

From: [Schaller, Howard](#)
To: [Nanette Seto](#)
Cc: [Steve Haeseke](#); [Christina Wang](#); [Rich Johnson](#)
Subject: Double-crested cormorant predation
Date: Monday, March 16, 2015 4:18:55 PM
Attachments: [DRAFT -Evaluating the degree of compensatory mortality.docx](#)

Hi Nanette

I wanted to share with you the follow-up analysis that Steve Haeseke performed that is related to predation effects of double -crested cormorants on the Snake River steelhead population. I know Steve has been working with you and your folks on this issue and wanted to give you an opportunity to provide feedback on the analysis and draft paper. Here is a summary of the findings:

The effectiveness of actions to reduce predation by double-crested cormorants depend on the degree that predation by double-crested cormorants is an additive versus a compensatory source of mortality for salmonid populations. Using published methods and several long-term data sets, Steve evaluated this important question of whether cormorant-induced mortality is an additive or compensatory source of mortality for Snake River steelhead, the population that has shown the greatest predation impacts from double-crested cormorants. Results indicated that cormorant-induced mortality on steelhead is compensated-for through reductions in other sources of mortality, resulting in no change in population productivity as measured by smolt-to-adult return rates. Statistical tests strongly rejected ($p < 0.0001$) the additive mortality hypotheses that has been assumed. These results indicate that efforts to reduce cormorant predation on steelhead (e.g., culling) are expected to have little to no effect on Snake River steelhead population productivity or the abundance of returning adults. Because cormorant predation rates are lower on other Snake River salmonid populations compared to Snake River steelhead, culling efforts are similarly unlikely to benefit the productivity of these other salmonid populations.

Attached is the latest draft of the analysis write-up.

I am on leave the next two weeks, but if you have any questions feel free to contact Steve. We will be more than happy to go through the document and findings.

Thanks.

Howard

--

Howard Schaller, Project Leader
Columbia River Fisheries Program Office
U.S. Fish & Wildlife Service
1211 SE Cardinal Court, Suite 100
Vancouver, WA 98683

Phone: 360 604-2500
www.fws.gov/columbiariver/

DRAFT: Tests of whether double-crested cormorants are an additive versus compensatory source of mortality for Snake River steelhead

Steven L Haeseke
Columbia River Fisheries Program Office
Vancouver, Washington

Executive summary

The effectiveness of actions to reduce predation by double-crested cormorants depend on the degree that predation by double-crested cormorants is an additive versus compensatory source of mortality for salmonid populations. If the cormorant-induced mortality is additive, as is assumed, then reductions in predation are expected to result in increased population productivity and adult abundance through efforts to reduce the cormorant-induced mortality. However, if the cormorant-induced mortality is compensated-for by commensurate reductions in mortality from other sources, then population productivity and adult abundance will be unaltered by efforts to reduce cormorant-induced mortality. For example, reductions in predation risk from one predator can be compensated by increased risk from other predators in complex ecosystems where several predators compete for the same prey, with no change in overall productivity following single-predator controls or removal.

Snake River steelhead have been identified as the species that has experienced the highest estimated levels of cormorant-induced mortality and are assumed to benefit most from cormorant culling efforts. Although potential compensatory responses to culling efforts have been recognized as an important factor to consider, there has been no research to quantify the degree that cormorant-induced mortality is an additive or compensatory source of mortality for steelhead or other salmonids. Instead, cormorant-induced mortality has been assumed to be a completely additive source of mortality. Using three, long-term (1998-2009) data sources on Snake River steelhead (fish transported from Lower Granite Dam, fish detected at Lower Granite Dam, and fish detected at Bonneville Dam), we conducted statistical tests to determine whether cormorant predation on steelhead was an additive or compensatory source of mortality. We also evaluated cormorant-induced mortality within the context of other factors (e.g., water velocity, spill levels, and ocean conditions) that have been shown to influence smolt-to-adult survival rates in order to account-for variation that may obscure the effects of cormorant-induced mortality. For comparative purposes, we also conducted statistical tests to determine whether mortality during juvenile migration through the hydropower system was an additive or compensatory source of mortality.

Graphical analyses showed that as cormorant-induced mortality increased, there was a commensurate reduction in mortality from all other sources, consistent with expectations under complete compensation. Across the range of cormorant-induced mortality rates, there was no decline in smolt-to-adult return rates, also consistent with expectations under complete compensation. For all three data sets, statistical tests supported the hypothesis that cormorant-induced mortality was completely

compensatory and strongly rejected ($p < 0.0001$) the hypothesis that cormorants were an additive source of mortality. Regression models showed that cormorant-induced mortality had no effect on smolt-to-adult return rates after accounting for other sources of variation. In contrast, statistical tests supported the hypothesis that mortality during juvenile migration through the hydropower system was additive and strongly rejected ($p < 0.0001$) the hypothesis of complete compensation.

These research results indicate that cormorant-induced mortality on steelhead is compensated-for through reductions in other sources of mortality, resulting in no change in population productivity as measured by smolt-to-adult return rates. Results also showed that the additive mortality assumption is inconsistent with available data. As a consequence, efforts to reduce cormorant predation on steelhead (e.g., culling) are expected to have no effect on Snake River steelhead population productivity or adult abundance. Since Snake River steelhead were most likely to benefit from reductions in cormorant-induced mortality but showed none, benefits to other species are also unlikely. However, improvements to survival during juvenile migration are expected to increase population productivity because mortality through the hydropower system was found to be an additive source of mortality.

Introduction

The effects of avian predation on salmonid populations are a key issue facing fisheries and wildlife managers. Many avian species are protected under the Migratory Bird Treaty Act, but avian predation has been identified as a factor that has reduced the productivity of salmonid populations listed under the Endangered Species Act within the Columbia River basin (NOAA Fisheries 2014). Concerns over avian predation impacts led to Reasonable and Prudent Alternative (RPA) Action 46, an action to reduce the double-crested cormorant population from current abundance levels (ca. 13,000 pairs) to no more than 5,380 to 5,939 pairs on East Sand Island (NOAA Fisheries 2014).

The efficacy of actions to reduce predation by double-crested cormorants depends on the degree to which predation by double-crested cormorants is an additive versus compensatory source of mortality for salmonid populations (Roby et al. 2003). Predation by double-crested cormorants has been assumed to be a completely additive source of mortality (USACE 2014). Under this assumption, reductions in double-crested cormorant predation are expected to lead to a direct increase in the overall survival of salmonid populations (Roby et al. 2003, Lyons et al. 2014). Alternatively, mortality caused by cormorants could be compensated-for by a corresponding reduction in other sources of mortality (ISAB 2011), resulting in no change in overall survival rates.

