Response to Reviewers

# Reviewer 1

Comments:

General Comments

The paper is generally well-written with a very good Introduction and thorough Discussion sections. There are occasions where the paper is written with the Pacific Northwest (PNW) as the audience, and important details will be lost among the wider readership. This is particularly true when geographic locations are mentioned and their relevance to steelhead migration or study logistics are missing. The manuscript should be revised to catch these PNW-centric references without description or explanation. The section on Conservation Implications is way too long and needs to be better focused and shortened.

A serious disconnect in the paper is between the title, stated objectives, and reported results. The title references “Abundance” and the Results has two sections entitled “Overshoot fallback abundance” and “Overshoot abundance.” Neither of these sections provide a single abundance estimate. The authors are wrongly intermixing the concepts of abundance estimates with event probabilities (actually %). This is a serious error in the paper’s presentation and must be rectified throughout the manuscript. This oversight seems ironic because it is generally much more difficult to estimate abundance than it is an event probability. One need not estimate abundance to estimate transition probabilities; a good example is Richins and Skalski (2018). The authors seem not to appreciate the value of having both overshoot abundance and fallback probabilities.

*We did estimate abundance of fallbacks from Priest Rapids for every year (2010 – 2017) and presented those results in Table 1. Table 2 also includes estimates of fallback abundance to various downstream locations, by year and origin. It seems that I submitted an incomplete manuscript, or the journal software failed to add our table captions to the PDF that reviewers received, so that may be the source of confusion. To clarify this, we have added some text to the first and last sentences of the “Overshoot fallback abundance” section. Because the implications on monitoring and management rely more on the percentage of fish that are fallbacks from Priest, the text focuses more on these probabilities.*

Large overshoot abundance with a high fallback probability can be a much better situation than a low overshoot abundance with a very low fallback probability. Both abundance and the frequency of occurrence matter. This paper has both types of information but fails to use those results or convey their joint importance to readers. Having both of these pieces of information is also important to fish managers trying to prioritize which Columbia/Snake River dams to receive mitigation for steelhead overshoot.

*Table 3 presents annual estimates of both overshoot abundance at PRD, as well as the probability that overshoot fish successfully fallback. We also tried to address your example in the discussion using overshoots in the Snake River compared to the upper Columbia in figure 5 (higher abundance and lower fallback migration success)*

The statistical methods section lacks almost any mention of model assumptions. Providing priors in a Bayesian analysis is not a substitute for defining model assumptions and discussion of their robustness. Much more detail is needed.

*We have added text about the assumptions of the POM to the end of that section, and further assumptions at the end of “Overshoot abundance” section.*

Specific Comments

Line 33: Need to mention relevance of Bonneville Dam to the steelhead up-migration. It’s the first dam they encounter in the Columbia Basin.

*Added text*

Line 123: Provide river km to mentioned rivers.

*Added*

Line 139: Add PITAGIS after name is first mentioned.

*Added*

Line 146: Add assumptions of POM.

*Included a few sentences addressing these assumptions*

Lines 162–163: Unnecessarily complicated expression for Bernoulli distributed random variable.

*Removed the second line of this expression*

Lines 209–210: Symbols not defined.

*Clarified what Ri refers to, and changed order of expressions to better match text above.*

Lines 213–214: Explain the need for a Bayesian analysis of a straight-line regression.

*Added text in the “Fallback migration success” section to justify this. We used a Bayesian framework to easily incorporate the uncertainty in many of the dependent and independent variables.*

Lines 226–228: What are the assumptions when pooling across years? Do you expect the process to be stationary over time?

*We did update this analysis to include random effects in the intercept and slope for year. This allows for the relationship between overshoot success and number of dams to differ between years. In the end, the random effect variances were relatively small, suggesting the impact of dams on overshoot success to be fairly constant over this time period.*

Line 232: Wording; steelhead were not pooled.

*Changed to “Steelhead detections were pooled”*

Line 255: Characterize how atypical were the water temperatures in 2015.

