and Bonneville (rkm 234) Dams (Figure 1). The farthest downstream site of PIT-tag detections was in the Columbia River estuary between rkm 65 and 84, where a pair trawl towed a PIT-tag detector (Ledgerwood et al. 2004). During spring 2007, the corner collector at Bonneville Dam Second Powerhouse was operated with its PIT tag detection system. Sufficient PIT tag detections at this site allowed survival estimation through the reach from John Day tailrace to Bonneville Dam tailrace for both yearling Chinook salmon and steelhead.

A large proportion of PIT-tagged yearling Chinook salmon used in this analysis were released in the Snake River above Lower Granite Dam for a multi-agency comparative survival study (CSS) (Schaller et al. 2007). In addition, we utilized about 55,074 yearling Chinook salmon PIT tagged at Lower Granite Dam and released into the tailrace there for evaluation of “extra” or “latent” mortality related to passage through Snake River dams (Marsh et al. 2006). All other PIT-tagged fish detected at dams were diverted back to the river by slide gates, which allowed for the possibility of detection of a particular fish at more than one downstream site (Marsh et al. 1999).

For fish released in the Snake River Basin, we used records of downstream PIT-tag detections with the SR model to estimate survival in the following seven reaches:

- Point of release to Lower Granite Dam tailrace
- Lower Granite Dam tailrace to Little Goose Dam tailrace
- Little Goose Dam tailrace to Lower Monumental Dam tailrace

- Lower Monumental Dam tailrace to Ice Harbor Dam tailrace
- Ice Harbor Dam tailrace to McNary Dam tailrace
- McNary Dam tailrace to John Day Dam tailrace
- John Day Dam tailrace to Bonneville Dam tailrace

The PIT-tag detection system in the Ice Harbor Dam juvenile bypass facility began operating in 2005. Because of the high level of spill at this dam, too few smolts were detected there to partition survival between Lower Monumental and McNary Dams in 2005. However, in 2006 and 2007 there were sufficient detections at Ice Harbor to partition survival through this reach**.**

For fish released in the Upper Columbia River, we estimated survival in the following three reaches:

- Point of release to the tailrace of McNary Dam
- McNary Dam tailrace to John Day Dam tailrace
- John Day Dam tailrace to Bonneville Dam tailrace

Lower Granite Dam Tailrace Release Groups

During 2007, hatchery and wild steelhead and wild yearling Chinook salmon were collected at the Lower Granite Dam juvenile facility, PIT tagged, and released to the tailrace for survival estimates. Fish were collected in approximate proportion to the numbers arriving at Lower Granite Dam during the migration season. However, in the early and late periods of the season, we tagged relatively more fish in order to provide sufficient numbers for analysis over these periods. No hatchery yearling Chinook salmon were PIT tagged specifically for this study because the numbers of fish PIT tagged and released from Snake River Basin hatcheries, traps, and for other studies were sufficient for analysis. Further, we used 55,074 yearling Chinook salmon that were tagged at Lower Granite Dam for evaluation of “extra” or “latent” mortality related to passage through Snake River dams.

For both yearling Chinook salmon and steelhead tagged above Lower Granite Dam and subsequently detected at Lower Granite Dam and released to the tailrace, we created daily "release groups" by combining detections at Lower Granite Dam that occurred on the same day. These groups were then combined with fish tagged and released each day at Lower Granite Dam. These daily release groups were then pooled into weekly groups, and we estimated survival probabilities in reaches between Lower Granite Dam tailrace and McNary Dam tailrace for both the daily and weekly groups.

McNary Dam Tailrace Release Groups

For both yearling Chinook salmon and steelhead tagged at all locations in the Snake River Basin, and for fish tagged in the Upper Columbia River, we created daily "release groups" of fish according to the day of detection at McNary Dam. Daily groups consisted of fish that were detected and returned to the tailrace, and daily groups were pooled into weekly groups. For weekly groups leaving McNary Dam, we estimated survival from McNary Dam tailrace to John Day Dam tailrace and from John Day Dam tailrace to Bonneville Dam tailrace.

Hatchery and Trap Release Groups

In 2007, most hatcheries in the Snake River Basin released PIT-tagged fish as part of research separate from the NMFS survival study. We analyzed data from hatchery releases of PIT-tagged yearling Chinook salmon, sockeye salmon, coho salmon *O. kisutch*, and steelhead to provide survival estimates and detection probabilities from release to the tailrace of Lower Granite Dam and to points downstream. We estimated survival to the tailrace of McNary Dam for yearling spring Chinook salmon released from Cle Elum, Wells, Winthrop, Entiat, Leavenworth, and East Bank hatcheries. Survival to McNary Dam was also estimated for steelhead released from Turtle Rock, Chelan, East Bank, and Cassimer Bar hatcheries in the Upper Columbia River Basin, for Coho salmon released from Cascade, Eagle Creek, Willard, and Yakima hatcheries, and for sockeye salmon released from East Bank Hatchery. In the course of characterizing the various hatchery releases, preliminary analyses were performed to determine whether data from multiple release groups could be pooled to increase sample sizes.

We estimated survival to Lower Granite Dam tailrace and points downstream for releases of wild and hatchery PIT-tagged yearling Chinook salmon and steelhead from the Salmon (White Bird), Snake, and Clearwater River traps, and many more smolt traps throughout the Snake River Basin.

Data Analysis

Tagging and detection data were uploaded to, and later retrieved from, the PIT Tag Information System (PTAGIS), a regional database maintained by the Pacific States Marine Fisheries Commission (PSMFC 1996). Data were examined for erroneous records, inconsistencies, and data anomalies. Records were eliminated where appropriate, and all eliminated PIT-tag codes were recorded with the reasons for their elimination. For each remaining PIT-tag code, we constructed a record ("detection history") indicating all locations at which the tagged fish had been detected and all locations at which it had not been detected. Methods for data retrieval, database quality assurance/control, and construction of detection histories were the same as those used in past years (see Iwamoto et al. 1994 for detail).

These analyses were conducted using the data available at the time. It is possible, for a variety of reasons, that the data in the PTAGIS database may be updated. Thus, estimates provided by NMFS, or employed in analyses in the future, may differ slightly from those presented here.

Tests of Assumptions

As in past years, we evaluated assumptions of the SR model as applied to the data generated from PIT-tagged juvenile salmonids in the Snake and Columbia Rivers (Burnham et al. 1987). These evaluations are detailed in the Appendix.

Survival Estimation

Estimates of survival probability under the SR model are random variables, subject to sampling variability. When true survival probabilities are close to 1.0 and/or when sampling variability is high, it is possible for estimates of survival probabilities to exceed 1.0. For practical purposes, estimates should be considered equal to 1.0 in these cases.

When estimates for a particular river section or passage route were available from more than one release group, the estimates were often combined using a weighted average (Muir et al. 2001a). Weights were inversely proportional to the respective estimated relative variance (coefficient of variation squared). The variance of an estimated survival probability from the SR model is a function of the estimate itself. Consequently, lower survival estimates tend to have smaller estimated variance. Therefore, we did not use the inverse estimated absolute variance in weighting because lower survival estimates have disproportionate influence, and the resulting weighted mean is biased toward the lower survival estimates.

All survival estimates presented are from point of release (or the tailrace of a dam) to the tailrace of a dam downstream. All survival and detection probability estimates were computed using the statistical computer program SURPH ("Survival with Proportional Hazards") for analyzing release-recapture data, developed at the University of Washington (Skalski et al. 1993; Smith et al. 1994).

Survival Estimates from Point of Release to Bonneville Dam

We estimated survival from point of release to the tailrace of Bonneville Dam (the last dam encountered by seaward-migrating juvenile salmonids) for various stocks from both the Snake and Upper Columbia Rivers. These estimates were obtained by first estimating weighted average estimated survival over shorter reaches for daily or weekly release groups using the same weighting scheme described above. These average survival estimates were then multiplied to compute the estimated survival probabilities through the entire reach.

We pooled similar fish from different release sites when we re-formed release groups at downstream sites. For example, for Snake River yearling Chinook salmon, we multiplied the weighted mean survival estimate for daily groups from Lower Granite Dam tailrace to McNary Dam tailrace by the weighted mean estimate for weekly groups from McNary Dam tailrace to Bonneville Dam tailrace to obtain an overall estimated mean survival probability from Lower Granite Dam tailrace to Bonneville Dam tailrace. Finally, we multiplied this result by the survival estimate from fish released from the Snake River trap to Lower Granite Dam to compute estimated survival from the head of Lower Granite reservoir to the tailrace of Bonneville Dam; essentially the entire eight-project hydropower system negotiated by juvenile salmonids from the Snake River Basin.

Travel Time and Migration Rate

Travel times of yearling Chinook salmon and steelhead were calculated for the following reaches:

1) Lower Granite Dam to Little Goose Dam (60 km)
2) Little Goose Dam to Lower Monumental Dam (46 km)
3) Lower Monumental Dam to McNary Dam (199 km)
4) Lower Granite Dam to McNary Dam (225 km)
5) Lower Granite Dam to Bonneville Dam (461 km)
6) McNary Dam to John Day Dam (123 km)
7) John Day Dam to Bonneville Dam (113 km)
8) McNary Dam to Bonneville Dam (236 km).

Travel time between any two dams was calculated for each fish detected at both dams as the number of days between last detection at the upstream dam (generally at a PIT-tag detector close enough to the outfall site that fish arrived in the tailrace within minutes after detection) and first detection at the downstream dam. Travel time included the time required to move through the reservoir to the forebay of the downstream dam and any delay associated with residence in the forebay, gatewells, or collection channel prior to detection in the juvenile bypass system.

Migration rate through a river section was calculated as the length of the section (km) divided by the travel time (d) (which included any delay at dams as noted above). For each group, the 20th percentile, median, and 80th percentile travel times and migration rates were determined.

The true complete set of travel times for a release group includes travel times of both detected and nondetected fish. However, using PIT tags, travel times cannot be determined for a fish that traverses a river section but is not detected at both ends of the section. Travel time statistics are computed only from travel times for detected fish, which represent a sample of the complete set. Nondetected fish pass dams via turbines and spill; thus, their time to pass a dam is typically minutes to hours shorter than that of detected fish, which pass to the tailrace via the juvenile bypass system.

Comparison of Annual Survival Estimates

We made two comparisons of 2007 results to those obtained in previous years of the NMFS survival study. First, we related migration distance to survival estimates from specific hatcheries to Lower Granite Dam. Second, we compared season-wide survival estimates for specific reaches across years.

Flow and Spill In Relation to Juvenile Salmonid Survival and Travel Time

Annual travel time and reach survival estimates were compared across years to investigate relationships with general flow and spill conditions during the spring migration. Trends within the 2007 season were also examined.

RESULTS

Lower Granite Dam Tagging and Release Information

During 2007, a total of 125,147 yearling Chinook salmon (104,602 hatchery origin, 20,485 wild) were detected and released or PIT tagged and released to the river in the tailrace of Lower Granite Dam. Steelhead we tagged at Lower Granite Dam and released to the tailrace were combined with those released upstream, detected at the dam, and returned to the river, for a total of 32,610 (20,724 hatchery origin and 11,886 wild).

For both species, not all detections were included in the analyses because some fish passed Lower Granite Dam early or late in the season, when sample sizes were too small to produce reliable survival or travel time estimates. Survival estimates for wild and hatchery fish combined were predominately based on fish of hatchery origin for yearling Chinook salmon (84% hatchery) and steelhead (64% hatchery) during 2007.

Survival Estimation

Tests of Assumptions

Assumption tests for 2007 indicated more significant differences between observed and expected detection proportions than would be expected by chance alone. In many cases, sample sizes were such that the contingency table-based tests had power to detect cases where violations had minimal effect on survival estimates. We present a detailed discussion of the assumption tests, the extent of violations, possible reasons for the occurrence of the violations, and their implications in the Appendix.

Snake River Yearling Chinook Salmon

Survival probabilities were estimated for weekly groups of yearling Chinook salmon released to the tailrace of Lower Granite Dam for 10 consecutive weeks from 23 March through 31 May. Survival estimates from Lower Granite Dam tailrace to Little Goose Dam tailrace averaged 0.938 (s.e. 0.006; Table 1). From Little Goose Dam tailrace to Lower Monumental Dam tailrace, estimated survival averaged 0.957 (s.e. 0.010). From Lower Monumental Dam tailrace to McNary Dam tailrace, estimated survival averaged 0.876 (s.e. 0.012). For the combined reach from Lower Granite Dam tailrace to McNary Dam tailrace, survival averaged 0.783 (s.e. 0.006).

We estimated survival probabilities for weekly groups of yearling Chinook salmon released in the tailrace at McNary Dam for eight consecutive weeks from 20 April through 14 June. From McNary Dam tailrace to John Day Dam tailrace, estimated survival averaged 0.920 (s.e. 0.016; Table 2). From John Day Dam tailrace to Bonneville Dam tailrace estimated survival averaged 0.824 (s.e. 0.043). For the combined reach from McNary Dam to Bonneville Dam, estimated survival averaged 0.763 (s.e. 0.044).

The product of the average estimates from Lower Granite Dam to McNary Dam and from McNary Dam to Bonneville Dam provided an overall survival estimate from Lower Granite Dam tailrace to Bonneville Dam tailrace of 0.597 (s.e. 0.035). Estimated survival probability through Lower Granite reservoir and Dam for Snake River wild and hatchery Chinook salmon released from the Snake River trap was 0.943 (s.e. 0.028). Thus, estimated survival probability through all eight hydropower projects encountered by Snake River yearling Chinook salmon was 0.563 (s.e. 0.037).

We also calculated separate survival probability estimates for weekly groups of hatchery and wild yearling Chinook salmon from Lower Granite Dam tailrace to McNary Dam tailrace (Tables 3 and 4). Weighted mean survival estimates for hatchery and wild yearling Chinook salmon were similar for the combined reach from the tailrace of Lower Granite Dam to the tailrace of McNary Dam in 2007.

Estimated survival probabilities for daily release groups of yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at Lower Granite Dam did not show any consistent increase or decrease through Snake River reaches during the 2007 migration season (Table 5; Figure 2).

Estimates of detection probability varied throughout the season for most weekly groups as flows and spill levels changed (Tables 6-9). Detection probabilities were generally highest at McNary and John Day Dams.

Snake River Steelhead

We estimated survival probabilities for weekly groups of steelhead from the tailrace of Lower Granite Dam for eight consecutive weeks from 6 April through 31 May. Survival estimates from Lower Granite Dam tailrace to Little Goose Dam tailrace averaged 0.887 (s.e. 0.009; Table 10). From Little Goose Dam tailrace to Lower Monumental Dam tailrace, estimated survival averaged 0.911 (s.e. 0.022). From Lower Monumental Dam tailrace to McNary Dam tailrace, estimated survival averaged 0.852

(s.e. 0.030). For the combined reach from Lower Granite Dam tailrace to McNary Dam tailrace, estimated survival averaged 0.694 (s.e. 0.020).

We estimated survival probabilities for weekly groups of steelhead released in the tailrace of McNary Dam for six consecutive weeks from 20 April through 31 May. From McNary Dam tailrace to John Day Dam tailrace, estimated survival averaged 0.988 (s.e. 0.098; Table 11). Estimated survival from John Day Dam tailrace to Bonneville Dam tailrace averaged 0.579 (s.e. 0.059), and for the combined reach from McNary Dam tailrace to Bonneville Dam tailrace, 0.524 (s.e. 0.064).

The product of the average estimates from Lower Granite Dam to McNary Dam and from McNary Dam to Bonneville Dam provided an overall survival estimate from Lower Granite Dam tailrace to Bonneville Dam tailrace of 0.364 (s.e. 0.050). Estimated survival probability through Lower Granite reservoir and Dam for Snake River wild and hatchery steelhead released from the Snake River trap was 1.016 (s.e. 0.026). Thus, estimated survival probability through all eight hydropower projects encountered by Snake River steelhead was 0.369 (0.047).

Survival probabilities were estimated separately for weekly groups of hatchery and wild steelhead from Lower Granite Dam tailrace to McNary Dam tailrace (Tables 12 and 13). Survival estimates for wild steelhead through most individual reaches and the reaches combined were higher than for hatchery steelhead.

Similar to yearling Chinook salmon, estimated survival probabilities for daily release groups of steelhead (hatchery and wild combined) detected and released to the tailrace of Lower Granite Dam did not show any consistent increase or decrease through Snake River reaches during the 2006 migration season (Table 14; Figure 3).

Estimates of detection probability at Snake River dams for the weekly steelhead groups varied throughout the season as the level of spill changed (Tables 15-18). Detection probability estimates were generally lowest at McNary, John Day, and Bonneville Dams.

Snake River Hatchery Release Groups

Survival probabilities were estimated for PIT-tagged hatchery yearling Chinook salmon, sockeye salmon, coho salmon, and steelhead from release at Snake River Basin hatcheries to the tailrace of Lower Granite Dam and to downstream dams. These estimates varied among hatcheries and release locations (Tables 19-21), as did estimated detection probabilities among detection sites (Tables 22-24). For yearling Chinook salmon, estimated survival from release to Lower Granite Dam tailrace was highest for fish released from the Clearwater Hatcheries' Red River Pond (0.816) and lowest for fish released from McCall Hatchery into Johnson Creek (0.319). For sockeye salmon, estimated survival from release to Lower Granite Dam tailrace ranged from 0.776 from the Sawtooth trap to 0.338 from Redfish Lake Creek trap for fish PIT-tagged and released in the spring. Estimated survival was lower for sockeye salmon PIT-tagged and release the previous fall (0.123 to 0.204).

Snake River Smolt Trap Release Groups

Survival probability estimates for juvenile salmonids PIT tagged and released from Snake River Basin smolt traps were generally inversely related to distance of the traps from Lower Granite Dam (Table 25). Estimated detection probabilities were similar among release groups of the same species from different traps (Table 26).

Upper Columbia River Hatchery Release Groups

Survival probability estimates for PIT-tagged hatchery yearling Chinook salmon, coho salmon, sockeye, and steelhead from release at Upper Columbia River hatcheries to the tailrace of McNary Dam and dams downstream varied among hatcheries and release locations (Table 27) as did detection probability estimates (Table 28). For yearling spring Chinook salmon released in the Upper Columbia River, estimated survival from point of release to McNary Dam tailrace ranged from 0.659 (s.e. 0.028) for East Bank Hatchery fish released from Chiwawa Pond to 0.260 (s.e. 0.068) for fish released from Wells Hatchery.

For steelhead released in the Upper Columbia River, estimated survival from point of release to McNary Dam tailrace ranged from 0.659 (s.e. 0.046) for fish from Turtle Rock Hatchery released in the Wenatchee River to 0.179 (s.e. 0.017) for fish from Cassimer Bar Hatchery released in the Okanagon River. Survival of sockeye salmon released to the Wenatchee River from East Bank Hatchery through this reach was 0.299 (s.e. 0.013).

Travel Time and Migration Rate

Travel time estimates for yearling Chinook salmon and juvenile steelhead released in the tailraces of Lower Granite and McNary Dams varied throughout the season (Tables 29-36). For both species, estimated migration rates were generally highest in the lower river sections. Estimated migration rates for yearling Chinook salmon generally increased over time as flow and water temperature increased, and presumably as fish became more smolted, while travel time for steelhead was faster than in recent years and changed little through the season (Figure 4). Travel time estimates for yearling Chinook salmon from Lower Granite to McNary Dam decreased during early- to mid-April independent of flow (i.e., estimated travel times decreased considerably without corresponding changes in flow) whereas travel time estimates for steelhead did not (Figure 5).

Tagging Details for Fish PIT Tagged at Lower Granite Dam

We PIT-tagged and released 19,352 hatchery steelhead, 11,286 wild steelhead, and 14,576 wild yearling Chinook salmon from 10 April through 16 June at Lower Granite Dam for survival estimates (Table 37-39). Total mortalities of hatchery steelhead, wild steelhead, and yearling Chinook salmon were 17, 3, and 37, respectively. Each of these numbers represented less than 1% of the total number of fish handled.

Comparison of Annual Survival Estimates

Estimates of yearling Chinook salmon survival from Snake River Basin hatcheries to Lower Granite Dam tailrace for 2007 were similar to those made in past recent years for most hatcheries. The mean of the hatchery estimates was higher compared to the long-term mean (Table 40), though the difference is not statistically significant. Over the years of the study, we have consistently observed an inverse relationship between the migration distance from the release site to Lower Granite Dam and the estimated survival through that reach (Figure 6). For 1993-2007 estimates, the negative linear correlation between migration distance and average estimated survival was significant ($R^2 = 0.948$, $P < 0.001$).

For yearling Chinook salmon and steelhead (hatchery and wild combined), estimated survival in 2007 was similar to that estimated in 2006 through the Lower Granite Dam to McNary Dam reach but lower from the McNary Dam to Bonneville Dam reach (Table 41-43; Figures 7-8). Steelhead estimated survival was depressed through the John Day Dam to Bonneville Dam reach, but was improved in the Lower Monumental to McNary Dam reach (Table 42; Figures 7-8).

For yearling Chinook salmon, estimated mean survival for all years combined was similar through each of the Snake River reaches and from John Day Dam to Bonneville Dam reach in the Columbia River (0.90-0.93), but was lower through the McNary to John Day Reach on the Columbia River (0.85; Table 41). For steelhead, estimated mean survival across years showed a slight decline through successive reaches, but similar to yearling Chinook salmon, was lowest through the McNary to John Day reach (0.75), the reach with the longest reservoir (Table 42).

For several years, we have combined empirical survival estimates for yearling Chinook salmon and steelhead over various reaches to derive estimates of survival throughout the entire Snake River hydropower system, from the head of Lower Granite reservoir (Snake River smolt trap) to the tailrace of Bonneville Dam (Table 43). Data were sufficient for these estimates starting in 1999 for yearling Chinook and 1997 for steelhead, but were not sufficient through the final reach for steelhead in 2004 and 2005 when the new corner collector (without PIT tag interrogation) was operated at Bonneville Dam's second powerhouse. In 2006, a new PIT tag interrogation system was operated in the corner collector increasing the detection probability at this site. For yearling Chinook salmon in 2007, estimated hydropower system survival was 0.563 (95% C.I. 0.491-0.636), the second highest survival estimate to date. For steelhead, estimated hydropower system survival was 0.369 (95% C.I. 0.277-0.461), higher than that estimated from 2001-2003 (estimates not available for 2004-2005), and lower than estimated from 1997-2000, and in 2006.

Flow and Spill In Relation to Juvenile Salmonid Survival and Travel Time

Snake River flow volume during the yearling Chinook salmon migration period was expressed as flow exposure index at Lower Monumental Dam for each release group. The flow exposure index is derived from average flow per day weighted by the numbers of fish detected that day. Thus, values of the exposure index are very similar to those of daily average flow at the dam.

The average flow exposure index in 2007 for yearling Chinook salmon (85.9 kcfs) and steelhead (81.4 kcfs) were much lower than in 2006 (130.5 and 135.4 kcfs, respectively), without an obvious peak as observed in most years (Figure 9 and 10).

In 2007, transport was delayed until 2 May at Lower Granite Dam, 9 May at Little Goose Dam, and 12 May at Lower Monumental Dam. Until these dates, smolts collected at Snake River dams were bypassed back to the river.

In comparisons among years, yearling Chinook salmon and steelhead estimated travel times between Lower Granite and Bonneville Dams in 2007 were similar to past years through most of the season, but were considerably faster than observed in 2001 (Figure 4).

Survival Estimates from Point of Release to McNary Dam

In 2007, estimated survival to McNary Dam was generally lower for yearling spring Chinook salmon released at hatcheries in the Upper Columbia River than for their counterparts released in the Snake River (Tables 19 and 27). For Upper Columbia River fish, average survival to McNary Dam was estimated at 0.594 (0.011) for fish from Leavenworth Hatchery (4 projects; 564 km) and 0.321 (0.035) for fish from Entiat Hatchery (5 projects; 559 km) in the Upper Columbia River. For Snake River fish released at Dworshak Hatchery (5 projects; 575 km), average survival to McNary Dam was estimated at 0.662 (0.004).

For steelhead from Snake River Basin hatcheries, estimated survival to the tailrace of McNary Dam was also generally higher to that of their counterparts from Upper Columbia hatcheries passing a similar number of dams (Tables 20 and 27).

Partitioning Survival Between Lower Monumental and Ice Harbor Dams

Although a PIT-tag detection system was operational at Ice Harbor Dam in 2005, the high spill rate there resulted in low numbers of fish entering the bypass system for detection. Thus, we were still unable to partition survival between Lower Monumental and McNary Dams into reach-specific estimates in 2005. However, sufficient detections occurred in 2006 and 2007 to partition survival estimates through the individual reaches (Tables 44 and 45). Estimated survival for yearling Chinook salmon was 0.930 (s.e. 0.017) from the tailrace of Lower Monumental Dam to the tailrace of Ice Harbor dam and 0.959 (s.e. 0.030) from Ice Harbor Dam tailrace to McNary Dam tailrace. For steelhead, estimated survival through these reaches was 0.902 (s.e. 0.026) and 0.953 (s.e. 0.033), respectively.

DISCUSSION

Flow volume was considerably lower and water was less turbid during the spring migration in 2007 than in 2006, which had high flows and turbid water throughout the migration (Faulkner et al. 2007). Despite moderately low flows during 2007, estimated travel times through the system were similar to other recent years, although migration for steelhead was slower than in 2006. For yearling Chinook salmon, estimated survival through the hydropower system was the second highest yet observed; about 56% from the Snake River trap to Bonneville Dam tailrace. For steelhead, estimated survival through the hydropower system was lower, at about 37%.

Between Lower Monumental Dam and McNary Dam, where steelhead survival has been depressed since 2001, estimated steelhead survival was higher in 2007 than in recent years. Loss of PIT-tagged steelhead to piscivorous birds in the McNary pool in 2007 was the lowest since 1998 (indexed by the percentage of tags detected in bird colonies). Loss to birds was also relatively low in 2006. The decrease in percentage of smolts taken by birds was due in part to an increase in the total number of smolts (tagged and untagged) remaining in the river, which resulted from increased spill and initiation of the smolt transportation program later in the year (see below for more on avian predation and total numbers of smolts).

Migration conditions and associated hydropower system survival estimates from 2005 through 2007 show suggestive correlations among flow, spill, and estimated survival. In spring 2005, flows were low during early- to mid-April, but increased substantially from late April through the remainder of the migration season, resulting in an annual flow index for yearling Chinook salmon of 95.3 kcfs. Spill did not occur (i.e., transportation was maximized) in 2005 at Lower Granite, Little Goose, and Lower Monumental Dams until 17 May, when flows exceeded powerhouse capacities. By that time, most of the yearling Chinook salmon migration had passed. Spill continued through about 27 May at Lower Granite and Lower Monumental Dams, while spill ended at Little Goose Dam on 23 May.

In contrast, 2006 was a high-flow year (annual flow index of 130.5 for yearling Chinook salmon), and spill was provided throughout the migration. The 2007 migration season was a relatively low-flow year (annual flow index of 85.9 for yearling Chinook salmon), with spill again provided throughout the migration. Estimated hydropower system survival for yearling Chinook salmon was highest in 2006 at 61.2% (high flow with spill), but similar between 2005 at 53.0% (moderately low flow, very limited spill) and 2007 at 56.3% (moderately low flow, with spill).

For steelhead we could not make the same annual comparisons, because operation of the corner collector at Bonneville Dam decreased detection efficiencies in 2005, and hydropower system survival could not be estimated for that year. However, we can compare estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace from 2005 through 2007. Estimated survival was lowest in 2005 (59.3%), but similar in 2006 (70.2%) and 2007 (69.4%). For yearling Chinook salmon, estimated survival through this reach was 73.2, 76.4, and 78.3% in 2005, 2006, and 2007, respectively. Thus, spill may have directly or indirectly provided greater benefit to migrating steelhead than for yearling Chinook salmon.

Because juvenile diversion screens have higher collection efficiency for steelhead than for Chinook, when there is no spill almost all (95% or more) non PIT-tagged steelhead are barged from Lower Granite, Little Goose, or Lower Monumental Dam. Fish that remain in the river to migrate downstream of Lower Monumental dam are the very small percentage (tagged and untagged) that passed through turbines at all three collector dams, those released from hatcheries or tributaries downstream of Lower Granite Dam, and PIT-tagged fish that were intentionally returned to the river from the bypass system at collector dams. Because of transportation, the total number of smolts remaining in the river decreases as the population moves downstream. Guidance efficiency of the turbine intake screens is lower for Chinook salmon, so the number of Chinook salmon remaining in the river does not decrease as quickly, as more of them pass through turbines.

Analyses based on early data (1973-1979) suggested that increases in spill directly increased survival (Sims and Ossiander 1981). From our own research, estimated survival through the Snake River was lower in 1993 and 1994, when spill occurred only in excess of powerhouse capacity, than it was in subsequent years, after the 1995 BiOp (NMFS 1995) prescribed spill at all dams. Estimated survival was lowest during the 2001 migration, when spill was eliminated or severely reduced at all dams. However, demonstrating positive correlation between spill and survival within a single migration season has been more problematic (Smith et al. 2002; Zabel et al. 2002; Williams et al. 2005).

Predation is one factor that unquestionably directly affects survival of migrating smolts (Collis et al. 2002). Avian piscivores are abundant along the Columbia River downstream of the confluence with the Snake River, and bird population sizes and consumption rates are well monitored. Crescent Island, in the McNary Dam reservoir, harbors the second largest Caspian tern *Hydroprogne caspia* colony in North America (about 500 breeding pairs annually on average in the last 10 years), as well as large populations of gulls *Larus* spp. Other avian piscivores reside within the McNary pool, including the American white pelican *Pelecanus erythrorhynchos,* cormorant *Phalacrocorax auritus*, and heron *Ardea alba, A. herodias*, and *Nycticorax nycticorax.* Steelhead smolts are particularly susceptible to predation by birds. For example,Collis et al. (2001) reported over 15% of the tags from PIT-tagged steelhead detected at Bonneville Dam in 1998 were later found on estuarine bird colonies, while only 2% of the tags from PIT-tagged yearling Chinook salmon were found.

For 10 years, the sites of bird colonies in McNary pool have been sampled for deposited PIT tags after the end of the nesting season, and we have combined bird-colony detection data with records of detection and return-to-river at Lower Monumental Dam. Assuming that PIT-tagged fish that remain in the river downstream of Lower Monumental Dam are representative of the untagged population that remains in the river, the percentage of smolts detected at the dam that are later recovered on a bird colony represents an estimate of the proportion of the entire smolt population that was consumed by birds. (Actually, it is a minimum estimate, as not all remains of smolts consumed are deposited with PIT tags recoverable on the colony site).

From smolts detected and returned to the river at Lower Monumental Dam, the percentage of tags later found on bird colonies upstream from McNary Dam is higher for steelhead than for Chinook, and highly variable from year to year (Table 47). Overall survival estimates for steelhead in the reach from Lower Monumental to McNary Dam (Table 42) have been strongly negatively correlated with the percentage of Lower Monumental-detected PIT tags recovered on bird colonies (Figure 11) ($R^2 = 0.934$, $P < 0.001$; excluding 2003 when only Crescent Island was sampled). There is also a negative correlation for yearling Chinook salmon ($R^2 = 0.884$; $P < 0.001$; excluding 2003) (Figure 11), although percentages detected on bird colonies have been much lower.

Roby et al. (2008) provide estimates of the breeding population size and salmonid consumption rates of the Caspian tern colony on Crescent Island for 2000 through 2007. The peak number of breeding pairs was in 2001 with 720 pairs and breeding pairs have generally declined since then, to 355 pairs in 2007. The estimated total consumption of steelhead by the colony generally tracked the fluctuations in breeding population size, with the highest estimates of approximately 160,000 steelhead smolts consumed in 2001 and 2002, followed by fairly constant estimates ranging between 48,000 to 58,000 between 2003 and 2006, and then an estimate of 74,000 in 2007.

The variation in the estimates of total steelhead consumption is not enough to explain all the variation in the percentage of steelhead PIT tags recovered. The estimate of total steelhead consumption in 2004 was about 1.25 times greater than that in 2007, but there was greater than a fivefold difference between the percentages of steelhead PIT tags recovered in 2004 compared to 2007. Total steelhead consumption is less variable because it largely depends on the dietary needs for energy and nutrients of the bird colonies, which are relatively stable from year to year because the bird colony sizes have not fluctuated widely (maximum 2-fold difference). The percentage of PIT tags recovered from bird colonies (and by extension, the mortality rate due to bird predation of the population as a whole) varies annually to a much greater degree because it depends both on the total bird take and on the total number of smolts remaining in the river; a quantity that varies much more than does bird take.

It follows that if the total consumption requirement of the bird colonies were constant in absolute terms (i.e., they must take a fixed *number* of smolts to sustain the colony and fledge young), then the mortality rate (*proportion*) due to bird predation would depend on the total number of smolts in the river. Moreover, the effect on survival of additional fish remaining in river would diminish as the total number increased (Figure 12). In fact, from 1998 through 2007, the percentage of PIT tags recovered from McNary pool bird colonies has been negatively correlated with estimates of the total number of steelhead smolts remaining in the river downstream of Lower Monumental Dam (our unpublished estimates using the methods of Sandford and Smith 2002), and the relationship between overall survival and the total number of smolts in the river generally shows the predicted curved pattern (Figure 13).

Many factors affect the number of smolts remaining in the river downstream of Lower Monumental Dam in any given year, but the major influence is the collection and transportation of smolts from Snake River dams. During years when transportation was maximized (e.g. 2001, 2004, and 2005), an extremely high proportion (as high as 99%) of steelhead smolts were transported, and we estimated that only about 350,000-530,000 steelhead smolts entered the tailrace below Lower Monumental Dam. In 2006 and 2007, greater numbers of smolts remained in the river. During 2006, about 60% of non-PIT-tagged yearling Chinook salmon and about 75% of non PIT-tagged steelhead were transported, and we estimated that 850,000 steelhead smolts remained in-river. During 2007, even fewer non-PIT-tagged yearling Chinook salmon (25%) and steelhead (41%) were transported, because the start of transportation was later in the Snake River, and spill continued at the same time as transportation. We estimated that 1,500,000 steelhead smolts remained in the river in 2007.

Estimated in-river survival was higher in 2006 and 2007 than in the years (2001, 2004, and 2005) when transport was maximized, and much less water was spilled. Direct effects of spillway passage have been suggested as the reason for the increase in survival for in-river migrants, but it is very likely that the simple increase in total number of smolts remaining in the river in 2006 and 2007 resulted in a smaller overall proportion of smolts taken by avian predators. This was an indirect effect of increased spill in those years, but there are other management options for keeping more fish in the river, including transporting fewer fish that enter the bypass system at upstream dams, releasing more hatchery fish downstream of Lower Monumental Dam, increasing turbine passage, etc. All of these are likely to decrease the mortality rate of in-river migrants due to predation by birds, but will ultimately lead to fewer adult returns unless the overall life-cycle survival probability for in-river migrants exceeds that for fish that are removed from the river for transport.

Results from the 2007 studies provide estimates of survival only during the downstream portion of the migration. We will analyze these data in conjunction with adult returns over the next three years to determine whether variations in spill, flow, temperature, and passage-route produce patterns in smolt-to-adult survival consistent with those observed during the downstream migration phase.

RECOMMENDATIONS

1) Coordination of future survival studies with other projects should continue to maximize the data-collection effort and minimize study effects on salmonid resources.

2) Estimates of survival from hatcheries to Lower Granite Dam suggest that substantial mortality occurs upstream from the Snake and Clearwater River confluence. Efforts to identify where this mortality occurs should continue.

3) Increasing the number of detection facilities in the Columbia River Basin will improve survival investigations. We recommend installation of detectors and diversion systems at The Dalles and Upper Columbia River dams. Although there is now a PIT-tag detection system in the juvenile bypass facility at Ice Harbor Dam, because of the high rate of spill, too few fish are detected for survival estimation in some years. Development of flat-plate and full-flow detector technology in bypass systems and other suitable locations at dams (including spillways), and portable streambed flat-plate detectors for use in tributaries would greatly enhance survival estimation capabilities.

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TABLES

Table 1. Estimated survival probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
23 Mar–29 Mar	56	0.720 (0.121)	1.714 (1.359)	0.508 (0.431)	0.627 (0.178)
30 Mar–05 Apr	268	0.749 (0.086)	0.869 (0.262)	1.069 (0.331)	0.696 (0.094)
06 Apr–12 Apr	3,134	0.919 (0.029)	0.897 (0.075)	0.882 (0.072)	0.727 (0.020)
13 Apr–19 Apr	9,142	0.921 (0.022)	1.006 (0.056)	0.835 (0.045)	0.774 (0.013)
20 Apr–26 Apr	15,956	0.962 (0.018)	0.895 (0.023)	0.940 (0.019)	0.809 (0.010)
27 Apr–03 May	34,853	0.932 (0.011)	0.968 (0.020)	0.911 (0.018)	0.822 (0.008)
04 May–10 May	33,902	0.900 (0.008)	0.994 (0.014)	0.859 (0.012)	0.768 (0.008)
11 May–17 May	25,878	0.975 (0.010)	0.966 (0.019)	0.796 (0.016)	0.750 (0.008)
18 May–24 May	1,786	0.944 (0.048)	1.038 (0.128)	0.796 (0.100)	0.780 (0.044)
25 May–31 May	172	0.875 (0.158)	NA	NA	NA
Weighted mean*		**0.938 (0.006)**	**0.957 (0.010)**	**0.876 (0.012)**	**0.783 (0.006)**

* Weighted means of the independent estimates for daily groups (25 March –31 May), with weights inversely proportional to respective estimated relative variances (see Table 5).

Table 2. Estimated survival probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Daily groups pooled weekly. Estimates based on the single-release model. Standard errors in parentheses. .

