

**BENEFITS TO COLUMBIA RIVER ANADROMOUS SALMONIDS
FROM POTENTIAL REDUCTIONS IN AVIAN PREDATION
ON THE COLUMBIA PLATEAU**

FINAL REPORT

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This report has been prepared for the U.S. Army Corps of Engineers – Walla Walla District for the purpose of assessing potential management actions to reduce avian predation on anadromous salmonids from the Columbia and Snake rivers.

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SUMMARY

Predation on juvenile salmonids (*Oncorhynchus* spp.) during out-migration to the Pacific Ocean is considered potentially limiting to the recovery of anadromous salmonid populations from the Columbia River basin that are listed under the U.S. Endangered Species Act. We examined the potential benefits of reducing avian predation associated with five colonies of piscivorous waterbirds in the Columbia Plateau region for three evolutionarily significant units (ESUs) of Chinook salmon (*O. tshawytscha*), one ESU of sockeye salmon (*O. nerka*), and two distinct population segments (DPSs) of steelhead trout (*O. mykiss*) from the Upper Columbia River and Snake River basins. Using predation rate data based on recoveries of smolt passive integrated transponder (PIT) tags at bird colonies and the framework of a simple deterministic, age-structured, matrix population growth model, we translated potential changes in smolt survival due to reductions in avian predation into increases in the average annual population growth rate (λ) at the ESU/DPS level. Estimates were produced for a range of reductions in avian predation and for a range of levels of compensatory mortality.

The greatest potential benefit from reductions in predation by birds from a single colony in the Columbia Plateau region was for Upper Columbia River steelhead when predation by Caspian terns (*Hydroprogne caspia*) nesting at Goose Island (in Potholes Reservoir near Othello, WA) was reduced; up to a 4.2% (hatchery-raised smolts) or 3.2% (wild smolts) increase in λ was possible if predation were completely eliminated and compensatory mortality did not occur. Potential benefits for Snake River ESUs were lower, in part because significant portions of those ESUs are transported and thus inaccessible to avian predators in the Columbia Plateau region. The greatest potential benefit possible for a Snake River salmonid ESU/DPS resulting from

reductions in predation by birds from a single colony was for steelhead, if predation by Caspian terns nesting at the Crescent Island colony (near Pasco, WA) was eliminated (0.5% increase in λ if no compensatory mortality occurred).

Management to reduce predation on salmonids by Caspian terns nesting at the Goose Island colony would offer the greatest benefits per managed bird. Management to reduce predation by Caspian terns from two other colonies in the Columbia Plateau region (Crescent Island and the Blalock Island Complex) would provide the next largest incremental benefit. Adding reductions in predation by double-crested cormorants (*Phalacrocorax auritus*) nesting on Foundation Island (near Pasco, WA) and gulls (*Larus* spp.) nesting on Miller Rocks (near Maryhill, WA) to reductions in Caspian tern predation would somewhat enhance benefits to salmonids, but at a much lower marginal benefit rate per managed bird. Cumulative potential benefits for eliminating predation by birds nesting at all five colonies in the Columbia Plateau region considered here were generally comparable to estimates of benefits from dispersing approximately two thirds of the large Caspian tern colony in the Columbia River estuary (USFWS 2005); benefits were greater, however, for Upper Columbia River steelhead from eliminating predation by birds nesting at the five Columbia Plateau colonies.

Our analysis indicates that, at current bird colony sizes, actions to reduce avian predation on juvenile salmonids in the Columbia Plateau region will not by themselves recover any ESA-listed population of anadromous salmonids. Reductions in avian predation in this region could, however, result in increases in salmonid population growth rates comparable to some other salmonid recovery efforts in the Columbia Basin, particularly for Upper Columbia River and Snake River steelhead populations.