*Added clarifying language*

Lines 291–294: Was the number of fish 7 or 8?

*Added clarifying language. 8 known overshoot wild steelhead were detected in tributaries overall, and of those 8, 7 of them were detected in tributaries above Wells dam (the remaining fish was detected in a tributary between Priest Rapids and Wells dams)*

Lines 386–389: Run on sentence.

*Revised.*

Tables: Tables lack captions.

*The captions were entered when the manuscript was submitted but did not appear in the PDF sent to reviewers. Hopefully the journal can correct this.*

# Reviewer 2

Comments:

This is an interesting paper and generally well written. However, it is not clear to an uninformed reader how much it adds to our knowledge beyond Richins and Skalski 2018 and Boggs et al. 2004. It would be helpful to identify in the Introduction section how this paper differs from Richins and Skalski 2018 and why it is an important contribution to science. The stock specific differences between the overshoots in the Snake and the Columbia is particularly interesting (Figure 4).

*Added clarifying language.*

There is also much citation of grey literature and a number of typos in the paper and the Table descriptions were not included making the tables difficult to evaluate.

*The captions were entered when the manuscript was submitted but did not appear in the PDF sent to reviewers. We have corrected that in the revision.*

I do not have expertise in Bayesian modeling so I cannot comment on the veracity of the modeling work. Perhaps someone with more expertise can evaluate the modeling.

*Please refer to Waterhouse et al 2020 for modeling simulations*

Maybe I missed it, but I didn’t see any mention about the possibility of PIT tag loss or failure. This may be a potential source of unexplained detections and mortality. Please include text or an assessment of this possibility.

*Pelvic girdle reportedly has high retention (99%) in walleye. Added reference.*

The introduction would benefit from additional references and information about natural overshoot and fallback (e.g., without dams or temperature alterations) as well as behavioral thermoregulation (Berman and Quinn in the Yakima)

*Berman and Quinn is a great paper, but describes movements within a spawning tributary and immediately before spawning (different spatial and temporal scales). The only paper we can find is for Chinook in the Yukon (Eiler et al 2015) and reported very low rates of overshooting (<1%). I also found some steelhead data from the Skeena and Upper Columbia in English et al 2006.*

Line 3 – do you mean warm water temperatures? If so, then please specify.

*Added clarifying language*

Line 13 – what years does this represent? Please insert years of the study.

*Added clarifying language*

13-15, 296-297 – is it the number of dams or the distance they migrate? How do you separate the two factors when they are correlated? If you used distance migrated in your model would you generate the same finding?

*The distance overshoot fish migrate is certainly correlated with the number of dams they must cross and therefore it would be impossible to fit a model with both number of dams and distance migrated. However, given the already great distances these fish swim during their lifespans, and their freshwater migration especially, as well as the fact that many Upper Columbia steelhead successfully swim at least that far to spawn in the Methow or Okanogan rivers, or even farther to spawn in tributaries of the Upper Salmon River, we find it an unlikely explanation that the extra river miles traversed is what leads to a reduction in overshoot fallback success. What separates overshoot fallback fish from fish that continue swimming upstream is that the dam passage moving downstream through turbine passage routes is a source of mortality.*

Line 80 – the authors claim they are the first to report overshoot and fallback in the abstract, but here it provides previously reported estimates. Which is correct?

*Estimates of overshoot and fallback abundance have not been reported to our knowledge. Previous research has described only the proportion of PIT tagged or radio tagged steelhead exhibiting this behavior.*

195-197 – were the assumptions of linear regression met when the ln transformation was made? How much of the variance was explained by the model? This seems like a very important analysis and should be included as a figure in the manuscript.

*We have revised the beginning of the first paragraph of the “Overshoots abundance” section within Results to present a pseudo-R2 and discuss whether the regression assumptions were met.*

216-219 – how was hooking mortality or unreported harvest of unclipped fish accounted for? Was it assumed that there was no harvest related mortality? How would this influence the results/conclusions?