Date at McNary	Number released	McNary to John Day Dam	John Day to Bonneville Dam	McNary to Bonneville Dam
20 Apr–26 Apr	1,344	0.955 (0.076)	0.763 (0.268)	0.729 (0.249)
27 Apr–03 May	11,709	0.872 (0.018)	0.940 (0.113)	0.820 (0.097)
04 May–10 May	37,880	0.960 (0.015)	0.877 (0.057)	0.841 (0.053)
11 May–17 May	28,473	0.921 (0.018)	0.860 (0.069)	0.792 (0.062)
18 May–24 May	16,429	0.906 (0.021)	0.609 (0.057)	0.552 (0.050)
25 May–31 May	2,310	0.712 (0.068)	0.875 (0.414)	0.623 (0.288)
01 Jun–07 Jun	695	0.728 (0.112)	1.116 (1.058)	0.813 (0.761)
08 Jun–14 Jun	607	0.655 (0.124)	0.452 (0.230)	0.296 (0.140)
Weighted mean*		**0.920 (0.016)**	**0.824 (0.043)**	**0.763 (0.044)**

* Weighted means of the independent estimates for weekly pooled groups (20 April–14 June), with weights inversely proportional to respective estimated relative variances.

Table 3. Estimated survival probabilities for Snake River hatchery yearling Chinook salmon detected and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
30 Mar–05 Apr	125	0.867 (0.260)	0.693 (0.316)	0.885 (0.351)	0.532 (0.106)
06 Apr–12 Apr	1,176	0.908 (0.067)	0.800 (0.103)	1.059 (0.121)	0.769 (0.039)
13 Apr–19 Apr	4,266	0.907 (0.039)	1.101 (0.100)	0.817 (0.070)	0.817 (0.022)
20 Apr–26 Apr	13,226	0.962 (0.022)	0.890 (0.026)	0.943 (0.022)	0.808 (0.011)
27 Apr–03 May	31,229	0.931 (0.012)	0.982 (0.024)	0.906 (0.020)	0.828 (0.009)
04 May–10 May	31,195	0.896 (0.009)	1.000 (0.015)	0.858 (0.013)	0.769 (0.008)
11 May–17 May	22,745	0.976 (0.012)	0.968 (0.021)	0.786 (0.017)	0.742 (0.009)
18 May–24 May	640	0.970 (0.082)	0.938 (0.164)	0.934 (0.174)	0.850 (0.091)
Weighted mean*		**0.931 (0.013)**	**0.977 (0.015)**	**0.869 (0.021)**	**0.788 (0.013)**

* Weighted means of the independent estimates for weekly pooled groups (30 March–24 May), with weights inversely proportional to respective estimated relative variances.

Table 4. Estimated survival probabilities for Snake River wild yearling Chinook salmon detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
23 Mar– 29 Mar	45	0.608 (0.109)	1.518 (1.163)	0.438 (0.368)	0.404 (0.125)
30 Mar–05 Apr	143	0.752 (0.084)	0.667 (0.096)	1.688 (0.264)	0.846 (0.153)
06 Apr–12 Apr	1,958	0.924 (0.032)	0.971 (0.110)	0.789 (0.089)	0.708 (0.023)
13 Apr–19 Apr	4,876	0.924 (0.026)	0.939 (0.066)	0.859 (0.058)	0.745 (0.015)
20 Apr–26 Apr	2,730	0.985 (0.033)	0.902 (0.043)	0.921 (0.038)	0.818 (0.022)
27 Apr–03 May	3,624	0.966 (0.024)	0.906 (0.039)	0.893 (0.038)	0.782 (0.020)
04 May–10 May	2,707	0.967 (0.024)	0.951 (0.035)	0.858 (0.034)	0.788 (0.022)
11 May–17 May	3,133	0.994 (0.024)	0.969 (0.040)	0.840 (0.039)	0.809 (0.026)
18 May–24 May	1,146	0.928 (0.060)	1.123 (0.196)	0.718 (0.126)	0.749 (0.049)
25 May–31 May	123	0.812 (0.144)	NA	NA	NA
Weighted mean*		**0.958 (0.013)**	**0.935 (0.018)**	**0.885 (0.038)**	**0.773 (0.013)**

* Weighted means of the independent estimates for weekly pooled groups (23 March–31 May), with weights inversely proportional to respective estimated relative variances.

Table 5. Estimated survival probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled as necessary to calculate estimates. Estimates based on the single–release model. Standard errors in parentheses. Abbreviations: LGR–Lower Granite Dam; Little Goose–Little Goose Dam; LMO–Lower Monumental Dam; MCN-McNary Dam.

Date at LGR	Number released	LGR to LGO	LGO to LMO	LMO to MCN	LGR to MCN
25 Mar–03 Apr	169	0.735 (0.092)	1.062 (0.526)	0.786 (0.408)	0.613 (0.107)
04–05 Apr	155	0.705 (0.096)	1.121 (0.418)	0.967 (0.380)	0.765 (0.131)
06 Apr	82	0.766 (0.102)	1.371 (0.957)	0.623 (0.445)	0.654 (0.099)
07 Apr	82	1.312 (0.408)	0.417 (0.142)	1.364 (0.155)	0.746 (0.114)
08 Apr	179	1.176 (0.254)	0.662 (0.307)	0.947 (0.397)	0.738 (0.090)
09 Apr	812	0.842 (0.046)	1.323 (0.267)	0.648 (0.132)	0.722 (0.036)
10 Apr	866	0.939 (0.060)	0.738 (0.102)	0.993 (0.128)	0.688 (0.034)
11 Apr	813	0.916 (0.051)	0.840 (0.117)	0.975 (0.134)	0.750 (0.041)
12 Apr	300	1.112 (0.190)	0.723 (0.235)	1.008 (0.292)	0.810 (0.092)
13 Apr	601	0.908 (0.100)	1.060 (0.254)	0.766 (0.172)	0.738 (0.051)
14 Apr	846	0.990 (0.083)	1.023 (0.194)	0.957 (0.180)	0.970 (0.073)
15 Apr	632	0.904 (0.102)	1.142 (0.297)	0.802 (0.199)	0.829 (0.057)
16 Apr	748	0.863 (0.077)	1.260 (0.317)	0.694 (0.171)	0.754 (0.047)
17 Apr	2,116	0.882 (0.037)	0.900 (0.086)	0.967 (0.088)	0.769 (0.026)
18 Apr	2,675	0.959 (0.042)	1.016 (0.109)	0.770 (0.079)	0.750 (0.021)
19 Apr	1,524	0.911 (0.054)	0.992 (0.129)	0.837 (0.103)	0.757 (0.027)
20 Apr	793	1.074 (0.162)	0.680 (0.150)	1.083 (0.177)	0.791 (0.050)
21 Apr	1,053	0.932 (0.094)	0.756 (0.100)	1.169 (0.103)	0.823 (0.041)
22 Apr	1,122	0.965 (0.094)	0.919 (0.134)	0.900 (0.109)	0.798 (0.036)
23 Apr	6,062	0.972 (0.029)	0.889 (0.035)	0.943 (0.029)	0.815 (0.016)
24 Apr	948	0.837 (0.050)	1.150 (0.109)	0.776 (0.071)	0.747 (0.037)
25 Apr	5,402	0.960 (0.029)	0.876 (0.034)	0.965 (0.032)	0.812 (0.018)
26 Apr	576	1.177 (0.176)	0.800 (0.150)	0.891 (0.109)	0.840 (0.055)
27 Apr	5,568	0.944 (0.022)	0.955 (0.034)	0.858 (0.030)	0.773 (0.017)
28 Apr	748	1.013 (0.090)	0.890 (0.124)	0.956 (0.115)	0.862 (0.055)
29 Apr	387	0.923 (0.079)	1.059 (0.203)	0.807 (0.163)	0.789 (0.073)
30 Apr	5,391	0.901 (0.021)	0.980 (0.041)	0.905 (0.038)	0.798 (0.018)
01 May	1,792	0.933 (0.036)	0.925 (0.068)	1.012 (0.075)	0.873 (0.034)
02 May	11,976	0.955 (0.023)	0.970 (0.048)	0.900 (0.042)	0.835 (0.014)
03 May	8,991	0.979 (0.031)	0.980 (0.058)	0.881 (0.048)	0.846 (0.018)

Table 5. Continued.

Date at LGR	Number released	LGR to LGO	LGO to LMO	LMO to MCN	LGR to MCN
04 May	8,807	0.882 (0.025)	1.032 (0.040)	0.895 (0.030)	0.815 (0.017)
05 May	5,918	0.915 (0.031)	1.026 (0.047)	0.833 (0.033)	0.782 (0.020)
06 May	1,102	0.862 (0.056)	0.975 (0.082)	0.898 (0.072)	0.755 (0.045)
07 May	4,640	0.904 (0.020)	0.942 (0.029)	0.875 (0.031)	0.745 (0.021)
08 May	1,527	0.944 (0.033)	0.968 (0.051)	0.735 (0.043)	0.671 (0.029)
09 May	5,932	0.917 (0.014)	0.998 (0.027)	0.827 (0.027)	0.756 (0.018)
10 May	5,976	0.933 (0.016)	0.919 (0.026)	0.875 (0.027)	0.750 (0.017)
11 May	6,212	0.939 (0.018)	1.012 (0.044)	0.775 (0.034)	0.736 (0.015)
12 May	6,698	0.997 (0.021)	0.968 (0.044)	0.772 (0.035)	0.746 (0.016)
13 May	1,257	0.910 (0.045)	1.242 (0.124)	0.685 (0.070)	0.774 (0.039)
14 May	6,189	1.002 (0.026)	0.900 (0.035)	0.815 (0.030)	0.735 (0.017)
15 May	4,569	0.979 (0.026)	0.923 (0.038)	0.855 (0.037)	0.772 (0.023)
16 May	506	0.995 (0.060)	0.976 (0.107)	0.930 (0.125)	0.904 (0.088)
17 May	447	1.002 (0.073)	0.968 (0.145)	0.819 (0.136)	0.795 (0.080)
18 May	466	1.092 (0.093)	1.097 (0.229)	0.710 (0.159)	0.851 (0.099)
19 May	247	0.956 (0.111)	1.310 (0.488)	0.578 (0.223)	0.724 (0.106)
20 May	218	1.008 (0.156)	0.640 (0.165)	1.230 (0.303)	0.793 (0.122)
21 May	162	0.846 (0.168)	0.780 (0.233)	1.331 (0.411)	0.878 (0.201)
22 May	343	0.975 (0.169)	1.016 (0.384)	0.716 (0.256)	0.710 (0.088)
23 May	160	0.656 (0.122)	1.231 (0.889)	0.792 (0.570)	0.639 (0.107)
24–31 May	362	0.816 (0.090)	1.611 (1.321)	0.660 (0.545)	0.868 (0.121)
Weighted mean*		**0.938 (0.006)**	**0.957 (0.010)**	**0.876 (0.012)**	**0.783 (0.006)**

* Weighted means of the independent estimates for daily groups (25 March –31 May), with weights inversely proportional to respective estimated relative variances.

Table 6. Estimated detection probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
23 Mar–29 Mar	56	0.422 (0.099)	0.062 (0.058)	0.312 (0.116)
30 Mar–05 Apr	268	0.294 (0.045)	0.072 (0.029)	0.353 (0.059)
06 Apr–12 Apr	3,134	0.228 (0.011)	0.046 (0.006)	0.417 (0.015)
13 Apr–19 Apr	9,142	0.158 (0.005)	0.051 (0.004)	0.400 (0.009)
20 Apr–26 Apr	15,956	0.119 (0.003)	0.159 (0.004)	0.398 (0.006)
27 Apr–03 May	34,853	0.144 (0.003)	0.082 (0.002)	0.340 (0.004)
04 May–10 May	33,902	0.190 (0.003)	0.214 (0.003)	0.358 (0.005)
11 May–17 May	25,878	0.214 (0.003)	0.135 (0.003)	0.392 (0.005)
18 May–24 May	1,786	0.202 (0.014)	0.057 (0.008)	0.345 (0.023)
25 May–31 May	172	0.213 (0.050)	NA	0.281 (0.080)

Table 7. Estimated detection probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at McNary Dam	Number released	John Day Dam	Bonneville Dam
20 Apr–26 Apr	1,344	0.443 (0.038)	0.128 (0.045)
27 Apr–03 May	11,709	0.526 (0.012)	0.144 (0.017)
04 May–10 May	37,880	0.368 (0.006)	0.155 (0.010)
11 May–17 May	28,473	0.343 (0.007)	0.142 (0.011)
18 May–24 May	16,429	0.415 (0.010)	0.198 (0.018)
25 May–31 May	2,310	0.338 (0.034)	0.114 (0.054)
01 Jun–07 Jun	695	0.356 (0.058)	0.105 (0.099)
08 Jun–14 Jun	607	0.292 (0.059)	0.285 (0.138)

Table 8. Estimated detection probabilities for Snake River hatchery yearling Chinook salmon detected and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
30 Mar–05 Apr	125	0.148 (0.056)	0.140 (0.061)	0.356 (0.089)
06 Apr–12 Apr	1,176	0.157 (0.016)	0.067 (0.011)	0.358 (0.024)
13 Apr–19 Apr	4,266	0.134 (0.008)	0.063 (0.006)	0.353 (0.012)
20 Apr–26 Apr	13,226	0.106 (0.004)	0.151 (0.004)	0.392 (0.007)
27 Apr–03 May	31,229	0.133 (0.003)	0.074 (0.002)	0.334 (0.004)
04 May–10 May	31,195	0.184 (0.003)	0.208 (0.003)	0.351 (0.005)
11 May–17 May	22,745	0.207 (0.004)	0.122 (0.003)	0.392 (0.006)
18 May–24 May	640	0.210 (0.024)	0.082 (0.017)	0.289 (0.036)

Table 9. Estimated detection probabilities for Snake River wild yearling Chinook Salmon detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
23 Mar–29 Mar	45	0.584 (0.122)	0.108 (0.097)	0.444 (0.166)
30 Mar–05 Apr	143	0.400 (0.062)	0.017 (0.017)	0.351 (0.078)
06 Apr–12 Apr	1,958	0.271 (0.014)	0.036 (0.006)	0.452 (0.019)
13 Apr–19 Apr	4,876	0.180 (0.008)	0.039 (0.004)	0.439 (0.012)
20 Apr–26 Apr	2,730	0.173 (0.009)	0.197 (0.010)	0.425 (0.015)
27 Apr–03 May	3,624	0.236 (0.009)	0.153 (0.008)	0.388 (0.013)
04 May–10 May	2,707	0.248 (0.010)	0.269 (0.012)	0.425 (0.016)
11 May–17 May	3,133	0.257 (0.010)	0.220 (0.010)	0.390 (0.015)
18 May–24 May	1,146	0.197 (0.018)	0.043 (0.009)	0.376 (0.029)
25 May–31 May	123	0.290 (0.068)	NA	0.421 (0.113)

Table 10. Estimated survival probabilities for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
06 Apr–12 Apr	754	0.813 (0.039)	1.158 (0.313)	0.776 (0.239)	0.731 (0.110)
13 Apr–19 Apr	2,717	0.852 (0.024)	1.004 (0.080)	0.784 (0.082)	0.670 (0.049)
20 Apr–26 Apr	4,468	0.862 (0.019)	0.880 (0.031)	0.965 (0.066)	0.732 (0.046)
27 Apr–03 May	6,966	0.900 (0.016)	1.008 (0.045)	0.853 (0.055)	0.774 (0.038)
04 May–10 May	6,484	0.907 (0.016)	0.906 (0.033)	0.729 (0.048)	0.599 (0.034)
11 May–17 May	6,591	0.891 (0.020)	0.886 (0.049)	0.840 (0.080)	0.662 (0.053)
18 May–24 May	4,479	0.851 (0.040)	0.974 (0.158)	0.708 (0.169)	0.587 (0.106)
25 May–31 May	151	0.550 (0.140)	0.812 (0.731)	NA	NA
Weighted mean*		**0.887 (0.009)**	**0.911 (0.022)**	**0.852 (0.030)**	**0.694 (0.020)**

* Weighted means of the independent estimates for daily groups (26 March–31 May), with weights inversely proportional to respective estimated relative variances (see Table 14).

Table 11. Estimated survival probabilities for juvenile Snake River steelhead (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at McNary Dam	Number released	McNary to John Day Dam	John Day to Bonneville Dam	McNary to Bonneville Dam
20 Apr–26 Apr	541	1.749 (0.557)	0.345 (0.325)	0.603 (0.534)
27 Apr–03 May	893	0.986 (0.167)	0.464 (0.177)	0.457 (0.157)
04 May–10 May	2,242	1.004 (0.108)	0.711 (0.168)	0.713 (0.150)
11 May–17 May	1,781	0.985 (0.186)	0.419 (0.120)	0.413 (0.089)
18 May–24 May	1,136	0.700 (0.150)	0.652 (0.251)	0.457 (0.147)
25 May–31 May	464	0.417 (0.204)	0.658 (0.503)	0.274 (0.161)
Weighted mean*		**0.988 (0.098)**	**0.579 (0.059)**	**0.524 (0.064)**

* Weighted means of the independent estimates for weekly pooled groups (20 April– 31 May), with weights inversely proportional to respective estimated relative variances.

Table 12. Estimated survival probabilities for juvenile Snake River hatchery steelhead detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
06 Apr–12 Apr	463	0.846 (0.048)	0.949 (0.260)	0.857 (0.279)	0.688 (0.126)
13 Apr–19 Apr	1,837	0.855 (0.026)	0.981 (0.079)	0.750 (0.086)	0.629 (0.055)
20 Apr–26 Apr	4,073	0.873 (0.020)	0.854 (0.030)	0.961 (0.069)	0.716 (0.048)
27 Apr–03 May	4,215	0.885 (0.020)	0.996 (0.056)	0.968 (0.102)	0.853 (0.078)
04 May–10 May	3,529	0.911 (0.020)	0.873 (0.041)	0.701 (0.062)	0.557 (0.043)
11 May–17 May	3,974	0.894 (0.023)	0.886 (0.062)	0.840 (0.112)	0.666 (0.078)
18 May–24 May	2,541	0.802 (0.046)	1.054 (0.219)	0.719 (0.220)	0.607 (0.141)
25 May–31 May	92	0.489 (0.154)	0.476 (0.406)	NA	NA
Weighted mean*		**0.881 (0.010)**	**0.897 (0.022)**	**0.856 (0.047)**	**0.680 (0.039)**

* Weighted means of the independent estimates for weekly pooled groups (06 April –31 May), with weights inversely proportional to respective estimated relative variances.

Table 13. Estimated survival probabilities for juvenile Snake River wild steelhead detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single-release model. Standard errors in parentheses.

Date at Lower Granite	Number released	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Lower Granite to McNary Dam
06 Apr–12 Apr	291	0.754 (0.067)	2.762 (2.539)	0.372 (0.356)	0.775 (0.202)
13 Apr–19 Apr	880	0.912 (0.071)	1.049 (0.292)	0.748 (0.224)	0.716 (0.092)
20 Apr–26 Apr	395	0.689 (0.069)	1.419 (0.282)	0.785 (0.193)	0.768 (0.128)
27 Apr–03 May	2,751	0.922 (0.024)	0.898 (0.062)	0.951 (0.080)	0.787 (0.043)
04 May–10 May	2,955	0.900 (0.027)	0.948 (0.054)	0.755 (0.074)	0.644 (0.054)
11 May–17 May	2,617	0.877 (0.035)	0.872 (0.078)	0.869 (0.118)	0.665 (0.073)
18 May–24 May	1,938	0.937 (0.076)	0.863 (0.225)	0.666 (0.251)	0.538 (0.152)
25 May–31 May	59	0.633 (0.264)	NA	NA	NA
Weighted mean*		**0.896 (0.018)**	**0.939 (0.051)**	**0.854 (0.039)**	**0.730 (0.027)**

* Weighted means of the independent estimates for weekly pooled groups (06 April–31 May), with weights inversely proportional to respective estimated relative variances.

Table 14. Estimated survival probabilities for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled as necessary to calculate estimates. Estimates based on the single–release model. Standard errors in parentheses. Abbreviations: LGR–Lower Granite Dam; Little Goose–Little Goose Dam; LMO–Lower Monumental Dam; MCN–McNary Dam.

Date at LGR	Number released	LGR to LGO	LGO to LMO	LMO to MCN	LGR to MCN
26 Mar–12 Apr	781	0.818 (0.040)	1.147 (0.310)	0.765 (0.234)	0.717 (0.106)
13–16 Apr	104	0.796 (0.107)	0.527 (0.144)	1.367 (0.539)	0.573 (0.205)
17 Apr	1,055	0.830 (0.032)	1.087 (0.133)	0.706 (0.111)	0.637 (0.067)
18 Apr	1,351	0.887 (0.041)	1.004 (0.124)	0.786 (0.125)	0.699 (0.077)
19 Apr	207	0.853 (0.105)	0.881 (0.224)	1.050 (0.410)	0.789 (0.255)
20 Apr	26	0.654 (0.159)	1.867 (1.519)	0.536 (0.589)	0.654 (0.487)
21 Apr	65	1.072 (0.438)	0.750 (0.443)	1.031 (0.723)	0.829 (0.470)
22 Apr	56	0.756 (0.268)	1.031 (0.689)	0.390 (0.253)	0.304 (0.112)
23 Apr	2,101	0.878 (0.028)	0.892 (0.047)	0.973 (0.099)	0.762 (0.071)
24 Apr	2,058	0.857 (0.027)	0.850 (0.042)	0.982 (0.100)	0.716 (0.068)
25–26 Apr	162	0.792 (0.095)	1.010 (0.207)	0.853 (0.224)	0.682 (0.135)
27 Apr	226	0.965 (0.094)	0.879 (0.141)	1.040 (0.271)	0.882 (0.200)
28 Apr	54	1.006 (0.385)	0.818 (0.463)	1.500 (1.430)	1.235 (1.067)
29 Apr	59	0.723 (0.154)	0.691 (0.254)	0.987 (0.328)	0.493 (0.121)
30 Apr	849	0.985 (0.045)	0.754 (0.076)	1.160 (0.168)	0.861 (0.100)
01 May	3,191	0.883 (0.022)	1.008 (0.067)	0.820 (0.087)	0.730 (0.062)
02 May	1,443	0.884 (0.030)	1.217 (0.144)	0.682 (0.096)	0.734 (0.059)
03 May	1,144	0.890 (0.049)	1.089 (0.134)	0.992 (0.190)	0.963 (0.150)
04 May	971	0.799 (0.053)	1.139 (0.143)	0.857 (0.155)	0.780 (0.112)
05 May	269	0.992 (0.139)	1.069 (0.262)	0.485 (0.166)	0.514 (0.140)
06 May	214	0.720 (0.062)	1.450 (0.293)	0.632 (0.262)	0.659 (0.240)
07 May	1,365	0.884 (0.032)	0.902 (0.063)	0.878 (0.139)	0.701 (0.103)
08 May	921	0.924 (0.040)	0.802 (0.066)	0.754 (0.130)	0.559 (0.088)
09 May	1,496	0.948 (0.034)	0.855 (0.065)	0.752 (0.113)	0.610 (0.082)
10 May	1,248	0.952 (0.036)	0.801 (0.065)	0.609 (0.075)	0.464 (0.046)
11 May	1,126	0.829 (0.031)	0.762 (0.067)	1.310 (0.300)	0.828 (0.177)
12 May	275	0.960 (0.086)	0.766 (0.203)	0.675 (0.300)	0.496 (0.180)

Table 14. Continued.

Date at LGR	Number released	LGR to LGO	LGO to LMO	LMO to MCN	LGR to MCN
13 May	327	1.003 (0.087)	1.121 (0.303)	0.803 (0.412)	0.903 (0.398)
14 May	865	0.851 (0.059)	1.094 (0.184)	0.584 (0.136)	0.544 (0.094)
15 May	1,405	0.907 (0.049)	0.955 (0.126)	0.764 (0.158)	0.661 (0.110)
16 May	1,142	0.894 (0.046)	0.948 (0.134)	0.780 (0.175)	0.660 (0.120)
17 May	1,451	0.974 (0.058)	0.799 (0.113)	0.854 (0.210)	0.665 (0.139)
18 May	881	0.926 (0.071)	1.041 (0.262)	0.748 (0.309)	0.721 (0.241)
19–20 May	243	0.741 (0.109)	0.800 (0.309)	1.594 (1.587)	0.945 (0.878)
21–22 May	1,353	0.964 (0.094)	1.530 (0.739)	0.622 (0.416)	0.917 (0.431)
23–31 May	2,153	0.782 (0.062)	0.909 (0.246)	0.584 (0.208)	0.415 (0.101)
Weighted mean*		**0.887 (0.009)**	**0.911 (0.022)**	**0.852 (0.030)**	**0.694 (0.020)**

* Weighted means of the independent estimates for daily groups (26 March–31 May), with weights inversely proportional to respective estimated relative variances.

Table 15. Estimated detection probabilities for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
06 Apr–12 Apr	754	0.543 (0.032)	0.048 (0.015)	0.187 (0.033)
13 Apr–19 Apr	2,717	0.422 (0.016)	0.135 (0.012)	0.193 (0.017)
20 Apr–26 Apr	4,468	0.320 (0.010)	0.368 (0.013)	0.141 (0.011)
27 Apr–03 May	6,966	0.407 (0.009)	0.163 (0.008)	0.182 (0.010)
04 May–10 May	6,484	0.372 (0.009)	0.335 (0.012)	0.198 (0.013)
11 May–17 May	6,591	0.402 (0.011)	0.197 (0.011)	0.126 (0.011)
18 May–24 May	4,479	0.338 (0.018)	0.072 (0.012)	0.078 (0.015)
25 May–31 May	151	0.458 (0.124)	0.138 (0.127)	NA

Table 16. Estimated detection probabilities for juvenile Snake River steelhead (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at McNary Dam	Number released	John Day Dam	Bonneville Dam
20 Apr–26 Apr	541	0.115 (0.038)	0.202 (0.180)
27 Apr–03 May	893	0.199 (0.036)	0.261 (0.092)
04 May–10 May	2,242	0.152 (0.018)	0.206 (0.044)
11 May–17 May	1,781	0.097 (0.020)	0.256 (0.057)
18 May–24 May	1,136	0.108 (0.026)	0.243 (0.080)
25 May–31 May	464	0.083 (0.045)	0.286 (0.171)

Table 17. Estimated detection probabilities for juvenile Snake River hatchery steelhead detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
06 Apr–12 Apr	463	0.580 (0.040)	0.067 (0.022)	0.174 (0.038)
13 Apr–19 Apr	1,837	0.478 (0.018)	0.180 (0.017)	0.177 (0.019)
20 Apr–26 Apr	4,073	0.331 (0.011)	0.391 (0.014)	0.132 (0.011)
27 Apr–03 May	4,215	0.412 (0.012)	0.201 (0.012)	0.105 (0.011)
04 May–10 May	3,529	0.424 (0.013)	0.359 (0.017)	0.190 (0.017)
11 May–17 May	3,974	0.451 (0.014)	0.208 (0.015)	0.103 (0.013)
18 May–24 May	2,541	0.367 (0.023)	0.073 (0.016)	0.088 (0.022)
25 May–31 May	92	0.533 (0.175)	0.250 (0.216)	NA

Table 18. Estimated detection probabilities for juvenile Snake River wild steelhead detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

Date at Lower Granite Dam	Number released	Little Goose Dam	Lower Monumental Dam	McNary Dam
06 Apr–12 Apr	291	0.483 (0.052)	0.016 (0.015)	0.211 (0.061)
13 Apr–19 Apr	880	0.282 (0.027)	0.043 (0.013)	0.232 (0.034)
20 Apr–26 Apr	395	0.206 (0.031)	0.153 (0.033)	0.253 (0.049)
27 Apr–03 May	2,751	0.401 (0.014)	0.123 (0.010)	0.280 (0.018)
04 May–10 May	2,955	0.310 (0.013)	0.309 (0.018)	0.209 (0.020)
11 May–17 May	2,617	0.330 (0.016)	0.184 (0.017)	0.161 (0.020)
18 May–24 May	1,938	0.296 (0.026)	0.070 (0.018)	0.066 (0.020)
25 May–31 May	59	0.375 (0.171)	NA	NA

Table 19. Estimated survival probabilities for PIT-tagged yearling Chinook salmon released from Snake River Basin hatcheries in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Release site	Number released	Release to Lower Granite Dam	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Release to McNary Dam
Clearwater Hatchery						
Crooked River	15,460	0.657 (0.016)	0.957 (0.054)	0.961 (0.082)	0.956 (0.069)	0.578 (0.012)
Powell Pond	14,970	0.774 (0.016)	0.906 (0.053)	1.041 (0.103)	0.913 (0.078)	0.667 (0.013)
Red River Pond	14,967	0.816 (0.022)	0.892 (0.055)	1.035 (0.099)	0.889 (0.074)	0.670 (0.016)
Dworshak Hatchery						
N.F. Clearwater River	104,186	0.817 (0.007)	0.931 (0.012)	0.956 (0.015)	0.911 (0.013)	0.662 (0.004)
Kooskia Hatchery						
Kooksia Hatchery	9,892	0.654 (0.015)	0.819 (0.064)	0.950 (0.127)	1.028 (0.116)	0.523 (0.019)
Lookingglass Hatchery						
Catherine Creek Pond	20,828	0.340 (0.007)	0.933 (0.037)	0.993 (0.057)	0.902 (0.052)	0.285 (0.009)
Grande Ronde P. (3/19)	496	0.361 (0.046)	1.016 (0.204)	0.812 (0.200)	1.019 (0.246)	0.303 (0.053)
Grande Ronde P. (4/2)	1,481	0.541 (0.025)	0.956 (0.072)	0.858 (0.086)	0.966 (0.093)	0.429 (0.028)
Imnaha Weir	20,888	0.682 (0.010)	0.908 (0.025)	0.972 (0.038)	0.968 (0.036)	0.582 (0.010)
Lostine Pond (3/16)	2,432	0.533 (0.024)	0.877 (0.056)	1.184 (0.131)	0.797 (0.090)	0.441 (0.023)
Lostine Pond (4/7)	4,011	0.631 (0.016)	0.970 (0.042)	0.986 (0.067)	0.843 (0.060)	0.509 (0.022)

Table 19. Continued.

Release site	Number released	Release to Lower Granite Dam	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Release to McNary Dam
McCall Hatchery						
Johnson Creek	12,060	0.319 (0.024)	0.960 (0.162)	0.980 (0.256)	0.864 (0.200)	0.260 (0.014)
Knox Bridge	52,128	0.554 (0.007)	0.972 (0.023)	1.019 (0.033)	0.864 (0.024)	0.474 (0.006)
Pahsimeroi Hatchery						
Pahsimeroi Pond	498	0.530 (0.038)	1.216 (0.241)	0.816 (0.228)	0.884 (0.204)	0.465 (0.054)
Rapid River Hatchery						
Rapid River H.	104,672	0.748 (0.004)	0.937 (0.010)	0.968 (0.013)	0.908 (0.012)	0.616 (0.005)
Sawtooth Hatchery						
Sawtooth H.	14,942	0.581 (0.015)	0.969 (0.054)	0.954 (0.071)	0.908 (0.060)	0.488 (0.015)

Table 20. Estimated survival probabilities for PIT-tagged juvenile steelhead released from Snake River Basin hatcheries in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Release site	Number released	Release to Lower Granite Dam	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Release to McNary Dam
Clearwater Hatchery						
S.F. Clearwater River	300	0.859 (0.158)	0.884 (0.194)	0.779 (0.175)	2.458 (2.362)	1.454 (1.371)
Crooked River Pond	599	0.805 (0.058)	0.956 (0.092)	0.872 (0.125)	0.758 (0.236)	0.508 (0.145)
Lolo Creek	300	0.787 (0.106)	0.880 (0.149)	0.840 (0.174)	0.931 (0.402)	0.542 (0.215)
Meadow Creek	300	0.870 (0.092)	0.840 (0.114)	0.942 (0.194)	0.846 (0.392)	0.582 (0.245)
Mill Creek	299	0.495 (0.059)	0.759 (0.120)	1.466 (0.890)	0.180 (0.149)	0.099 (0.054)
Red River Pond	600	0.753 (0.069)	1.093 (0.143)	1.200 (0.360)	0.313 (0.146)	0.309 (0.112)
Dworshak Hatchery						
N.F. Clearwater River	1,491	0.838 (0.043)	0.876 (0.054)	0.897 (0.059)	0.798 (0.103)	0.525 (0.061)
Hagerman Hatchery						
Little Salmon River	597	0.899 (0.074)	0.800 (0.084)	1.121 (0.205)	0.628 (0.176)	0.506 (0.111)
East Fork Salmon R.	290	1.074 (0.137)	0.636 (0.115)	0.732 (0.230)	1.250 (1.198)	0.624 (0.571)
Sawtooth Hatchery	298	0.596 (0.085)	0.970 (0.178)	0.840 (0.228)	1.574 (1.058)	0.765 (0.481)
Yankee Fork	300	0.588 (0.065)	1.068 (0.204)	2.037 (1.925)	NA	NA
Irrigon Hatchery						
Big Canyon Facility	595	0.799 (0.093)	0.880 (0.139)	1.013 (0.242)	1.220 (0.841)	0.870 (0.569)
Little Sheep Facility	295	0.604 (0.047)	1.163 (0.129)	1.517 (0.498)	0.439 (0.297)	0.467 (0.279)
Wallowa H. (4/8)	5,370	0.734 (0.078)	1.264 (0.362)	0.754 (0.420)	0.691 (0.399)	0.484 (0.124)
Wallowa H. (4/28)	1,786	0.676 (0.222)	2.093 (1.896)	NA	NA	NA

Table 20. Continued.

Release site	Number released	Release to Lower Granite Dam	Lower Granite to Little Goose Dam	Little Goose to Lower Monumental Dam	Lower Monumental to McNary Dam	Release to McNary Dam
Magic Valley Hatchery						
East Fork Salmon R.	300	0.934 (0.143)	0.615 (0.121)	1.280 (0.500)	NA	NA
Little Salmon R.	300	0.826 (0.075)	1.095 (0.152)	1.220 (0.382)	0.443 (0.249)	0.488 (0.233)
Salmon R. (rkm 385)	293	0.929 (0.103)	1.030 (0.165)	0.850 (0.222)	0.494 (0.203)	0.401 (0.136)
Salmon R. (rkm 476)	300	0.796 (0.099)	1.062 (0.174)	1.128 (0.312)	0.806 (0.534)	0.768 (0.470)
Salmon R. (rkm 506)	297	0.793 (0.103)	1.207 (0.222)	0.988 (0.318)	1.745 (1.730)	1.651 (1.564)
Slate Creek (4/18)	293	0.640 (0.071)	0.852 (0.128)	0.917 (0.258)	1.079 (0.603)	0.539 (0.267)
Slate Creek (5/1)	292	0.609 (0.058)	0.931 (0.130)	0.839 (0.235)	0.750 (0.326)	0.356 (0.126)
Squaw Creek	972	0.691 (0.036)	0.972 (0.074)	0.711 (0.098)	0.918 (0.283)	0.439 (0.125)
Valley Creek	299	0.941 (0.107)	0.773 (0.118)	1.015 (0.383)	0.598 (0.432)	0.441 (0.272)
Yankee Fork	298	1.092 (0.189)	0.468 (0.100)	0.778 (0.202)	1.540 (1.027)	0.613 (0.384)
Niagara Springs Hatchery						
Hells Canyon Dam	289	0.866 (0.173)	0.792 (0.203)	0.675 (0.271)	1.367 (0.832)	0.633 (0.308)
Little Salmon R.	592	0.970 (0.076)	0.840 (0.087)	0.861 (0.122)	0.963 (0.294)	0.676 (0.188)
Pahsimeroi Weir	297	1.464 (0.330)	0.543 (0.142)	0.797 (0.197)	1.670 (1.119)	1.057 (0.673)

Table 21. Estimated survival probabilities for PIT-tagged juvenile sockeye salmon from Snake River Basin hatcheries released in 2007. Estimates based on the single-release model. Standard errors in parentheses. Abbreviations: LGR-Lower Granite Dam; Little Goose-Little Goose Dam; LMO-Lower Monumental Dam; MCN-McNary Dam.

Release site	Release date	Number released	Release to LGR	LGR to LGO	LGO to LMO	LMO to MCN	LGR to MCN	Release to MCN
Eagle Creek NFH								
Redfish Lk Cr Trap	08 May 07	330	0.338 (0.121)	NA	NA	NA	NA	NA
Oxbow Hatchery								
Redfish Lk Cr Trap	08 May 07	1,020	0.571 (0.070)	2.770 (1.101)	0.326 (0.155)	0.502 (0.210)	0.454 (0.151)	0.259 (0.080)
Sawtooth Hatchery								
Alturus Lake	02 Oct 06	1,016	0.174 (0.019)	0.890 (0.126)	0.903 (0.159)	0.922 (0.196)	0.741 (0.139)	0.129 (0.023)
Pettit Lake	02 Oct 06	1,021	0.123 (0.024)	1.350 (0.606)	0.547 (0.381)	0.963 (0.701)	0.712 (0.357)	0.088 (0.042)
Redfish Lake	02 Oct 06	1,016	0.204 (0.026)	0.873 (0.156)	0.783 (0.171)	1.238 (0.340)	0.846 (0.212)	0.173 (0.040)
Sawtooth Trap	08 May 07	909	0.776 (0.133)	0.686 (0.175)	0.826 (0.256)	0.824 (0.264)	0.468 (0.126)	0.363 (0.076)

Table 22. Estimated detection probabilities for PIT-tagged yearling Chinook salmon released from Snake River Basin hatcheries in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Release site	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
			Clearwater Hatchery		
Crooked River Pond	15,460	0.162 (0.005)	0.110 (0.006)	0.087 (0.006)	0.333 (0.008)
Powell Pond	14,970	0.147 (0.004)	0.114 (0.007)	0.075 (0.006)	0.330 (0.008)
Red River Pond	14,967	0.164 (0.006)	0.117 (0.007)	0.087 (0.007)	0.314 (0.008)
			Dworshak Hatchery		
N.F. Clearwater River	104,186	0.142 (0.002)	0.127 (0.002)	0.094 (0.002)	0.348 (0.003)
			Kooskia Hatchery		
Kooskia Hatchery	9,892	0.259 (0.008)	0.233 (0.018)	0.147 (0.015)	0.416 (0.014)
			Lookingglass Hatchery		
Catherine Creek Pond	20,828	0.312 (0.008)	0.213 (0.009)	0.149 (0.009)	0.339 (0.012)
Grande Ronde P. (3/19)	496	0.234 (0.041)	0.163 (0.038)	0.138 (0.038)	0.315 (0.063)
Grande Ronde P. (4/2)	1,481	0.326 (0.021)	0.189 (0.019)	0.136 (0.017)	0.360 (0.028)
Imnaha Weir	20,888	0.242 (0.005)	0.177 (0.005)	0.126 (0.005)	0.343 (0.008)
Lostine Pond (3/16)	2,432	0.218 (0.015)	0.180 (0.014)	0.074 (0.010)	0.348 (0.022)
Lostine Pond (4/7)	4,011	0.323 (0.012)	0.203 (0.011)	0.125 (0.010)	0.328 (0.017)

Table 22. Continued.