Double-crested cormorants are but one of many piscivorous predators that consume juvenile salmonids. Other known predators of juvenile salmonids include: Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), chub mackerel (*Scomber japonicus*), spiny dogfish (*Squalus acanthias*), adult salmonids, walleye (*Sander vitreus*), northern pikeminnow (*Ptychocheilus oregonensis*), pinnipeds, Caspian terns (*Hydroprogne caspia*), brown pelicans (*Pelecanus occidentalis*), sooty shearwaters

(*Puffinus griseus*), common murre (*Uria aalge*), mergansers (*Mergus* spp.), gulls (*Larus* spp.), belted kingfisher (*Megaceryle alcyon*), grebes and loons (*Gavia* spp.), herons (family Ardeidae), osprey (*Pandion haliaetus*), and bald eagles (*Haliaeetus leucocephalus*). Because juvenile salmonids have many potential predators, predation mortality by double-crested cormorants may be compensatory, where juvenile salmonids not consumed by double-crested cormorants are instead consumed by other predators with no change in overall survival or productivity (Ellis-Felege et al. 2012). For example, Ellis-Felege et al. (2012) found that reductions in predation risk from one predator can be compensated by increased risk from other predators in complex ecosystems where several predators compete for the same prey. A critical question that has not been examined is whether reductions in cormorant predation are compensated-for through reductions in mortality from other sources or species. If predation by double-crested cormorants is completely compensatory, actions to reduce the double-crested cormorant population will have zero efficacy in terms of increasing salmonid productivity or survival rates (Roby et al. 2003, Lyons et al. 2014).

Both the USACE (2014) and NOAA Fisheries (2014) recognize that the level of compensation is a critical factor for understanding the effects of predation and for characterizing the efficacy of predator control efforts on salmonid populations. However, both agencies state that the magnitude of compensation associated with avian predation on juvenile salmonids is “unknown” (USACE 2014, NOAA Fisheries 2014). Despite this uncertainty, economic and survival benefits associated with reduced predation by double-crested cormorants have assumed that predation mortality is completely additive (i.e., zero compensation) (USACE 2014). To date, there have been no efforts to quantify the degree to which predation by double-crested cormorants is completely compensatory, completely additive, or at some intermediate level between these two possibilities.

Of the salmonid species and populations that have been assessed, estimates of double-crested cormorant predation mortality have been highest on Snake River steelhead (USACE 2014, Evans et al. 2012), and therefore the benefits of reductions in double-crested cormorant predation have been calculated to be highest for Snake River steelhead (Lyons et al. 2014). Because Snake River steelhead have been consistently tagged with Passive Integrated Transponder (PIT) tags for nearly two decades, tagging has occurred over years when the abundance of double-crested cormorants has varied extensively, and tagged fish are present over the migration season and therefore across the seasonal range of double-crested cormorant predation intensity, Snake River steelhead provide an ideal case study to assess the degree of compensatory versus additive predation mortality caused by double-crested cormorants. Because the estimates of predation mortality by double-crested cormorants have been highest on Snake River steelhead, this population is most likely to demonstrate that double-crested cormorant predation mortality is additive, if this in fact is the case.

Methods for quantifying the degree that mortality is compensatory versus additive were first described by Anderson and Burnham (1976). Burnham and Anderson (1984) subsequently developed a discriminant function test of the two opposing hypotheses of complete compensation versus total additivity. Burnham and Anderson (1984) also conducted Monte Carlo studies to validate the procedure and demonstrate the power of the test. Burnham et al. (1984) further described a more direct, general methodology to assess the degree of compensatory versus additive mortality along with hypothesis

tests. The main objective of this study is to quantitatively determine the degree to which double-crested cormorant predation on Snake River steelhead is compensatory or additive using the methods described by Burnham et al. (1984). For comparative purposes, we also evaluated the degree to which mortality of Snake River steelhead during migration through the Federal Columbia River Power System (FCRPS) is compensatory or additive using the same methods.

Another method to evaluate whether predation by cormorants reduces steelhead productivity is to examine cormorant predation rates within the context of other freshwater and ocean environmental factors that have been associated with steelhead survival rates (Haeseke et al. 2012, Hall and Marmorek 2013). By accounting for the various factors that explain variations in survival rates, the variation due to cormorant predation can be assessed. If cormorant predation is an important factor that contributes to reduced survival of steelhead, the expectation is that there would be a significant, negative association between cormorant predation rates and survival after accounting for other freshwater and ocean factors that have been identified as important factors for steelhead (Haeseke et al. 2012, Hall and Marmorek 2013, Schaller et al. 2014). Using the data and models described by Hall and Marmorek (2013), we evaluated whether cormorant predation reduced smolt-to-adult return rates of steelhead, accounting for the other freshwater and ocean environmental conditions that have been identified as important factors associated with steelhead survival rates.

Methods

Four sets of data on Snake River steelhead were used for the analysis. A cohort approach was used to identify groups of PIT-tagged steelhead that were detected over two-week intervals at either Lower Granite Dam or Bonneville Dam during 1998-2009. The first data set consisted of fish that were tagged or collected at Lower Granite Dam and subsequently transported to below Bonneville Dam (Appendix A). The second data set consisted of fish that were tagged or collected at Lower Granite Dam and subsequently bypassed to continue their in-river migration (Appendix B). The third data set consisted of fish that were detected passing Bonneville Dam (Appendix C). The use of Lower Granite Dam as the starting point allowed for higher sample sizes than were available at Bonneville Dam, and separately analyzing transported versus in-river migrants provides for the opportunity to evaluate whether there are differences in the level of compensation between the two groups. The use of Bonneville Dam as the starting point is consistent with the approach used by other researchers estimating the levels of cormorant predation using PIT tags (Evans et al. 2012, USACE 2014). Cohorts were limited to cases where at least 200 fish were available for analysis. The fourth data set was similar to the second data set on in-river migrants with the exception that it was limited to cohorts where in-river survival estimates ($S_{LGR-BON}$) from Lower Granite Dam to Bonneville Dam cohorts were available (Appendix B). This data set was used to evaluate the degree that mortality experienced during passage through the hydrosystem, $1 - S_{LGR-BON}$, was a compensatory or additive form of mortality.