*These types of mortality are all incorporated into the fallback migration success, . Added clarifying language. Included estimates of impacts in results (~1%)*

278-280 – can you provide an estimate of how many wild fish may be unmarked (e.g., bad clip) or scale misread hatchery fish? How might that effect estimates?

*Hatchery fish were identified using clips, PIT and CWT tags and finally scale pattern analysis. (Lines 137-138). Every effort was made to identify hatchery fish prior to our analysis. Hatchery smolts released as yearlings have a distinct scale pattern compared to wild fish. Hence, we do not have an estimate of misidentified fish.*

298-301 How much natural mortality above PRD would you expect given the length of time that they are in the river and also the potential of incidental or unreported harvest or mistaken hatchery broodstock collection? The amount that is predicted from the model (e.g., 0 dams) seems very low.

*PRD is actually the first dam overshoot fish in this system cross, so mortality above PRD corresponds to crossing one dam. 0 dams correspond to fish tagged in the Yakima basin as juveniles that have crossed McNary Dam (downstream of the Yakima River) but did not overshoot to PRD (which is upstream of the Yakima River) or Ice Harbor Dam on the Snake. For the logistic model, we did not use those 0-dam fish, but we did compare the intercept of the model (95.5% success) with the observed proportion of 0 dam fish that were detected in the Yakima (94.9%). The model predicts 88.9% success for fish that only cross one dam (PRD) and then return to the Yakima. Additionally, a radio telemetry study was conducted for two years during our study period and reported consistent mortality rates prior to Jan 1 (~9%) See Fuchs et al 2021. Unfortunately separating natural mortality from overshoot/fallback related mortality was not possible in that study, but the ~5% for non-overshoots from July through September seems very reasonable.*

*Fuchs, N. T., C. C. Caudill, A. R. Murdoch, and B. L. Truscott. 2021. Overwintering distribution and postspawn survival of steelhead in the Upper Columbia Basin. North American Journal of Fisheries Management 41 (3):757-774.*

390-392 – Why do you assume these sources of mortality when it is not clear what the other sources of mortality might be (e.g., hooking mortality, handling mortality, poaching, predation, etc.)? It seems that there needs to be more justification about why this assumption was made and why it is reasonable.

*Clarified this sentence to read, “While several potential minor spawning areas were not monitored using IPDSs (Fuchs et al. (2021), we assumed that most unsuccessful overshoot steelhead suffered the same rate of mortality in the mainstem as non-overshoot fish or downstream passage-related mortality from turbine strikes, as opposed to successfully spawning in an unmonitored tributary above PRD”*

450-459 – This seems to come way too late in the paper and finally acknowledges that there are multiple possible sources of mortality. What about the possibility of handling effects of tagged fish, particularly during warmer times, or disease associated with PIT tagging?

*All the fish discussed here (known overshoot fish) were tagged as juveniles, years before being detected as adults. We are assuming that any effects due to tagging them are negligible or have been overcome at this point. Low fallback migration success rate may be related to turbine strikes or high rates of straying. In summary, overshoots in the snake river and upper Columbia are different in magnitude and fallback migration success and warrant further study.*

460-463 – What about the possibility of increased straying?

*Yes. Good point. Line 452-453 we highlighted potentially higher straying in the Snake compared to upper Columbia*

480-482 – This assumes their survival would be higher in places that they overshot. If the places they overshot are warm (e.g., Yakima), then overshooting may help the population because they are able to be in cold water. Are there data that would allow you to evaluate this scenario? Otherwise, the statement should probably be modified.

*Added clarifying language. This sentence refers to the low fallback migration success as a factor, not overshoots per se. In theory, overshooting behavior in response to warm temperatures should provide a benefit but only if all overshooting fish were able to return to their natal stream without being delayed.*

493-495 – This is a policy statement and should be removed unless it can be tied to the science.

*Policy makers have already prioritized upstream migration survival to maximize escapement. Our research simply extends that concept for steelhead to downstream migration.*

496-499 – Unclear as written. Please revise

*Added clarifying language.*

523-527 – This isn’t clear to me. Are you saying that their should be genetic evaluation of the fishery to see if harvest is capturing overshoots?