Release site	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
McCall Hatchery					
Johnson Creek	12,060	0.214 (0.017)	0.137 (0.020)	0.114 (0.024)	0.352 (0.017)
Knox Bridge	52,128	0.220 (0.004)	0.116 (0.003)	0.101 (0.003)	0.350 (0.005)
Pahsimeroi Hatchery					
Pahsimeroi Pond	498	0.402 (0.038)	0.086 (0.023)	0.078 (0.023)	0.343 (0.048)
Rapid River Hatchery					
Rapid River H.	104,672	0.280 (0.002)	0.167 (0.002)	0.134 (0.002)	0.330 (0.003)
Sawtooth Hatchery					
Sawtooth H.	14,942	0.307 (0.009)	0.197 (0.010)	0.166 (0.010)	0.327 (0.011)

Table 23. Estimated detection probabilities for PIT-tagged juvenile steelhead released from Snake River Basin hatcheries in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Release site	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
Clearwater Hatchery					
S.F. Clearwater River	300	0.097 (0.026)	0.321 (0.050)	0.324 (0.070)	0.029 (0.028)
Crooked River Pond	599	0.205 (0.023)	0.398 (0.035)	0.313 (0.046)	0.103 (0.034)
Lolo Creek	300	0.157 (0.031)	0.366 (0.050)	0.259 (0.056)	0.076 (0.036)
Meadow Creek	300	0.207 (0.033)	0.440 (0.050)	0.312 (0.067)	0.114 (0.054)
Mill Creek	299	0.338 (0.052)	0.565 (0.077)	0.185 (0.115)	0.250 (0.153)
Red River Pond	600	0.177 (0.024)	0.335 (0.039)	0.162 (0.049)	0.107 (0.045)
Dworshak Hatchery					
N.F. Clearwater River	1,491	0.158 (0.013)	0.411 (0.020)	0.376 (0.026)	0.156 (0.022)
Hagerman Hatchery					
Little Salmon R.	597	0.196 (0.023)	0.446 (0.036)	0.188 (0.037)	0.161 (0.041)
East Fork Salmon R.	290	0.234 (0.038)	0.458 (0.065)	0.257 (0.082)	0.046 (0.044)
Sawtooth Hatchery	298	0.174 (0.037)	0.368 (0.058)	0.208 (0.060)	0.054 (0.037)
Yankee Fork	300	0.306 (0.046)	0.396 (0.074)	0.052 (0.049)	0.000 (0.000)
Irrigon Hatchery					
Big Canyon Facility	595	0.160 (0.025)	0.293 (0.038)	0.211 (0.049)	0.036 (0.025)
Little Sheep Facility	295	0.309 (0.040)	0.408 (0.052)	0.188 (0.063)	0.061 (0.042)
Wallowa H. (4/8)	5,370	0.179 (0.020)	0.235 (0.061)	0.165 (0.074)	0.066 (0.017)
Wallowa H. (4/28)	1,786	0.198 (0.066)	0.144 (0.117)	NA	0.073 (0.034)

Table 23. Continued

Release site	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
Magic Valley Hatchery					
East Fork Salmon R.	300	0.189 (0.037)	0.435 (0.062)	0.174 (0.070)	NA
Little Salmon R.	300	0.234 (0.034)	0.349 (0.048)	0.180 (0.057)	0.077 (0.043)
Salmon R. (rkm 385)	293	0.187 (0.031)	0.346 (0.049)	0.222 (0.058)	0.114 (0.048)
Salmon R. (rkm 476)	300	0.151 (0.029)	0.339 (0.048)	0.181 (0.052)	0.040 (0.028)
Salmon R. (rkm 506)	297	0.144 (0.029)	0.298 (0.049)	0.169 (0.054)	0.027 (0.027)
Slate Creek (4/18)	293	0.277 (0.043)	0.467 (0.063)	0.212 (0.065)	0.107 (0.058)
Slate Creek (5/1)	292	0.343 (0.046)	0.460 (0.064)	0.229 (0.069)	0.200 (0.080)
Squaw Creek	972	0.296 (0.022)	0.449 (0.033)	0.312 (0.043)	0.115 (0.036)
Valley Creek	299	0.210 (0.034)	0.517 (0.060)	0.192 (0.075)	0.095 (0.064)
Yankee Fork	298	0.187 (0.039)	0.486 (0.066)	0.250 (0.071)	0.074 (0.050)
Niagara Springs Hatchery					
Hells Canyon Dam	289	0.124 (0.032)	0.318 (0.060)	0.100 (0.045)	0.080 (0.044)
Little Salmon R.	592	0.188 (0.022)	0.403 (0.034)	0.279 (0.041)	0.100 (0.032)
Pahsimeroi Weir	297	0.090 (0.025)	0.344 (0.052)	0.203 (0.052)	0.042 (0.029)

Table 24. Estimated detection probabilities for PIT-tagged juvenile sockeye salmon from Snake River Basin hatcheries released in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Release site	Release date	Number released	Lower Granite	Little Goose	Lower Monumental	McNary
Eagle Creek National Fish Hatchery						
Redfish Lk Cr Trap	08 May 07	330	0.215 (0.085)	NA	0.167 (0.108)	NA
Oxbow Hatchery						
Redfish Lk Cr Trap	08 May 07	1,020	0.187 (0.028)	0.043 (0.017)	0.081 (0.026)	0.062 (0.024)
Sawtooth Hatchery						
Alturus Lake	02 Oct 06	1,016	0.317 (0.044)	0.276 (0.047)	0.251 (0.050)	0.308 (0.064)
Pettit Lake	02 Oct 06	1,021	0.286 (0.064)	0.120 (0.056)	0.077 (0.051)	0.150 (0.080)
Redfish Lake	02 Oct 06	1,016	0.270 (0.043)	0.241 (0.046)	0.169 (0.043)	0.291 (0.073)
Sawtooth Trap	08 May 07	909	0.113 (0.023)	0.109 (0.025)	0.078 (0.023)	0.137 (0.034)

Table 25. Estimated survival probabilities for juvenile salmonids released from fish traps in Snake River Basin in 2007. Estimates based on the single-release model. Standard errors in parentheses. Abbreviations: LGR-Lower Granite Dam; Little Goose-Little Goose Dam; LMO-Lower Monumental Dam; MCN-McNary Dam.

Trap	Release dates	Number released	Release to LGR	LGR to LGO	LGO to LMO	LMO to MCN	Release to MCN
			Wild Chinook salmon				
American River	20 Mar-31 May	703	0.475 (0.050)	0.888 (0.122)	0.737 (0.141)	1.295 (0.262)	0.402 (0.053)
Catherine Creek	02 Feb-26 May	364	0.310 (0.036)	1.095 (0.296)	0.667 (0.192)	1.504 (0.200)	0.341 (0.059)
Crooked Fork Cr	23 Mar-28 May	109	0.574 (0.122)	1.202 (0.545)	0.641 (0.397)	1.061 (0.670)	0.469 (0.204)
Clearwater	11 Mar-09 May	658	0.811 (0.046)	0.833 (0.077)	1.043 (0.198)	0.794 (0.154)	0.559 (0.040)
Crooked River	19 Mar-31 May	400	0.370 (0.058)	0.870 (0.167)	0.764 (0.196)	1.290 (0.390)	0.318 (0.070)
Grande Ronde	07 Mar-26 May	2,571	0.891 (0.022)	0.995 (0.053)	0.920 (0.088)	0.891 (0.082)	0.726 (0.028)
Imnaha (early)	08 Mar-31 May	6,635	0.840 (0.014)	0.913 (0.029)	1.003 (0.056)	0.892 (0.049)	0.686 (0.018)
Imnaha (late)	01 Jun-21 Jun	864	0.394 (0.139)	1.031 (0.454)	NA	NA	NA
Johnson Creek	05 Mar-17 May	339	0.454 (0.048)	0.925 (0.144)	1.014 (0.218)	0.775 (0.171)	0.330 (0.049)
Knox Bridge	08 Mar-30 May	1,950	0.389 (0.020)	0.911 (0.072)	0.957 (0.119)	0.945 (0.126)	0.320 (0.027)
Lemhi River Weir	09 Mar-26 May	166	0.753 (0.127)	0.752 (0.190)	1.889 (1.509)	0.478 (0.395)	0.511 (0.091)
Lostine River	20 Feb-09 May	505	0.615 (0.054)	0.996 (0.194)	1.227 (0.503)	0.648 (0.262)	0.487 (0.070)
Marsh Creek	21 Mar-21 May	78	0.603 (0.394)	0.659 (0.506)	1.125 (0.798)	0.656 (0.482)	0.293 (0.097)
Minam	20 Feb-09 May	217	0.560 (0.066)	0.972 (0.210)	1.231 (0.590)	0.774 (0.404)	0.518 (0.100)
Pahsimeroi	06 Mar-31 May	1,200	0.414 (0.033)	0.970 (0.135)	1.083 (0.309)	0.740 (0.204)	0.322 (0.029)
Red River	19 Mar-31 May	922	0.336 (0.045)	0.980 (0.177)	0.827 (0.256)	0.930 (0.296)	0.253 (0.040)
Salmon	10 Mar-11 May	5,201	0.796 (0.017)	1.003 (0.047)	0.826 (0.060)	0.962 (0.060)	0.634 (0.018)
Sawtooth	20 Mar-31 May	569	0.581 (0.050)	0.731 (0.102)	1.069 (0.213)	1.141 (0.250)	0.518 (0.075)
Snake	23 Mar-25 May	379	0.903 (0.062)	1.691 (0.493)	0.441 (0.145)	0.912 (0.146)	0.614 (0.061)
Spoolcart*	07 Mar-23 May	501	0.376 (0.039)	0.981 (0.212)	0.816 (0.306)	0.882 (0.352)	0.265 (0.060)

Table 25. Continued.

Trap	Release dates	Number released	Rel to LGR	LGR to LGO	LGO to LMO	LMO to MCN	Rel to MCN
			Wild steelhead				
American River	21 Mar-30 May	86	0.349 (0.122)	0.622 (0.304)	0.750 (0.564)	NA	NA
Asotin Creek	08 Apr-31 May	1,818	0.410 (0.039)	NA	NA	NA	NA
Catherine Creek	02 Mar-31 May	349	0.089 (0.027)	0.881 (0.447)	NA	NA	NA
Crooked Fork Cr	26 Mar-31 May	331	0.795 (0.067)	0.959 (0.116)	0.811 (0.177)	0.892 (0.230)	0.552 (0.093)
Clearwater	11 Mar-09 May	1,060	0.966 (0.061)	0.986 (0.112)	0.651 (0.123)	0.961 (0.195)	0.596 (0.075)
Grande Ronde	10 Mar-24 May	369	0.944 (0.091)	0.980 (0.170)	0.742 (0.190)	0.660 (0.232)	0.453 (0.125)
Imnaha (early)	11 Mar-31 May	6,524	0.832 (0.023)	0.916 (0.044)	0.844 (0.076)	1.008 (0.136)	0.649 (0.067)
Imnaha (late)	01 Jun-21 Jun	668	0.693 (0.418)	0.403 (0.322)	NA	NA	NA
Knox Bridge	10 Mar-31 May	647	0.074 (0.020)	2.000 (1.816)	NA	NA	NA
Lookingglass Cr	27 Mar-30 May	299	0.335 (0.057)	1.725 (0.674)	0.456 (0.264)	0.546 (0.338)	0.144 (0.062)
Minam River	08 Mar-31 May	295	0.413 (0.131)	2.184 (2.034)	0.262 (0.278)	0.629 (0.484)	0.148 (0.082)
Pahsimeroi	07 Mar 31 May	647	0.063 (0.014)	2.500 (2.183)	NA	NA	NA
Salmon	17 Mar-11 May	407	0.879 (0.081)	0.985 (0.136)	1.091 (0.350)	0.875 (0.345)	0.826 (0.204)
Snake	23 Mar-25 May	964	1.050 (0.056)	0.765 (0.070)	1.137 (0.182)	0.789 (0.190)	0.720 (0.138)
Spoolcart*	07 Mar-08 May	600	0.252 (0.037)	1.193 (0.335)	0.640 (0.298)	1.833 (1.833)	0.352 (0.320)
			Hatchery Chinook salmon				
Grande Ronde	18 Mar-23 May	1,406	0.872 (0.039)	0.849 (0.057)	1.190 (0.121)	0.749 (0.079)	0.660 (0.036)
Salmon	15 Mar-11 May	3,937	0.755 (0.021)	0.923 (0.043)	0.933 (0.055)	0.941 (0.050)	0.612 (0.019)
Snake	23 Mar-25 May	1,666	0.949 (0.031)	0.960 (0.055)	1.014 (0.082)	0.761 (0.061)	0.703 (0.032)
			Hatchery steelhead				
Grande Ronde	05 May-23 May	1,528	0.977 (0.050)	0.860 (0.059)	0.857 (0.077)	1.273 (0.306)	0.917 (0.209)
Imnaha	11 Apr-19 May	1,492	0.970 (0.045)	0.882 (0.057)	0.951 (0.098)	1.006 (0.237)	0.818 (0.176)
Salmon	31 Mar-11 May	2,298	0.966 (0.040)	0.864 (0.048)	0.862 (0.073)	0.925 (0.157)	0.665 (0.101)
Snake	23 Mar-25 May	2,545	0.997 (0.029)	0.880 (0.040)	0.870 (0.069)	1.133 (0.216)	0.864 (0.153)

* Grande Ronde River

Table 26. Estimated detection probabilities for juvenile salmonids released from fish traps in Snake River Basin in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Trap	Release dates	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
			Wild Chinook salmon			
American River	20 Mar-31 May	703	0.198 (0.029)	0.259 (0.035)	0.071 (0.021)	0.327 (0.050)
Catherine Creek	02 Feb-26 May	364	0.372 (0.055)	0.162 (0.055)	0.136 (0.045)	0.389 (0.081)
Crooked Fork Creek	23 Mar-28 May	109	0.288 (0.080)	0.176 (0.085)	0.171 (0.095)	0.273 (0.134)
Clearwater	11 Mar-09 May	658	0.288 (0.025)	0.314 (0.031)	0.118 (0.026)	0.480 (0.042)
Crooked River	19 Mar-31 May	400	0.202 (0.044)	0.309 (0.056)	0.114 (0.041)	0.320 (0.079)
Grande Ronde	07 Mar-26 May	2,571	0.322 (0.012)	0.237 (0.014)	0.112 (0.012)	0.392 (0.019)
Imnaha (early)	08 Mar-31 May	6,635	0.335 (0.008)	0.230 (0.009)	0.107 (0.007)	0.388 (0.012)
Imnaha (late)	01 Jun-21 Jun	864	0.074 (0.029)	0.147 (0.041)	NA	0.286 (0.066)
Johnson Creek	05 Mar-17 May	339	0.325 (0.047)	0.221 (0.045)	0.176 (0.044)	0.444 (0.074)
Knox Bridge	08 Mar-30 May	1,950	0.359 (0.023)	0.259 (0.024)	0.142 (0.021)	0.384 (0.037)
Lemhi River Weir	09 Mar-26 May	166	0.240 (0.055)	0.233 (0.061)	0.056 (0.048)	0.394 (0.085)
Lostine River	20 Feb-09 May	505	0.351 (0.039)	0.216 (0.044)	0.080 (0.034)	0.333 (0.057)
Marsh Creek	21 Mar-21 May	78	0.106 (0.082)	0.276 (0.120)	0.185 (0.134)	0.571 (0.187)
Minam	20 Feb-09 May	217	0.329 (0.054)	0.195 (0.053)	0.138 (0.069)	0.343 (0.080)
Pahsimeroi	06 Mar-31 May	1,200	0.222 (0.024)	0.196 (0.030)	0.069 (0.021)	0.373 (0.040)
Red River	19 Mar-31 May	922	0.158 (0.029)	0.215 (0.036)	0.053 (0.021)	0.370 (0.063)
Salmon	10 Mar-11 May	5,201	0.281 (0.009)	0.196 (0.010)	0.114 (0.009)	0.419 (0.014)
Sawtooth	20 Mar-31 May	569	0.354 (0.038)	0.329 (0.045)	0.182 (0.042)	0.373 (0.063)
Snake	23 Mar-25 May	379	0.356 (0.035)	0.108 (0.034)	0.235 (0.042)	0.520 (0.059)
Spoolcart*	07 Mar-23 May	501	0.420 (0.051)	0.250 (0.059)	0.167 (0.062)	0.312 (0.082)

Table 26. Continued.

Trap	Release dates	Number released	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam
Wild steelhead						
American River	05 May-23 May	86	0.333 (0.136)	0.375 (0.171)	0.143 (0.132)	NA
Asotin Creek	11 Apr-19 May	1,818	0.344 (0.036)	NA	NA	0.163 (0.056)
Catherine Creek	31 Mar-11 May	349	0.419 (0.139)	0.270 (0.136)	NA	NA
Crooked Fork Creek	23 Mar-25 May	331	0.247 (0.033)	0.395 (0.047)	0.155 (0.040)	0.262 (0.054)
Clearwater	18 Mar-23 May	1,060	0.199 (0.018)	0.311 (0.032)	0.166 (0.030)	0.246 (0.036)
Grande Ronde	15 Mar-11 May	369	0.264 (0.035)	0.228 (0.040)	0.228 (0.054)	0.167 (0.054)
Imnaha (early)	23 Mar-25 May	6,524	0.310 (0.010)	0.370 (0.015)	0.214 (0.018)	0.148 (0.017)
Imnaha (late)	21 Mar-30 May	668	0.080 (0.050)	0.363 (0.177)	NA	0.500 (0.354)
Knox Bridge	08 Apr-31 May	647	0.333 (0.103)	0.062 (0.060)	NA	0.333 (0.192)
Lookingglass Creek	02 Mar-31 May	299	0.269 (0.060)	0.171 (0.069)	0.183 (0.091)	0.200 (0.103)
Minam River	26 Mar-31 May	295	0.205 (0.073)	0.104 (0.092)	0.195 (0.114)	0.182 (0.116)
Pahsimeroi	11 Mar-09 May	647	0.490 (0.112)	0.125 (0.114)	NA	NA
Salmon	10 Mar-24 May	407	0.221 (0.030)	0.307 (0.040)	0.077 (0.027)	0.177 (0.048)
Snake	11 Mar-31 May	964	0.310 (0.022)	0.260 (0.025)	0.166 (0.027)	0.170 (0.036)
Spoolcart*	01 Jun-21 Jun	600	0.344 (0.059)	0.338 (0.087)	0.282 (0.116)	0.091 (0.087)
Hatchery Chinook salmon						
Grande Ronde	05 May-23 May	1,406	0.228 (0.016)	0.196 (0.016)	0.100 (0.012)	0.320 (0.022)
Salmon	11 Apr-19 May	3,937	0.240 (0.010)	0.136 (0.008)	0.111 (0.008)	0.375 (0.015)
Snake	31 Mar-11 May	1,666	0.276 (0.014)	0.185 (0.013)	0.138 (0.013)	0.379 (0.022)
Hatchery steelhead						
Grande Ronde	05 May-23 May	1,528	0.188 (0.014)	0.350 (0.021)	0.290 (0.026)	0.066 (0.016)
Imnaha	11 Apr-19 May	1,492	0.211 (0.014)	0.390 (0.022)	0.228 (0.024)	0.068 (0.016)
Salmon	31 Mar-11 May	2,298	0.186 (0.011)	0.401 (0.018)	0.233 (0.021)	0.101 (0.017)
Snake	23 Mar-25 May	2,545	0.280 (0.012)	0.392 (0.017)	0.253 (0.020)	0.079 (0.015)

* Grande Ronde River

Table 27. Estimated survival probabilities for PIT-tagged yearling Chinook salmon and steelhead from upper-Columbia River hatcheries released in 2007. Estimates based on the single-release model. Standard errors in parentheses. Abbreviations: Rel-Release site; MCN-McNary Dam; JDA-John Day Dam; BON-Bonneville Dam.

Hatchery	Release site	Number released	Rel to MCN	MCN to JDA	JDA to BON	MCN to BON	Rel to BON
Yearling Chinook salmon							
Cle Elum	Yakima R. (rkm 27)	12,860	0.334 (0.009)	0.930 (0.049)	0.715 (0.152)	0.665 (0.139)	0.222 (0.046)
Cle Elum	Yakima R. (rkm 325)	12,931	0.285 (0.008)	0.837 (0.047)	0.869 (0.234)	0.727 (0.194)	0.207 (0.055)
Cle Elum	Jack Creek Pond	12,959	0.296 (0.008)	0.858 (0.047)	0.759 (0.194)	0.651 (0.164)	0.193 (0.048)
East Bank	Chiwawa Pond (4/13)	4,988	0.636 (0.028)	0.896 (0.081)	0.721 (0.212)	0.645 (0.185)	0.410 (0.117)
East Bank	Chiwawa Pond (5/1)	4,992	0.659 (0.028)	1.041 (0.094)	0.569 (0.133)	0.592 (0.132)	0.390 (0.086)
Entiat	Entiat Hatchery	999	0.321 (0.035)	0.642 (0.116)	NA	NA	NA
Leavenworth	Leavenworth Hatchery	14,968	0.594 (0.011)	0.868 (0.033)	0.908 (0.136)	0.789 (0.117)	0.468 (0.069)
Wells	Wells Hatchery (5/17)	5,983	0.267 (0.042)	1.012 (0.322)	0.626 (0.604)	0.634 (0.593)	0.169 (0.156)
Wells	Wells Hatchery (6/15)	5,882	0.260 (0.068)	4.511 (4.610)	NA	NA	NA
Winthrop	Winthrop NFH	3,833	0.492 (0.022)	0.857 (0.083)	0.838 (0.356)	0.718 (0.300)	0.354 (0.147)
Sockeye salmon							
East Bank	Wenatchee R. (rkm 9)	14,859	0.299 (0.013)	1.013 (0.087)	0.837 (0.134)	0.848 (0.125)	0.253 (0.036)
Steelhead							
Cassimer Bar	Okanagon R.	9,878	0.179 (0.017)	0.921 (0.213)	0.457 (0.179)	0.421 (0.145)	0.075 (0.025)
Cassimer Bar	Omak Creek	9,911	0.260 (0.022)	0.708 (0.114)	0.580 (0.150)	0.411 (0.096)	0.107 (0.024)
Chelan	Wenatchee R (rkm 0)	1,497	0.338 (0.074)	0.756 (0.250)	0.713 (0.380)	0.539 (0.281)	0.182 (0.087)
East Bank	Wenatchee R. (rkm 0)	1,563	0.386 (0.119)	0.903 (0.459)	1.037 (1.059)	0.936 (0.925)	0.361 (0.339)
Turtle Rock	Chiwawa River	4,164	0.534 (0.059)	0.810 (0.143)	0.864 (0.278)	0.700 (0.217)	0.374 (0.109)
Turtle Rock	Nason Creek	7,306	0.424 (0.033)	1.155 (0.174)	0.475 (0.115)	0.549 (0.120)	0.233 (0.048)
Turtle Rock	Wenatchee R. (rkm 75)	13,629	0.659 (0.046)	1.040 (0.122)	0.662 (0.118)	0.689 (0.115)	0.454 (0.069)

Table 27. Continued.

Hatchery	Release Site	Number released	Rel to MCN	MCN to JDA	JDA to BON	MCN to BON	Rel to BON
			Coho Salmon				
Cascade	Leavenworth Hatchery	2,879	0.269 (0.030)	0.659 (0.118)	1.116 (0.498)	0.736 (0.322)	0.198 (0.084)
Cascade	Nason Creek	3,408	0.334 (0.044)	0.879 (0.170)	0.778 (0.335)	0.684 (0.291)	0.228 (0.093)
Cascade	Wenatchee R. (rkm 76)	3,130	0.474 (0.060)	0.916 (0.178)	0.814 (0.282)	0.745 (0.252)	0.353 (0.111)
Eagle Creek	Natches River (rkm 10)	2,464	0.322 (0.034)	1.256 (0.301)	0.836 (0.577)	1.050 (0.696)	0.338 (0.222)
Eagle Creek	Natches River (rkm 62)	2,481	0.449 (0.106)	0.593 (0.195)	NA	NA	NA
Eagle Creek	Yakima River (rkm 75)	1,246	0.545 (0.046)	0.840 (0.127)	0.590 (0.256)	0.495 (0.209)	0.270 (0.112)
Eagle Creek	Yakima River (rkm 256)	2,479	0.090 (0.025)	0.923 (0.528)	0.339 (0.250)	0.312 (0.187)	0.028 (0.015)
Willard	Leavenworth Hatchery	9,038	0.422 (0.030)	1.049 (0.139)	0.582 (0.119)	0.610 (0.112)	0.257 (0.044)
Willard	Nason Creek (4/27)	3,494	0.334 (0.050)	0.767 (0.179)	0.850 (0.349)	0.652 (0.260)	0.218 (0.081)
Willard	Nason Creek (5/7)	3,992	0.298 (0.043)	0.830 (0.182)	1.105 (0.585)	0.917 (0.479)	0.273 (0.137)
Willard	Wenatchee R. (rkm 76)	3,116	0.439 (0.087)	0.711 (0.205)	0.975 (0.629)	0.694 (0.445)	0.305 (0.186)
Yakima	Natches River (rkm 10)	2,398	0.239 (0.030)	0.781 (0.189)	1.255 (1.208)	0.979 (0.928)	0.234 (0.220)
Yakima	Natches River (rkm 62)	2,484	0.162 (0.021)	1.174 (0.413)	0.501 (0.479)	0.588 (0.533)	0.095 (0.086)
Yakima	Yakima River (rkm 75)	2,498	0.527 (0.025)	0.821 (0.086)	0.860 (0.462)	0.706 (0.375)	0.372 (0.197)
Yakima	Yakima River (rkm 256)	1,201	0.082 (0.030)	0.587 (0.325)	NA	NA	NA

Table 28. Estimated detection probabilities for PIT-tagged yearling Chinook salmon and steelhead from upper-Columbia River hatcheries released in 2007. Estimates based on the single-release model. Standard errors in parentheses.

Hatchery	Release Site	Number released	McNary Dam	John Day Dam	Bonneville Dam
			Yearling Chinook salmon		
Cle Elum	Yakima R. (rkm 27)	12,860	0.337 (0.011)	0.428 (0.022)	0.145 (0.031)
Cle Elum	Yakima R. (rkm 325)	12,931	0.336 (0.012)	0.462 (0.024)	0.122 (0.033)
Cle Elum	Jack Creek Pond	12,959	0.363 (0.012)	0.448 (0.024)	0.151 (0.038)
East Bank	Chiwawa Pond (4/13)	4,988	0.266 (0.014)	0.262 (0.022)	0.167 (0.048)
East Bank	Chiwawa Pond (5/1)	4,992	0.259 (0.013)	0.239 (0.020)	0.189 (0.042)
Entiat	Entiat Hatchery	999	0.328 (0.042)	0.536 (0.085)	NA
Leavenworth	Leavenworth Hatchery	14,968	0.323 (0.008)	0.384 (0.014)	0.150 (0.022)
Wells	Wells Hatchery (5/17)	5,983	0.120 (0.020)	0.074 (0.021)	0.143 (0.132)
Wells	Wells Hatchery (6/15)	5,882	0.074 (0.020)	0.012 (0.012)	NA
Winthrop	Winthrop NFH	3,833	0.318 (0.017)	0.396 (0.036)	0.099 (0.042)
			Sockeye salmon		
East Bank	Wenatchee R. (rkm 9)	14,859	0.229 (0.011)	0.136 (0.011)	0.20 (0.029)
			Steelhead		
Cassimer Bar	Okanagon R.	9,878	0.220 (0.023)	0.103 (0.023)	0.201 (0.068)
Cassimer Bar	Omak Creek	9,911	0.197 (0.018)	0.127 (0.019)	0.247 (0.055)
Chelan	Wenatchee R (rkm 0)	1,497	0.115 (0.029)	0.126 (0.035)	0.303 (0.146)
East Bank	Wenatchee R. (rkm 0)	1,563	0.084 (0.028)	0.076 (0.033)	0.102 (0.096)
Turtle Rock	Chiwawa River	4,164	0.112 (0.014)	0.100 (0.016)	0.220 (0.065)
Turtle Rock	Nason Creek	7,306	0.140 (0.012)	0.095 (0.013)	0.262 (0.055)
Turtle Rock	Wenatchee River (rkm 75)	13,629	0.079 (0.006)	0.067 (0.007)	0.198 (0.030)

Table 28. Continued.

Hatchery	Release Site	Number released	McNary Dam	John Day Dam	Bonneville Dam
			Coho salmon		
Cascade	Leavenworth Hatchery	2,879	0.212 (0.027)	0.186 (0.031)	0.255 (0.110)
Cascade	Nason Creek	3,408	0.104 (0.016)	0.118 (0.020)	0.333 (0.136)
Cascade	Wenatchee R. (rkm 76)	3,130	0.096 (0.014)	0.091 (0.016)	0.294 (0.093)
Eagle Creek	Natches River (rkm 10)	2,464	0.228 (0.027)	0.136 (0.032)	0.125 (0.083)
Eagle Creek	Natches River (rkm 62)	2,481	0.079 (0.020)	0.147 (0.036)	NA
Eagle Creek	Yakima River (rkm 75)	1,246	0.270 (0.028)	0.332 (0.046)	0.275 (0.116)
Eagle Creek	Yakima River (rkm 256)	2,479	0.188 (0.056)	0.097 (0.053)	0.400 (0.219)
Willard	Leavenworth Hatchery	9,038	0.134 (0.011)	0.077 (0.010)	0.309 (0.053)
Willard	Nason Creek (4/27)	3,494	0.103 (0.018)	0.090 (0.019)	0.297 (0.111)
Willard	Nason Creek (5/7)	3,992	0.098 (0.016)	0.093 (0.018)	0.232 (0.117)
Willard	Wenatchee R. (rkm 76)	3,116	0.066 (0.015)	0.067 (0.016)	0.250 (0.153)
Yakima	Natches River (rkm 10)	2,398	0.251 (0.035)	0.231 (0.052)	0.100 (0.095)
Yakima	Natches River (rkm 62)	2,484	0.296 (0.043)	0.157 (0.054)	0.170 (0.155)
Yakima	Yakima River (rkm 75)	2,498	0.381 (0.021)	0.409 (0.041)	0.135 (0.072)
Yakima	Yakima River (rkm 256)	1,201	0.192 (0.077)	0.345 (0.159)	NA

Table 29. Travel time statistics for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at Lower Granite Dam in 2007. Abbreviations: LGR–Lower Granite Dam; LGO–Little Goose Dam; LMO–Lower Monumental Dam; MCN–McNary Dam; BON–Bonneville Dam; N–Number of fish on which statistics are based; Med.–Median.

	LGR to LGO (d)				LGO to LMO (d)				LMO to MCN (d)			
Date at Lower Granite	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
23 Mar–29 Mar	17	12.2	16.3	19.1	2	2.8	3.1	3.3	0	NA	NA	NA
30 Mar–05 Apr	59	10.9	13.2	15.9	4	2.9	4.0	5.3	4	4.3	5.2	12.2
06 Apr–12 Apr	658	6.8	8.2	13.3	23	2.9	3.8	14.2	33	3.1	4.0	5.2
13 Apr–19 Apr	1,332	6.0	7.4	10.3	54	2.8	4.0	5.6	82	3.0	3.8	5.0
20 Apr–26 Apr	1,821	6.0	7.2	9.1	275	1.7	2.1	2.7	667	2.8	3.2	4.1
27 Apr–03 May	4,693	4.1	4.8	6.2	475	1.6	1.9	2.5	692	2.8	3.2	4.1
04 May–10 May	5,792	4.4	5.2	6.3	1,369	1.3	1.6	2.1	1,877	2.6	3.0	3.7
11 May–17 May	5,395	3.9	4.7	5.8	660	1.3	1.7	2.2	924	2.6	3.1	4.0
18 May–24 May	340	3.9	4.7	6.1	12	1.4	1.6	2.0	25	3.0	3.4	4.2
25 May–31 May	32	4.2	5.3	6.1	0	NA	NA	NA	0	NA	NA	NA

	LGR to MCN (d)				LGR to BON (d)			
Date at Lower Granite	N	20%	Med.	80%	N	20%	Med.	80%
23 Mar–29 Mar	10	25.2	32.1	34.3	2	41.3	47.5	53.6
30 Mar–05 Apr	56	22.1	25.0	28.4	13	26.8	29.3	34.4
06 Apr–12 Apr	904	16.4	20.1	26.3	245	24.1	28.8	33.4
13 Apr–19 Apr	2,657	12.4	15.0	19.9	795	18.5	21.8	27.2
20 Apr–26 Apr	4,853	11.0	12.3	14.7	1,429	15.9	17.7	20.4
27 Apr–03 May	9,508	8.7	9.9	11.6	3,196	12.9	14.1	16.0
04 May–10 May	9,133	8.9	9.9	11.2	2,766	12.8	14.0	15.7
11 May–17 May	7,476	8.0	9.0	10.4	2,006	11.7	13.0	14.8
18 May–24 May	471	8.7	10.7	13.0	123	12.3	15.0	17.2
25 May–31 May	44	9.8	10.9	13.0	9	13.2	13.7	14.7

Table 30. Migration rate statistics for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at Lower Granite Dam in 2007. Abbreviations: LGR–Lower Granite Dam; LGO–Little Goose Dam; LMO–Lower Monumental Dam; MCN–McNary Dam; BON–Bonneville Dam; N–Number of fish observed; Med–Median.

	LGR to LGO (km/d)				LGO to LMO (km/d)				LMO to MCN (km/d)			
Date at Lower Granite	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
23 Mar–29 Mar	17	3.1	3.7	4.9	2	13.8	15.0	16.4	0	NA	NA	NA
30 Mar–05 Apr	59	3.8	4.6	5.5	4	8.6	11.4	15.8	4	9.7	22.9	27.6
06 Apr–12 Apr	658	4.5	7.3	8.8	23	3.3	12.0	16.1	33	22.9	29.5	38.5
13 Apr–19 Apr	1,332	5.8	8.1	9.9	54	8.2	11.5	16.7	82	23.9	31.1	39.7
20 Apr–26 Apr	1,821	6.6	8.4	9.9	275	17.2	22.1	26.4	667	28.9	37.1	42.7
27 Apr–03 May	4,693	9.7	12.5	14.5	475	18.8	23.7	29.1	692	29.2	36.6	43.3
04 May–10 May	5,792	9.5	11.5	13.7	1,369	22.0	27.9	35.7	1,877	32.1	39.1	46.5
11 May–17 May	5,395	10.3	12.7	15.5	660	21.3	27.5	34.8	924	29.9	37.9	45.8
18 May–24 May	340	9.9	12.8	15.3	12	22.4	28.6	31.7	25	28.0	35.5	39.0
25 May–31 May	32	9.9	11.4	14.4	0	NA	NA	NA	0	NA	NA	NA

	LGR to MCN (km/d)				LGR to BON (km/d)			
Date at Lower Granite	N	20%	Med.	80%	N	20%	Med.	80%
23 Mar–29 Mar	10	6.6	7.0	8.9	2	8.6	9.7	11.2
30 Mar–05 Apr	56	7.9	9.0	10.2	13	13.4	15.7	17.2
06 Apr–12 Apr	904	8.5	11.2	13.8	245	13.8	16.0	19.2
13 Apr–19 Apr	2,657	11.3	15.0	18.2	795	16.9	21.1	25.0
20 Apr–26 Apr	4,853	15.3	18.3	20.4	1,429	22.6	26.1	28.9
27 Apr–03 May	9,508	19.4	22.8	25.9	3,196	28.8	32.6	35.8
04 May–10 May	9,133	20.1	22.6	25.4	2,766	29.3	32.9	36.1
11 May–17 May	7,476	21.5	25.0	28.3	2,006	31.2	35.6	39.3
18 May–24 May	471	17.3	21.0	25.9	123	26.8	30.7	37.5
25 May–31 May	44	17.3	20.6	22.9	9	31.4	33.6	35.0

Table 31. Travel time statistics for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Abbreviations: N–number of fish on which statistics are based; Med.-median.