For each cohort, the number of juveniles was enumerated along with the number of subsequent recoveries of the associated PIT tags from those juveniles on the East Sand Island within the double-crested cormorant nesting and rearing area. Recoveries included those fish that were detected in the year of migration as well as those detected in subsequent years. Preliminary analyses indicated that

tags can be detected up to several years after deposition. By using the cumulative number of recovered tags, the need to account for variable, first-year detection probabilities using sown tags (Evans et al. 2012) is reduced. The recovery rate was calculated as the cumulative number of PIT tags detected on the double-crested cormorant colony divided by the starting number of PIT-tagged juveniles for each cohort (i) and data set using

$$Recovery Rate_i = \frac{Cumulative\ detections_i}{PIT\text{-}tagged\ juveniles_i}$$

As recognized by Evans et al. (2012), not all PIT tags consumed by double-crested cormorants are deposited on the colony and available for possible recovery. The term for this is deposition probability. Lyons et al. (2014b) estimated through feeding studies that the mean deposition probability for double-crested cormorants on East Sand Island was 0.51. The consumption rate was calculated as the recovery rate divided by the deposition probability of 0.51 for each cohort (i) and data set:

$$Consumption Rate_i = \frac{Recovery Rate_i}{0.51}$$

Because compensatory mortality processes can occur at any point over the life-cycle, we used the Smolt-to-Adult Return rate (SAR) to measure the cumulative effects of mortality over the life-cycle. In addition, SARs and changes in SARs (e.g., lambda analyses) were used by the USACE (2014) to characterize economic and productivity benefits of various control options for double-crested cormorants, and therefore SARs are an appropriate metric to evaluate the degree that cormorant predation is a compensatory versus additive source of mortality. SARs were calculated using

$$SAR_i = \frac{Adults_i}{PIT\text{-}tagged\ juveniles_i}$$

where $Adults_i$ is the number of adult steelhead detected at Lower Granite Dam from cohort (i).

Anderson and Burnham (1976) provide graphical illustrations of the relationship between hunting mortality rates (K), nonhunting mortality rates (V), and survival rates (S) under the hypothesis of complete compensation. Adapting these figures and terminology to the case of double-crested cormorant predation as the source of mortality and using SARs as the measure of steelhead survival, these figures define the expected relationship between non-cormorant mortality and cormorant mortality as well as the relationship between SARs and cormorant mortality under the hypothesis of complete compensation (Figure 1). As defined by Anderson and Burnham (1976), below a level of mortality (C), populations are resilient and can compensate for increased levels of mortality. But beyond this level, increasing mortality levels reduce survival rates. At mortality levels less than C , the relationship between mortality rates and survival rates is

$$S = S_0 \text{ if } K \leq C.$$

Under the complete compensation hypothesis, the non-cormorant mortality rate (V) decreases as the cormorant mortality rate (K) increases with a slope (b) equal to -1. The illustrations of Anderson and Burnham (1976) therefore provide two graphical patterns that would be expected under the hypothesis

of complete compensation. First, there should be a negative association between the non-cormorant mortality rate (V) and the cormorant mortality rate (K) with a slope equal to -1. Second, there should be no association between SARs and the cormorant mortality rate (i.e., a slope equal to zero). Under this framework, the cormorant mortality rate (K) is defined to be the cormorant consumption rate. The non-cormorant mortality rate (V) is then calculated as

$$V_i = 1 - SAR_i - K_i .$$

Using graphical presentations of the data on cormorant mortality rates, non-cormorant mortality rates and SARs, we evaluated whether the data were consistent with the expectations listed above under the hypothesis of complete compensation (Anderson and Burnham 1976, Allen et al. 1998).

Formal tests for evaluating the degree of compensatory versus additive mortality developed by Burnham and Anderson (1984) and Burnham et al. (1984) were originally applied to the question of whether the effects of hunting on mallards (*Anas platyrhynchos*) were additive or compensatory using band recovery data. They developed a structural model that described the relationship between survival rates and hunting rates. Adapting their structural model to the topic of steelhead survival rates and double-crested cormorant consumption rates, the model used to test the degree of compensatory versus additive mortality is

$$S_i = S_0(1 - bK_i),$$

where S_i is the SAR in period i , S_0 is the SAR in the absence of cormorant predation, K_i is the cormorant consumption rate in period i , b is the slope of the linear relationship between the SAR and the cormorant consumption rate, normalized such that $0 \leq b \leq 1$ (Burnham et al. 1984). For the fourth data set where mortality during migration through the FCRPS is being evaluated, K_i is equal to $1 - S_{LGR-BON}$. When b is equal to zero, the data support a hypothesis of complete compensation. When b is equal to one, the data support a hypothesis of total additivity. Intermediate values between zero and one (e.g., 0.5) indicate that mortality is neither completely compensatory nor totally additive. The null hypothesis of complete compensation ($H_0: b = 0$) is evaluated using the test statistic

$$z = (\hat{b} - 0) / \widehat{se}(\hat{b}) .$$

The null hypothesis of total additivity is evaluated using the test statistic

$$z = (\hat{b} - 1) / \widehat{se}(\hat{b}).$$

Both parameters (S_0 and b) of the structural model of Burnham et al. (1984) are defined with $0 \leq S_0 \leq 1$ and $0 \leq b \leq 1$. Therefore inverse-logit functions $\hat{S}_0 = 1/[1 + \exp(-\beta_1)]$ and $\hat{b} = 1/[1 + \exp(-\beta_2)]$ were used to constrain estimates \hat{S}_0 and \hat{b} within these boundaries. Maximum likelihood methods were used to estimate model parameters. Bootstrapping techniques (Efron and Tibshirani 1993) consisting of 3,000 replicates with replacement were used to estimate the variability in \hat{b} ($\widehat{se}(\hat{b})$) for testing the complete compensation and total additivity null hypotheses listed above.

The second approach for evaluating whether cormorant predation levels reduce smolt-to-adult return rates was to include cormorant consumption estimates within the multivariate regression models described by Hall and Marmorek (2013). Those models showed that most of the variability in steelhead SARs was associated with migration timing (i.e., day of release), water transit time (a measure of water velocity), spillway passage, and ocean conditions as indexed by the Pacific Decadal Oscillation (PDO). The data for this analysis consisted of the SARs and cormorant consumption rate estimates presented in Appendix B along with the associated estimates of water transit time (WTT), spillway passage rates, and summer PDO values that were used in Hall and Marmorek (2013). Spillway passage rates were estimated using models that quantified the effects of flow and the proportion of water spilled on spillway passage proportions, using methods described by Tuomikoski et al. (2012) and Hall and Marmorek (2013). Model-averaged coefficients and their unconditional standard errors (Burnham and Anderson 2002) were calculated using all-subsets regression using standardized estimates for each of the freshwater, ocean, and predation factors analyzed. If cormorant consumption rates were a significant factor that reduced steelhead SARs, then the estimated coefficient for cormorant consumption rates is expected to be negative with confidence bounds that do not overlap zero.

Results

The graphical presentations were consistent with the hypothesis of complete compensation for all three data sets that examined the effects of cormorant consumption rates on non-cormorant mortality and SARs. Estimates of non-cormorant mortality rates declined with increases in cormorant consumption rates (Figure 2). The slope of the relationships between non-cormorant mortality rates and cormorant consumption rates were all near -1. Consistent with the compensatory mortality hypothesis, there was no association between SARs and cormorant consumption rates (Figure 3). Therefore the data are consistent with expectations under the compensatory mortality hypothesis.