*Yes. Periodic genetic evaluations could be used to ensure fishery models are still accurate under climate change.*

574 – year not specified

*Corrected*

706-709 – The text lists this as 2020 and there is a typo “form”. Please check all citations in text to see if they match with the lit cited.

*Corrected*

- Is the survival at the dams with surface passage better than the ones that don’t have it? This would support the recommendation alluded to in the paper, but if not then it should be explained and the recommendation should be reevaluated.

*You are correct. That is what the research is strongly suggesting. But it has not been explicitly incorporated into a study design that we are aware of.*

How is the mortality that occurs below PRD (e.g., in the Yakima River below Prosser) and before detections at the next downstream location handled and how might it effect the results?

*Good question. Any mortality in the lower Yakima below Prosser (or any mortality downstream of any tributary detection site) is incorporated into our results and outside the scope of the study.*

- The discussion would be improved with a paragraph about the influence of overshoot on straying. On the one had the paper describes issues with genetic introgression and then on the other hand it appears that there are very few fish that are on the spawning grounds above PRD.

*You are correct. Straying is not an issue above PRD, but maybe a huge issue in the Snake. We had a section on genetic introgression in the previous version but removed it based on previous reviewers comments. Some results from Blankenship et al 2011 can be simply explained by overshoot patterns, straying and genetic introgression*

*Blankenship, S. M., M. R. Campbell, J. E. Hess, M. A. Hess, T. K. Kassler, C. C. Kozfkay, A. P. Matala, S. R. Narum, M. M. Paquin, M. P. Small, J. J. Stephenson, and K. I. Warheit. 2011. Major lineages and metapopulations in Columbia River Oncorhynchus mykiss are structured by dynamic landscape features and environments. Transactions of the American Fisheries Society 140:665–684.*

- It would be interesting and relevant to compare survival of fish that overshot and returned to the Snake or Yakima vs. those that didn’t overshoot. It would be important to control for factors such as run timing etc.

*Please see lines 297-301. We used Yakima steelhead non-overshoot for comparison purposes but survival of non-overshoots (e.g., ~95%) from other populations may be different. Estimating survival to spawning or as part of a relative reproductive success study would give us the final missing piece.*

- Figure 2 – Is the first point referring to PRD or to PRD and Wanapum Dam? In other words should it be 1 or 2 dams. If it is 2 dams then should the model be rerun?

*The first point refers to PRD only. The lack of detections at Wanapum is reflected in the lack of points at dam = 2. Fish that make it to Rock Island (dam = 3) and further must have crossed Wanapum.*

- Tables – Please insert Table descriptions. I did not see the descriptions for the tables. Also, how do the very large annual confidence intervals factor into the interpretations

*The captions for tables were entered when the manuscript was submitted but did not appear in the PDF sent to reviewers. That was an oversight on our part. Large confidence intervals are due to small sample size issues and were outside our control. We did recommend ways to improve uncertainty related to juvenile PIT tagging programs within overshoot populations (line 325-330)*

*.*

# Associate Editor

Comments to the Author:

This manuscript describes a study where the authors used two PIT tag datasets to evaluate large-scale adult steelhead movements in the main stem Columbia River and entry into spawning tributaries. One dataset was comprised of adult steelhead collected and tagged at Priest Rapids Dam, several hundred river kilometers upstream from the Pacific Ocean. The second dataset included adult steelhead that were PIT tagged as juveniles at sites downstream from Priest Rapids Dam. In their analyses, the authors estimated that substantial proportions of the adults counted at the dam originated at downstream locations (i.e., they swam past or swam past or ‘overshot’ their natal tributary); the proportions that eventually moved back downstream varied considerably as a function of origin and upstream overshoot distance.