Date at Lower	McNary to John Day Dam (d)				John Day to Bonneville Dam (d)				McNary to Bonneville Dam (d)			
Granite Dam	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
13 Apr–19 Apr	20	4.8	5.7	9.6	1	2.2	2.2	2.2	3	5.6	5.9	6.7
20 Apr–26 Apr	568	4.7	5.6	7.1	51	1.8	1.9	2.3	125	6.7	7.2	8.2
27 Apr–03 May	5,374	4.0	4.7	5.7	731	1.8	2.0	2.3	1,376	5.7	6.4	7.8
04 May–10 May	13,366	3.9	4.5	5.4	1,803	1.6	1.8	2.1	4,920	5.1	5.9	6.9
11 May–17 May	8,985	3.7	4.3	5.0	1,090	1.5	1.7	2.0	3,191	5.0	5.4	6.3
18 May–24 May	6,169	3.5	4.0	4.7	751	1.6	1.7	2.0	1,789	4.9	5.3	6.0
25 May–31 May	556	3.7	4.5	5.2	54	1.6	1.8	2.0	163	5.0	5.4	6.4
01 Jun–07 Jun	180	3.4	3.9	4.7	22	1.4	1.5	1.9	59	4.9	5.3	5.9
08 Jun–14 Jun	116	3.4	3.9	4.7	15	1.5	1.6	1.9	51	4.8	5.2	6.0
15 Jun–21 Jun	18	3.3	3.4	4.3	2	2.3	2.4	2.6	14	4.9	5.2	6.2

Table 32. Migration rate statistics for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to the tailrace at McNary Dam in 2007. Abbreviations: N–number of fish on which statistics are based; Med.–median.

	McNary to John Day Dam (d)				John Day to Bonneville Dam (d)				McNary to Bonneville Dam (d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
13 Apr–19 Apr	20	12.8	21.8	25.4	1	51.8	51.8	51.8	3	35.1	40.0	42.3
20 Apr–26 Apr	568	17.3	22.1	26.0	51	49.6	58.2	63.8	125	28.6	32.6	35.1
27 Apr–03 May	5,374	21.4	26.2	30.4	731	48.3	56.5	64.6	1,376	30.4	37.0	41.2
04 May–10 May	13,366	22.7	27.6	31.3	1,803	54.3	63.1	71.1	4,920	34.3	39.9	45.9
11 May–17 May	8,985	24.7	28.7	33.3	1,090	57.1	66.1	73.4	3,191	37.6	43.5	47.4
18 May–24 May	6,169	26.1	30.5	34.9	751	56.5	65.7	72.9	1,789	39.3	44.5	48.2
25 May–31 May	556	23.7	27.4	32.9	54	55.4	62.8	71.5	163	37.0	43.5	47.0
01 Jun–07 Jun	180	26.3	31.9	36.5	22	58.9	76.4	80.1	59	39.9	44.8	48.4
08 Jun–14 Jun	116	26.0	31.5	36.5	15	60.8	70.6	74.8	51	39.7	45.7	49.0
15 Jun–21 Jun	18	28.5	36.0	37.5	2	44.1	46.3	48.9	14	38.2	45.0	48.0

Table 33. Travel time statistics for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Abbreviations: LGR–Lower Granite Dam; LGO–Little Goose Dam; LMO–Lower Monumental Dam; MCN–McNary Dam; BON–Bonneville Dam; N-Number of fish on which statistics are based; Med.–Median.

	LGR to LGO (d)				LGO to LMO (d)				LMO to MCN (d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
06 Apr–12 Apr	333	4.9	6.0	7.5	18	3.1	7.5	14.5	3	2.7	3.7	4.8
13 Apr–19 Apr	977	4.7	5.8	8.6	138	3.0	6.2	9.5	44	2.4	2.8	3.4
20 Apr–26 Apr	1,234	5.7	7.6	9.1	391	2.1	3.2	4.9	169	2.2	2.6	3.0
27 Apr–03 May	2,555	3.5	4.0	4.7	406	1.9	2.6	6.2	141	2.2	2.6	3.1
04 May–10 May	2,187	4.3	4.7	5.7	684	1.8	2.2	3.2	252	2.4	2.8	3.3
11 May–17 May	2,359	3.5	4.2	5.0	413	1.7	2.2	3.9	97	2.1	2.6	3.1
18 May–24 May	1,286	3.8	4.7	6.7	86	1.8	2.4	3.5	11	2.8	3.5	4.0
25 May–31 May	38	3.9	4.8	7.1	5	3.3	3.8	5.2	0	NA	NA	NA

	LGR to MCN (d)				LGR to BON (d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%
06 Apr–12 Apr	98	11.1	12.6	16.9	77	17.2	21.0	28.9
13 Apr–19 Apr	341	10.8	12.4	16.9	270	16.8	20.1	24.5
20 Apr–26 Apr	446	10.8	12.4	15.3	525	15.8	17.4	20.4
27 Apr–03 May	953	8.1	9.0	11.4	696	12.0	13.4	18.3
04 May–10 May	733	8.4	9.6	11.0	482	13.1	15.1	19.3
11 May–17 May	532	7.5	8.7	11.6	552	12.3	14.3	18.8
18 May–24 May	201	9.3	11.4	13.7	212	13.8	17.0	23.3
25 May–31 May	5	10.9	12.4	12.9	2	15.0	15.4	15.8

Table 34. Migration rate statistics for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Abbreviations: LGR–Lower Granite Dam; LGO–Little Goose Dam; LMO–Lower Monumental Dam; MCN–McNary Dam; BON–Bonneville Dam; N-Number of fish on which statistics are based; Med.–Median.

	LGR to LGO (km/d)				LGO to LMO (km/d)				LMO to MCN (km/d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
06 Apr–12 Apr	333	8.0	10.0	12.2	18	3.2	6.1	15.0	3	24.8	31.9	43.8
13 Apr–19 Apr	977	6.9	10.4	12.8	138	4.8	7.4	15.4	44	35.1	43.1	49.0
20 Apr–26 Apr	1,234	6.6	7.9	10.6	391	9.5	14.2	21.9	169	39.7	45.8	54.1
27 Apr–03 May	2,555	12.9	15.1	16.9	406	7.4	17.6	24.2	141	38.6	45.9	53.1
04 May–10 May	2,187	10.5	12.7	13.8	684	14.5	20.8	25.6	252	36.3	42.0	49.4
11 May–17 May	2,359	12.0	14.3	17.0	413	11.8	20.7	27.1	97	38.5	45.4	56.4
18 May–24 May	1,286	9.0	12.7	16.0	86	13.0	19.1	25.4	11	29.8	33.9	42.7
25 May–31 May	38	8.4	12.5	15.4	5	8.8	12.1	13.8	0	NA	NA	NA

	LGR to MCN (km/d)				LGR to BON (km/d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%
06 Apr–12 Apr	98	13.3	17.8	20.3	77	15.9	21.9	26.8
13 Apr–19 Apr	341	13.3	18.1	20.8	270	18.8	22.9	27.4
20 Apr–26 Apr	446	14.7	18.2	20.9	525	22.6	26.5	29.1
27 Apr–03 May	953	19.8	25.0	27.8	696	25.1	34.4	38.5
4 May–10 May	733	20.4	23.5	26.8	482	23.8	30.6	35.2
11 May–17 May	532	19.4	25.9	29.9	552	24.6	32.1	37.5
18 May–24 May	201	16.4	19.7	24.2	212	19.8	27.1	33.5
25 May–31 May	5	17.5	18.2	20.5	2	29.2	29.9	30.7

Table 35. Travel time statistics for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at McNary Dam in 2007. Abbreviations: N–Number of fish on which statistics are based; Med.–Median.

	McNary to John Day Dam (d)				John Day to Bonneville Dam (d)				McNary to Bonneville Dam (d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
13 Apr–19 Apr	14	4.5	8.0	13.7	2	1.5	1.8	2.0	11	6.0	6.9	14.2
20 Apr–26 Apr	109	5.4	8.0	13.4	7	1.4	1.5	2.3	66	6.2	8.1	13.7
27 Apr–03 May	175	3.9	5.1	7.0	22	1.3	1.4	1.6	106	5.1	6.1	7.4
04 May–10 May	341	3.5	4.1	5.0	46	1.4	1.5	1.6	330	4.9	5.7	6.9
11 May–17 May	170	4.0	4.7	6.0	16	1.3	1.5	1.8	188	5.0	6.0	8.1
18 May–24 May	86	4.0	4.6	6.1	15	1.5	1.7	2.0	126	5.2	6.3	9.1
25 May–31 May	16	4.5	5.0	7.4	2	1.6	1.7	1.7	36	5.8	7.1	14.0
01 Jun–07 Jun	8	4.3	5.5	10.9	3	1.6	1.8	2.8	20	5.7	7.2	13.2
08 Jun–14 Jun	4	4.6	4.7	4.8	3	1.9	1.9	2.9	10	6.4	7.8	12.8

Table 36. Migration rate statistics for juvenile Snake River steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at McNary Dam in 2007. Abbreviations: N–Number of fish on which statistics are based; Med.–Median.

	McNary to John Day Dam (d)				John Day to Bonneville Dam (d)				McNary to Bonneville Dam (d)			
Date at LGR	N	20%	Med.	80%	N	20%	Med.	80%	N	20%	Med.	80%
13 Apr–19 Apr	14	9.0	15.5	27.2	2	55.9	64.6	76.4	11	16.6	34.2	39.0
20 Apr–26 Apr	109	9.1	15.4	22.7	7	48.3	74.3	81.3	66	17.2	29.1	37.8
27 Apr–03 May	175	17.6	24.0	31.7	22	71.1	78.5	85.0	106	31.9	38.5	46.4
04 May–10 May	341	24.5	29.7	35.2	46	68.9	74.8	81.3	330	34.4	41.2	48.3
11 May–17 May	170	20.7	26.5	30.9	16	63.1	76.4	84.3	188	29.0	39.7	46.7
18 May–24 May	86	20.1	26.9	31.0	15	57.4	66.5	76.4	126	25.8	37.7	45.2
25 May–31 May	16	16.7	24.6	27.3	2	65.7	67.7	69.8	36	16.9	33.1	40.6
01 Jun–07 Jun	8	11.3	22.4	28.9	3	40.6	63.1	72.4	20	17.9	32.9	41.4
08 Jun–14 Jun	4	25.4	26.5	26.8	3	39.4	59.2	60.8	10	18.5	30.3	37.0

Table 37. Number of PIT–tagged hatchery steelhead released at Lower Granite Dam by day for survival estimates in 2007. Also included are tagging mortalities and lost tags by date.

Release date	Number released	Mortalities	Lost tags
10–Apr	96		
11–Apr	97		
12–Apr	260		
18–Apr	711		1
19–Apr	929		
20–Apr	109	1	
24–Apr	1,871	1	
25–Apr	2,013	2	
26–Apr	3		
28–Apr	2		
1–May	26		
2–May	2,714	6	
3–May	296		
4–May	464		
5–May	228		
8–May	583	1	
9–May	328		
10–May	793	1	
11–May	707		
12–May	805		
15–May	257		1
16–May	632		
17–May	466		
18–May	739	1	2
19–May	365		
23–May	731	1	
24–May	449		
25–May	574		
30–May	299	1	
31–May	299		1
1–Jun	313	1	
2–Jun	141		
5–Jun	151		
6–Jun	172		
7–Jun	153		
8–Jun	138	1	
9–Jun	38		
12–Jun	81		1
13–Jun	80		
14–Jun	81		
15–Jun	81		
16–Jun	77		
Total	19,352	17	6

Table 38. Number of PIT–tagged wild steelhead released at Lower Granite Dam by day for survival estimates in 2007. Also included are tagging mortalities and lost tags by date.

Release date	Number released	Mortalities	Lost tags	Release date	Number released	Mortalities	Lost tags
10–Apr	533			17–May	471		
11–Apr	15			18–May	522		
12–Apr	200			19–May	386		
18–Apr	291			23–May	472		
19–Apr	377			24–May	416		
20–Apr	71			25–May	469		
24–Apr	172			30–May	171		
25–Apr	17			31–May	173	1	
26–Apr	79			1–Jun	116		
28–Apr	185			2–Jun	114		
1–May	675			5–Jun	72		
2–May	254			6–Jun	60		
3–May	816			7–Jun	79	1	
4–May	232	1		8–Jun	44		
5–May	412			9–Jun	82		
8–May	605		1	12–Jun	69		
9–May	396			13–Jun	58		
10–May	529			14–Jun	41		
11–May	407			15–Jun	35		
12–May	161			16–Jun	39		
15–May	392						
16–May	574			Total	11,286	3	1

Table 39. Number of PIT–tagged wild yearling Chinook salmon released at Lower Granite Dam by day for survival estimates in 2007. Also included are tagging mortalities and lost tags by date.

Release date	Number released	Mortalities	Lost Tags	Release date	Number released	Mortalities	Lost tags
10–Apr	564	2		17–May	271		
11–Apr	508	2	1	18–May	174	4	
12–Apr	611	1		19–May	222		1
18–Apr	1,131	2	1	23–May	264		
19–Apr	1,615	6		24–May	100		
20–Apr	798			25–May	131		
24–Apr	941	4		30–May	79		
25–Apr	213			31–May	85		
26–Apr	585	3	2	1–Jun	33		
28–Apr	1,087	6	2	2–Jun	23		
1–May	278						
2–May	306						
3–May	425						
4–May	410	1					
5–May	331	1					
8–May	277						
9–May	350						
10–May	354						
11–May	634	1					
12–May	264	1					
15–May	587	1					
16–May	925			Total	14,576	37	7

Table 40. Estimated survival for yearling Chinook salmon from selected Snake River Basin hatcheries to the tailrace of Lower Granite Dam, 1993–2007. Distance from each hatchery to Lower Granite Dam in parentheses in header. Standard errors in parentheses following each survival estimate.

Year	Dworshak (116)	Kooskia (176)	Lookingglass* (209)	Rapid River (283)	McCall (457)	Pahsimeroi (630)	Sawtooth (747)	Mean
1993	0.647 (0.028)	0.689 (0.047)	0.660 (0.025)	0.670 (0.017)	0.498 (0.017)	0.456 (0.032)	0.255 (0.023)	0.554 (0.060)
1994	0.778 (0.020)	0.752 (0.053)	0.685 (0.021)	0.526 (0.024)	0.554 (0.022)	0.324 (0.028)	0.209 (0.014)	0.547 (0.081)
1995	0.838 (0.034)	0.786 (0.024)	0.617 (0.015)	0.726 (0.017)	0.522 (0.011)	0.316 (0.033)	0.230 (0.015)	0.576 (0.088)
1996	0.776 (0.017)	0.744 (0.010)	0.567 (0.014)	0.588 (0.007)	0.531 (0.007)	—	0.121 (0.017)	0.555 (0.096)
1997	0.576 (0.017)	0.449 (0.034)	0.616 (0.017)	0.382 (0.008)	0.424 (0.008)	0.500 (0.008)	0.508 (0.037)	0.494 (0.031)
1998	0.836 (0.006)	0.652 (0.024)	0.682 (0.006)	0.660 (0.004)	0.585 (0.004)	0.428 (0.021)	0.601 (0.033)	0.635 (0.046)
1999	0.834 (0.011)	0.653 (0.031)	0.668 (0.009)	0.746 (0.006)	0.649 (0.008)	0.584 (0.035)	0.452 (0.019)	0.655 (0.045)
2000	0.841 (0.009)	0.734 (0.027)	0.688 (0.011)	0.748 (0.007)	0.689 (0.010)	0.631 (0.062)	0.546 (0.030)	0.697 (0.035)
2001	0.747 (0.002)	0.577 (0.019)	0.747 (0.003)	0.689 (0.002)	0.666 (0.002)	0.621 (0.016)	0.524 (0.023)	0.653 (0.032)
2002	0.819 (0.011)	0.787 (0.036)	0.667 (0.012)	0.755 (0.003)	0.592 (0.006)	0.678 (0.053)	0.387 (0.025)	0.669 (0.055)
2003	0.720 (0.008)	0.560 (0.043)	0.715 (0.012)	0.691 (0.007)	0.573 (0.006)	0.721 (0.230)	0.595 (0.149)	0.654 (0.028)
2004	0.821 (0.003)	0.769 (0.017)	0.613 (0.004)	0.694 (0.003)	0.561 (0.002)	0.528 (0.017)	0.547 (0.018)	0.648 (0.044)
2005	0.823 (0.003)	0.702 (0.021)	0.534 (0.004)	0.735 (0.002)	0.603 (0.003)	0.218 (0.020)	0.220 (0.020)	0.549 (0.092)
2006	0.853 (0.007)	0.716 (0.041)	0.639 (0.014)	0.764 (0.004)	0.634 (0.006)	0.262 (0.024)	0.651 (0.046)	0.645 (0.071)
2007	0.817 (0.007)	0.654 (0.015)	0.682 (0.010)	0.748 (0.004)	0.554 (0.007)	0.530 (0.038)	0.581 (0.015)	0.652 (0.040)
Mean	**0.782 (0.021)**	**0.682 (0.024)**	**0.652 (0.014)**	**0.675 (0.027)**	**0.576 (0.018)**	**0.484 (0.042)**	**0.430 (0.046)**	**0.618 (0.031)**

* Released at Imnaha River Weir.

Table 41. Annual weighted means of survival probability estimates for yearling Chinook salmon (hatchery and wild combined), 1993–2007. Standard errors in parentheses. Reaches with asterisks comprise two dams and reservoirs (i.e., two projects); the following column gives the square root (i.e., geometric mean) of the two–project estimate to facilitate comparison with other single–project estimates. Simple arithmetic means across all years, and across all years excluding 2001 are given. Abbreviations: Trap–Snake River Trap; LGR–Lower Granite Dam; Little Goose–Little Goose Dam; LMO–Lower Monumental Dam; IHR–Ice Harbor Dam; MCN–McNary Dam; JDA–John Day Dam; TDA–The Dalles Dam; BON–Bonneville Dam.

Year	Trap–LGR	LGR–LGO	LGO–LMO	LMO–MCN*	LMO–IHR IHR–MCN	MCN–JDA	JDA–BON*	JDA–TDA TDA–BON
1993	0.828 (0.013)	0.854 (0.012)						
1994	0.935 (0.023)	0.830 (0.009)	0.847 (0.010)					
1995	0.905 (0.010)	0.882 (0.004)	0.925 (0.008)	0.876 (0.038)	0.936			
1996	0.977 (0.025)	0.926 (0.006)	0.929 (0.011)	0.756 (0.033)	0.870			
1997	NA	0.942 (0.018)	0.894 (0.042)	0.798 (0.091)	0.893			
1998	0.925 (0.009)	0.991 (0.006)	0.853 (0.009)	0.915 (0.011)	0.957	0.822 (0.033)		
1999	0.940 (0.009)	0.949 (0.002)	0.925 (0.004)	0.904 (0.007)	0.951	0.853 (0.027)	0.814 (0.065)	0.902
2000	0.929 (0.014)	0.938 (0.006)	0.887 (0.009)	0.928 (0.016)	0.963	0.898 (0.054)	0.684 (0.128)	0.827
2001	0.954 (0.015)	0.945 (0.004)	0.830 (0.006)	0.708 (0.007)	0.841	0.758 (0.024)	0.645 (0.034)	0.803
2002	0.953 (0.022)	0.949 (0.006)	0.980 (0.008)	0.837 (0.013)	0.915	0.907 (0.014)	0.840 (0.079)	0.917
2003	0.993 (0.023)	0.946 (0.005)	0.916 (0.011)	0.904 (0.017)	0.951	0.893 (0.017)	0.818 (0.036)	0.904
2004	0.893 (0.009)	0.923 (0.004)	0.875 (0.012)	0.818 (0.018)	0.904	0.809 (0.028)	0.735 (0.092)	0.857
2005	0.919 (0.015)	0.919 (0.003)	0.886 (0.006)	0.903 (0.010)	0.950	0.772 (0.029)	1.028 (0.132)	1.014
2006	0.952 (0.011)	0.923 (0.003)	0.934 (0.004)	0.887 (0.008)	0.942	0.881 (0.020)	0.944 (0.030	0.972
2007	0.943 (0.028)	0.938 (0.006)	0.957 (0.010)	0.876 (0.012)	0.978	0.920 (0.016)	0.824 (0.043)	0.908
Mean	**0.932 (0.011)**	**0.924 (0.010)**	**0.903 (0.011)**	**0.855 (0.019)**	**0.927**	**0.851 (0.018)**	**0.815 (0.040)**	**0.901**
Excl. 2001	0.930 (0.011)	0.922 (0.011)	0.908 (0.011)	0.867 (0.015)	0.934	0.862 (0.017)	0.836 (0.038)	0.913

Table 42. Annual weighted means of survival probability estimates for steelhead (hatchery and wild combined), 1993–2007. Standard errors in parentheses. Reaches with asterisks comprise two dams and reservoirs (i.e., two projects); the following column gives the square root (i.e., geometric mean) of the two–project estimate to facilitate comparison with other single–project estimates. Simple arithmetic means across all years, and across all years excluding 2001 are given. Abbreviations: Trap–Snake River Trap; LGR–Lower Granite Dam; Little Goose–Little Goose Dam; LMO–Lower Monumental Dam; IHR–Ice Harbor Dam; MCN–McNary Dam; JDA–John Day Dam; TDA–The Dalles Dam; BON–Bonneville Dam.

Year	Trap–LGR	LGR–LGO	LGO–LMO	LMO–MCN*	LMO–IHR IHR–MCN	MCN–JDA	JDA–BON*	JDA–TDA TDA–BON
1993	0.905 (0.006)							
1994	NA	0.844 (0.011)	0.892 (0.011)					
1995	0.945 (0.008)	0.899 (0.005)	0.962 (0.011)	0.858 (0.076)	0.926			
1996	0.951 (0.015)	0.938 (0.008)	0.951 (0.014)	0.791 (0.052)	0.889			
1997	0.964 (0.015)	0.966 (0.006)	0.902 (0.020)	0.834 (0.065)	0.913			
1998	0.924 (0.009)	0.930 (0.004)	0.889 (0.006)	0.797 (0.018)	0.893	0.831 (0.031)	0.935 (0.103)	0.967
1999	0.908 (0.011)	0.926 (0.004)	0.915 (0.006)	0.833 (0.011)	0.913	0.920 (0.033)	0.682 (0.039)	0.826
2000	0.964 (0.013)	0.901 (0.006)	0.904 (0.009)	0.842 (0.016)	0.918	0.851 (0.045)	0.754 (0.045)	0.868
2001	0.911 (0.007)	0.801 (0.010)	0.709 (0.008)	0.296 (0.010)	0.544	0.337 (0.025)	0.753 (0.063)	0.868
2002	0.895 (0.015)	0.882 (0.011)	0.882 (0.018)	0.652 (0.031)	0.807	0.844 (0.063)	0.612 (0.098)	0.782
2003	0.932 (0.015)	0.947 (0.005)	0.898 (0.012)	0.708 (0.018)	0.841	0.879 (0.032)	0.630 (0.066)	0.794
2004	0.948 (0.004)	0.860 (0.006)	0.820 (0.014)	0.519 (0.035)	0.720	0.465 (0.078)	NA	NA
2005	0.967 (0.004)	0.940 (0.004)	0.867 (0.009)	0.722 (0.023)	0.850	0.595 (0.040)	NA	NA
2006	0.920 (0.013)	0.956 (0.004)	0.911 (0.006)	0.808 (0.017)	0.899	0.795 (0.045)	0.813 (0.083)	0.902
2007	1.016 (0.026)	0.887 (0.009)	0.911 (0.022)	0.852 (0.030)	0.955	0.988 (0.098)	0.579 (0.059)	0.761
Mean	**0.942 (0.009)**	**0.905 (0.013)**	**0.887 (0.016)**	**0.732 (0.045)**	**0.851**	**0.751 (0.067)**	**0.720 (0.042)**	**0.846**
Excl. 2001	0.945 (0.009)	0.913 (0.011)	0.900 (0.010)	0.768 (0.029)	0.877	0.797 (0.055)	0.715 (0.048)	0.843

Table 43. Hydropower system survival estimates derived by combining empirical survival estimates from various reaches for Snake River yearling Chinook salmon and steelhead (hatchery and wild combined), 1997–2007. Standard errors in parentheses. Abbreviations: Trap–Snake River Trap; LGR–Lower Granite Dam; BON–Bonneville Dam.

	Yearling Chinook Salmon			Steelhead		
Year	Trap–LGR	LGR–BON	Trap–BON	Trap–LGR	LGR–BON	Trap–BON
1997	NA	NA	NA	0.964 (0.015)	0.474 (0.069)	0.457 (0.067)
1998	0.925 (0.009)	NA	NA	0.924 (0.009)	0.500 (0.054)	0.462 (0.050)
1999	0.940 (0.009)	0.557 (0.046)	0.524 (0.043)	0.908 (0.011)	0.440 (0.018)	0.400 (0.016)
2000	0.929 (0.014)	0.486 (0.093)	0.452 (0.087)	0.964 (0.013)	0.393 (0.034)	0.379 (0.032)
2001	0.954 (0.015)	0.279 (0.016)	0.266 (0.015)	0.911 (0.007)	0.042 (0.003)	0.038 (0.003)
2002	0.953 (0.022)	0.578 (0.060)	0.551 (0.057)	0.895 (0.015)	0.262 (0.050)	0.234 (0.045)
2003	0.993 (0.023)	0.532 (0.023)	0.528 (0.023)	0.932 (0.015)	0.309 (0.011)	0.288 (0.011)
2004	0.893 (0.009)	0.395 (0.050)	0.353 (0.045)	0.948 (0.004)	NA	NA
2005	0.919 (0.015)	0.577 (0.068)	0.530 (0.063)	0.967 (0.004)	NA	NA
2006	0.952 (0.011)	0.643 (0.017)	0.612 (0.016)	0.920 (0.013)	0.455 (0.056)	0.418 (0.052)
2007	0.943 (0.028)	0.597 (0.035)	0.563 (0.037)	1.016 (0.026)	0.364 (0.045)	0.369 (0.047)

Table 44. Estimated survival and detection probabilities for Snake River yearling Chinook salmon (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

		Survival probability		
Date at Lower Granite	Number released	Lower Monumental to Ice Harbor Dam	Ice Harbor to McNary Dam	Detection probability Ice Harbor Dam
23 Mar–29 Mar	56	0.333 (0.272)	1.524 (0.349)	0.048 (0.046)
30 Mar–05 Apr	268	0.667 (0.192)	1.604 (0.179)	0.020 (0.014)
06 Apr–12 Apr	3,134	0.784 (0.085)	1.119 (0.089)	0.021 (0.004)
13 Apr–19 Apr	9,142	0.893 (0.068)	0.956 (0.057)	0.021 (0.002)
20 Apr–26 Apr	15,956	0.954 (0.027)	0.999 (0.026)	0.066 (0.003)
27 Apr–03 May	34,853	0.983 (0.028)	0.944 (0.024)	0.042 (0.002)
04 May–10 May	33,902	0.932 (0.020)	0.922 (0.020)	0.068 (0.002)
11 May–17 May	25,878	0.864 (0.027)	0.923 (0.026)	0.043 (0.002)
18 May–24 May	1,786	0.721 (0.120)	1.108 (0.150)	0.032 (0.006)
Weighted mean*		**0.930 (0.017)**	**0.959 (0.030)**	**0.044 (0.006)**

* Weighted means of the independent estimates for weekly pooled groups (23 March –24 May), with weights inversely proportional to respective estimated relative variances.

Table 45. Estimated survival and detection probabilities for Snake River Steelhead (hatchery and wild combined) detected and released to or PIT tagged and released to the tailrace at Lower Granite Dam in 2007. Daily groups pooled weekly. Estimates based on the single–release model. Standard errors in parentheses.

		Survival probability		
Date at Lower Granite Dam	Number released	Lower Monumental to Ice Harbor Dam	Ice Harbor Dam to McNary Dam	Detection probability Ice Harbor Dam
06 Apr–12 Apr	754	0.881 (0.528)	0.965 (0.546)	0.009 (0.006)
13 Apr–19 Apr	2,717	0.837 (0.152)	0.962 (0.174)	0.025 (0.006)
20 Apr–26 Apr	4,468	0.933 (0.074)	1.050 (0.102)	0.066 (0.007)
27 Apr–03 May	6,966	0.904 (0.076)	0.988 (0.088)	0.048 (0.005)
04 May–10 May	6,484	0.828 (0.071)	0.871 (0.085)	0.064 (0.006)
11 May–17 May	6,591	1.040 (0.140)	0.805 (0.120)	0.036 (0.005)
18 May–24 May	4,479	0.838 (0.243)	0.977 (0.306)	0.024 (0.007)
Weighted mean*		**0.902 (0.026)**	**0.953 (0.033)**	**0.039 (0.007)**

* Weighted means of the independent estimates for weekly pooled groups (06 April –24 May), with weights inversely proportional to respective estimated relative variances.

Table 46. Average survival estimates (with standard errors in parentheses) from McNary Dam tailrace to Bonneville Dam tailrace for various spring–migrating salmonid stocks (hatchery and wild combined) in 2007 that were detected and returned to the tailrace at McNary Dam. For each reach, the survival estimate represents a weighted average of daily or weekly estimates (some of which are presented in other tables in this document). Dam release sites are in tailraces. Abbreviations: Sp–spring Chinook salmon; Sp–Su–spring/summer; S–F–summer/fall Chinook salmon.

		Number	Survival estimates (standard errors)		
Stock	Initial release location	released from McNary Dam	McNary to John Dam Dam	John Day to Bonneville Dam	McNary to Bonneville Dam
Snake R. Chinook (Sp–Su)	Snake River sites[a]	99,447	0.920 (0.016)	0.824 (0.043)	0.763 (0.044)
U. Columbia Chinook (S–F)	Upper Columbia sites[b]	7,223	0.891 (0.033)	0.862 (0.145)	0.761 (0.138)
U. Columbia Chinook (S–F)	Yakima River sites[c]	6,070	0.832 (0.031)	0.772 (0.220)	0.578 (0.206)
Upper Columbia Coho	Upper Columbia sites	1,204	0.811 (0.094)	1.365 (0.279)	1.142 (0.158)
Upper Columbia Coho	Yakima River sites	1,638	0.853 (0.095)	0.453 (0.094)	0.424 (0.048)
Snake River Steelhead	Snake River sites	7,057	0.988 (0.098)	0.579 (0.059)	0.524 (0.064)
Upper Columbia Steelhead	Upper Columbia sites	3,032	0.821 (0.170)	0.530 (0.091)	0.408 (0.047)

a. Snake River sites include any release sites on the Snake River or its tributaries.

b. Upper Columbia sites include any release sites on the Columbia River or its tributaries that are above the confluence with the Yakima River.

c. Yakima River sites include any release sites on the Yakima River or its tributaries.

Table 47. Percentage of PIT–tagged smolts (wild and hatchery combined) detected at Lower Monumental Dam later detected on McNary pool bird colonies, 1998-2007.

Year	Yearling Chinook salmon	Steelhead
1998	0.49	4.20
1999	0.90	4.51
2000	0.98	3.66
2001	5.59	21.06
2002	1.62	10.09
2003[a]	1.06	3.71
2004[b]	2.08	19.42
2005	1.37	9.15
2006	0.92	4.81
2007	0.80	3.59

[a] Only Crescent Island Caspian tern colony sampled.

[b] Only Crescent Island and Foundation Island colonies sampled.

FIGURES

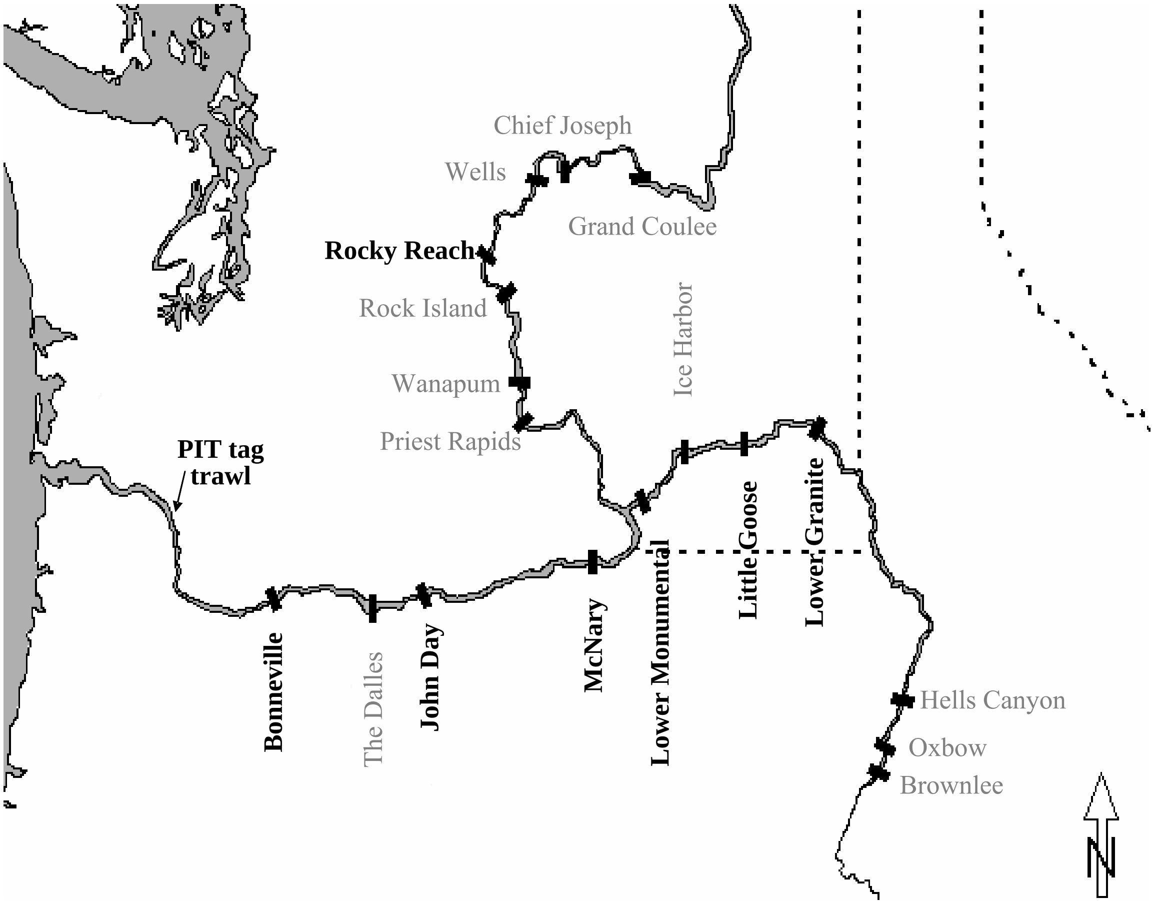

Figure 1. Study area showing sites with PIT-tag detection facilities (names in black), including dams and the PIT-tag trawl in the Columbia River estuary. Dams with names in gray do not have detection facilities.

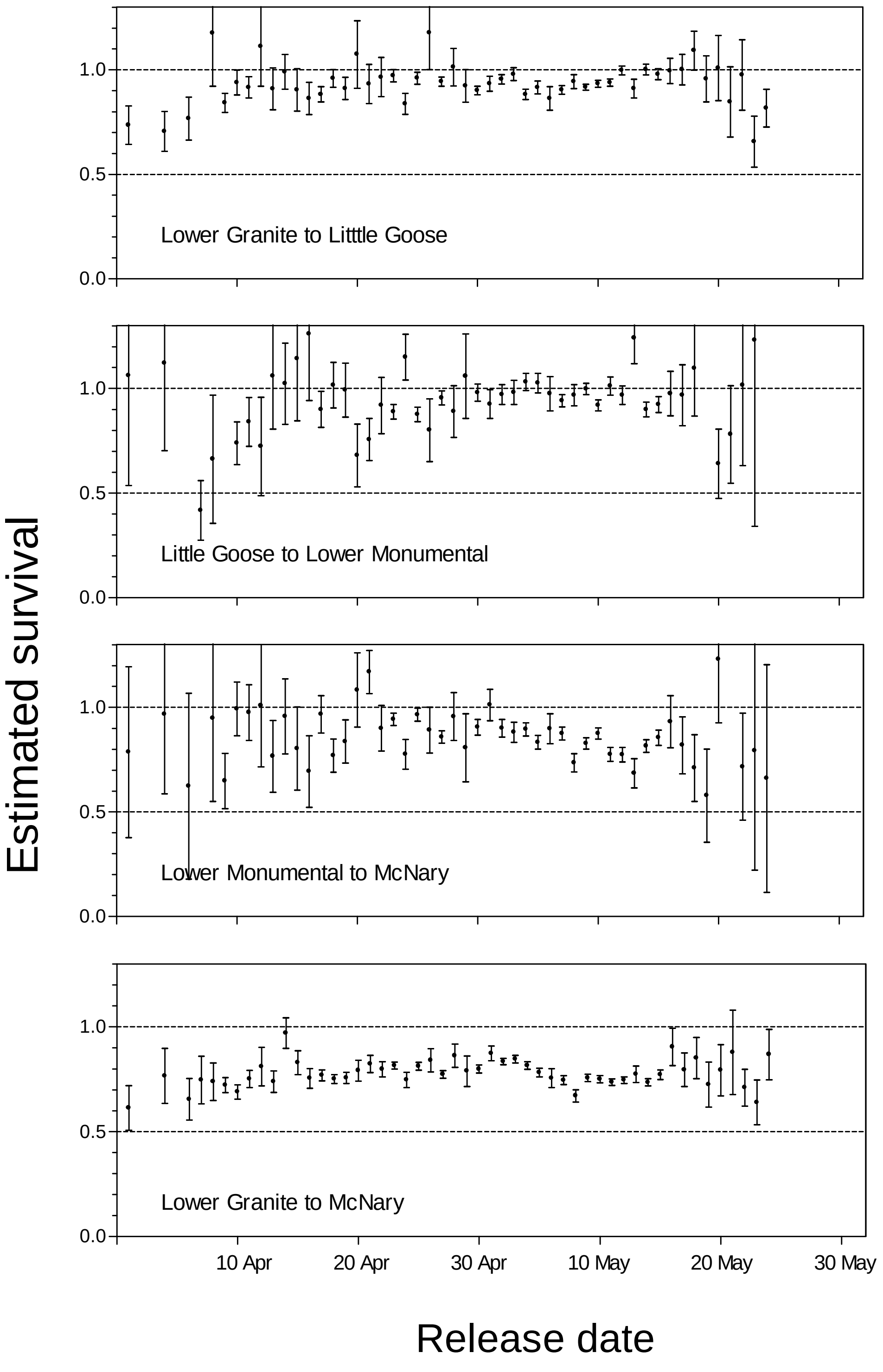

Figure 2. Estimated survival through various reaches vs. release date at Lower Granite Dam for daily release groups of Snake River yearling Chinook salmon, 2007. Bars extend one standard error above and below point estimates.