Maximum likelihood estimates of b and the associated standard errors for each data set are provided in Table 1. All three data sets that analyzed double-crested cormorant consumption as the mortality source support the hypothesis of complete compensation ($p = 0.78$ for steelhead transported from LGR, $p = 0.82$ for in-river detections at LGR, and $p = 0.53$ for in-river detections at BON). All estimates of b were near zero, ranging from 0.008 to 0.053. All three data sets rejected the hypothesis that cormorants are an additive source of mortality ($p < 0.0001$). In contrast, the data set that analyzed mortality during migration through the hydrosystem supported the hypothesis of total additivity ($p = 0.99$) and rejected the hypothesis that mortality during migration through the hydrosystem is compensatory ($p < 0.0001$), with a maximum likelihood estimate of b near one (0.99).

After incorporating cormorant consumption rates into the multivariate regression model described by Hall and Marmorek (2013), we found that cormorant consumption rates were not a significant factor that explained variability in steelhead SARs (Figure 4). As evidenced by coefficient confidence intervals that did not overlap zero, increases in steelhead SARs were significantly associated with earlier migration timing (Day), faster water transit time (WTT), increased spillway passage (Spill), and cooler ocean temperatures (PDO). However, the estimated coefficient for the cormorant consumption rate

was near and overlapped zero, indicating that cormorant consumption rates were not a significant factor for steelhead SARs after accounting for the other freshwater and ocean factors.

Discussion

Numerous research efforts have evaluated whether hunting is an additive or compensatory source of mortality in avian populations (Anderson and Burnham 1976, Burnham and Anderson 1984, Burnham et al. 1984, Nichols and Hines 1983). With the notable exception of Allen et al. (1998), this research is one of the first to examine hypotheses on additive versus compensatory sources of mortality for fish populations. The PIT tag data that are available provide independent estimates of the levels of mortality caused by double-crested cormorants and the overall survival rate (SAR). Although SARs vary within and across years, Burnham et al. (1984) concluded that variability in S_0 would not produce a bias in estimates of b . Simulations conducted by Barker et al. (1991) also demonstrate that the model used in this analysis is robust to temporal variation in S_0 , which can occur both within and across years.

Results from the three data sets used to assess the effects of cormorant consumption rates strongly rejected the hypothesis that cormorant predation is an additive source of mortality, and supported the hypothesis that cormorant predation is a compensatory source of mortality, for Snake River steelhead. This conclusion is also supported by the multivariate regression model that found that cormorant consumption rates had no influence on steelhead SARs after accounting for other important freshwater and ocean environmental factors. These results indicate that the total additivity assumption used by USACE (2014) to project the benefits of double-crested cormorant reductions is inconsistent with available data. As a result, the benefits to population productivity or adult abundance associated with reductions in cormorant abundance and predation are likely overestimated. Contrary to the total additivity assumption applied by the USACE (2014), the three data sets that were analyzed indicated that predation by double-crested cormorants is completely compensatory and the multivariate regression results showed that cormorants had little effect on steelhead SARs after accounting for other freshwater and ocean environmental factors. Across the analyses that have been conducted, the data indicate that efforts to reduce predation by double-crested cormorants are unlikely to have an effect on Snake River steelhead abundance or productivity. Because other species (e.g., Snake River spring Chinook salmon, Snake River fall Chinook salmon) are consumed at lower rates than Snake River steelhead, efforts to reduce predation by double-crested cormorants are also unlikely to affect the abundance or productivity of other Snake and upper Columbia River species as well. In total, the data indicate that efforts to reduce predation by double-crested cormorants are expected to result in no changes or benefits to these fish populations in terms of increasing adult returns or abundance.

In this complex river-estuary-ocean ecosystem, numerous predators are in competition for the same smolt resources. For a single-species control effort to be effective (e.g., cormorant population reductions), it must be assumed that other species will not increase consumption rates in response to those single-species reductions. For example, it must be assumed that hake and other predators will not respond to increased steelhead availability through increased consumption. This is a strong assumption that does not appear to be consistent with the available data. Ellis-Felege et al. (2012) found that reductions in predation risk from one predator species were compensated-for by increases in predation

risk from other predator species. The data from these analyses support the hypothesis that there are compensatory shifts in predation impacts among smolt predators. Shifts in predation impacts among predators are expected to limit or eliminate the benefits that could be achieved through single-species (e.g., cormorant) population reductions (Ellis-Felege et al. 2012). Quantifying the total and seasonal consumption by all of the predators that consume smolts is likely infeasible in this aquatic ecosystem where it is difficult to “see” who the aquatic predators are and how much they consume. However, the data indicate that other (i.e., non-cormorant) mortality factors decline as cormorant consumption rates increase and conversely that those mortality factors increase as cormorant consumption rates decline (Figure 2). Due to these shifts between cormorant and non-cormorant sources of mortality, SARs did not decline as cormorant consumption rates increased. We speculate that compensatory shifts in predation are the cause of these patterns that are evident in the data.

In contrast to the effects of variable cormorant consumption rates, analyses on the effects of hydrosystem mortality on SARs found that mortality during hydrosystem passage was an additive source of mortality. As a result, the data indicate that efforts to reduce mortality during passage through the hydrosystem are expected to result in increased productivity and abundance of steelhead. Based on these analyses, reducing mortality during hydrosystem migration is likely to increase adult abundance and productivity. Haeseker et al. (2012) showed that increases in spill levels and reductions in water transit times were associated with reduced mortality during hydrosystem passage. There is evidence that reductions in mortality during hydrosystem migration also reduce mortality during ocean residence (Haeseker et al. 2012). These findings on the importance of mortality during hydrosystem passage are also supported by the multivariate regression model in this analysis indicated that reductions in water transit time and increases in spillway passage are expected to increase steelhead SARs.