INTRODUCTION

Predation on juvenile salmonids (*Oncorhynchus* spp.) during out-migration to the Pacific Ocean is considered a factor potentially limiting the recovery of anadromous salmonid populations from the Columbia River basin that are listed under the U.S. Endangered Species Act (ESA; NOAA 2008). Most studies of avian predation in the Columbia River basin have focused on colonial waterbirds nesting in the estuary (Collis et al. 2001; Roby et al. 2003; Ryan et al. 2003; Lyons 2010), where the largest known colonies of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants (*Phalacrocorax auritus*) in western North America currently reside (Lyons 2010). Management of avian predation to enhance recovery of ESA-listed salmonids has been ongoing in the estuary since 1999 (USACE 1999, 2000; Roby et al. 2002; USFWS 2005). Breeding colonies of piscivorous colonial waterbirds are not limited to the Columbia River estuary, however, but are distributed throughout the Columbia River basin. Work began to systematically evaluate predation on salmonids by colonial nesting birds in the interior Columbia Basin, or Columbia Plateau, in 1997 (Collis et al. 2002). The initial focus of this investigation was Caspian tern colonies at Crescent Island, near the confluence of the Columbia and Snake rivers and Pasco, WA (Antolos et al. 2005), and in Potholes Reservoir near Othello, WA (Antolos et al. 2004; Maranto et al. 2010). In 2004, comprehensive research was initiated with funding from the Walla Walla District of the U.S. Army Corps of Engineers to identify waterbird nesting colonies with the greatest impacts to survival of salmonids and to evaluate those impacts over a broad range of environmental (e.g., river flows) and management (e.g., smolt transportation levels and magnitudes of spill at hydropower facilities) conditions (Roby 2011). Over 100,000 piscivorous colonial waterbirds, representing five different species

nesting at 18 different colonies, were documented nesting in the Columbia Plateau region (upstream of the estuary) during 2004-2009 (Adkins et al. 2011).

A variety of approaches have been used to assess the impacts of avian predators on salmonid smolts in the Columbia River basin, including predator diet composition (Collis et al. 2002), bioenergetics-based estimates of smolt consumption (Roby et al. 2003, Antolos et al. 2005, Maranto et al. 2010, Lyons 2010, Lyons et al. 2011), recovery rates of smolt passive integrated transponder (PIT) tags at bird colonies (Collis et al. 2001, Ryan et al. 2003, Maranto et al. 2010, Evans et al. 2011), and salmonid population-level demographic benefits, where avian predation reduced (Roby et al. 2003, Antolos et al. 2005, Good et al. 2007, Lyons 2010, Maranto et al. 2010). Of these potential indicators, salmonid population-level demographic benefits, as quantified by the potential increase in average annual population growth rates (λ) (McClure et al. 2003), have been used to justify potentially significant management actions to reduce avian predation as part of environmental analysis procedures dictated by the National Environmental Protection Act (NEPA; USFWS 2005).

The goal of this analysis is to estimate benefits to salmonid populations from potential reductions in avian predation by colonies of piscivorous waterbirds in the Columbia Plateau region. The first objective was to identify for further analysis the most significant interactions between particular waterbird colonies and specific salmonid populations, where appropriate data exist. The second objective was to estimate potential increases in λ of salmonid populations for those high priority interactions. The third and final objective was to explore these estimated potential benefits in the context of constraints in available data and methodological uncertainties. This analysis focuses on reductions in avian predation at the level of individual colonies, rather than focusing on reductions in avian predation at particular foraging sites (e.g., certain dams),

where the breeding status and origin of foraging birds are often unclear. Reductions in predation on juvenile salmonids by birds from a particular breeding colony could be achieved by management that reduces colony size (e.g., habitat management, disturbance, lethal control, or others) and the analyses are considered in this context; however, other approaches could potentially also accomplish this outcome – for example, actions that would reduce the availability or susceptibility of smolts to predation by birds from the colonies. The estimated benefits presented here to salmonid populations from reduced avian predation are applicable regardless of what type of management action achieves a reduction in predation and in juvenile salmonid mortality.

METHODS

Waterbird Colonies and Salmonid Populations Considered for Analysis

Our investigation into avian predation on juvenile salmonids across the Columbia Plateau region has focused primarily on five species of native piscivorous colonial waterbirds, all having historically nested in this region: Caspian terns, double-crested cormorants, American white pelicans (*Pelecanus erythrorhynchos*), California gulls (*Larus californicus*), and ring-billed gulls (*L. delawarensis*). Preliminary data were collected from 18 waterbird breeding colonies used by these five species during 2004 – 2010 (Adkins et al. 2011, Table 1.1) to identify colonies with the greatest potential to reduce survival of juvenile salmonids (smolts) during their out-migration (map shown in Figure 1). Using a variety of measures, including colony size (Adkins et al. 2011), diet composition (Collis et al. 2002, Lyons et al. 2011), and recovery rates of smolt PIT-tags (Evans et al. 2011), colonies were ranked based on their potential impact on smolt survival.

The colonies deemed potentially most significant were Caspian tern colonies on Goose Island in Potholes Reservoir near Othello, WA, on Crescent Island in the McNary Pool reach of the mainstem Columbia River, near Pasco, WA, and on multiple islands in the Blalock Island Complex above John Day Dam, near Boardman, OR; a double-crested cormorant colony on Foundation Island in the McNary Pool; and a mixed California gull and ring-billed gull colony on Miller Rocks just upstream of the confluence of the Deschutes and Columbia rivers near Maryhill, WA. Expert opinion from the Inland Avian Predation Working Group (e.g., Gary Fredericks, National Oceanic and Atmospheric Administration [NOAA] Fisheries; Chris Pinney and David Trachtenberg, U.S. Army Corps of Engineers [USACE]; and others) confirmed that the colonies selected by this ranking were an appropriate set for comprehensive analysis.