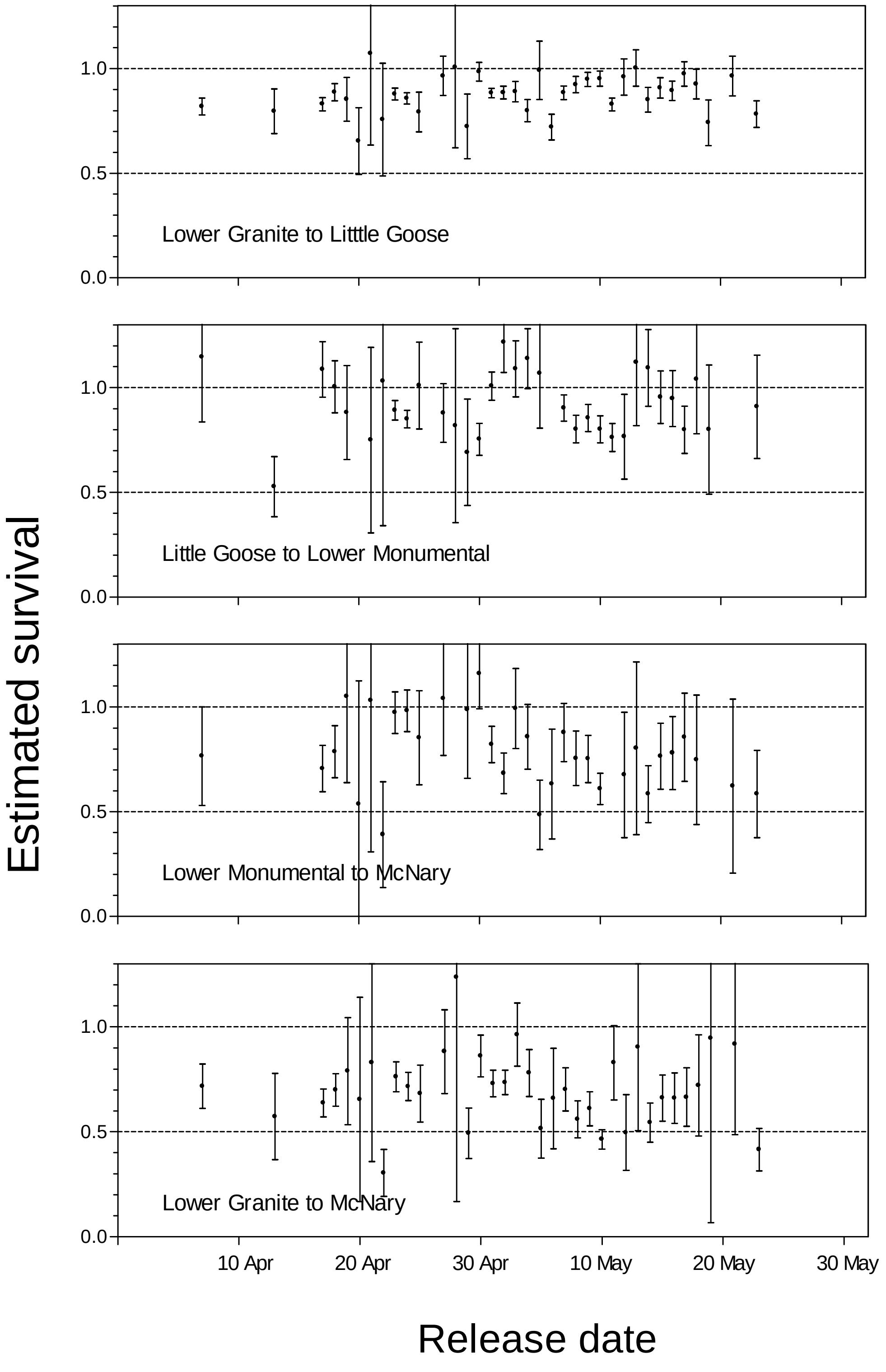

Figure 3. Estimated survival through various reaches versus release date at Lower Granite Dam for daily release groups of Snake River steelhead, 2007. Bars extend one standard error above and below point estimates.

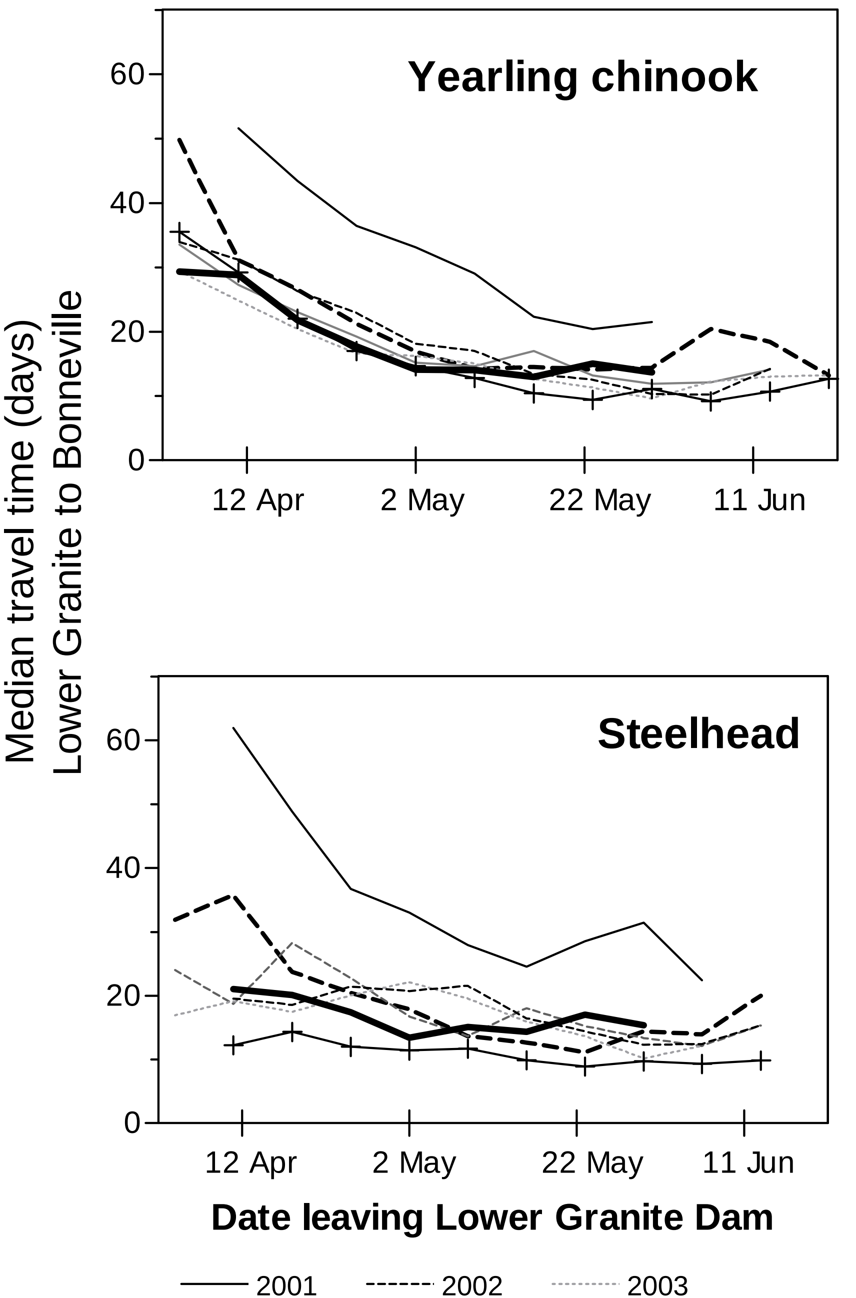

Figure 4. Median travel time (days) from Lower Granite Dam to Bonneville Dam for weekly release groups of Snake River yearling Chinook salmon and steelhead from Lower Granite Dam, 2001-2007.

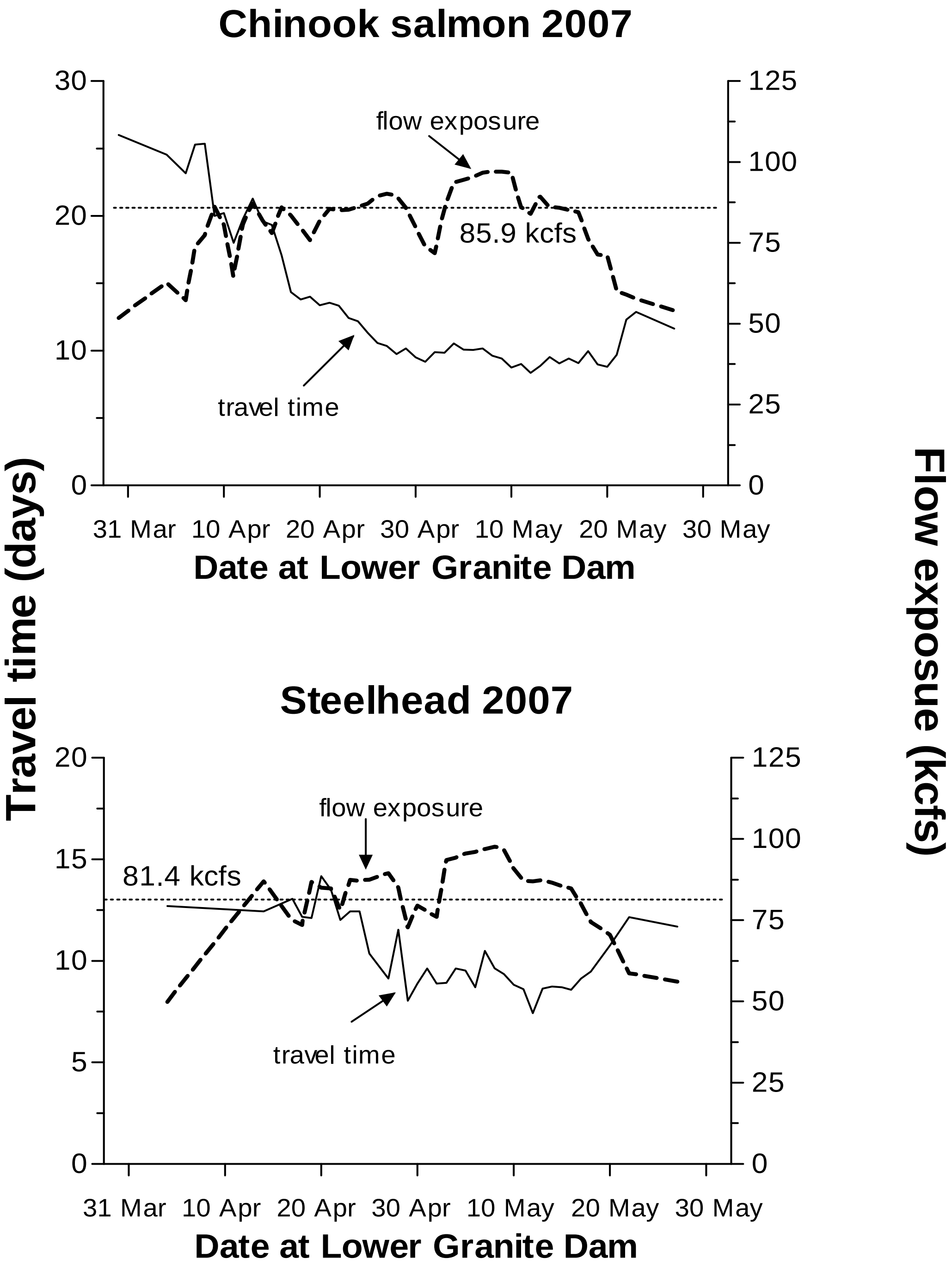

Figure 5. Travel time (days) for yearling Chinook salmon and steelhead from Lower Granite Dam to McNary Dam and index of flow exposure at Lower Granite Dam (kcfs) for daily groups of PIT-tagged fish during 2007. Dashed horizontal lines represent the annual average flow exposure index, weighted by the number of PIT-tagged fish in each group.

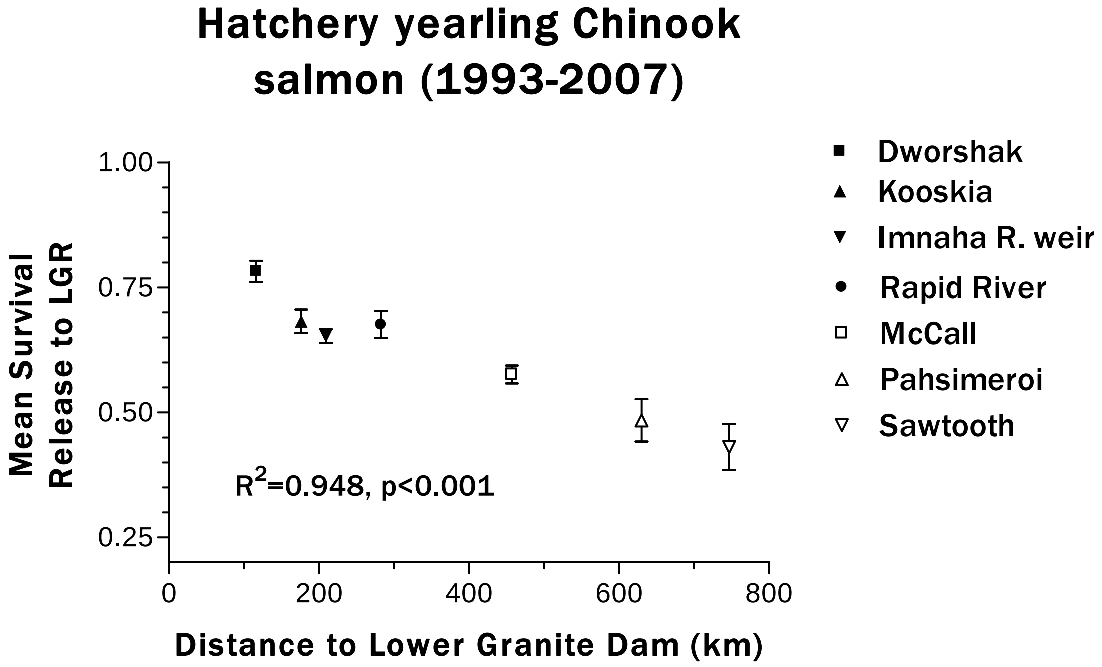

Figure 6. Estimated survival with standard errors from release at Snake River Basin hatcheries to Lower Granite Dam tailrace, 1993-2007 vs distance (km) to Lower Granite Dam. The correlation between survival and migration distance is also shown.

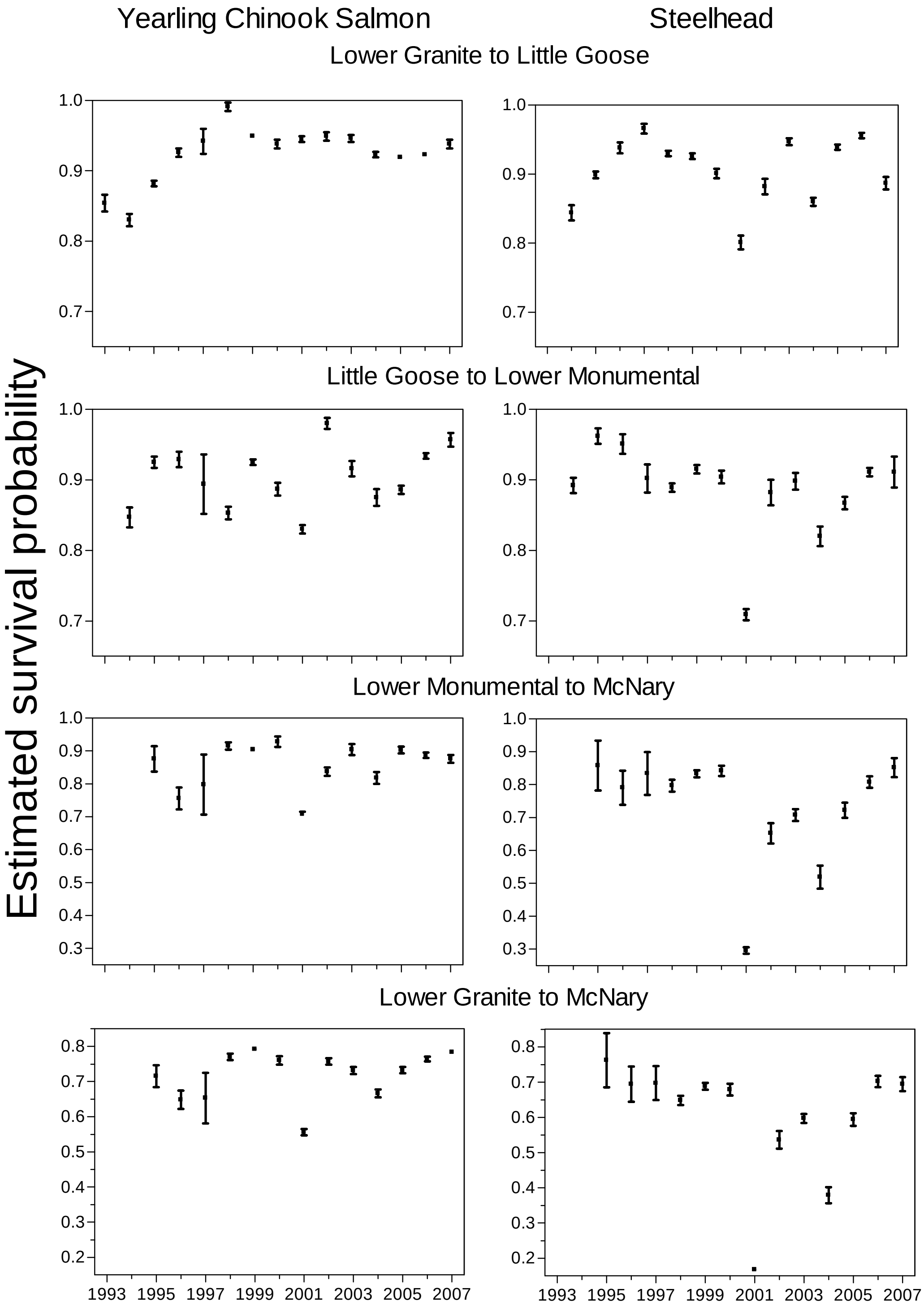

Figure 7. Annual average survival estimates for PIT-tagged yearling Chinook salmon and steelhead through Snake River reaches, 1993-2007. Estimates are from tailrace to tailrace with standard errors.

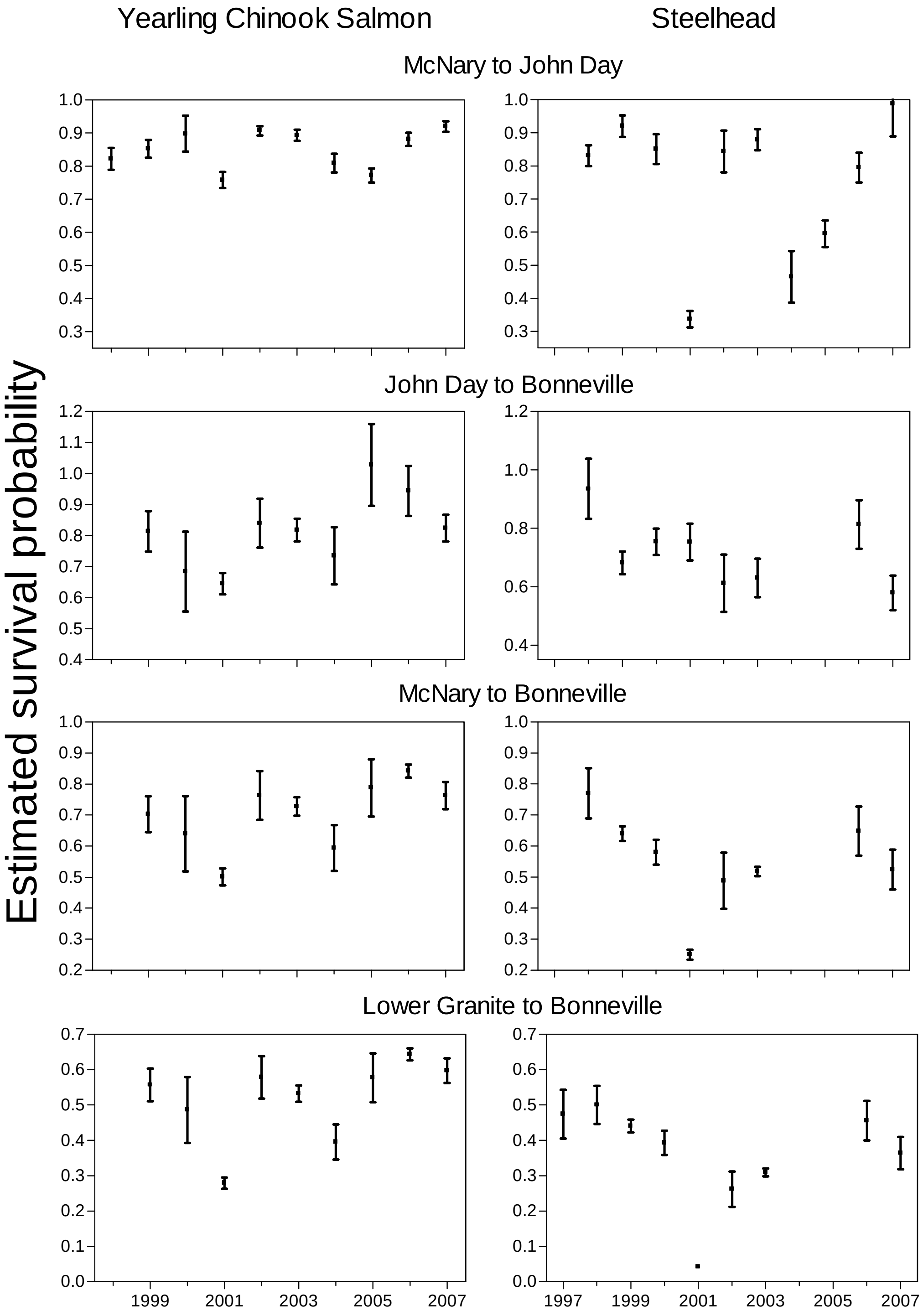

Figure 8. Annual average survival estimates for PIT-tagged Snake River yearling Chinook salmon and steelhead through Columbia River reaches and from Lower Granite Dam to Bonneville Dam, 1993-2007. Estimates are from tailrace to tailrace with standard errors.

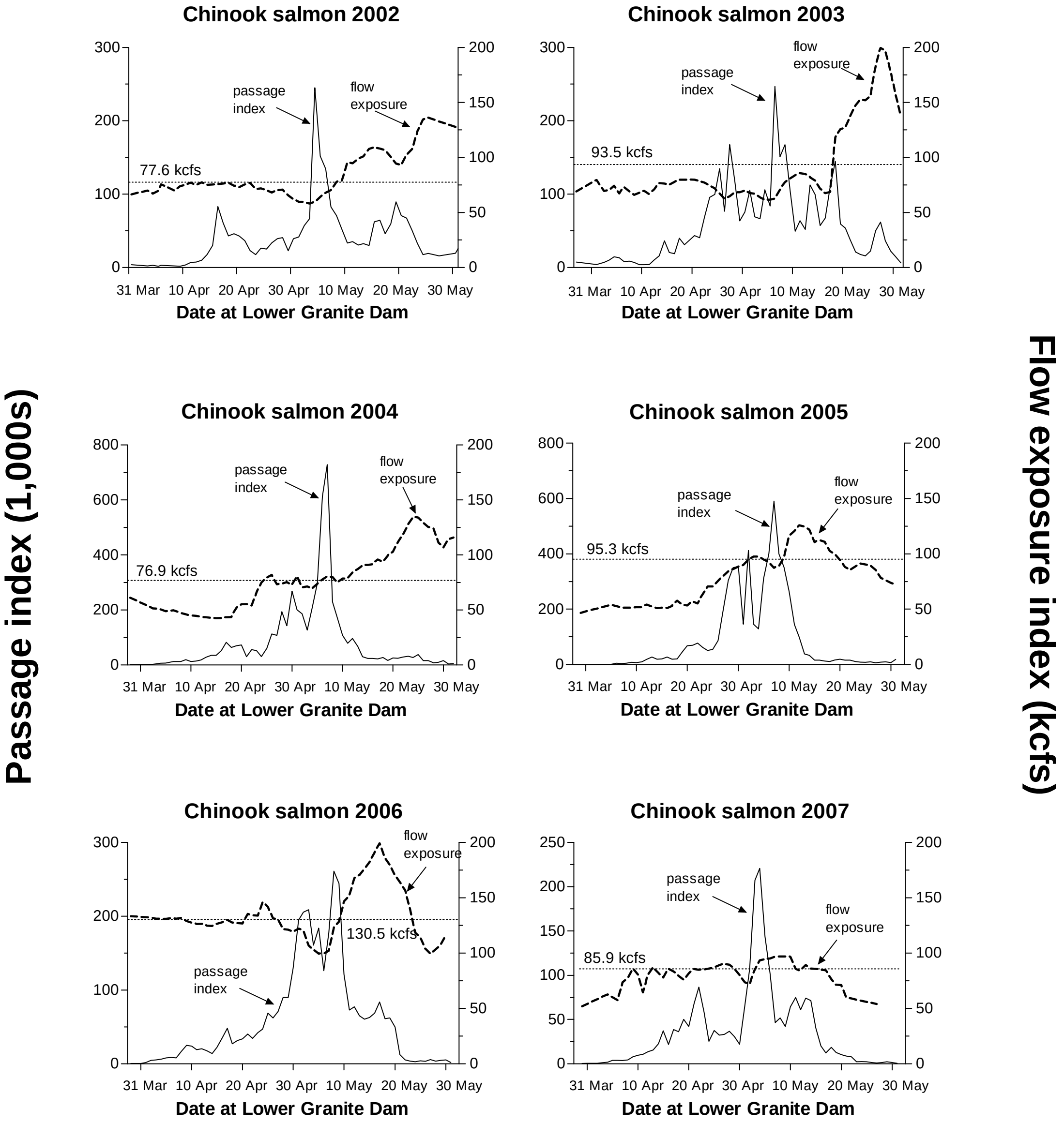

Figure 9. Passage index (per 1,000 fish) and flow exposure index (kcfs) for daily groups of PIT-tagged yearling Chinook salmon passing Lower Granite Dam from 2002 through 2007. Dashed horizontal lines represent the annual average flow exposure index, weighted by the number of PIT-tagged fish in each group.

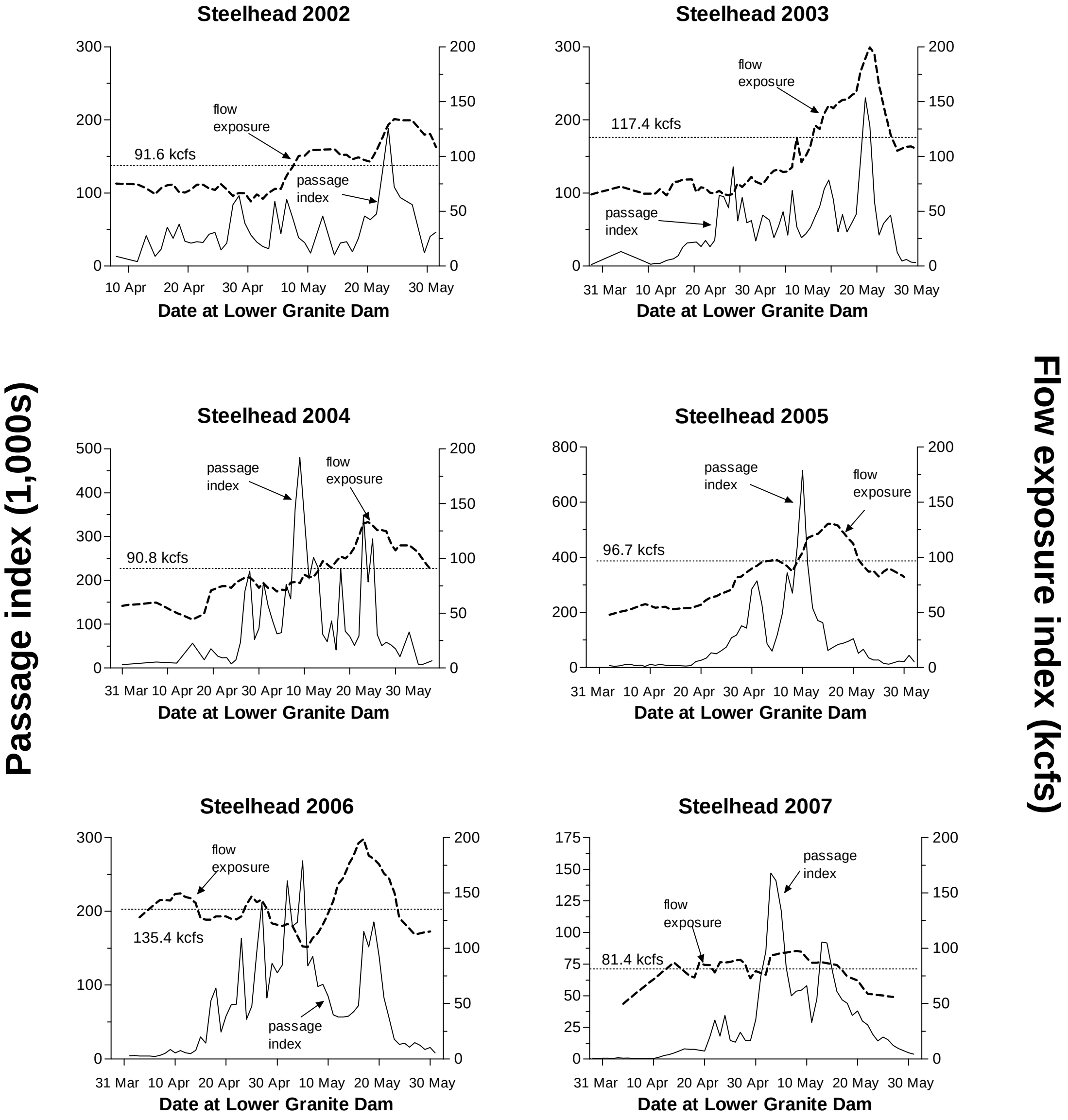

Figure 10. Passage index (per 1,000 fish) and flow exposure index (kcfs) for daily groups of PIT-tagged steelhead passing Lower Granite Dam from 2002 through 2007. Dashed horizontal lines represent the annual average flow exposure index, weighted by the number of PIT-tagged fish in each group.

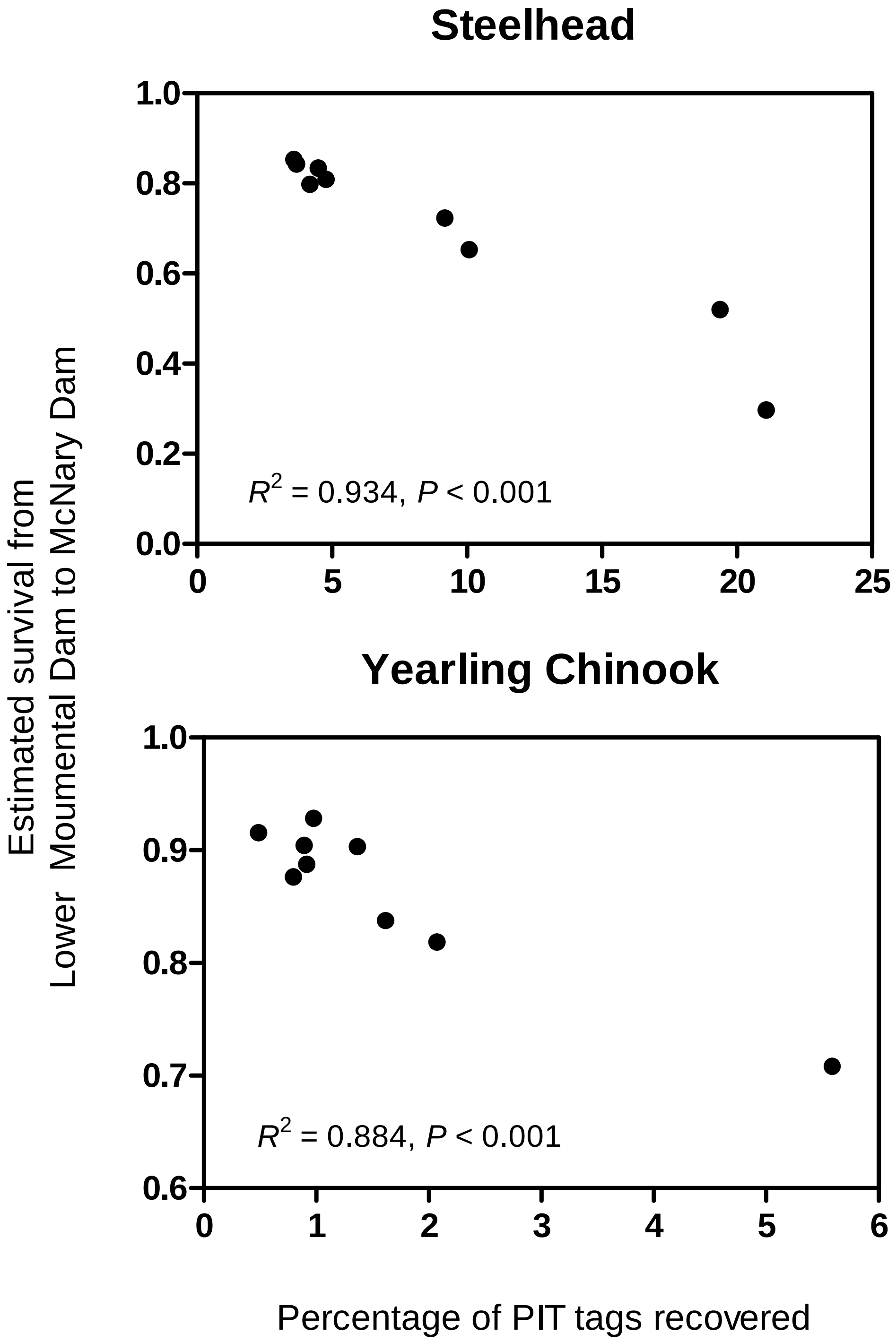

Figure 11. Estimated survival between Lower Monumental and McNary Dams versus percentage of Lower Monumental Dam-detected PIT tags recovered on bird colonies, 1998-2007 (excluding 2003, which had incomplete recovery).

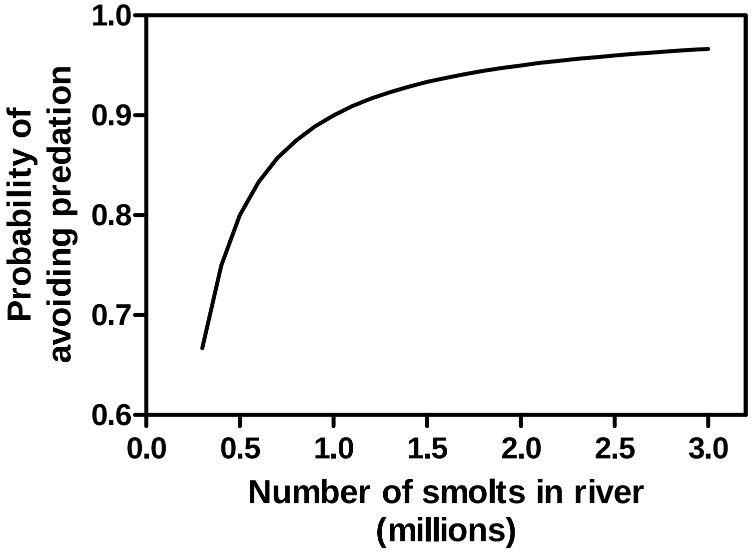

Figure 12. Idealized illustration of effect of total smolt population size on probability of avoiding predation. Assumes constant take of 100,000 smolts over range of population sizes.