References:

- Allen, M.S., L.E. Miranda, and R.E. Brock. 1998. Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes & Reservoirs: Research and Management* 3:67-79.
- Anderson, D.R., and K.P. Burnham. 1976. Population ecology of the mallard: VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publication 128. 66pp.
- Burnham, K.P., and D.R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. *Ecology* 65:105-112.
- Burnham, K.P. and D.R. Anderson. 2002. Model selection and inference – a practical information-theoretic approach. Second edition. Springer-Verlag. New York.
- Burnham, K.P., G.C. White, and D.R. Anderson. 1984. Estimating the effect of hunting on annual survival rates of adult mallards. *Journal of Wildlife Management* 48:350-361.
- Ellis-Felege, S.N., M.J. Conroy, W.E. Palmer, and J.P. Carroll. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. *Journal of Applied Ecology* 49:661-669.
- Evans, A.F., N.J. Hostetter, D.D. Roby, K. Collis, D.E. Lyons, B.P. Sandford, R.D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. *Transactions of the American Fisheries Society* 141:975-989.
- Haeseker, S.L., J.M. McCann, J.E. Tuomikoski, and B. Chockley. 2012. Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring/summer Chinook salmon and steelhead. *Transactions of the American Fisheries Society*, 141:1, 121–138.
- Hall, A. and D. Marmorek. 2013. Comparative Survival Study (CSS) 2013 Workshop Report. Prepared by ESSA Technologies Ltd., Vancouver, B.C. for the Fish Passage Center (Portland, OR) and U.S. Fish and Wildlife Service (Vancouver WA). xi + 47 pp. + Appendices.
- ISAB (Independent Scientific Advisory Board). 2011. Columbia River food webs: developing a broader scientific foundation for fish and wildlife restoration. ISAB 2011-1. Northwest Power and Conservation Council, Portland, Oregon.
- Lyons, D.E., D.D. Roby, A.F. Evans, N.J. Hostetter, and K. Collis. 2014. Benefits to Columbia River anadromous salmonids from potential reductions in predation by double-crested cormorants nesting at the East Sand Island Colony in the Columbia River estuary. Final Report prepared for the U.S. Army Corps of Engineers- Portland District.
- Lyons, D.E., A.F. Evans, N.J. Hostetter, A. Piggott, L. Weitkamp, T.P. Good, D.D. Roby, K. Collis, P.J. Loschl, and B. Cramer. 2014b. Factors influencing predation on juvenile salmonids by double-crested

cormorants in the Columbia River estuary: a retrospective analysis. Report prepared for the U.S. Army Corps of Engineers – Portland District.

NOAA Fisheries. 2014. Endangered Species Act Section 7(a)(2) Supplemental Biological Opinion Consultation on Remand for Operation of the Federal Columbia River Power System. NOAA Fisheries Log Number NWR-2013-9562.

Roby, D.D., D.E. Lyons, D.P. Craig, K. Collis, and G.H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Canadian Journal of Zoology* 81: 250–265.

Schaller, H. A., C.E. Petrosky, and E.S. Tinus. 2013. Evaluating river management during seaward migration to recover Columbia River stream-type Chinook salmon considering the variation in marine conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 71(2), 259-271.

Tuomikoski, J., J. McCann, B. Chockley, H. Schaller, P. Wilson, S. Haeseker, J. Fryer, C. Petrosky, E. Tinus, T. Dalton, R. Ehlke, and R. Lessard. 2012. Comparative Survival Study (CSS) of PIT-tagged Spring/Summer Chinook and Summer Steelhead 2012 Annual Report, BPA Contract #19960200.

USACE (U.S. Army Corps of Engineers- Portland District). 2014. Double-crested Cormorant Management Plan to Reduce Predation of Juvenile Salmonids in the Columbia River Estuary Draft Environmental Impact Statement.

DRAFT

Table 1. Number of cohorts analyzed, maximum likelihood estimates \hat{S}_0 and \hat{b} , bootstrap estimates of the standard error of b ($\widehat{se}(\hat{b})$), and z-scores and p-values for testing the complete compensation hypothesis (z comp.) and for testing the total additivity hypothesis (z additive) for each of the four data sets analyzed.

Data set	Mortality source	n (cohorts)	S_0	b	se(b)	z (comp.)	p-value	z (additive)	p-value
Transported LGR	Cormorant	45	1. 80%	0.055	0.172	0.32	0.75	-5.49	< 0.0001
In-river LGR	Cormorant	48	0. 81%	0.008	0.031	0.26	0.79	-31.55	< 0.0001
In-river BON	Cormorant	40	1. 82%	0.004	0.036	0.11	0.91	-27.29	< 0.0001
In-river LGR	Hydrostem	30	2. 34%	0. 998	0.164	6. 07	< 0.0001	-0.02	0.99