Two Reviewers with extensive familiarity with Columbia River steelhead and their behaviors have provided insightful comments on the manuscript. The Reviewers agreed that the findings of this study may be of interest to steelhead managers in the Columbia River basin but they also identified numerous areas for potential improvement, including a need to make it less colloquial. Their suggestions should be carefully addressed to improve the manuscript. Furthermore, two previous publications are fundamentally enmeshed with the current study: the first (Waterhouse at al. 2020) provides background on the occupancy and movement model the authors used in their evaluation; the second (Richins and Skalski 2018) provides a large group of comparable overshoot and fallback estimates for steelhead populations throughout the Columbia River basin. I think the current manuscript could be improved by providing more of the Waterhouse model details and assumptions and, importantly, by including more direct comparisons of the estimates in Richins and Skalski with the new study results, paying particular attention to the terminology used for the various behaviors and migration outcomes (confusing metrics are a weakness of the current manuscript). Aside from some qualitative similarity statements the “new” results are not especially well differentiated from the earlier work, recognizing that the data sources only partially overlap and so the results are largely confirmatory which is useful.

Line by line comments.

Line 6. I think there is potential for confusion around the term “fallback”. It has been used to describe downstream fish movement generally, as in Frank et al. (2009) and more specifically to describe passage downstream at dams through turbines and over spillways, as in Boggs et al. (2004). ‘Fallback success’ might have very different meanings in these two applications. Along these lines, the authors might consider adding a table where all terms and metrics are clearly defined.

*Fallback is a term that does need context. Thank you for the reference. We did not fully standardize terminology from the last revision. Our mistake. We have now and provided complete descriptions at the first usage within the main text. We believe the term fallback is used consistently as related to overshoot steelhead in Boggs et al. 2004; Naughton et al 2006; Keefer et al 2008; Khan et al 2013; Richins and Skalski 2020.*

Frank HJ, Mather ME, Smith JM, Muth RM, Finn JT, McCormick SD. What is "fallback"?: metrics needed to assess telemetry tag effects on anadromous fish behavior. Hydrobiologia. 2009;635:237-49.

Line 9. “was modified” – probably better to use active voice here and elsewhere.

*Sentence was changed*

Line 10. Insert “between” after “relationship”?

*added*

Line 20. affect = affected?

*Sentence was changed*

Line 27. Insert “Adult” to begin sentence?

*Added*

Line 37. Greater risk than what – some other population?

*Added clarification*

Line 42. Consider defining overshoot here at first mention.

*Added clarification*

Line 74. Eiler citation is for the Yukon River not the Columbia.

*Deleted*

Line 77. Rates = percentages to match 71%. Also see reviewer comments.

*Corrected*

Line 82. Should fall back be two words here?

*Corrected*

Line 95. Downstream-migrating. Hyphen.

*Corrected*

Line 97. Define non-spill periods.

*Added clarifying language*

Line 108. Please provide more geographic details about the dam location.

*Added clarifying language*

Line 112. The long preamble in the introduction about water temperature, steelhead behavior, and harvest does not set up the objectives especially well. Did the authors have hypotheses about temperature effects on behavior? It might help to provide some expectations at the end of this important paragraph.

*Added clarifying language*

Line 119. Again, providing some details on the locations of these dams in relation to each other or at least generally would help unfamiliar readers orient.

*An important figure with lots of information. Some additional language was added.*

Line 142. It would be appropriate to mention approximately how many IPDS there were.

*Added this.*

Line 151. Citations should be chronological.

*Corrected*

Line 152, 167. Verb tense should be past for completed work.

*Corrected*

Line 168. Total abundance in this case means the total count of steelhead at PRD?

*It means the adjusted total count, after accounting for re-ascension / double counting at PRD.*

Line 178. On first read, not clear that the three letter abbreviations reference sites on the map.

Line 204. See general comments about adding a table summarizing the metrics. Fallback migration success, fallback abundance, overshoot abundance, and overshoot fallback abundance are all mentioned in this paragraph and the lines separating them seem a little blurry.

*We have reduced the number of terms and standardized their usage. Also clearly defined terms when first used in the text.*

Line 212. Was a specific R package used?