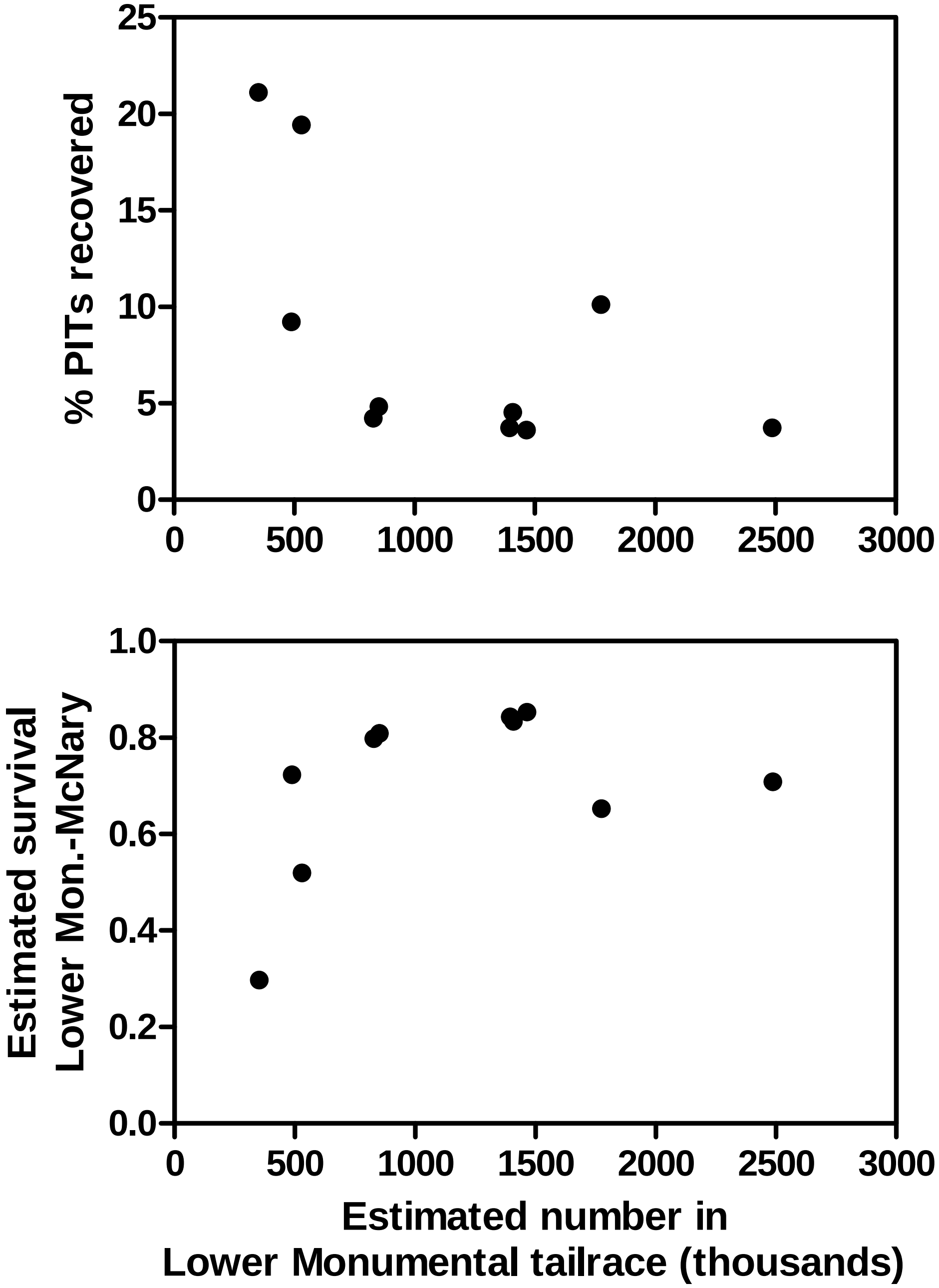

Figure 13. Relationship between percentage of Lower Monumental Dam-detected PIT tags (steelhead) recovered on bird colonies (top) and estimated overall steelhead survival between Lower Monumental and McNary Dams versus estimated number of steelhead in the tailrace of Lower Monumental Dam, 1998-2007.

APPENDIX

Tests of Model Assumptions

Background

Using the Cormack-Jolly-Seber (CJS), or single-release (SR) model, the passage of a single PIT-tagged salmonid through the hydropower system is modeled as a sequence of events. Examples of such events are survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam, and detection at Little Goose Dam. Each event has an associated probability of occurrence (technically, these probabilities are "conditional", as they are defined only if a certain condition is met, for example "probability of detection at Little Goose Dam *given* that the fish survived to Little Goose Dam").

The detection history, then, is the record of the outcomes of the series of events. (The detection history is an imperfect record of outcomes; if the history ends with one or more "zeroes," we cannot distinguish mortality from survival without detection). The SR Model represents detection history data for a group of tagged fish as a multinomial distribution; each multinomial cell probability (detection history probability) is a function of the underlying survival and detection event probabilities. Three key assumptions lead to the multinomial cell probabilities used in the SR Model:

A1) Fish in a single group of tagged fish have common event probabilities (each conditional detection or survival probability is common to all fish in the group).
A2) Event probabilities for each individual fish are independent from those for all other fish.
A3) Each event probability for an individual fish is conditionally independent from all other probabilities.

For a migrating PIT-tagged fish, assumption A3 implies that detection at any particular dam does not affect (or give information regarding) probabilities of subsequent events. For the group as a whole, this means that detected and nondetected fish at a given dam have the same probability of survival in downstream reaches, and have the same conditional probability of detection at downstream dams.

Methods

We used the methods presented by Burnham et al. (1997; pp 71-77) to assess the goodness-of-fit of the SR model to observed detection history data. In these tests, we compiled a series of contingency tables from detection history data for each group of tagged fish, and used χ^2 tests to identify systematic deviations from what was expected if the assumptions were met. We applied the tests to weekly groups of yearling Chinook salmon and steelhead (hatchery and wild combined) leaving Lower Granite and McNary dams (Snake River-origin fish only) in 2007 (i.e., the fish used for survival estimates reported in Tables 1, 2, 10, and 11).

If goodness-of-fit tests for a series of release groups resulted in more significant tests than expected by chance, we compared observed and expected tables to determine the nature of the violation. While consistent patterns of violations in the assumption testing do not unequivocally pinpoint the cause of the violation, they can be suggestive, and some hypothesized causes may be ruled out.

Potential causes of assumption violations include inherent differences between individuals in survival or detectability (e.g., propensity to be guided by bypass screens); differential mortality between the passage route that is monitored for PIT tags (juvenile collection system) and those that are not (spillways and turbines); behavioral responses to bypass and detection; and differences in passage timing for detected and non-detected fish if such differences result in exposure to different conditions downstream. Using detection information, inherent differences and behavioral responses are virtually indistinguishable. Conceptually, we make the distinction that inherent traits are those that characterized the fish before any hydrosystem experience, while behavioral responses occur as a result of particular hydrosystem experiences. For example, developing a preference for a particular passage route is a behavioral response, while size-related differences in passage-route selection are inherent. Of course, response to passage experience may also depend on inherent characteristics.

To describe each test we conducted, we follow the nomenclature of Burnham et al. (1987). For release groups from Lower Granite Dam, we analyzed 4-digit detection histories indicating status at Little Goose, Lower Monumental, and McNary Dams, and the final digit for detection anywhere below McNary Dam.

The first test for Lower Granite Dam groups was "Test 2.C2," which is based on the contingency table:

Test 2.C2	First site detected below LGO		
df = 2	LMN	MCN	JDA or below
Not detected at LGO	n_{11}	n_{12}	n_{13}
Detected at LGO	n_{21}	n_{22}	n_{23}

In this table, all fish that were detected somewhere below Little Goose Dam are cross-classified according to their history at Little Goose Dam and according to their first detection site below Little Goose Dam (e.g., n_{11} is the number of fish not detected at Little Goose Dam that were first detected downstream at Lower Monumental Dam). If all assumptions were met, the counts for fish detected at LGO should be in constant proportion to those for fish not detected (i.e., n_{11}/n_{21}, n_{12}/n_{22}, and n_{13}/n_{23} should be equal). Because this table counts only fish detected below LGO (i.e., all fish survived LGO passage), differential *direct* mortality for fish detected and not detected at LGO will not cause violations of Test 2.C2 by itself. However, differential *indirect* mortality related to LGO passage could cause violations if differences are not expressed until fish are below LMO. Behavioral response to guidance at LGO could cause violations of Test 2.C2: if fish detected at LGO become more likely to be detected downstream, then they will tend to have more first downstream detections at LMO. If detected fish at LGO become less likely to be detected downstream, then they will have fewer first detections at LMO. Inherent differences among fish could also cause violations of Test 2.C2, and would be difficult to distinguish from behavioral responses.

The second test for Lower Granite Dam groups was Test 2.C3, based on the contingency table:

Test 2.C3	First site detected below LMN	
df = 1	MCN	JDA or below
Not detected at LMN	n_{11}	n_{12}
Detected at LMN	n_{21}	n_{22}

This table and corresponding implications are similar to Test 2.C2. All fish that were detected somewhere below LMN are cross-classified according to their history at LMN and according to their first detection site below LMN. If the respective counts for fish first detected at MCN are not in the same proportion as those first detected at JDA or below, it could indicate behavioral response to detection at LMN, inherent differences in detectability (i.e., guidability) among tagged fish in the group, or long-term differential mortality caused by different passage routes at LMN.

The next series of tests for Lower Granite Dam groups is called Test 3. The first in the series is called Test 3.SR3, based on the contingency table:

Test 3.SR3	Detected again at MCN or below?	
df = 1	YES	NO
Detected at LMN, not detected at LGO	n_{11}	n_{12}
Detected at LMN, detected at LGO	n_{21}	n_{22}

In this table, all fish detected at LMN are cross-classified according to their status at LGO and whether or not they were detected again downstream from LMN. As with the Test 2 series, differential mortality in different passage routes at LGO will not be detected by this test if all the mortality is expressed before the fish arrive at LMN. Differences in mortality expressed below MCN could cause violations, however, as could behavioral responses (possibly somewhat harder to detect because of the conditioning on detection at LMN) or inherent differences in detectability or survival between fish detected at LGO and those not detected there.

The second test in the Test 3 series is Test 3.Sm3, based on the contingency table:

Test 3.Sm3	Site first detected below LMN	
df = 1	MCN	JDA
Detected at LMN, not detected at LGO	n_{11}	n_{12}
Detected at LMN, detected at LGO	n_{21}	n_{22}

This test is sensitive to the same sorts of differences as Test 3.SR3, but tends to have somewhat less power. Because the table classifies only fish detected somewhere below LMN, it is not sensitive to differences in survival between LMN and MCN.

The final test for Lower Granite Dam groups is Test 3.SR4, based on the contingency table:

Test 3.SR4	Detected at JDA or below?	
df = 1	Yes	No
Detected at MCN, not detected previously	n_{11}	n_{12}
Detected at MCN, also detected previously	n_{21}	n_{22}

This table classifies all fish detected at MCN according to whether they had been detected at least once at LGO and LMN and whether they were detected again below MCN. A significant test indicates that some below-MCN parameter(s) differ between fish detected above MCN and those not detected. The cause of such an assumption violation could be differences in indirect survival associated with detection at LGO and/or LMN (mortality expressed between MCN and the estuary PIT-trawl), inherent differences in survival or detection probabilities, or behavioral responses.

We did not include any contingency table tests when any of the expected cells of the table were less than 1.0, as the test statistic does not sufficiently approximate the asymptotic χ^2 distribution in these cases. (For Test 2.C2, when the expected values in the "LMN" and "MCN" columns were all greater than 1.0, but one or two of the expected values in the "JDA or below" column were less than 1.0, we collapsed the "MCN" and "JDA or below" and calculated a one-degree-of-freedom test of the resulting 2-by-2 table). We combined the two test statistics in the Test 2 series and the three in the Test 3 series and then all tests together in a single overall χ^2 test statistic.

For release groups from McNary Dam, we analyzed 3-digit detection histories indicating status at John Day Dam, Bonneville Dam, and the estuary PIT-trawl.

Only two tests are possible for 3-digit detection histories. The first of these was Test 2.C2, based on the contingency table:

Test 2.C2	First site detected below JDA	
df = 1	BON	Trawl
Not detected at JDA	n_{11}	n_{12}
Detected at JDA	n_{21}	n_{22}

and the second is Test 2.SR3, based on the contingency table:

Test 3.SR3	Detected at Trawl	
df = 1	Yes	No
Detected at BON,	n_{11}	n_{12}
Detected at BON,	n_{21}	n_{22}

These tests are analogous to Tests 2.C3 and 3.SR4, respectively, for the Lower Granite Dam release groups. Potential causes of violations of the tests for McNary Dam groups are the same as those for Lower Granite Dam groups.

Results

For weekly Lower Granite Dam release groups in 2007 there were more significant ($\alpha = 0.05$) tests than expected by chance alone for both yearling Chinook salmon and steelhead (Appendix Table 1). There were 10 weekly groups of yearling Chinook salmon. For these, the overall sum of the χ^2 test statistics was significant 4 times. For 8 steelhead groups, the overall test was significant 2 times. Counting all individual component tests (i.e., 2.C2, 3.SR3, etc.), 12 tests of 41 (29%) were significant for yearling Chinook salmon and 5 of 36 (14%) were significant for steelhead (Appendix Tables 1-3). Significant tests occurred with about equal frequency.

We diagnosed the patterns in the contingency tables that led to significant tests and results were similar to those we reported in past years: in 14 of the 17 significant cases (individual component tests) for Lower Granite Dam groups of yearling Chinook salmon and steelhead, and in all of the most highly significant cases, there was evidence that fish previously detected were more likely to be detected again at downstream dams.

Significant contingency table test results were far less common (1 significant test of 21) for weekly groups from McNary Dam (Appendix Tables 4-6).

Discussion

We believe that inherent differences in detectability (guidability) of fish within a release group are the most likely cause of the patterns we observed in the contingency table tests in 2007, as in previous years. Zabel et al. (2002) provided evidence of inherent differences related to length of fish at tagging, and similar observations were made in 2007 data. Fish size probably does not explain all inherent differences, but it appears to explain some. The relationship between length at tagging and detection probability at Little Goose Dam, the first dam encountered after release by fish in these data sets (all fish in the data set were detected at Lower Granite Dam; Little Goose Dam is the first encountered after leaving LGR), suggests that the heterogeneity is inherent, and not a behavioral response.

As in previous years (Zabel et al. 2002), results in 2007 lead us to conclude, as did Burnham et al. (1987), that a reasonable amount of heterogeneity in the survival and detection process did not seriously affect the performance of estimators of survival.

Appendix Table 1. Number of tests of goodness of fit to the single release model conducted for weekly release groups of yearling Chinook salmon and steelhead (hatchery and wild combined) from Lower Granite Dam, and number of significant ($\alpha = 0.05$) test results, 2007.

	Test 2.C2		Test 2.C3		Test 3.SR3		Test 3.Sm3		Test 3.SR4		Test 2 sum		Test 3 sum		**Test 2 + 3**	
Species	No.	sig.	No.	sig.	No.	sig.	No.	sig.	No.	sig.	No.	sig.	No.	sig.	**No.**	**sig.**
Chinook	9	3	8	1	7	2	7	3	10	3	9	3	10	4	**10**	**4**
Steelhead	8	1	7	1	7	2	7	0	7	1	8	1	7	2	**8**	**2**
Total	17	4	15	2	14	4	14	3	17	4	17	4	17	6	**18**	**6**

Appendix Table 2. Results of tests of goodness of fit to the single release model for release groups of yearling Chinook salmon (hatchery and wild) from Lower Granite to McNary Dam in 2007.

	Overall		Test 2		Test 2.C2		Test 2.C3	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
23 Mar–29 Mar	2.64	0.45	2.24	0.33	2.24	0.33	NA	NA
30 Mar–05 Apr	7.49	0.19	5.77	0.12	2.57	0.28	3.20	0.07
06 Apr–12 Apr	10.47	0.11	0.15	0.99	0.04	0.98	0.11	0.74
13 Apr–19 Apr	7.41	0.29	2.08	0.56	0.75	0.69	1.33	0.25
20 Apr–26 Apr	41.77	<0.001	37.40	<0.001	32.94	<0.001	4.46	0.04
27 Apr–03 May	98.56	<0.001	86.37	<0.001	86.35	<0.001	0.03	0.87
04 May–10 May	77.28	<0.001	52.78	<0.001	49.17	<0.001	3.61	0.06
11 May–17 May	13.72	0.03	3.24	0.36	2.89	0.24	0.35	0.55
18 May–24 May	9.51	0.15	5.30	0.15	5.18	0.08	0.12	0.73
25 May–31 May	0.002	0.97	NA	NA	NA	NA	NA	NA
Total (d.f.)	268.9 (51)	<0.001	195.3 (26)	<0.001	182.1 (18)	<0.001	13.2 (8)	0.11

Appendix Table 2. Continued.

	Test 3		Test 3.SR3		Test 3.Sm3		Test 3.SR4	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
23 Mar–29 Mar	0.40	0.53	NA	NA	NA	NA	0.40	0.53
30 Mar–05 Apr	1.72	0.42	NA	NA	NA	NA	1.72	0.19
06 Apr–12 Apr	10.32	0.02	3.21	0.07	0.01	0.92	7.10	0.008
13 Apr–19 Apr	5.33	0.15	0.35	0.55	4.72	0.03	0.26	0.61
20 Apr–26 Apr	4.37	0.22	1.74	0.19	0.10	0.75	2.53	0.11
27 Apr–03 May	12.19	0.007	0.05	0.83	10.18	0.001	1.96	0.16
04 May–10 May	24.50	<0.001	8.27	0.004	6.72	0.01	9.52	0.002
11 May–17 May	10.47	<0.001	4.02	0.045	1.86	0.17	4.59	0.03
18 May–24 May	4.20	<0.001	1.11	0.29	0.49	0.48	2.60	0.11
25 May–31 May	0.00	0.97	NA	NA	NA	NA	0.00	0.97
Total (d.f.)	73.5 (25)	<0.001	18.7 (8)	0.016	24.1 (7)	0.001	30.7 (10)	0.001

Appendix Table 3. Results of tests of goodness of fit to the single release model for release groups of juvenile steelhead (hatchery and wild) from Lower Granite to McNary Dam in 2007.

	Overall		Test 2		Test 2.C2		Test 2.C3	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
06 Apr–12 Apr	2.88	0.82	1.66	0.65	1.13	0.57	0.53	0.47
13 Apr–19 Apr	2.82	0.83	2.25	0.52	2.16	0.34	0.09	0.77
20 Apr–26 Apr	11.57	0.07	3.53	0.32	1.33	0.51	2.19	0.14
27 Apr–03 May	19.96	0.003	0.10	0.99	0.07	0.97	0.03	0.85
04 May–10 May	20.26	0.002	16.58	0.001	6.43	0.04	10.15	0.001
11 May–17 May	6.35	0.39	1.53	0.68	1.32	0.52	0.21	0.65
18 May–24 May	4.33	0.63	1.40	0.71	0.76	0.69	0.65	0.42
25 May–31 May	1.17	0.28	1.17	0.28	1.17	0.28	NA	NA
Total (d.f.)	69.3 (43)	0.007	28.2 (22)	0.17	14.4 (15)	0.50	13.8 (7)	0.054

Appendix Table 3. Continued.

	Test 3		Test 3.SR3		Test 3.Sm3		Test 3.SR4	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
06 Apr–12 Apr	1.22	0.75	0.01	0.91	0.90	0.34	0.31	0.58
13 Apr–19 Apr	0.57	0.90	0.45	0.50	0.08	0.78	0.04	0.84
20 Apr–26 Apr	8.05	0.045	3.86	0.049	1.02	0.31	3.16	0.08
27 Apr–03 May	19.86	<0.001	11.81	0.001	0.38	0.54	7.67	0.01
04 May–10 May	3.67	0.30	0.24	0.63	2.31	0.13	1.13	0.29
11 May–17 May	4.82	0.19	1.75	0.19	0.96	0.33	2.11	0.15
18 May–24 May	2.93	0.40	0.14	0.71	2.36	0.13	0.43	0.51
25 May–31 May	NA	NA	NA	NA	NA	NA	NA	NA
Total (d.f.)	41.1 (21)	0.005	18.3 (7)	0.011	8.0 (7)	0.33	14.8 (7)	0.038

Appendix Table 4. Number of tests of goodness of fit to the single release model conducted for weekly release groups of yearling Chinook salmon and steelhead (hatchery and wild combined) from McNary Dam, and number of significant (a = 0.05) test results, 2007.

	Test 2.C2		Test 3.SR3		Test 2 + 3	
Species	No.	sig.	No.	sig.	No.	sig.
Chinook	8	0	6	1	8	0
Steelhead	4	0	3	0	4	0
Total	12	0	9	1	12	0

Appendix Table 5. Results of tests of goodness of fit to the single release model for release groups of yearling Chinook salmon (hatchery and wild) from McNary to Bonneville Dam in 2007.

	Overall		Test 2.C2		Test 3.SR3	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
20 Apr–26 Apr	4.17	0.13	1.82	0.18	2.35	0.13
27 Apr–03 May	2.29	0.32	1.12	0.29	1.18	0.28
04 May–10 May	0.04	0.98	0.04	0.83	0.00	0.98
11 May–17 May	4.68	0.10	0.03	0.86	4.64	0.03
18 May–24 May	2.46	0.29	1.87	0.17	0.59	0.44
25 May–31 May	0.15	0.93	0.00	0.98	0.15	0.70
01 Jun–07 Jun	0.78	0.38	0.78	0.38	NA	NA
08 Jun–14 Jun	0.07	0.80	0.07	0.80	NA	NA
Total (d.f.)	14.6 (14)	0.40	5.7 (8)	0.68	8.9 (6)	0.18

Appendix Table 6. Results of tests of goodness of fit to the single release model for release groups of steelhead (hatchery and wild) from McNary to Bonneville Dam in 2007.

	Overall		Test 2.C2		Test 3.SR3	
Release	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
20 Apr–26 Apr	NA	NA	NA	NA	NA	NA
27 Apr–03 May	2.42	0.30	0.75	0.39	1.67	0.20
04 May–10 May	2.53	0.28	2.26	0.13	0.27	0.60
11 May–17 May	1.17	0.56	1.09	0.30	0.08	0.78
18 May–24 May	1.05	0.31	1.05	0.31	NA	NA
25 May–31 May	NA	NA	NA	NA	NA	NA
Total (d.f.)	7.17 (7)	0.41	5.16 (4)	0.27	2.02 (3)	0.57

EXHIBIT 4

DECLARATION OF RICHARD W. ZABEL

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SURVIVAL AND SELECTION OF MIGRATING SALMON FROM CAPTURE–RECAPTURE MODELS WITH INDIVIDUAL TRAITS

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Abstract. Capture–recapture studies are powerful tools for studying animal population dynamics, providing information on population abundance, survival rates, population growth rates, and selection for phenotypic traits. In these studies, the probability of observing a tagged individual reflects both the probability of the individual surviving to the time of recapture and the probability of recapturing an animal, given that it is alive. If both of these probabilities are related to the same phenotypic trait, it can be difficult to distinguish effects on survival probabilities from effects on recapture probabilities. However, when animals are individually tagged and have multiple opportunities for recapture, we can properly partition observed trait-related variability into survival and recapture components. We present an overview of capture–recapture models that incorporate individual variability and develop methods to incorporate results from these models into estimates of population survival and selection for phenotypic traits. We conducted a series of simulations to understand the performance of these estimators and to assess the consequences of ignoring individual variability when it exists. In addition, we analyzed a large data set of $>$153 000 juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) of known length that were PIT-tagged during their seaward migration. Both our simulations and the case study indicated that the ability to precisely estimate selection for phenotypic traits was greatly compromised when differential recapture probabilities were ignored. Estimates of population survival, however, were far more robust. In the chinook salmon and steelhead study, we consistently found that smaller fish had a greater probability of recapture. We also uncovered length-related survival relationships in over half of the release group/river segment combinations that we observed, but we found both positive and negative relationships between length and survival probability. These results have important implications for the management of salmonid populations.

Key words: behavioral variability; capture–recapture; chinook salmon; individual covariates; mark–recapture; model averaging; Oncorhynchus mykiss; Oncorhynchus tshawytscha; *PIT tag; selection; steelhead; survival.*

INTRODUCTION

Animal populations typically exhibit behavioral heterogeneity, and this can confound efforts to understand population dynamics. Capture–recapture experiments, for example, yield information on population abundance, life-stage-specific survival, population growth rate, and selection for phenotypic traits (Seber and Schwarz 2002), but behavioral variability arising from genetic heterogeneity, variability in developmental level, or phenotypic plasticity can lead to differential probabilities of recapture within populations. Studies that ignore differential recapture probabilities can produce biased estimates of population abundance (MacKenzie and Kendall 2002), selection coefficients (Endler 1986), or survival (Lebreton et al. 1992). Of particular concern is when a phenotypic trait is related to both recapture and survival probabilities, because studies that only have one opportunity to recapture animals cannot distinguish between differential recapture rates and selection. For example, Janzen et al. (2000) obtained different estimates of size-based selection of slider turtles depending on which assumptions they made about non-observed individuals. Thus, understanding the behavioral variability within populations is often critical for estimating population-level attributes such as life-stage-specific survival rates, information that is crucial for managing at-risk populations.

To address this, recent advances in capture–recapture methodology have focused on incorporating individually varying traits into capture–recapture models (Pol-

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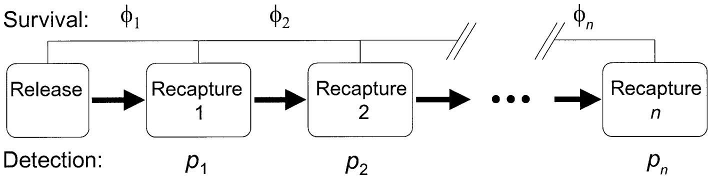

FIG. 1. Schematic diagram of the recapture and survival processes. Note that we cannot estimate ϕ_n and p_n separately, so they are combined such that $\beta = \phi_n p_n$.

lock 2002). When individuals are uniquely identifiable and have multiple opportunities for recapture, it is possible to distinguish differential effects on recapture and survival probabilities. Also, advances in tagging techniques have enhanced our ability to monitor populations. A notable example is the passive integrated transponder (PIT) tag (Prentice et al. 1990*a*), which lends itself to multiple recaptures of uniquely tagged individuals. Tagging animals with the small (12-mm) tag is relatively benign because ''recapturing'' individuals often does not require handling: many PIT-tag experiments deploy automatic detectors that record the presence of individuals in both natural habitats (Roussel et al. 2000) and man-made structures (Prentice et al. 1990*b*). Worldwide, researchers have used PIT tags to study taxa as wide-ranging as sea urchins (Hagen 1996) and manatees (Wright et al. 1998). In the Columbia River Basin, hundreds of thousands of juvenile salmonids (*Oncorhynchus* spp.) are PIT-tagged annually and have multiple opportunities for detection as they pass hydroelectric dams during their seaward migration.

Here we examine the importance of incorporating individually varying recapture rates into the estimation of population survival and selection for phenotypic traits. First we present an overview of the underlying capture–recapture models and discuss how to estimate model parameters for a fully specified model. We then develop methods to use results from these models to estimate population-level parameters (survival and selection coefficients), taking into account individually varying survival and recapture probabilities. We conduct a series of simulations to address the following two questions: (1) how well do our estimates of population parameters perform and (2) what are the consequences of ignoring individual variability when it is present? Next, we turn our attention to natural populations where underlying relationships are unknown. Therefore, we first present methods for selecting the best performing models among a suite of alternative models. Finally, as a case study, we analyze an extensive data set based on PIT-tagged juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*), both listed as threatened under the U.S. Endangered Species Act. We examine the effect of length at tagging on the probabilities of survival and recapture during migration. In analyzing these data, we also address the physiological and behavioral mechanisms that lead to length-based recapture probabilities, and the management implications of our results.

METHODS

Survival and selection estimation using capture–recapture and individual traits

In typical capture–recapture experiments, individuals are marked and released in a group and have several opportunities for recapture (at least two are necessary to estimate survival). The recapture opportunities are separated temporally or spatially, such as along a migration route. Based on recapture information, capture histories are constructed for each individual. The capture history reflects whether an individual was recaptured (1), not recaptured (0), or removed (-1) for each recapture opportunity. To conduct the type of analysis that we present here, individuals are uniquely tagged and are distinguishable by a measurable trait (or traits) important for determining their behavior and survival.

Two underlying processes determine whether individuals are recaptured: probability of survival between two recapture sites and probability of recapturing an individual, given that it is alive. Thus we incorporate survival and recapture probabilities into a multinomial model of the probabilities of observing all possible realizations of the capture history (Burnham et al. 1987, Lebreton et al. 1992, Skalski et al. 1998). To do this we introduce three terms (based on terminology from Lebreton et al. 1992) for the site-specific survival and recapture probabilities (Fig. 1): ϕ_j is the probability of fish surviving through the *j*th encounter segment; p_j is the probability of recapturing an individual at the *j*th recapture event, given that the individual was alive; and β is the combined probability of an individual surviving the last encounter segment and being recaptured at the last site, because the data cannot distinguish between these two probabilities. The multinomial model provides a probability density function (pdf) for each potential capture history (by release group), given specified values for the probabilities. When each probability is uniquely specified by release group, this model is often referred to as the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965). Thus, the CJS model assumes that all individuals in a release group behave identically (that is, they have common survival and recapture probabilities), and that all of the survival and recapture probabilities are independent. Burnham et al. (1987) provide several tests to evaluate these assumptions.

Obviously, if within-population behavioral variability exists, the assumptions are violated. A way to overcome assumption violations is to incorporate behavioral variability directly into the models. To achieve this, we modify the CJS model (for details, see Hoffmann and Skalski 1995, Pollock 2002, Zabel and Achord 2004) by expressing survival and recapture probabilities as functions of a trait *x*. We use a logit link to ensure that survival and recapture probabilities range from 0 to 1. For example, the relationship between recapture probability (substitute $s_j(x)$ for $p_j(x)$ for survival probability) at site *j* and trait *x* is

$$p_j(x) = \frac{\exp(\alpha_{0,j} + \alpha_{x,j}x)}{1 + \exp(\alpha_{0,j} + \alpha_{x,j}x)} \tag{1}$$

where *x* is standardized to have zero mean and the α's are coefficients. If *x* is not included in the probability, this equation reduces to $p_j = \exp(\alpha_{0,j})/(1 + \exp(\alpha_{0,j}))$, which is a constant.

Model parameters are estimated using maximum likelihood (Mood et al. 1974) by numerically optimizing the log-likelihood function with respect to the parameters. Standard errors are estimated based on numerical approximations of the Hessian matrix (Burnham et al. 1987). The readily available software MARK (White and Burnham 1999) and SURPH (Lady et al. 2001) can conduct these analyses.

Estimating population-level parameters when individuals vary

Using CJS methodology, estimated population survival between sampling events is simply a model parameter, and thus we simply use the maximum likelihood estimate for this. One element of the CJS population estimates is that R_j, the number of individuals recaptured at site *j*, is divided by the estimated recapture probability ($\hat{p}_j$) to estimate the actual number of individuals alive ($\hat{N}_j$) during sampling event *j*. When individual covariates are included in the recapture probabilities, we can use this same approach, but it is more complicated. We must iterate across all individuals recaptured at site *j* and divide by the estimated probability of recapturing an individual with attribute x_i ($\hat{p}_j(x_i)$). This gives an estimate of the total number of individuals alive at the recapture site. We divide this by an estimate of the total number of individuals alive during the previous sampling event, which is obtained by multiplying the total number of fish released by the survival estimates between the previous sampling events and subtracting any removed fish:

$$\hat{N}_j = \sum_{i=1}^{R_j} 1/\hat{p}_j(x_i) \tag{2a}$$

$$\hat{\phi}_j = \frac{\hat{N}_j}{\hat{N}_{j-1} - r_{j-1}}. \tag{2b}$$

In this equation, r_{j-1} is the number of fish removed at site $j-1$, and site 0 corresponds to the release site. Thus $\hat{N}_0$ is the number of fish released, and $r_0 = 0$.

Another population-level attribute is the directional selection coefficient (Endler 1986), defined as follows:

$$\delta = \frac{\bar{X}_{\text{NEW}} - \bar{X}_{\text{RLS}}}{\sqrt{\text{var}(X_{\text{RLS}})}} \tag{3}$$

where X_{RLS} is a random variable from the distribution of the trait in the release population, X_{NEW} is a random variable from the distribution of the trait after selection, and the bar above *X* designates the mean value. Thus the selection coefficient is determined by the trait-related survival relationship and the initial distribution of the trait.

If we assume that recapture probability is homogeneous in the population, then

$$\bar{X}_{\text{NEW}} = \frac{1}{R_j} \sum_{i=1}^{R_j} x_i \tag{4}$$

where R_j is the number of individuals recaptured at site *j*. If, however, recapture probability is related to *x*, then

$$\bar{X}_{\text{NEW}} = \frac{\displaystyle\sum_{i=1}^{R_j} \frac{x_i}{p_j(x_i)}}{\displaystyle\sum_{i=1}^{R_j} \frac{1}{p_j(x_i)}}. \tag{5}$$

Once again, the differential capture probability in the denominator of each summation inflates each observed individual to reflect the expected number of individuals of that size alive during the *j*th sampling event.

Simulations

We had two motivations for conducting the simulations. First, we assessed the efficacy of Eqs. 2 and 5 as means of incorporating individual heterogeneity into population-level estimates of survival and selection. Second, we wanted to determine under which scenarios we expect to see biases in population-level estimates when existing individual heterogeneity is ignored. Because these biases are likely to vary with sample size, parameter values, and complexity of the system, fully understanding their behavior is beyond the scope of this paper. Instead, we focused on establishing the most important effects. Accordingly, we adopted a simple system in which we set the number of released individuals at 1000, and individuals had two opportunities for recapture. Thus we could simulate trait-based effects for the recapture probability, $p_1(x)$, the survival probability, $\phi_1(x)$, and the combined survival and recapture probability at the second recapture site $\beta(x)$.

We assumed that trait *x* in the population was normally distributed with zero mean and variance = 1.0. We set each of the effects parameters (α_x) to −0.35, 0.0, or 0.35, with the magnitude of the trait effect chosen such that individuals with the 97.5th percentile value of the trait had approximately twice the probability of survival or recapture as individuals from the 2.5th percentile. We set α_0 for $\phi_1(x)$ to 2.0, so an individual with mean x had a survival probability through the first recapture site of 0.88, α_0 for $p_1(x)$ to 1.0, so an individual with mean x had a recapture probability at the first site of 0.73, and α_0 for $\beta(x)$ to 0.0, so an individual with mean x had a combined probability of survival and recapture at the second site of 0.5.

The first step of each simulation was to simulate each individual's capture history based on the underlying survival and recapture processes. To do this we first randomly assigned each individual a value of trait x. Then we determined the probabilities $p_1(x)$, $\phi_1(x)$, and $\beta(x)$ and repeatedly drew from a binomial distribution to determine each individual's fate. Based on these simulated data, we first calculated CJS survival estimates and selection coefficients based on Eq. 4. We then estimated model parameters (the α_0 and α_x parameters for each of the ϕ_1, p_1, and β terms) for each parameter that was set different from zero, and used these parameters to estimate population survival and selection coefficients using the individual covariate method, Eqs. 2 and 5, respectively. For each run of the simulation, we compared these alternative estimates to the true population survival and selection coefficients (which were calculated in each simulation), and determined the differences (a negative difference indicated that the estimated value was less than the true value). Based on 1000 simulations for each scenario, we calculated the mean and standard deviation of the differences for each estimation method. We considered an estimate to be biased if the mean difference between the estimate and true value was >0.001 or <0.001, because the means of the true values varied across simulations by this amount.

Model selection

One of the key questions in analyzing capture–recapture data from natural populations is whether to include the trait x in the various survival and recapture probabilities. Answering this question involves model selection. Because capture–recapture models are often complex, and because several alternative models might perform similarly, most capture–recapture studies now use AIC (or one of its variants) for model selection (Seber and Schwarz 2002), as opposed to more traditional methods such as likelihood ratio tests. Further, there is a trend in capture–recapture studies toward selecting a suite of well-performing models (Johnson and Omland 2004) as opposed to choosing a single "best" model. Model averaging (Burnham and Anderson 2002) is then used where all the selected models contribute to the final parameter estimates (for ecological examples, see MacKenzie and Kendall 2002, Mazerolle 2003, McPherson et al. 2003). An advantage of model averaging is that model uncertainty is incorporated into the estimation of model parameters (MacKenzie and Kendall 2002, Johnson and Omland 2004). We adopted this approach because it is particularly well-suited to our case study that follows.

The first step is to run all possible combinations of trait x included or not for each of the model terms (2^{2n-1} possible combinations, where n is the number of recapture sites). Clearly this is intractable if there are many recapture opportunities, but simplifying assumptions such as identical relationships across sites can reduce the number of models. AIC$_\mathrm{c}$ (AIC corrected for sample size; Burnham and Anderson 2002) is used to weight each model i according to

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{j=1}^{M}\exp(-\Delta_j/2)} \qquad (6)$$

where M is the number of alternative models, and Δ_i is the difference in AIC$_\mathrm{c}$ between model i and the one with the lowest AIC$_\mathrm{c}$. Note that the denominator normalizes the weights so that they sum to 1.0. Models are included one by one, beginning with the best-fitting one, until the sum of the weights is >0.95 (or some other predetermined value), and then are renormalized so that weights of the selected group of models sum to 1.0.

Once the models are selected, the next step is to estimate model-averaged parameters and standard errors. Model-averaged parameter estimates are weighted means across all selected models in which the parameter is included. If we use θ to generically signify any parameter, then the model-averaged estimate of θ is

$$\hat{\theta}_a = \sum_{i=1}^{S} w_i\hat{\theta}_i. \qquad (7)$$

The summation is across all selected models that contain the parameter, $\hat{\theta}_i$ is the estimate of θ from the ith model, and, again, the weights are renormalized to sum to 1.0. In this study, we are interested in estimating length relationships, so we only include the α_0's in the selected set when they are part of a length relationship and thus have a corresponding α_1. The standard errors associated with each parameter are estimated as

$$\mathrm{SE}(\hat{\theta}_a) = \sum_{i=1}^{S} w_i\sqrt{\mathrm{var}(\hat{\theta}_i) + (\hat{\theta}_i - \hat{\theta}_a)^2} \qquad (8)$$

(Burnham and Anderson 2002). Note that the estimated standard error reflects variability associated with each individual estimate and model uncertainty, reflected by the second term in the square root. The 95% confidence intervals about the estimated relationships (using recapture probability as an example) are

$$p_j(x) = \frac{\exp(\alpha_{0,j} + \alpha_{x,j}x \pm z_{0.975}\mathrm{SE})}{1 + \exp(\alpha_{0,j} + \alpha_{x,j}x \pm z_{0.975}\mathrm{SE})} \qquad (9)$$

where $z_{0.975}$ is the 97.5th percentile of the z distribution, and the standard error (SE) is defined as

$$\mathrm{SE} = \sqrt{\mathrm{var}(\alpha_0) + x^2\mathrm{var}(\alpha_x) + 2x\,\mathrm{cov}(\alpha_0, \alpha_x)} \qquad (10)$$

(Hosmer and Lemeshow 2000).