DRAFT

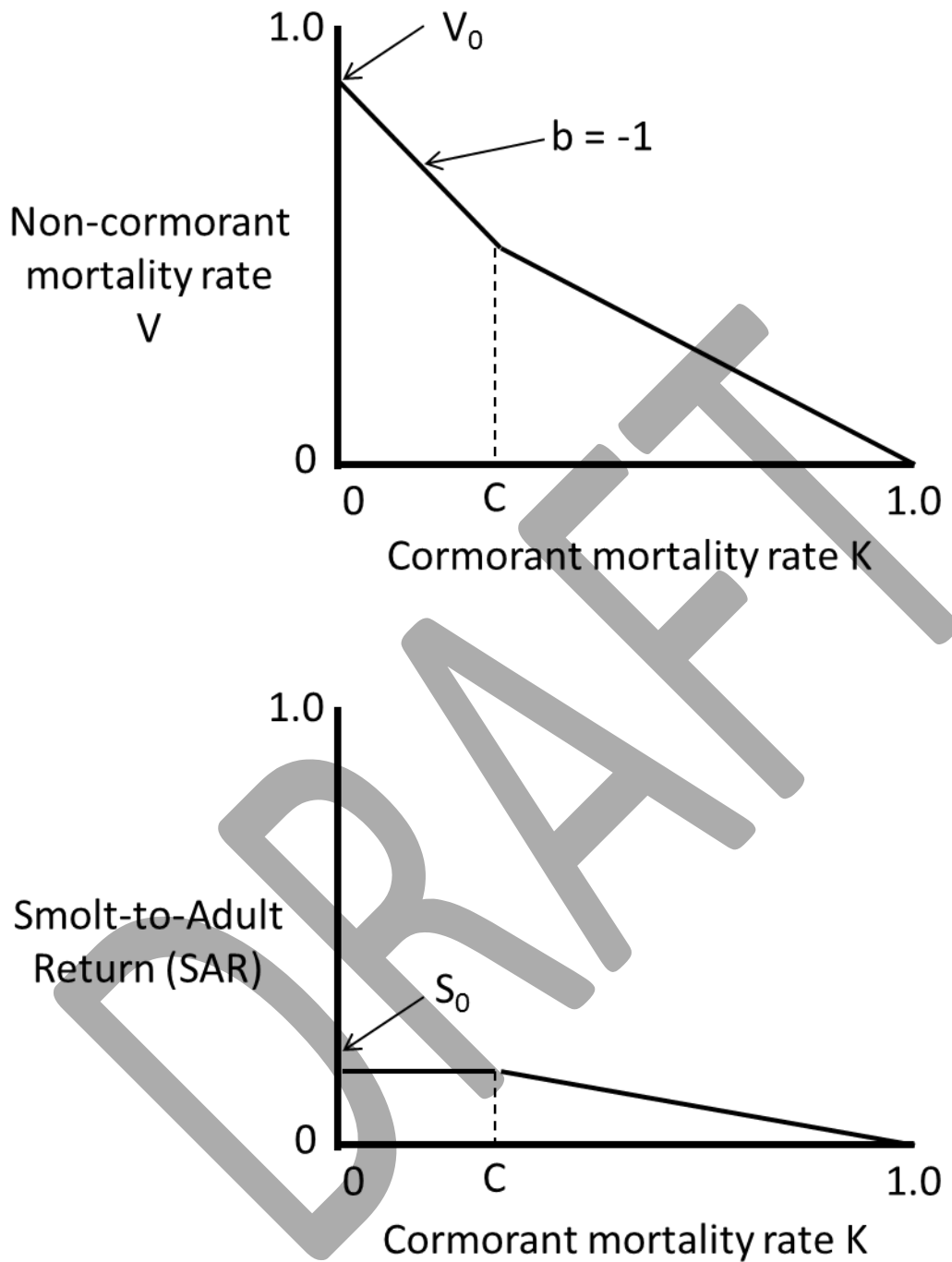


Figure 1. Predicted relationships between the non-cormorant mortality rate (V), the cormorant mortality rate (K), and the Smolt-to-Adult Return rate (SAR) under the completely compensatory hypothesis. Figure is adapted from Figure 1 of Anderson and Burnham (1976).

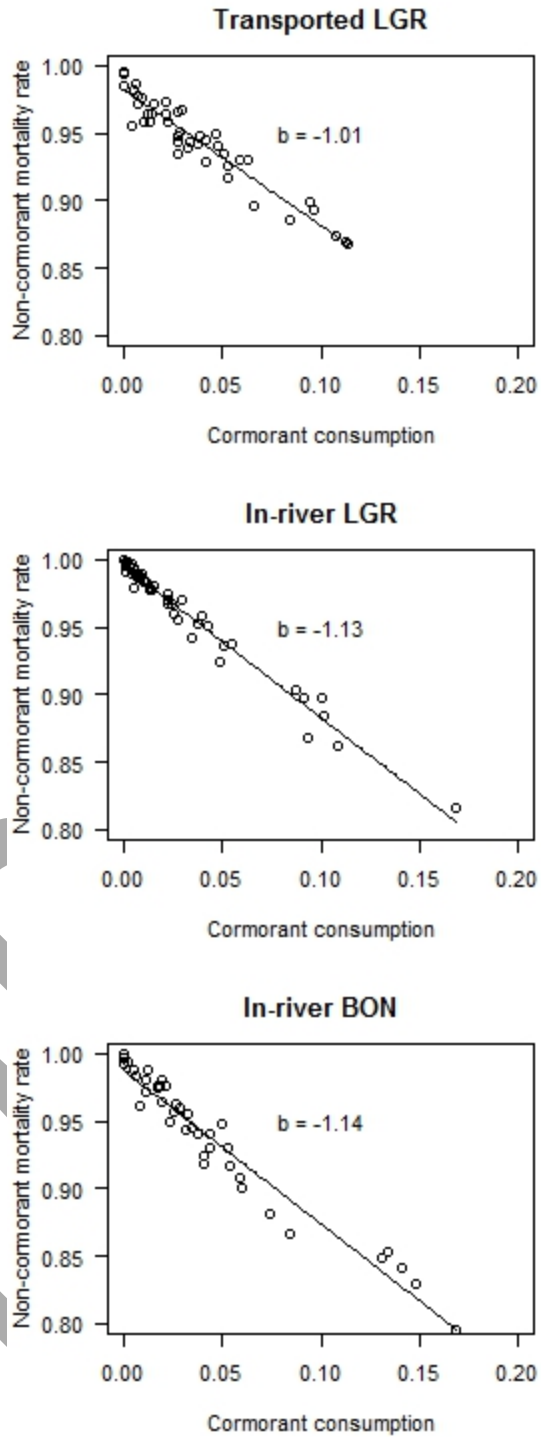


Figure 2. Associations between the non-cormorant mortality rate and cormorant consumption rate for the three data sets used to test the hypothesis of complete compensation.