*Noted specific R package, and changed citations to better match AFS style guide*

Line 221. Is “fallback migration success” a synonym for overshoot return?

*Yes. We have reduced the number of terms and standardized their usage. Sorry for the confusion.*

Line 230. This analysis of Yakima steelhead at McNary Dam was not included in the objectives statement that I recall.

*Revised the end of this paragraph to better clarify why those PIT tags were used (as model validation, not a separate analysis)*

Line 250. Why not instead include the monthly means for all study years?

*All years is not available. Our intent was to illustrate future conditions under climate change (prospective v. retrospective)*

Line 258. PIT-tagged adult steelhead. Hyphen. Check for consistent use.

*Corrected and checked*

Line 260. The final sentence in this paragraph seems divorced from the temperature and timing threads that preceded it.

*Created new paragraph and provided more context.*

Line 264. I think including a summary of the PIT-tagged samples would be appropriate at the start of the results section. It looks like about 120,000 adult steelhead were counted at PRD but the numbers of adults PIT tagged at the dam and the numbers of adults PIT tagged as juveniles are not obviously reported.

*Added summary statistics for wild fish*

Line 267. The count adjustment method was not described. Did this follow some previous procedure such as the one described by Boggs et al. or perhaps English at al.?

*Added a description of this method in the “Overshoot fallback abundance” methods section.*

Line 279. Verb tense – originated. Some of this material reads like methods.

*Changed. Some may be redundant but added clarifying language.*

Line 283. What is the relevance of this time series correlation?

*Added clarifying language. Estimates of overshoot abundance combined with upstream escapement did a good job of accounting for the number of fish counted at PRD.*

Line 288. Including sample size (n’s) for these percentages would put the effort into better perspective. Proportion should read percentage.

*Added sample sizes and changed proportion to percentage*

Line 310. Please add degree symbol after 20.

*Corrected*

Line 319. overwintering-related. Hyphen.

*Added*

Line 317. Does this manuscript report escapement estimates? Or only the aggregate count of wild steelhead at PRD?

*No. But we included them in a figure related to the total dam count.*

Line 327. This material about sample size needs might be better located later in the discussion under something like caveats and recommendations.

*Moved to later in discussion*

Line 340. “does compare well” is very imprecise. See general comments.

*Deleted and changed sentence*

Line 345. Should “dam counts” instead be “adult steelhead counts at dams”? Also the unpublished data referenced here and on lines 358 and 377 probably needs a bit more information. What if readers wanted to access this material? Perhaps a contact person and a pers. comm. citation.

*Reference added*

Line 371,372. observed = detected. are = were.

*Corrected*

Line 376. proportion = proportions.

*Corrected*

Line 380. are = were.

*Corrected*

Line 392. Mortality may also occur for fish passing via spillways, bypasses, or other routes mentioned in the text, not just turbines?

Line 417. have = had. proportion = percentage – check for consistent use.

*Corrected*

Line 435. This 507% finding would be appropriately noted in the results section. Perhaps an objective or hypotheses about differences between PRD and IHD groups would be appropriate as well.

*Language was changed to “over five times greater”. This information was introduced into the discussion only for comparison purposes and to highlight areas where a similar type of analysis is warranted. Lack of PIT tag detectors until 2014 was also an issue.*

Line 439. patterns…similar to those.

*Corrected*

Line 451. Verb tenses. Overshot, fell back.

*Corrected*

Table 1. Include rows with the mean and standard deviation as in tables 2 and 3?

*Done*

Table 2. Labeling or data error for row “Year”?

*Not sure what this refers to. The entire column has a column header called “Run Year”.*

Figure 1 caption. Perhaps define IPDS given similarity to DPS.

*Corrected*

Figure 2 caption. The figure shows perfect a probability and a confidence envelope derived from a logistic regression model, not a logistic regression per se.

*Revised*

Figure 3 caption. Why “Priest” instead of PRD or Priest Rapids Dam? Check for consistent use.

*Changed to “Priest Rapids Dam”*

Figure 4 caption. Insert “detected” after segment?

*Revised*