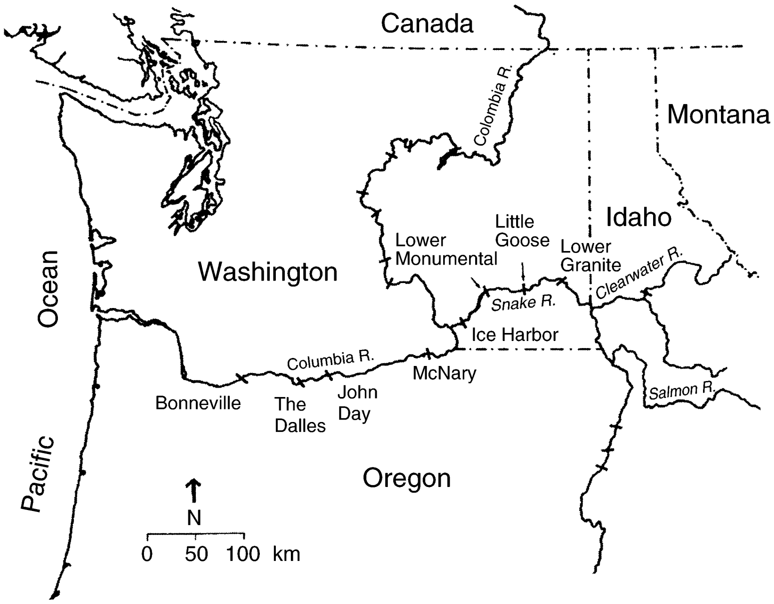

FIG. 2. Mainstem Snake and Columbia Rivers, including major hydroelectric dams. PIT-tagged fish are potentially detected at Lower Granite, Little Goose, Lower Monumental, McNary, John Day, and Bonneville Dams.

Case study: Snake River spring/summer chinook salmon and steelhead

We examined relationships between recapture and survival probabilities and fish length for juvenile chinook salmon (*O. tshawytscha*) and steelhead (*O. mykiss*) migrating out of the Snake River Basin in Idaho and Oregon, USA (Fig. 2). We chose to analyze the length phenotype because it is easily measured, reflects the developmental level of the fish (Zabel 2002), and is directly related to fish swimming ability (McDonald et al. 1998, Peake and McKinley 1998). Study fish were of both wild and hatchery origin, with the wild fish members of Evolutionarily Significant Units (ESUs, Waples 1995) listed as threatened under the U.S. Endangered Species Act. The fish were captured, PIT-tagged, and released (for details, see Harmon et al. 2000 and Marsh et al. 2001) at Lower Granite Dam on the Snake River (Fig. 2). We analyzed yearly release groups from 1998 to 2002, with groups separated by species and origin. Because the fish were not physically recaptured, we use the term ''detection'' analogously to the term ''recapture'' from typical capture–recapture studies. Survival and detection probabilities may vary over a season, so we analyzed fish from the 10-d period when the most fish were released per release group. The minimum sample size per release group over the 10-d periods was 5000, which ensured enough downstream detections to conduct the analysis.

The tagged fish were potentially detected in the juvenile fish bypass systems at Little Goose, Lower Monumental, McNary, John Day, and Bonneville Dams (Fig. 1). The detectors recorded individual tag codes and uploaded them into the Columbia Basin PIT Tag Information System (PTAGIS) operated by the Pacific States Marine Fisheries Commission (*available online*).[6] We combined detections at the last three sites together to increase the sample size, so an individual fish had three opportunities for detection. Thus the full capture history for fish *i* was a sequence of three digits, each digit taking on the values 1, 0, or -1. In addition, the fork length (tip of the snout to the fork in the tail, in millimeters) of each fish was measured at tagging.

Before conducting our analyses, we performed goodness-of-fit tests to determine whether the assumptions of the CJS model were violated, which would suggest that behavioral variability existed. We reported results from the overall goodness-of-fit test, which represents a summation of several tests (Burnham et al. 1987).

We estimated parameters and AIC_c values for all 32 possible models per release group. We then used the model-averaging approach to estimate model-averaged parameters and standard errors. If the effect parameter (α_x) estimate was greater than twice its standard error, this provided ad hoc evidence of a significant relationship.

Finally, we compared estimates of population survival and selection coefficients using individually varying recapture probabilities to those that ignored this information. To assess the consistency among methods, we calculated mean differences in estimates and the correlation in estimates produced by the two methods.

RESULTS

Simulations

Although we ran all combinations of parameter values (27 separate simulations), we only presented those

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[6] ⟨http://www.psmfc.org/pittag/⟩

TABLE 1. Simulation results for survival estimation.

Value of effect parameter (α_x)			True mean survival	Difference between true and estimated survival			
				CJS method		Indiv. trait method	
p_1	ϕ_1	β		Mean	SD	Mean	SD
0.0	0.0	0.0	0.880	0.000	0.0171	0.000	0.0145
−0.35	0.0	0.0	0.880	−0.001	0.0178	−0.001	0.0152
0.0	−0.35	0.0	0.876	0.000	0.0179	0.000	0.0156
0.0	0.0	−0.35	0.881	0.001	0.0179	0.000	0.0156
−0.35	−0.35	0.0	0.876	0.001	0.0178	−0.001	0.0150
−0.35	0.35	0.0	0.876	0.000	0.0186	−0.001	0.0152
−0.35	0.0	−0.35	0.881	**−0.013**	0.0171	0.001	0.0147
−0.35	0.0	0.35	0.881	**0.015**	0.0190	0.000	0.0155
0.35	0.0	−0.35	0.881	**0.014**	0.0193	0.000	0.0151
0.35	0.0	0.35	0.881	**−0.014**	0.0169	−0.001	0.0144
0.0	−0.35	−0.35	0.876	0.000	0.0177	0.000	0.0154
−0.35	−0.35	−0.35	0.876	**−0.013**	0.0176	0.000	0.0170
−0.35	0.35	−0.35	0.875	**−0.013**	0.0178	−0.001	0.0164
−0.35	−0.35	0.35	0.876	**0.014**	0.0190	−0.001	0.0155

Notes: Values highlighted in boldface type varied by more than 0.001 from the true survival and were considered biased. The CJS method refers to the Cormack-Jolly-Seber method, and the individual trait method refers to Eq. 2. See *Methods: Simulations* for a description of the simulations and *Methods: Estimating population-level parameters where individuals vary* for survival estimation methods.

that were necessary to establish important results (Tables 1 and 2). For all combinations of parameters, estimates of population survival and selection coefficients that incorporated individual heterogeneity were unbiased (Tables 1 and 2, Fig. 3). This indicates that the proposed methods to account for individual heterogeneity were effective.

The consequence of ignoring individual heterogeneity in recapture probabilities was much more severe for estimating selection coefficients than for estimating population survival. The distribution of selection coefficients estimated with the standard method were far more shifted away from the true value than were population survival estimates using the standard (CJS) method (Fig. 3). Although the overall magnitude of bias was relatively small using the CJS method (typically <1% of the true survival, and the mean of the bias was less than the standard deviation; Table 1), the magnitude of bias was extremely large when using the standard method to estimate selection coefficients. When biases existed, they were more than twice as large as the true selection coefficients observed under the scenarios with trait-related survival, and the mean of the bias was ~4–10 times greater than the standard deviations (Table 2).

Population survival estimates using the CJS method were biased if trait relationships existed in both the p_1 term (first recapture probability) and the β term (combined survival and recapture probability at the last site, Table 1). The direction of bias was dependent on the signs of the effect parameters (α_x's): if the signs were the same, the CJS survival estimates were negatively biased. Recall that with the CJS method, the number of individuals observed at a site is divided by the estimated recapture probability to yield an estimate of the actual number of fish alive at the sampling site. This, then, is used to estimate survival. When the signs of the effect parameters for the p_1 and β terms were the same, the chance of observing individuals with capture history "11" (recaptured twice) was greater than expected with no relationships, leading to positively biased estimates of the recapture probability and, consequently, negatively biased estimates of survival. The opposite occurred when the signs were opposite. The presence or absence of a trait relationship with the survival parameter (ϕ_1) had no effect on the magnitude or direction of bias. The variance about the population survival estimates, regardless of method, generally increased with the number of length relationships, but the effects of the particular parameters on variance varied, with some cases of variance decreasing with added parameters. Further study is necessary to completely understand the statistical properties of the population survival estimators.

Estimates of selection coefficients were biased if a trait relationship existed in the first recapture probability term (p_1) and it was ignored (Table 2). If the effect parameter was negative, the selection coefficient was negatively biased. This occurred because the greater probability of observing individuals with lower values of x led to a negative bias in the calculation of mean x. The opposite occurred when the effect parameter for p_1 was positive. The magnitude of the bias remained relatively constant, regardless of the values of the parameters. Note that the value of the true selection coefficient was determined by the value of the effect parameter for ϕ_1, as expected. An unexpected result with these simulations was that in the cases in which the effect term for p_1 was not equal to zero, the standard deviation about the estimated selection co-

TABLE 2. Simulation results for estimation of selection coefficients (δ).

Value of effect parameter (α_x)			True mean δ	Difference between true and estimated δ			
				Standard method		Indiv. trait method	
p_1	ϕ_1	β		Mean	SD	Mean	SD
0.0	0.0	0.0	0.001	0.000	0.0204	0.000	0.0204
−0.35	0.0	0.0	0.001	**−0.094**	0.0200	−0.001	0.0103
0.35	0.0	0.0	0.000	**0.094**	0.0214	0.000	0.0105
0.0	−0.35	0.0	−0.043	0.000	0.0201	0.000	0.0201
0.0	0.0	−0.35	0.000	0.000	0.0202	0.000	0.0202
−0.35	−0.35	0.0	−0.043	**−0.092**	0.0204	0.000	0.0182
−0.35	0.35	0.0	0.043	**−0.093**	0.0206	0.000	0.0146
−0.35	0.0	−0.35	0.000	**−0.094**	0.0212	0.000	0.0099
0.35	0.0	−0.35	0.001	**0.094**	0.0222	0.000	0.0109
0.0	−0.35	−0.35	−0.043	0.001	0.0200	0.001	0.0200
−0.35	−0.35	−0.35	−0.043	**−0.091**	0.0211	0.001	0.0236
−0.35	0.35	−0.35	0.043	**−0.093**	0.0216	−0.002	0.0165

Notes: Values highlighted in boldface type varied by more than 0.001 from the true selection coefficient and were considered biased. The standard method is based on Eq. 4, and the individual covariate method is based on Eq. 5. See *Methods: Simulations* for a description of the simulations and *Methods: Estimating population-level parameters when individuals vary* for estimation methods.

efficients (using the individual trait method) was reduced compared to the other cases. We believe that this occurred as a result of differentially inflating observations based on their value of x (Eq. 5), leading to a decrease in variance. Again, further research is necessary to understand the statistical properties of the proposed selection coefficient estimator.

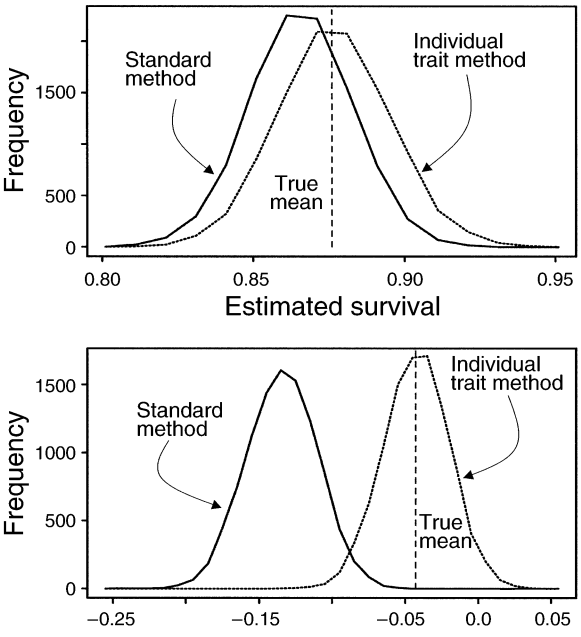

FIG. 3. Results from the simulations for estimated survival (top) and estimated selection coefficients (bottom) where negative trait relationships existed for all three model terms (p_1, ϕ_1, β). In each plot, the solid line represents the distribution of estimates when trait relationships were ignored, the dotted line represents the distribution of estimates when trait relationships were incorporated into the estimates, and the dashed vertical line represents the true mean value of survival (top plot) or the selection coefficient (bottom plot).

Chinook salmon and steelhead case study

We analyzed data from >153 000 PIT-tagged individuals in eight release groups (Table 3). Distinct size differences existed among groups, with steelhead being longer than chinook salmon and hatchery fish being longer than wild ones (Table 3). In five out of eight release groups, the assumptions of the CJS model were rejected, which suggested that behavioral variability existed within the release groups. Using the model selection techniques, we selected a broad range of ‘‘best’’ models per release group based on their AIC$_c$ weights, ranging from one model selected for wild steelhead released in 2000 to 26 models selected for hatchery steelhead released in 1999. In no case was the CJS model selected among the suite of ‘‘best’’ models, further reinforcing the existence of behavioral variability.

Detection probability was related to fish length for all release groups in at least one of the sites. Overall, the model selection process chose length relationships in 11 out of 16 year–site combinations (Figs. 4 and 5, Table 4). In all cases in which a length relationship was selected, the length effects coefficient, α_x, was negative, indicating that smaller fish had a higher probability of detection.

The relationship between estimated survival and fish length was not as consistent. Although the model selection process selected length relationships in 11 out of 16 year–site combinations (Figs. 4 and 5, Table 5), the direction of the relationships was variable. There was a greater tendency for positive survival–length relationships than negative ones, with eight out of 11

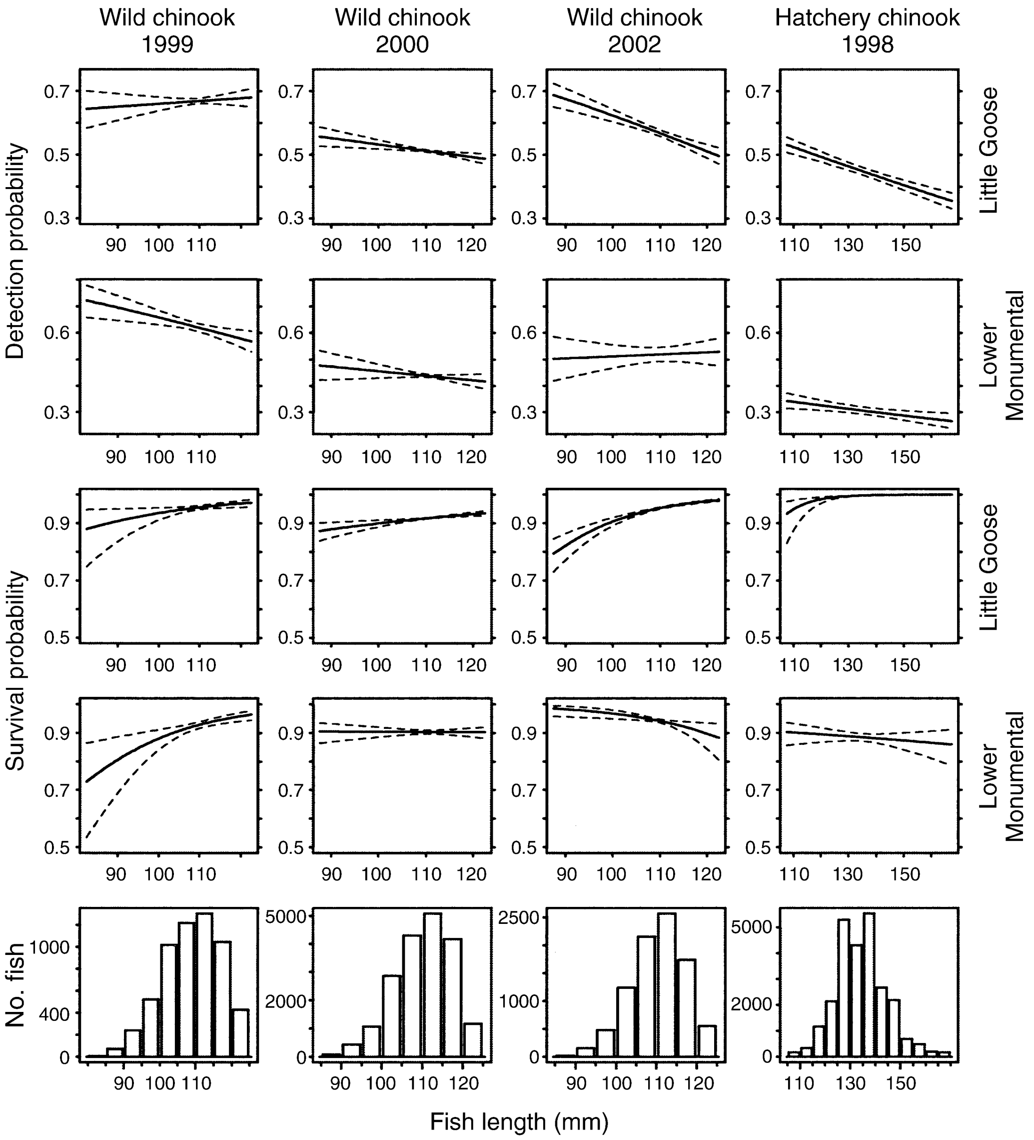

FIG. 4. Relationships between recapture and survival probabilities and fish length by release group and recapture site based on results from Tables 4 and 5. Dashed lines show the 95% confidence intervals about the relationships. The bottom row of plots is the distribution of lengths in each release group.

TABLE 3. Number of fish released, range of release dates, and length by species, origin (hatchery or wild), and year.

Year and fish type	No. fish released	Release dates	Fish length (mm) Mean	Fish length (mm) SD	GOF P	No. models selected
Wild chinook, 1999	5858	20 Apr–29 Apr	109.3	8.0	0.8822	12
Wild chinook, 2000	19 216	13 Apr–22 Apr	110.7	7.5	**0.0014**	13
Wild chinook, 2002	8913	17 May–26 May	109.8	6.7	0.0618	7
Hatchery chinook, 1998	25 560	19 Apr–28 Apr	135.1	10.9	**0.0000**	6
Hatchery chinook, 1999	32 370	26 Apr–5 May	137.8	13.6	0.6888	4
Wild steelhead, 2000	29 600	13 Apr–22 Apr	189.3	28.5	**0.0193**	1
Wild steelhead, 2002	13 696	17 May–26 May	171.2	18.7	**0.0156**	11
Hatchery steelhead, 1999	18 607	28 Apr–7 May	210.2	21.8	**0.0035**	26

Notes: P values of the goodness-of-fit (GOF) tests are presented in boldface when $P < 0.05$, which indicates that the assumptions of the CJS model were violated. The number of models selected refers to the number of models retained based on their AIC_c weights.

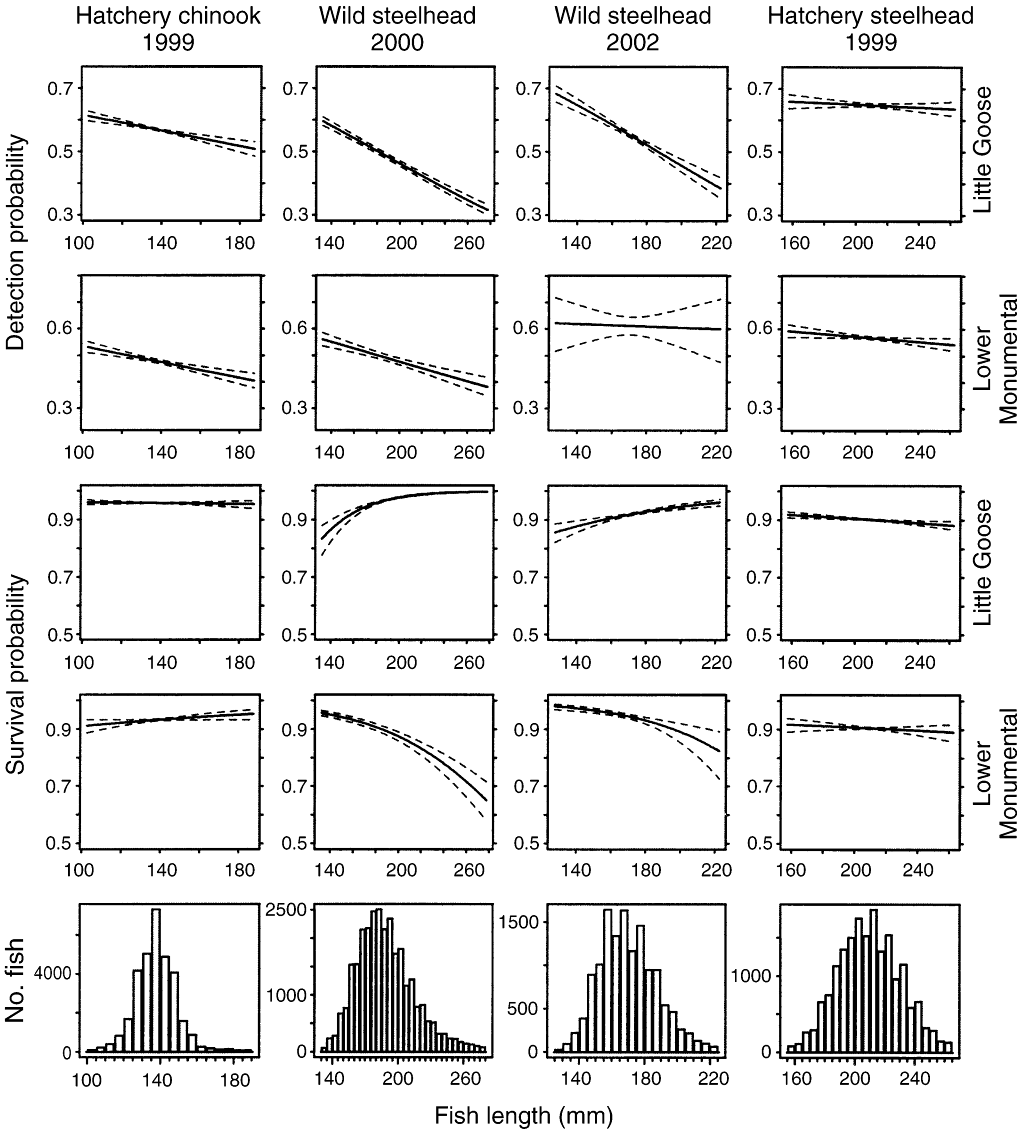

FIG. 5. Relationships between recapture and survival probabilities and fish length by release group and recapture site based on results from Tables 4 and 5. Dashed lines show the 95% confidence intervals about the relationships. The bottom row of plots is the distribution of lengths in each release group.

TABLE 4. Model-averaged parameter mean estimates for the recapture probability vs. fork length (FL, measured in millimeters) relationships by species, origin (hatchery or wild), detection site, and year.

	p_1 (Little Goose Dam)		p_2 (Lower Monumental Dam)	
Fish type and year	α_0 (SE)	α_x (SE)	α_0 (SE)	α_x (SE)
Wild chinook, 1999	0.702 (0.0200)	0.004 (0.0047)	0.497 (0.0325)	**−0.017 (0.0055)**
Wild chinook, 2000	0.046 (0.0075)	**−0.008 (0.0026)**	−0.254 (0.0118)	−0.007 (0.0048)
Wild chinook, 2002	0.281 (0.0209)	**−0.023 (0.0037)**	0.075 (0.0536)	0.003 (0.0071)
Hatchery chinook, 1998	−0.204 (0.0242)	**−0.012 (0.0015)**	−0.816 (0.0324)	**−0.006 (0.0020)**
Hatchery chinook, 1999	0.281 (0.0075)	**−0.005 (0.0009)**	−0.090 (0.0146)	**−0.006 (0.0011)**
Wild steelhead, 2000	−0.065 (0.0170)	**−0.008 (0.0004)**	−0.042 (0.0236)	**−0.005 (0.0008)**
Wild steelhead, 2002	0.201 (0.0158)	**−0.013 (0.0013)**	0.454 (0.0700)	−0.001 (0.0047)
Hatchery steelhead, 1999	0.611 (0.0129)	−0.001 (0.0009)	0.270 (0.0114)	**−0.002 (0.0009)**

Note: Boldface values of the effects parameters (α_x) indicate that the estimate is greater than twice its standard error.

TABLE 5. Model-averaged parameter mean estimates for the survival probability vs. fork length (FL, measured in millimeters) relationships by species, origin (hatchery or wild), detection site, and year.

	ϕ_1 (L. Granite to L. Goose)		ϕ_2 (L. Goose to L. Monumental)	
Fish type and year	α_0 (SE)	α_x (SE)	α_0 (SE)	α_x (SE)
Wild chinook, 1999	3.034 (0.0838)	**0.039 (0.0165)**	2.518 (0.0837)	**0.057 (0.0156)**
Wild chinook, 2000	2.416 (0.0136)	**0.021 (0.0060)**	2.227 (0.0396)	−0.001 (0.0086)
Wild chinook, 2002	2.998 (0.0390)	**0.074 (0.0077)**	2.791 (0.0569)	**−0.061 (0.0232)**
Hatchery chinook, 1998	5.888 (0.1910)	**0.118 (0.0176)**	2.035 (0.0651)	−0.007 (0.0077)
Hatchery chinook, 1999	3.136 (0.0121)	−0.002 (0.0031)	2.619 (0.0315)	**0.008 (0.0039)**
Wild steelhead, 2000	3.434 (0.0511)	**0.032 (0.0031)**	2.124 (0.0694)	**−0.017 (0.0015)**
Wild steelhead, 2002	2.442 (0.0306)	**0.015 (0.0029)**	2.823 (0.0761)	**−0.025 (0.0053)**
Hatchery steelhead, 1999	2.215 (0.0132)	−0.004 (0.0013)	2.252 (0.0210)	−0.003 (0.0029)

Note: Boldface values of the effects parameters (α_x) indicate that the estimate is greater than twice its standard error.

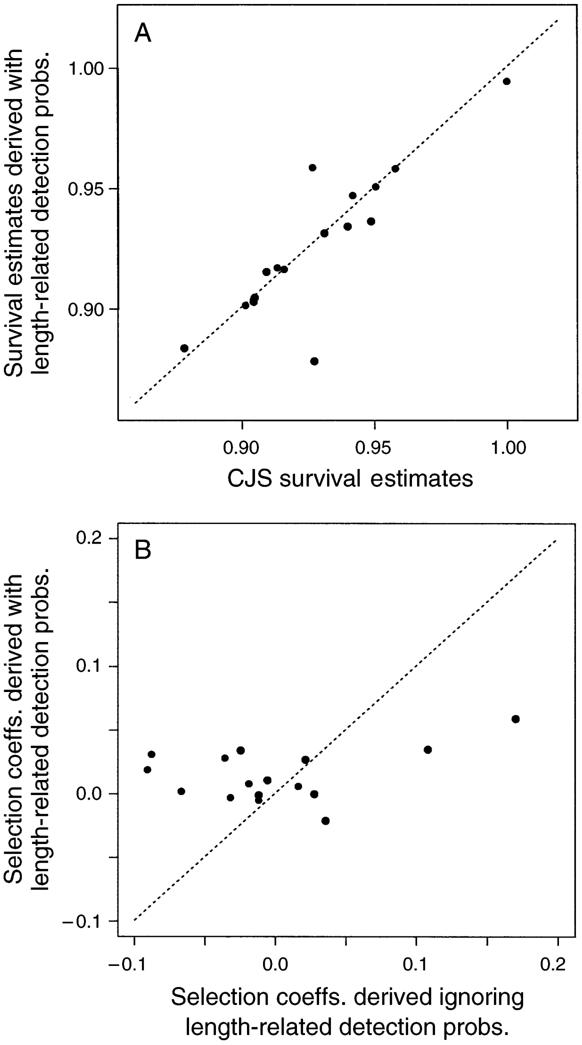

FIG. 6. Comparison of (A) survival estimates and (B) estimates of selection coefficients derived with length-related recapture probabilities to those that ignored these relationships.

significant length relationships having a positive value of α_x.

When we compared among methods for estimating population survival, we found a high level of correlation between methods and little evidence for bias in the CJS method when ignoring the individual trait (Fig. 6A). Survival estimates produced by the two methods were highly correlated ($r = 0.861$), and the CJS produced survival estimates that averaged 0.1% less than those produced when incorporating individually varying recapture probabilities. One release group, wild steelhead released in 2000, had relatively poor correlation between the two methods. When this group was removed, the correlation between the methods increased to 0.989. This group was different from the other groups in several ways: it only had one model selected (the model with all possible length relationships) in the model selection process; the difference in AIC_c between the best model and the CJS model was much larger compared to other groups (−381.1 compared to −123.5 for the next largest group); and it had relatively small standard errors for all the effect parameters (Tables 4 and 5). All of these effects lead to the conclusion that length effects were particularly strong for this release group, and that the CJS model poorly represented the survival and recapture process. We believe that this led to bias in the CJS survival estimates. We note, though, that the product of ϕ_1 and ϕ_2 for this release group was similar between the two methods, indicating that most of the discrepancy occurred in partitioning survival between the two river segments, not in estimating the overall survival through both segments.

When we examined selection coefficients produced by the two methods, we found striking differences (Fig. 6B). The estimated selection coefficients were poorly correlated between the methods ($r = 0.365$) and somewhat biased (mean difference of 0.015 between the two methods). The most striking result was that the selection coefficients derived from models with constant detection probabilities spanned a much greater range than those derived from models with length-related detection probabilities. Thus, ignoring differential recapture probabilities would lead to the conclusion that magnitude of selection was much greater than it actually was.

Overall, the results of the case study were consistent with the results from the simulation study. With the exception of one release group, the CJS method produced reasonable estimates of population survival that were within the range of biases produced in the simulations (Table 1, Fig. 6). Selection coefficients were extremely biased if differential recapture probabilities were ignored, and, again the range biases were consistent with those observed in the simulation study (Table 2, Fig. 6). Further, the majority of the selection coefficients estimated under the standard model were negatively biased (Fig. 6), consistent with the conclusion of the simulation study that negative trait relationships in the recapture probabilities lead to negative bias in selection coefficients.

DISCUSSION

Animal populations typically are behaviorally heterogeneous and inhabit heterogeneous environments. The same heterogeneity that leads to differential survival can also lead to differential capture rates, thus potentially obscuring population dynamics. Here we demonstrated that, with carefully planned experiments that allow for multiple recaptures of individually tagged animals, one can properly partition observed trait-related variability into survival and recapture probability components. This, in turn, allows for unbiased estimation of population survival and selection coefficients.

Probably our most striking result, obtained from both the simulation and the case study, is the demonstration of potential for extreme bias in estimating selection for phenotypic traits when differential recapture probabilities are ignored. Estimating selection for phenotypic traits is a key element of evolutionary ecology (Endler 1986), with selection coefficients routinely estimated for hundreds of taxa (Kingsolver et al. 2001). Unfortunately, many advances in capture–recapture methodology that can rectify these biases have not found their way into the evolutionary ecology literature (Clobert 1995; but see Kingsolver and Smith 1995). We note that with slight modifications, the methods that we presented here can be used to estimate more complex forms of selection such as stabilizing or disruptive selection or correlations in selection among multiple traits.

Our results indicate that population survival estimates are more robust in the face of a variety of assumption violations concerning recapture and survival probabilities, a result observed elsewhere (e.g., Lebreton 1995). This is encouraging news because CJS methodology (which ignores differential recapture and survival probabilities) is used extensively. However, an important consideration is that differential capture probabilities may result in a sample of tagged animals that is not representative of the entire population. When differential capture probabilities are combined with size-related selection, a nonrepresentative sample of individuals can produce a biased estimate of population survival, regardless of the estimation procedure.

Chinook salmon and steelhead case study

Our results clearly indicate that migrating juvenile salmonids exhibit behavioral variability. Thus, the type of analysis that we performed is warranted and can shed light on this behavioral variability. Although it is clear that seaward-migrating juvenile salmonids experience selective mortality in the mainstem Snake and Columbia Rivers, the lack of consistent pattern indicates that the selection probably arises from a variety of sources. The two primary sources of mortality for these fish are predation (by both piscivorous fish and birds) and mortality associated with dam passage. Further studies that specifically target these mortality sources are needed to elucidate these patterns.

Our analysis demonstrated a consistent negative relationship between detection probability at fish bypass systems and fish length of seaward-migrating salmonids. Size-related recapture rates can arise from two nonmutually exclusive mechanisms. First, spatial heterogeneity related to size may result in differential exposure to the trap or detection site. Second, individuals of different sizes may have differential abilities to escape the trap or detection site once they are in close vicinity. In the case of migrating juvenile salmonids, each of these mechanisms could contribute to the results that we observed, and we will examine them in more detail.

In the system that we studied, the vertical position of a fish in the water column is likely to be important in determining its probability of detection. Fish that are more surface-oriented are more likely to be diverted into bypass systems than fish swimming lower in the water column (Coutant and Whitney 2000). One key factor that influences the vertical position of salmonids is smoltification, the series of physiological, morphological, and behavioral changes that ready fish for a saltwater environment (Hoar 1976). Smolted fish are more buoyant than non-smolted ones and tend to migrate higher in the water column (Saunders 1965, Pinder and Eales 1969). We have some evidence that smaller fish may be more smolted than larger ones in the system that we studied. Gill Na^+, K^+-ATPase activity (an indicator of smoltification) was measured in juvenile wild and hatchery chinook salmon sampled from bypass systems in 2000, 2001, and 2002, and it was negatively correlated ($\alpha = 0.05$) with fish length in two of four analyses for wild fish and in four of seven analyses for hatchery fish (*unpublished data*, J. L. Congleton).

Our second hypothesis is that fish of different sizes react differently to flow patterns that they encounter at the face of the dam. Larger fish have longer swimming times-to-fatigue and greater burst-swimming abilities than smaller individuals (McDonald et al. 1998, Peake and McKinley 1998). The higher absolute burst-swimming speed and greater endurance of the larger fish may allow them to more successfully avoid guidance by diversion screens. Flow velocities approaching the screens are typically ~1 m/s (Coutant and Whitney 2000), equivalent to a velocity of 10 body lengths/s for a 100-mm fish, or 5 body lengths/s for a 200-mm fish. At these swimming velocities, the expected time to fatigue would be only a few seconds for a 100-mm salmonid (McDonald et al. 1998), but 12–15 s for a 200-mm fish (Brett 1964). Large fish would have more time to maneuver and might be able to swim around the bypass screen or sound below it.

The results of our case study have implications for the management of Columbia River Basin salmonids. PIT-tag studies are routinely used to estimate adult return rates, which are used to assess population performance. In these studies, juveniles are collected from bypass systems and are tagged, under the assumption that the collected fish represent the entire population. The tendency, demonstrated in this study, for bypass systems to divert smaller fish, on average, than the entire population, coupled with the tendency for smaller fish to return at lower rates (Zabel and Williams 2002) could lead to underestimates of population return rates. Further, studies that use bypassed fish as a treatment group and undetected fish as a control group (e.g., studies on the efficacy of transportation [Marsh et al. 2001] or examinations of the latent effects of bypass systems [Budy et al. 2002]) could produce misleading results. Williams et al. (2005) discuss this issue in much greater detail.

In summary, recent advances in tagging technology and analytical methods have enabled researchers to accurately portray survival and recapture processes in natural populations. The ability to elucidate within-population behavioral variability is crucial for describing population dynamics. This, in turn, will allow us to more effectively manage at-risk populations.

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EXHIBIT 5

DECLARATION OF RICHARD W. ZABEL

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SELECTIVE MORTALITY IN CHINOOK SALMON: WHAT IS THE ROLE OF HUMAN DISTURBANCE?

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Abstract. While many recovery programs for threatened species focus on acute sources of mortality, understanding some of the evolutionary processes of these species may lead to more effective recovery efforts, especially in cases where human-induced disturbances have resulted in artificial selection pressures. We developed a Monte Carlo test to determine whether Snake River spring/summer chinook salmon (*Oncorhynchus tshawytscha*) experienced selective mortality as a function of their juvenile length and timing of downstream migration. Actively migrating juvenile fish (smolts) were captured, tagged, and released in 1995 and 1996 approximately 700 km upstream from the Pacific Ocean, and returning adults were detected at the same location. We analyzed data from two groups of fish: those that migrated downstream in-river and those that were barged downstream as part of the juvenile-salmon transportation program. These groups were further separated into wild and hatchery fish. Length at release was significantly greater in returning adults than in the general population for fish that migrated downstream in-river (both wild and hatchery) or were transported (hatchery only). From the 1995 seaward migration, adult returns of both wild and hatchery fish that migrated in-river were composed of fish released significantly earlier than the general population. In contrast, the opposite trend existed for wild and hatchery transported fish. From the 1996 seaward migration, no significant difference in release date was found between returning adults and the original population for any of the groups analyzed. Fish length at migration is a result of factors encountered in early life stages but selectively determines mortality in the smolt-to-adult stage. Thus freshwater habitat improvements, such as salmon carcass supplementation, directed at increasing nutrient levels and thus fish length may result in an increase in overall survival. The development of hydroelectric dams in the migratory corridors of these fish has disrupted their arrival timing to the estuary. Mitigation efforts designed to shift arrival timing toward that experienced prior to impoundment may confer considerable survival benefits.

Key words: chinook salmon; endangered species, recovery planning; fish length; hydroelectric dams, effects on salmon; local adaptation; migration timing; Monte Carlo test; salmon vs. human disturbance; selection; selective mortality: fish length, migrational timing; Snake River (Pacific Northwest, USA).