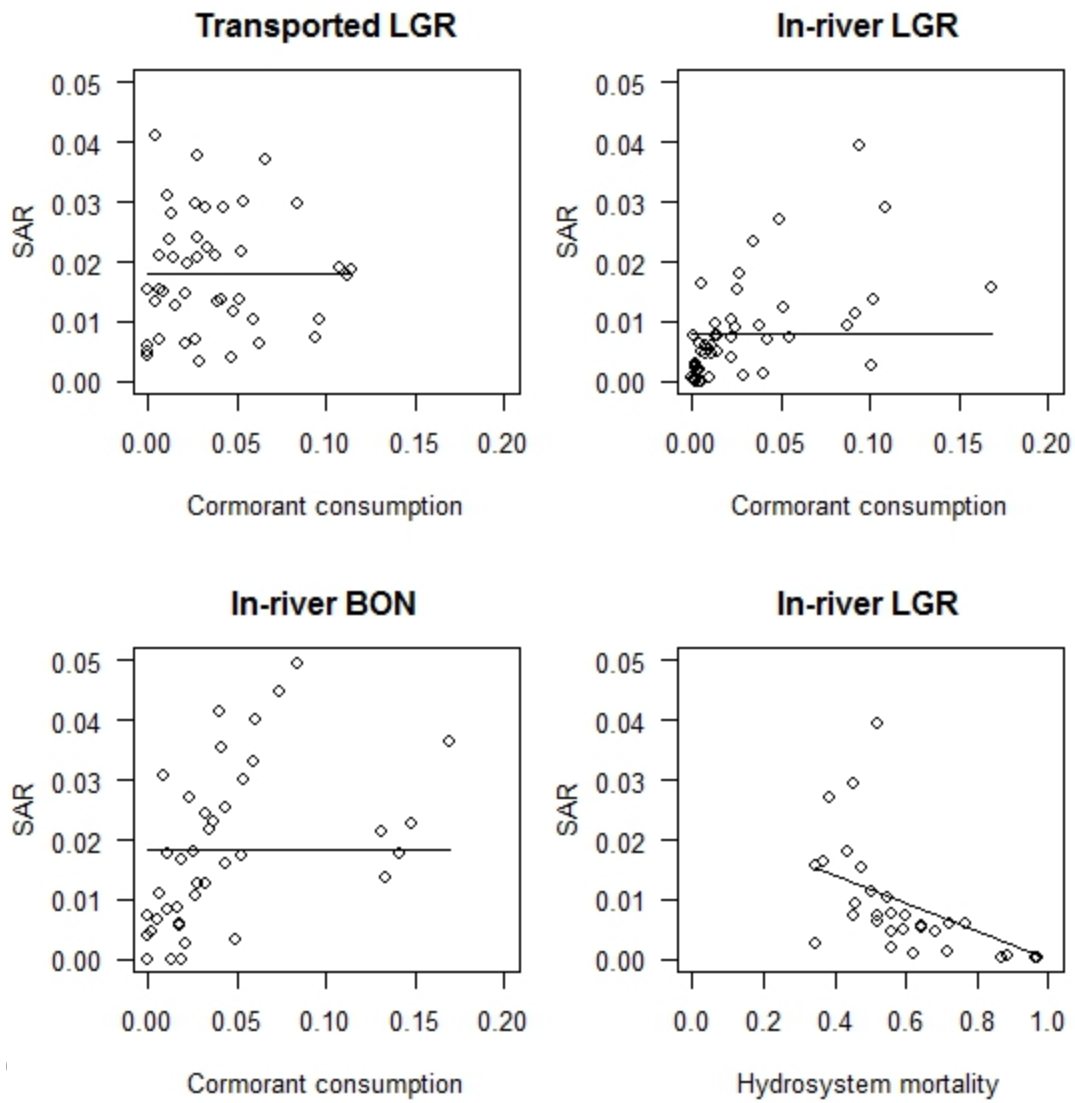


Figure 3. Associations between the SARs and cormorant consumption rates along with the association between SARs and hydrosystem mortality rates for hatchery and wild Snake River steelhead 1998-2009. The lines represent the predicted SAR using the structural model and maximum likelihood estimates of S_0 and b presented in Table 1.

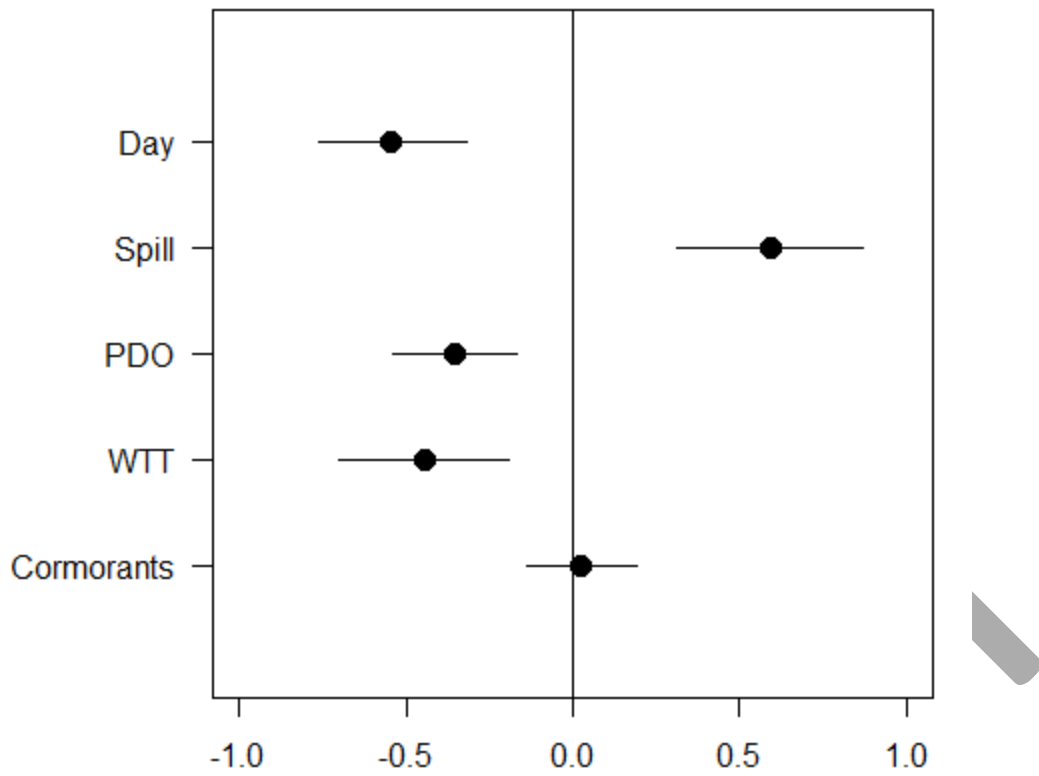


Figure 4. Model-averaged coefficients (closed circles) and 95% confidence intervals from the multivariate regression model of smolt-to-adult return rates for steelhead detected at Lower Granite Dam, 1998-2009.

Appendix A. Number of hatchery and wild Snake River steelhead PIT-tagged or detected with a PIT tag at Lower Granite Dam that subsequently were transported (Juveniles_{LGR}), the cumulative number of recoveries at the double-crested cormorant colony (DCCO Recoveries), number of PIT-tagged adults detected at Lower Granite Dam (Adults_{LGR}) for two-week juvenile cohorts (Date range) at Lower Granite Dam, 1998-2009.

Year	Date range	Juveniles _{LGR}	DCCO	
			Recoveries	Adults _{LGR}
1998	4/22 to 5/5	679	0	3
1998	5/6 to 5/19	588	0	3
1998	5/20 to 6/02	333	0	2
1999	4/8 to 4/21	2,290	7	16
1999	4/22 to 5/5	19,023	139	393
1999	5/6 to 5/19	15,815	124	202
1999	5/20 to 6/02	9,323	22	125
2000	4/8 to 4/21	275	3	4
2000	4/22 to 5/5	332	9	10
2000	5/6 to 5/19	335	2	8
2000	5/20 to 6/02	213	3	8
2001	4/8 to 4/21	736	4	23
2001	4/22 to 5/5	9,205	125	280
2001	5/6 to 5/19	3,654	77	50
2001	5/20 to 6/02	2,063	22	13
2002	4/8 to 4/21	972	2	40
2002	4/22 to 5/5	713	0	11
2002	5/6 to 5/19	668	3	10
2002	5/20 to 6/02	2,466	35	59
2003	4/8 to 4/21	1,183	4	25
2003	4/22 to 5/5	1,883	26	56
2003	5/6 to 5/19	2,858	56	38
2003	5/20 to 6/02	4,021	46	79
2004	4/8 to 4/21	2,030	29	42
2004	4/22 to 5/5	2,532	76	26
2004	5/6 to 5/19	4,728	227	35
2004	5/20 to 6/02	2,684	64	11
2005	4/8 to 4/21	870	12	6
2005	4/22 to 5/5	3,909	102	53
2005	5/6 to 5/19	11,947	384	75
2005	5/20 to 6/02	2,901	43	10
2006	4/22 to 5/5	16,025	917	285
2006	5/6 to 5/19	14,377	709	146
2006	5/20 to 6/02	3,103	76	36
2007	4/8 to 4/21	594	2	9
2007	4/22 to 5/5	4,121	88	120
2007	5/6 to 5/19	8,880	145	257
2007	5/20 to 6/02	3,334	57	75
2008	4/22 to 5/5	6,823	293	203
2008	5/6 to 5/19	31,797	1077	1181
2008	5/20 to 6/02	12,561	337	271
2009	4/8 to 4/21	890	6	25
2009	4/22 to 5/5	9,066	498	171
2009	5/6 to 5/19	30,790	1787	572
2009	5/20 to 6/02	13,969	267	295

Appendix B. Number of hatchery and wild Snake River steelhead PIT-tagged or detected with a PIT tag at Lower Granite Dam that subsequently migrated in-river (J_{LGR}), in-river survival estimates from Lower Granite Dam to Bonneville Dam ($S_{LGR-BON}$), the cumulative number of recoveries at the double-crested cormorant colony (DCCO Recoveries), number of PIT-tagged adults detected at Lower Granite Dam (A_{LGR}) for two-week juvenile cohorts (Date range) at Lower Granite Dam, 1998-2009. NA denotes cohorts where in-river survival estimates could not be calculated due to low sample size and/or poor detection probabilities.

Year	Date range	J_{LGR}	$S_{LGR-BON}$	DCCO	
				Recoveries	A_{LGR}
1998	4/8 to 4/21	1,945	NA	1	15
1998	4/22 to 5/5	16,311	NA	11	45
1998	5/6 to 5/19	15,916	NA	11	35
1998	5/20 to 6/02	8,227	NA	6	21
1999	4/8 to 4/21	5,828	0.439	40	45
1999	4/22 to 5/5	28,929	0.549	209	216
1999	5/6 to 5/19	28,506	0.478	66	182
1999	5/20 to 6/02	20,172	0.408	58	103
2000	4/8 to 4/21	23,541	0.616	584	636
2000	4/22 to 5/5	33,713	0.564	465	602
2000	5/6 to 5/19	23,014	0.275	92	137
2000	5/20 to 6/02	8,923	NA	21	16
2001	4/8 to 4/21	516	NA	1	0
2001	4/22 to 5/5	15,647	0.037	10	2
2001	5/6 to 5/19	20,235	0.030	7	5
2001	5/20 to 6/02	5,413	NA	0	3
2002	4/8 to 4/21	9,768	0.629	26	158
2002	4/22 to 5/5	11,803	0.356	44	68
2002	5/6 to 5/19	15,231	0.235	80	93
2002	5/20 to 6/02	16,510	0.318	66	76
2003	4/8 to 4/21	4,280	0.526	56	65
2003	4/22 to 5/5	6,345	0.400	71	47
2003	5/6 to 5/19	10,894	0.443	63	49
2003	5/20 to 6/02	14,261	0.438	24	30
2004	4/8 to 4/21	1,174	NA	52	11
2004	4/22 to 5/5	13,292	NA	150	50
2004	5/6 to 5/19	23,666	0.117	111	17
2004	5/20 to 6/02	13,959	NA	38	1
2005	4/8 to 4/21	2,570	NA	56	18
2005	4/22 to 5/5	16,731	0.284	339	24
2005	5/6 to 5/19	30,226	0.377	452	30
2005	5/20 to 6/02	6,680	NA	13	0
2006	4/8 to 4/21	7,120	NA	370	98
2006	4/22 to 5/5	19,870	0.499	924	225
2006	5/6 to 5/19	18,149	0.481	506	135
2006	5/20 to 6/02	6,271	NA	47	31
2007	4/8 to 4/21	4,234	0.544	82	40
2007	4/22 to 5/5	16,309	0.449	188	169
2007	5/6 to 5/19	15,971	0.358	81	84
2007	5/20 to 6/02	5,693	0.131	5	2
2008	4/8 to 4/21	4,471	0.480	213	176
2008	4/22 to 5/5	22,201	0.549	1232	649
2008	5/6 to 5/19	24,472	NA	429	569
2008	5/20 to 6/02	12,880	NA	160	115
2009	4/8 to 4/21	11,751	0.653	602	31
2009	4/22 to 5/5	37,500	0.653	3217	583
2009	5/6 to 5/19	22,356	NA	581	276
2009	5/20 to 6/02	11,582	NA	75	113

Appendix C. Number of PIT-tagged hatchery and wild Snake River steelhead detected as a juvenile at Bonneville Dam (Juveniles_{BON}), the cumulative number of recoveries at the double-crested cormorant colony (DCCO Recoveries), number of PIT-tagged adults detected at Lower Granite Dam (Adults_{LGR}) for two-week juvenile cohorts (Date range) at Bonneville Dam, 1998-2009.

Year	Date range	Juveniles _{BON}	DCCO	
			Recoveries	Adults _{LGR}
1998	4/29 to 5/12	1,066	3	7
1998	5/13 to 5/26	2,628	2	12
1998	5/27 to 6/9	1,580	0	6
1999	4/15 to 4/28	235	2	2
1999	4/29 to 5/12	3,183	52	40
1999	5/13 to 5/26	4,033	23	71
1999	5/27 to 6/9	4,893	15	54
1999	6/10 to 6/23	325	0	0
2000	4/15 to 4/28	1,604	49	64
2000	4/29 to 5/12	5,627	213	251
2000	5/13 to 5/26	2,438	67	73
2000	5/27 to 6/9	742	10	8
2001	5/27 to 6/9	368	4	1
2002	4/15 to 4/28	279	0	2
2002	4/29 to 5/12	1,893	8	58
2002	5/13 to 5/26	1,253	15	34
2002	5/27 to 6/9	2,536	44	55
2002	6/10 to 6/23	872	8	5
2003	4/29 to 5/12	943	21	24
2003	5/13 to 5/26	1,408	20	18
2003	5/27 to 6/9	4,871	27	40
2003	6/10 to 6/23	818	8	0
2004	5/13 to 5/26	301	9	10
2005	5/13 to 5/26	317	8	1
2006	4/29 to 5/12	1,457	105	26
2006	5/13 to 5/26	1,114	76	15
2006	5/27 to 6/9	314	7	5
2007	4/29 to 5/12	1,336	36	23
2007	5/13 to 5/26	1,955	37	45
2007	5/27 to 6/9	1,020	10	17
2007	6/10 to 6/23	312	2	0
2008	4/29 to 5/12	6,526	562	237
2008	5/13 to 5/26	6,981	299	345
2008	5/27 to 6/9	1,243	26	44
2008	6/10 to 6/23	242	5	10
2009	4/15 to 4/28	620	10	15
2009	4/29 to 5/12	9,176	692	207
2009	5/13 to 5/26	7,387	492	159
2009	5/27 to 6/9	1,624	21	29
2009	6/10 to 6/23	340	3	2