Introduction

Local adaptation is a means for populations to increase their average fitness in response to unique local conditions (Endler 1986). Local adaptation is encouraged when gene flow among populations is limited and environmental and ecological heterogeneity exists among populations (Wright 1931, Futuyma 1979). In fish populations, local adaptation has been demonstrated for a number of different traits in a wide variety of taxa (see Conover and Schultz [1997] for a review). Human-induced disturbances to natural systems may result in decreased average fitness of affected populations if these disturbances dramatically change the conditions compared to those under which the populations evolved. One such disturbance faced by many migratory fish populations is hydroelectric dams constructed in their migratory corridors. While many dams allow for fish passage, they can still impact migratory fish populations in a variety of ways. First, they create slack-water reservoirs where river velocities are greatly reduced. Since many migratory fish exhibit passive migration relying on river currents (Leggett 1977), dams can delay their downstream migration. Also, the altered riverine environment can affect the suite of predators encountered by fish during their migration and potentially increase predation (Ward et al. 1995) and associated selective pressures. With tens of thousands of dams in place worldwide and more planned, the resulting alteration of riverine habitats is potentially a strong evolutionary force for many populations of migratory fish.

Because of their complex migratory behavior, salmon species are particularly disposed to local adaptation (Ricker 1972, Schaffer and Elson 1975, Leggett 1977, Taylor 1991). Many populations have strong homing ability that limits gene flow by returning adults to geographically isolated sites to spawn. Salmon often undergo extensive migrations that lead them through a

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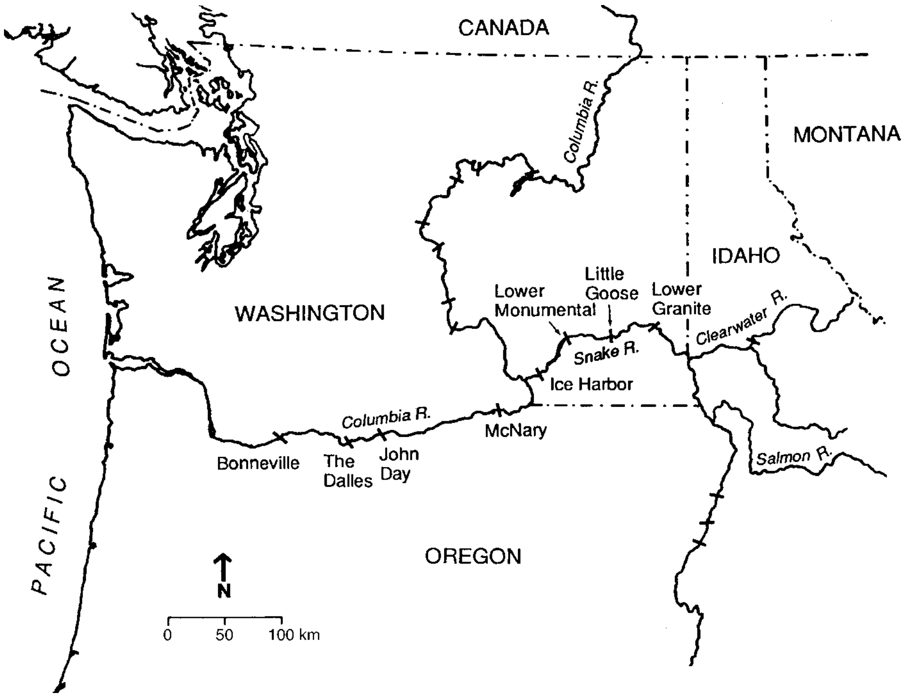

FIG. 1. Map of the Columbia and Snake rivers and some of the major tributaries. Locations of hydroelectric dams are indicated by bars across the rivers.

variety of habitats. Accordingly, salmon have developed extensive variability in life-history patterns both among and within species in terms of freshwater residence, migratory patterns, and length of ocean residence (Groot and Margolis 1991). For instance, chinook salmon (*Oncorhynchus tshawytscha*) exhibit two distinct life-history patterns, termed ''stream type'' and ''ocean type'' by Gilbert (1912). Ocean-type fish typically migrate downstream shortly after emergence while stream-type fish spend a year rearing in freshwater before migrating downstream. Taylor (1990*b*) demonstrated that these different strategies and their associated suite of traits are heritable.

Most salmon populations are anadromous, meaning that they spawn and undergo initial rearing in freshwater before migrating to saltwater. Anadromy occurs in a variety of fish taxa, including herring, lamprey, shad, and sturgeon (McDowall 1987), and is believed to have evolved to enable the utilization of freshwater habitats as nursery areas and the exploitation of higher nutrient levels available in the ocean (Gross 1987, Gross et al. 1988, Dodson 1997). Within anadromous fish populations, a trade-off exists between the size individuals attain before initiating migration and the timing of migration. It is well demonstrated that larger size confers a selective advantage for juveniles in many fish populations (Sogard 1997). Fish length at migration is a function of growth rate and residence time in the rearing habitat. Growth rate has been demonstrated to be heritable for some fish species (Conover and Schultz 1997) and involves trade-offs between foraging and predator avoidance (Werner and Gilliam 1984, Werner and Anholt 1993). Freshwater residence time is also heritable (Randall et al. 1987), and migrational timing is thought to have evolved, in part, to seasonally varying patterns in predation pressure and estuary/ocean productivity (Dodson 1997).

We examined these issues by studying selective mortality in Snake River spring/summer chinook salmon, listed as threatened under the U.S. Endangered Species Act. We tested for selective mortality by comparing the distributions of two traits in yearling smolts, length as juveniles and timing of migration, to the same traits in returning adults. Understanding some of the evolutionary processes of threatened species may result in more effective recovery planning than would result from programs directed exclusively on acute sources of mortality.

Snake River spring/summer chinook salmon natural history and hydroelectric development

These stream-type fish migrate as yearling smolts from their native streams in Oregon and Idaho through the mainstem Snake and Columbia Rivers and the estuary to feeding areas in the Pacific Ocean (Fig. 1). After 1–3 yr in the ocean, they return to their natal streams in the spring or summer (hence the designation) to spawn as adults. The migration from freshwater spawning/rearing areas to the ocean covers a distance of up to 1500 km.

Anadromous salmon populations migrating from the Snake River basin must pass eight hydroelectric dams during their downstream migration (Fig. 1). These dams are outfitted with juvenile-fish bypass systems and adult-fish ladders. Nonetheless, the impacts of dams and other human-induced disturbances, including overharvest, habitat destruction, and massive releases of hatchery fish, have resulted in serious depletion of salmonid populations (Lichatowich 1999) and the listing of four Snake River species as threatened or endangered under the U.S. Endangered Species Act: sockeye salmon (*O. nerka*), spring/summer and fall chinook salmon (both *O. tshawytscha*), and steelhead trout (*O. mykiss*).

To mitigate for these disturbances and to avoid direct mortality at dam passage, a juvenile transportation program was implemented where fish are collected at the uppermost dams on the Snake River and transported by barge to below Bonneville Dam, the lowermost dam (Ebel 1980). In this study we tested for selective mortality in both fish that were transported downstream and those that migrated volitionally.

Passive integrated transponder (PIT) tags

In the analysis reported here, we took advantage of an innovative fish tag, the passive integrated transponder (PIT) tag (Prentice et al. 1990). The small tag (∼12 mm in length) is inserted into the body cavity and remains in the individual for life. Each tag contains a unique code, and when fish are tagged, pertinent information such as length and time of tagging is recorded in a database. Individuals are detected at interrogation sites (primarily located in dam bypass systems for juveniles and fish ladders for adults) as they progress through their migrations, yielding information on survival and migrational timing. Researchers are beginning to use these tags worldwide, greatly enhancing our knowledge of fish populations.

PIT tags afford several advantages for studies of selection in fish populations since individuals are tracked and their attributes are known. Previous studies either had to undertake mass marking of categorical tag groups (Bilton et al. 1982) or infer juvenile traits in returning adults from scale or otolith samples (West and Larkin 1987, Holtby et al. 1990)—time-consuming and often imprecise methods. In addition, PIT tags allow for re-sampling of individuals (i.e., longitudinal sampling), which is the most effective means of measuring selection in populations (Miller 1997).

METHODS

Data

Hatchery and wild Snake River spring/summer chinook salmon were captured, tagged, and released at Lower Granite Dam (Fig. 1) in 1995 and 1996 as part of a transportation-effectiveness study (Marsh et al. 1996, 1997). Fish were collected from the juvenile bypass system and randomly assigned to either transportation or in-river migration groups. In 1995 the length of every fifth fish was measured; in 1996 almost all fish were measured. Fish that were not measured were removed from the length analysis but were included in the release-date analysis. Although we did not control for potential selective effects of tagging, Prentice et al. (1990) did not observe any size-selective effects or adverse effects on survival, growth, or swimming performance when comparing PIT-tagged juvenile salmon to control fish, and Peterson et al. (1994) did not observe any differences in overwinter growth or survival of PIT-tagged juvenile salmon compared to a group marked with a coded-wire tag.

Fish were transported in trucks (used only in the beginning of the season when few fish were present) or barges to a release site below Bonneville Dam (Fig. 1) within 36 h. We analyzed only fish that were barged so we would not introduce a conveyance effect. Fish for the in-river migration group were held for 24 h, and then released into the tailrace of Lower Granite Dam. They migrated to below Bonneville Dam in ∼10–20 d.

Adult returns were based on fish detected 1–3 yr after tagging as they returned upstream through ladders at Lower Granite Dam (Marsh et al. 1996, 1997). When an adult PIT-tagged fish returned, information was retrieved from a database about its size and release date as a juvenile. Essentially all adult PIT-tagged fish (>96%) were detected as they passed upstream through ladders at Lower Granite Dam.

Statistical analysis

We developed a Monte Carlo test (Manly 1997) to compare the distribution of traits measured at release to the distribution of the same traits in returning adults. The null hypothesis was that returning adults were a random sample of the original population. If selective mortality was detected in the traits observed, then this hypothesis would be rejected. We examined the traits (1) fish length at tagging and (2) release date.

The data consisted of two vectors of traits (measured at tagging) corresponding to individual fish. One of the vectors corresponded to the entire tagged population, and the other to returning adults:

$$\mathbf{x}_\mathrm{T} = (x_{\mathrm{T},1}, x_{\mathrm{T},2}, \ldots, x_{\mathrm{T},N_\mathrm{T}}) \qquad \mathbf{x}_\mathrm{R} = (x_{\mathrm{R},1}, x_{\mathrm{R},2}, \ldots, x_{\mathrm{R},N_\mathrm{R}})$$

where the subscripts T and R refer to the entire tagged group and returning adults, respectively, and N_T and N_R correspond to the total number of tagged fish and returning adults, respectively. Note that $\mathbf{x}_\mathrm{R}$ is a subset of $\mathbf{x}_\mathrm{T}$.

The first step in developing the Monte Carlo test was to define a test statistic *T*, which characterized the data in a biologically meaningful way. We chose the directional selection coefficient (Endler 1986):

$$T = \frac{\bar{x}_\mathrm{R} - \bar{x}_\mathrm{T}}{\sqrt{\mathrm{var}_\mathrm{T}}}$$

TABLE 1. Length at tagging (means with 1 SE in parentheses) for the total tagged chinook salmon population and returning adults.

	Total population		Returning adults			Monte Carlo test results	
Release group†	*N*	Length (mm)	*N*	Length (mm)	Percentage return‡	Selection coefficient	*P* value
1995							
In-river W	5331	107.37 (0.112)	5	113.80 (3.441)	0.094	0.790	0.039
In-river H	21,596	136.55 (0.119)	62	143.95 (2.200)	0.287	0.422	0.001
Transported W	3369	106.84 (0.140)	12	110.17 (2.873)	0.356	0.409	0.079
Transported H	15,583	136.17 (0.139)	93	141.62 (1.301)	0.597	0.315	0.002
1996							
In-river W	13,929	109.31 (0.07)	7	115.00 (1.83)	0.050	0.741	0.023
In-river H	53,420	139.45 (0.06)	53	146.59 (2.31)	0.099	0.479	0.001
Transported W	8656	110.49 (0.08)	10	113.00 (1.50)	0.116	0.351	0.139
Transported H	36,867	139.62 (0.07)	53	146.30 (2.14)	0.144	0.477	0.001

Notes: The year corresponds to year of downstream migration. *N* is the number of fish in each group.

† Fish were separated into wild (W) and hatchery (H) groups, and into fish that migrated downstream in-river and those that were transported.

‡ The percentage of the tagged population that returned as adults.

where $\bar{x}$ represents the mean of the trait. This measure incorporates information from all individuals and is a standard value that can be compared to a broad range of studies.

If mortality were random, we would expect an equally probable chance of observing each possible combination of traits measured as juveniles in a group of returning adults. Based on this, by repeatedly drawing random samples (without replacement) of size N_R from the original population ($\mathbf{x}_T$), we generated a distribution of the test statistic expected under the null hypothesis. We drew 100 000 samples, well above the number recommended by Manly (1997).

The *P* value for the test was determined by comparing the observed value of the test statistic to the distribution of randomly generated test statistics. The test can be set up as a one-tailed or two-tailed test. We used a one-tailed test with the length trait because we believed, a priori, that larger juveniles had a greater probability of returning as adults. For the release-date trait, we used a two-tailed test because we had no preconceived beliefs about the relationship between adult return rate and date of release. For the two-tailed test, the *P* value was either measured in the upper tail or the lower tail. We set α to 0.05.

Finally, we performed correlations between release date and release length to verify that the two variables were operating independently.

RESULTS

The evidence for size-selective mortality was similar for both the 1995 and 1996 migration years (Table 1). Returning adults of hatchery origin were highly significantly ($P < 0.005$) larger at tagging as juveniles than expected by chance (Table 1, Figs. 2 and 3). Returning adults from wild-origin juveniles that migrated in-river were significantly ($P < 0.05$) larger at tagging as juveniles than expected by chance. Returning adults of transported wild fish were not significantly different in size as juveniles than the general population. For these fish, however, the *P* values were relatively low (<0.15), and the number of returning adults was small, probably resulting in low power of the test to detect significant differences.

The results for the 1996 wild fish suggested that a size threshold may exist for naturally reared fish. For the in-river migrants, no adult fish returned that was <110 mm at tagging, and for transported groups no adult fish returned that was <108 mm at tagging. These size thresholds were exceeded by only 49% of the wild juveniles that migrated in-river and 65% of the wild juveniles that were transported.

All four categories of juvenile fish from migration year 1995 had returning adults with juvenile release dates that were highly significantly shifted compared to expectations under the null hypothesis (Table 2, Fig. 4). Fish that migrated in-river as juveniles were more likely to return as adults if they began migration early in the season, while fish that were transported as juveniles were more likely to return as adults if transported later in the season. In 1996 none of the four categories had returning adults that were significantly different from the entire tagged population in terms of release date (Table 2, Fig. 5).

The selection coefficients for length at tagging ranged from 0.315 to 0.790 (Table 1), while those for release date ranged (in absolute value) from 0.042 to 0.410 (Table 2). Endler (1986) compiled selection coefficients from studies on a broad range of organisms and found that approximately half the selection coefficients reported were <0.2. Thus, the selective mortality we observed, particularly for the length trait, was comparatively large.

When comparing release date to length, correlation coefficients for the eight data sets ranged from 0.00 to 0.024, indicating little correlation between the two traits.

Although the focus of our study was on selective

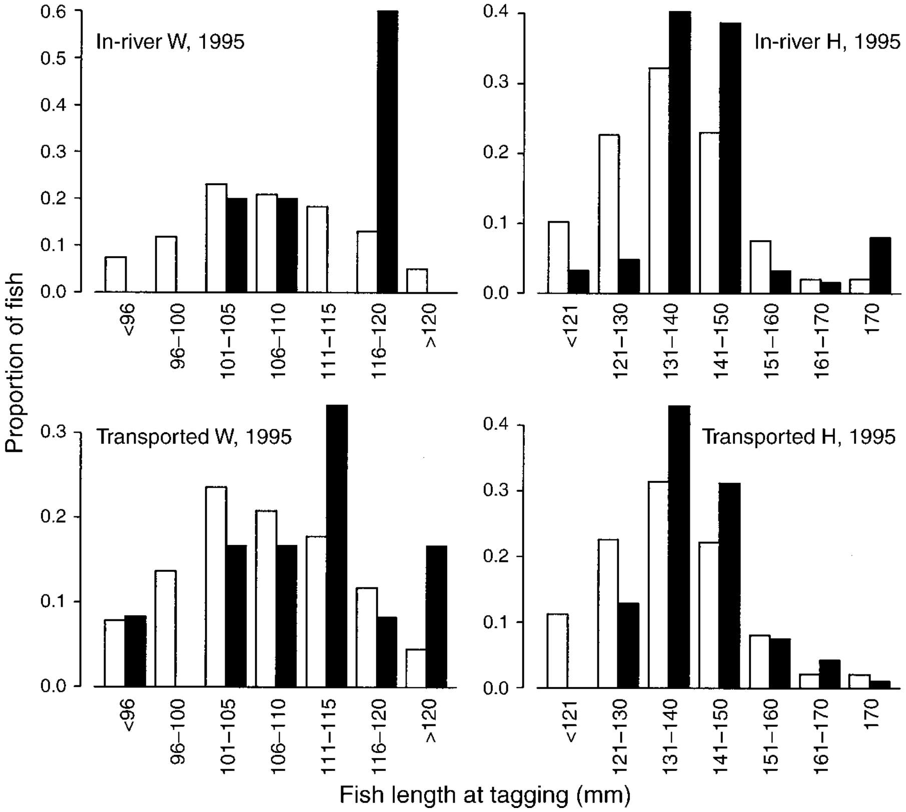

FIG. 2. Histograms of length at tagging for the entire tagged population (open bars) and for returning adults (solid bars) for 1995. Fish were separated into wild (W) and hatchery (H) groups, and into fish that migrated downstream in-river and those that were transported. The year corresponds to year of downstream migration.

mortality, we also presented return rates for the data groupings (Tables 1 and 2). Within transported and in-river migrating groups, hatchery fish always returned at a higher rate than wild fish, while within hatchery and wild groups, transported fish always returned at a higher rate than fish that migrated in-river. Return rates were at least three times higher in 1995 than in 1996 in comparable groups.

DISCUSSION

We observed marked trends in selective mortality related to migration timing and fish length in Snake River spring/summer chinook salmon. The combination of passive integrated transponder (PIT)-tag technology and the assumption-free Monte Carlo test we developed provides a strong method for measuring and testing for selection in natural populations. Although we did not examine whether these traits are heritable, the magnitude of the coefficients indicates a large potential for evolution if the traits are heritable, or a large potential for habitat management if they are environmentally determined.

Timing of migration

The hypothesis that salmonids optimize (within constraints) their seaward migrational timing, either to exploit peak feeding opportunities or avoid predation (Pearcy 1992), is supported both theoretically (Baker 1978, Walters et al. 1978, Godin 1982) and empirically (Ricker 1972, Brannon 1984, Tallman 1986, Beacham and Murray 1987, Randall et al. 1987, Taylor 1990*b*, 1991, Clarke et al. 1992). Migrational timing in salmonids is associated with the process of smoltification, which involves a series of behavioral, physiological, and morphological changes preparing fish for downstream migration and subsequent seawater entry (Hoar 1976). Thus the optimal timing of estuary/ocean entry involves an interplay between seasonally varying conditions of the seawater habitat and physiological condition of individuals. Arrival timing at the Columbia River estuary for Snake River spring/summer chinook populations is typically protracted over many weeks due to variability in the initiation of downstream migration (Achord et al. 1996) and the dispersal of populations as they move downstream (Zabel and Anderson 1997). This is typical of many salmonid populations and may serve as a ''bet-hedging'' strategy in the face of unpredictable environmental fluctuations (Pearcy 1992). However, any factor that *shifts* the migration timing of an entire population could result in suboptimal timing for the population (Walters et al. 1978).

Our results for migration year 1995 demonstrate the

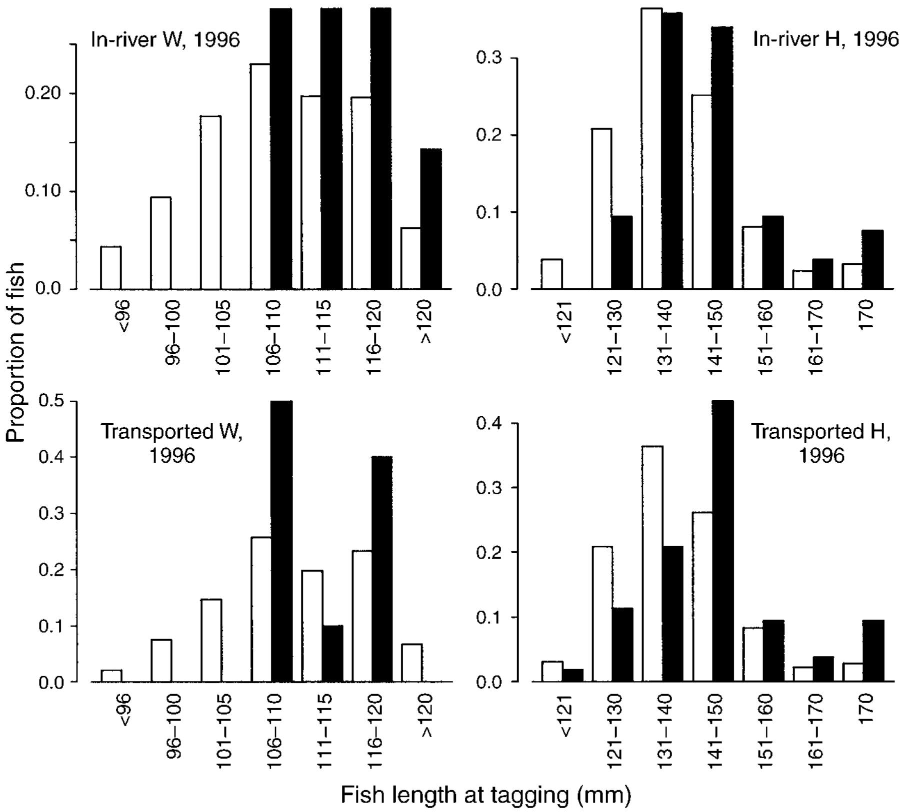

FIG. 3. Histograms of length at tagging for the entire tagged population (open bars) and for returning adults (solid bars) for 1996. Format is as in Fig. 2.

importance of migrational timing and the possibly deleterious effects of shifts in migrational timing resulting from hydroelectric dams and fish transportation. Dams have prolonged the downstream migration of Snake River spring/summer chinook by weeks by creating slack-water reservoirs and by acting as barriers to fish passage (Raymond 1979). In migration year 1995, fish that initiated migration earlier had higher smolt-to-adult survival than those initiating migration later. Late-migrating fish likely arrived at the estuary later than they would have under pre-dam conditions. Transported fish, however, completed the nearly 700-km downstream migration in two days (Marsh et al. 1996, 1997), several weeks faster than they would have migrating under pre-dam conditions. In migration year 1995, fish transported early in the season survived at

TABLE 2. The release day of year (mean with 1 SE in parentheses) for the total chinook population and returning adults.

	Total population		Returning adults			Monte Carlo test results	
Release group†	*N*	Mean release date (SE)	*N*	Mean release date (SE)	Percentage return‡	Selection coefficient	*P* value (tail)§
1995							
In-river W	31 766	119.81 (0.10)	63	114.81 (1.94)	0.198	−0.290	0.007 (L)
In-river H	104 279	121.06 (0.03)	321	118.42 (0.43)	0.308	−0.268	0.000 (L)
Transported W	21 359	119.84 (0.10)	78	125.77 (2.07)	0.365	0.410	0.000 (U)
Transported H	81 780	120.95 (0.03)	455	122.29 (0.40)	0.556	0.143	0.001 (U)
1996							
In-river W	14 078	117.62 (0.09)	7	116.43 (4.27)	0.050	−0.112	0.427 (L)
In-river H	53 976	126.52 (0.04)	53	126.23 (1.97)	0.098	−0.030	0.416 (L)
Transported W	8 699	117.80 (0.11)	10	114.5 (2.62)	0.115	−0.314	0.167 (L)
Transported H	37 027	126.09 (0.05)	53	125.68 (1.41)	0.143	−0.042	0.382 (L)

Notes: The year corresponds to year of downstream migration. *N* is the number of fish in each group.

† Fish were separated into wild (W) and hatchery (H) groups, and into fish that migrated downstream in-river and those that were transported.

‡ The percentage of the tagged population that returned as adults.

§ "U" corresponds to upper tail, and "L" to lower tail.

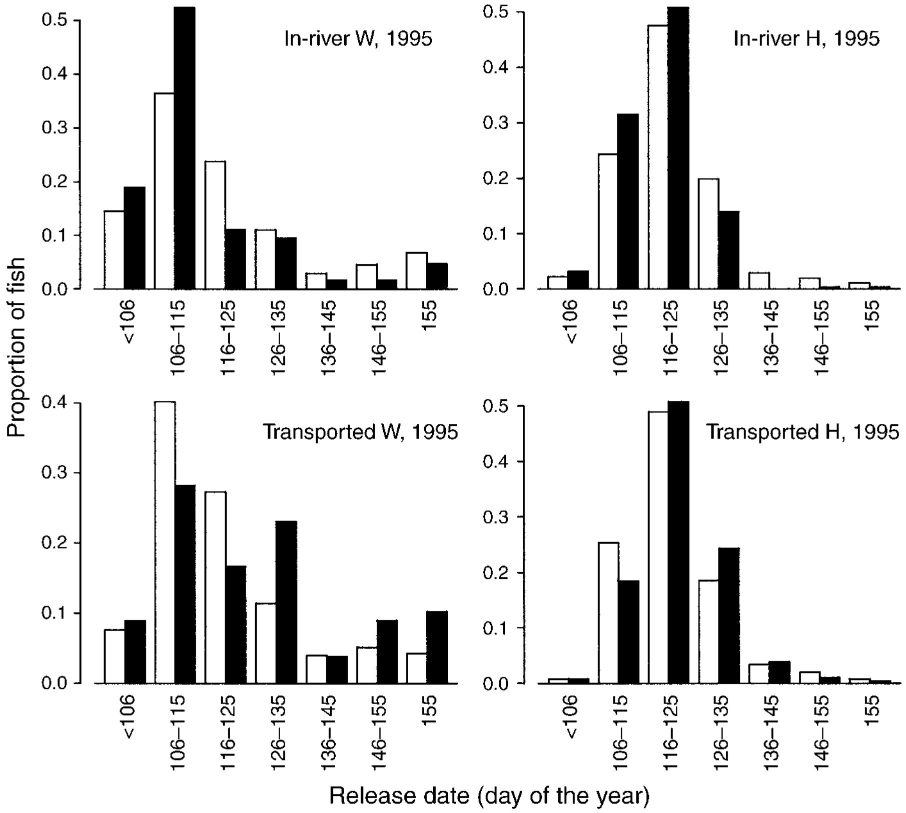

FIG. 4. Histograms of release date for the entire tagged population (open bars) and for returning adults (solid bars) for 1995. Fish were separated into wild (W) and hatchery (H) groups, and into fish that migrated downstream in-river and those that were transported. The year corresponds to year of downstream migration.

relatively poor rates compared to fish transported later. The early transported fish may have arrived in the estuary when conditions were suboptimal or before they were physiologically or behaviorally ready to enter seawater. Although the data presented here generally support the position that transportation improves overall survival (Tables 1 and 2), conditions may exist when it is better to allow fish to migrate volitionally.

Since the pattern observed in 1995 was not repeated in 1996, the timing process is likely complex, with year-to-year variation. Important factors in the estuary and nearshore ocean, such as temperature, food availability, and predator abundance, vary both seasonally and interannually (Pearcy 1992). Clearly, more years of data and studies designed to examine survival mechanisms will be required to further elucidate these patterns.

Fish length

While the question of where size-selective mortality occurs in the smolt-to-adult life phase of salmon is largely unanswered, Sogard (1997) suggested that in teleost fish it occurs through three mechanisms: differential vulnerability to predation; differential susceptibility to starvation or exhaustion; and differential tolerance of environmental extremes. The first two mechanisms appear most plausible for Pacific salmon. The majority of marine mortality incurred by salmonids occurs soon after ocean entry (Pearcy 1992), and size-selective predation on salmonids has been demonstrated in the early ocean phase (Parker 1971, Healy 1982, Hargreaves and LeBrasseur 1986, Holtby et al. 1990). Healy (1982) and Holtby et al. (1990) suggested that larger fish could escape predators with prey size thresholds. The starvation/exhaustion mechanism is supported by several recent studies that have demonstrated strong relationships between marine survival or overall salmon productivity and ocean conditions (Mantua et al. 1997, Hare et al. 1999, Beamish et al. 2000, Welch et al. 2000), which Welch et al. (2000) suggest is attributable to variability in ocean primary productivity. Upstream migration is energy costly for salmonids (Dodson 1997, Hinch and Rand 1998, Rand and Hinch 1998); long-distance migration in adult salmon can consume 75–95% of stored fat (Brett 1995). Further, adult body size has been related to cost of migration among populations (Schaffer and Elson 1975, Bernatchez and Dodson 1987). The larger early ocean growth rates experienced by larger smolts (Holtby et al. 1990) may confer a selective advantage in terms of the ability to accumulate enough energy to successfully complete the upstream migration.

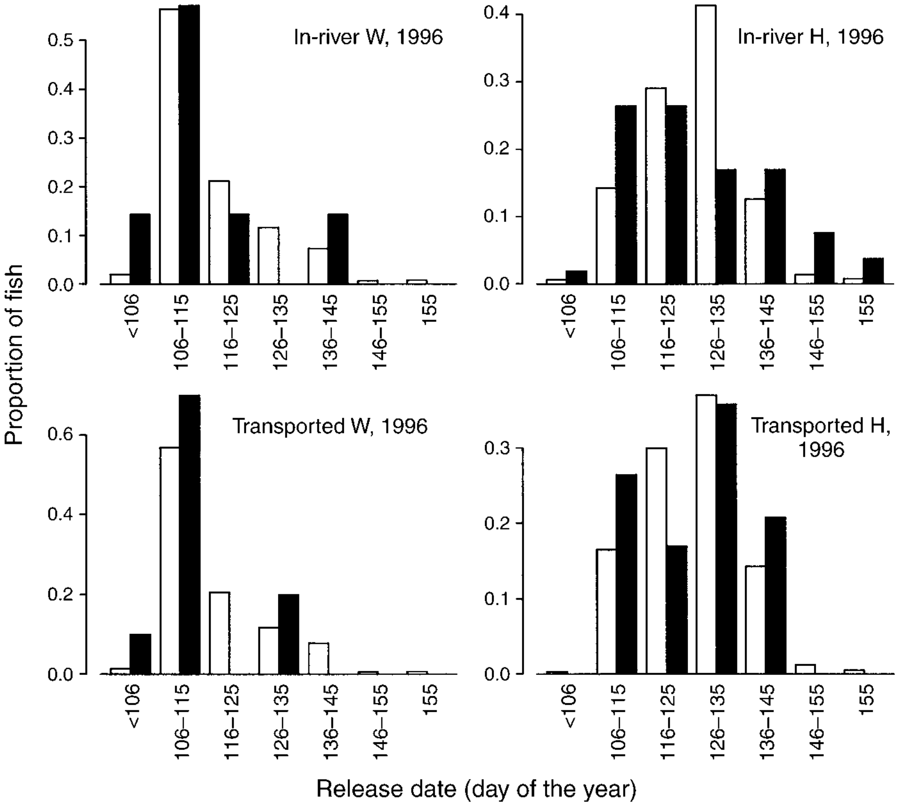

FIG. 5. Histograms of release date for the entire tagged population (open bars) and for returning adults (solid bars) for 1996. Format is as in Fig. 4.

An issue concerning many stocks of salmon in the Pacific Northwest is nutrient deficiency in rearing areas (Gresh et al. 2000). Bilby et al. (1996) demonstrated that marine-derived nutrients from adult carcasses are an important source for juvenile salmonids, and thus the reduced number of spawners that some streams have experienced recently may have led to nutrient deficiencies. Bilby et al. (1998) found that the size of juvenile coho salmon was increased by placing adult salmon carcasses in their rearing streams. In our analysis, Snake River spring/summer chinook salmon that attained larger sizes at the initiation of the seaward migration clearly had a better chance of returning as adults. Thus nutrient enhancement, which has been practiced for several decades in Alaska and British Columbia (Stockner and MacIsaac 1996, Bradford et al. 2000), may be a useful practice for wild populations of Snake River spring/summer chinook, particularly during periods of depressed adult returns.

Our results also suggest that increasing the size of hatchery fish at release would increase their smolt-to-adult survival. Hatchery fish, however, already are released substantially larger and in this study returned at a higher rate than wild fish (Tables 1 and 2). Since the potential exists for negative impacts of hatchery fish on wild fish (Levin et al. 2001) and since recovery efforts are directed at wild stocks, we do *not* recommend further increasing the release size of hatchery fish.

Quantifying potential effects of management actions

Given the existence of selective mortality, management actions that favorably shift distribution of traits within a population may result in increased survival. Here we estimate the potential magnitude of survival benefits resulting from this type of action. We calculate expected survival, S, for a population as

$$S = \frac{1}{N}\sum_{i=1}^{N} x_i \times s(x_i)$$

where N is the sample size, i is the ith individual, x is the level of the trait, and $s(x)$ is the survival probability for an individual with trait x. Potential survival benefits can be calculated by applying the above equation to the original distribution of traits and then to the distribution shifted by some increment.

To characterize the effects of selective mortality, we used logistic regression (Hosmer and Lemeshow 2000) to estimate the function $s(x)$. The logistic equation can capture a wide range of behaviors including nonlinear and threshold effects. We did not have adequate sample sizes to perform logistic regressions on all our data groupings, so we chose a single example: release date of wild fish migrating in-river in 1995 (Fig. 6).

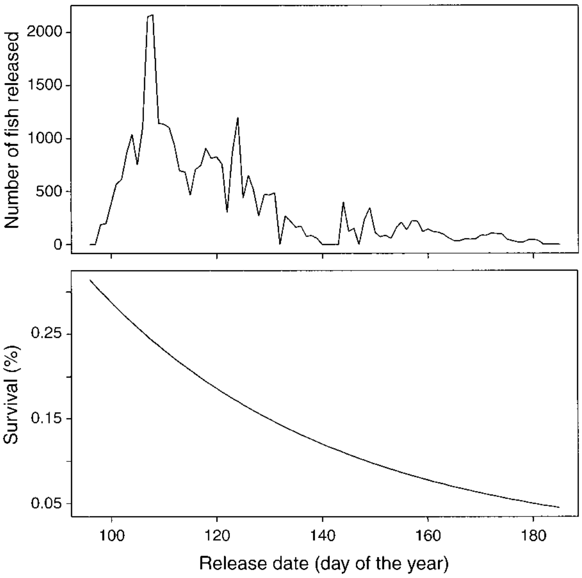

FIG. 6. The initial distribution of release dates (day of year; top plot) and survival probability as a function of release date (bottom plot) for the in-river, wild, 1995 data grouping. The survival probability function was estimated using logistic regression (See *Discussion: Quantifying potential effects. . .*).

TABLE 3. Potential salmonid survival benefits, measured in change in percentage survival (Δ% survival), in response to shifting the mean release date by one day for wild fish migrating in-river in 1995.

Mean release date (day of year)	Survival (%)	Δ% survival
119.8	0.198	0.00
118.8	0.203	2.21
117.8	0.207	4.46
116.8	0.212	6.77
115.8	0.216	9.12
114.8	0.221	11.53
113.8	0.226	13.99
112.8	0.231	16.50
111.8	0.236	19.07
110.8	0.241	21.70
109.8	0.247	24.38

For this exercise, we examined the effects of shifting the observed distribution of release dates by increments of one day (Table 3). Decreasing migrational timing by 2–10 d yielded survival benefits of 4–24%. If the survival benefits of earlier migration are due to earlier arrival at the estuary, then management actions to decrease migration time by increasing river velocity, such as flow augmentation or dam breaching, could result in increased survival in this range.

This approach is clearly simplistic: for instance, selection may operate on relative values of the trait within a population, not on absolute values; density-dependent effects may limit potential survival gains; or the survival model may be too simplistic. However, it serves to estimate the potential magnitude of benefits. In the example presented here, the magnitude of potential benefits warrants further study to better understand mechanisms of selective mortality or the development of an experimental management approach.

Managing migratory fish populations with evolutionary considerations

While the evolutionary effects of size-selective harvest on marine fish species is well documented (Borisov 1978, Brown and Parman 1993, Rijnsdorf 1993) other human-induced evolutionary forces on fish populations are not as well understood. Our results suggest that hydropower development and associated mitigation efforts (e.g., fish transportation) may present a new selective force on migratory fish populations. With thousands of large dams in the United States alone and many of them constructed in fish migration routes, they may substantially shape evolutionary processes in a variety of populations. In addition, human influences that diminish salmon populations may indirectly lead to the depletion of nutrients in rearing areas by reducing carcasses from spawning adults. Since growth opportunity is believed to be a factor in the selection of life-history traits in salmon populations (Gross 1987, Randall et al. 1987, Gross et al. 1988, Taylor 1990*a*), this depletion of nutrients in rearing areas may also have evolutionary consequences.

Managers need to recognize, though, that traits do not exist in isolation (Lande and Arnold 1983), and observed phenotypes are usually the results of tradeoffs (Roff 1992) or selection for suites of traits (Taylor 1990*b*). Further, artificially manipulating a population may have unforeseen consequences. For instance, increasing the size at migration of juvenile salmon may result in an increased proportion of precocious males (Gross 1985, 1991), potentially an undesirable effect. In perturbed systems such as the Snake and Columbia Rivers, however, humans have altered selective forces substantially. In cases where it is possible to demonstrate that human-induced shifts in selection pressure have resulted in negative impacts on populations, restoring selective forces to those under which populations evolved will potentially confer strong benefits. Any such actions, though, require caution, with full monitoring and experimental programs in place.

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