The conservation unit used to set most large-scale salmon and steelhead (*O. mykiss*) recovery objectives in the Columbia River basin is the distinct population segment (DPS) as defined under the U.S. Endangered Species Act (ESA; Waples 1991, McClure et al. 2003). Most salmonid DPSs in the Columbia Basin have unique evolutionary lineages and are referred to as evolutionarily significant units (ESUs), although this is not true for steelhead DPSs. For simplicity and following the example of others (e.g., McClure et al. 2003), we used the ESU term throughout this document to designate the conservation unit of interest. Examples of current, large scale recovery planning using ESUs as the conservation unit include efforts to reduce the impacts of the Federal Columbia River Power System (USACE et al. 2007, NOAA 2008) and ongoing management to reduce predation on juvenile salmonids by Caspian terns in the Columbia River estuary (USFWS 2005, Good et al. 2007). Consequently, we identified 11 recognized ESUs that were potentially preyed upon by waterbirds from colonies on the Columbia Plateau, which yielded a total of 40 possible interactions between distinct salmonid

ESUs and the five bird colonies of primary interest (Table 1). Interactions with coho salmon (*O. kisutch*) restored to the Snake and Columbia rivers were not considered because these coho stocks are not recognized as a distinct ESU and are thus not covered under the ESA. In addition, few coho salmon smolts have been PIT-tagged in some years, resulting in fewer data to assess avian predation impacts than for recognized ESUs (Evans et al. 2011). In years when appreciable numbers of coho smolts have been PIT-tagged, however, predation rates by waterbirds from the five priority colonies were similar to those for other salmonid ESUs (Evans et al. 2011). PIT-tags implanted in juvenile bull trout (*Salvelinus confluentus*) in the Walla Walla River have also been detected at Columbia Plateau waterbird colonies, but at low rates (33 PIT-tags recovered from 2002 – 2010, during which 10,650 bull trout were tagged; Allen Evans and Nathan Hostetter, unpublished data). We did not attempt to assess benefits to bull trout if avian predation were reduced because of small sample sizes and the difficulty in determining how many bull trout moved within the foraging range of birds from the colonies considered (i.e. how many actually became susceptible to avian predation).

Impacts to some salmonid ESUs from avian predation were eliminated from consideration for further analysis for the following reasons:

1. Upper Columbia River (UCR) summer/fall-run (UCR_{Su/F}) Chinook salmon (*O. tshawytscha*) is not an ESA-listed ESU and impacts on this ESU from the waterbird colonies of interest (where adequate data existed) were lower than or comparable to impacts on the UCR spring-run Chinook ESU (Evans et al. 2011). The ESA-listed UCR_{Sp} Chinook ESU was retained for analysis because of greater management interest in potential benefits to listed populations.

2. Middle Columbia River spring-run (MCR_{Sp}) Chinook salmon is not an ESA-listed ESU. Spawning for this ESU extends from the Klickitat River upstream to include the Yakima River (excluding the Snake River). Consequently, many of the major spawning tributaries for this ESU (e.g., John Day, Deschutes, and Klickitat sub-basins) are downstream from and outside the foraging range of most of the priority waterbird colonies. For the portion of this ESU that was exposed to predation by gulls at Miller Rocks and Caspian terns at the Blalock Island Complex, predation rates were < 1% (Evans et al. 2011) and impacts to the entire ESU would be proportionately less.
3. Okanogan River and Wenatchee Lake sockeye salmon (*O. nerka*) are not ESA-listed ESUs. Impacts to these Columbia River sockeye populations were generally less than for the ESA-listed Snake River sockeye ESU, often an order-of-magnitude lower, with predation rates < 1% for all colonies (Evans et al. 2011).
4. Middle Columbia River (MCR) steelhead trout is an ESA-listed (threatened) ESU. The spawning range of MCR steelhead, however, extends from above the Wind River (Washington) and the Hood River (Oregon) upstream to, and including, the Yakima River (excluding the Snake River). Consequently, as with MCR_{Sp} Chinook, much of the spawning activity by this ESU occurs well downstream of most of the waterbird colonies considered here (i.e., in the John Day, Deschutes, and Klickitat sub-basins). For the portion of this ESU that was exposed to predation by gulls nesting at Miller Rocks and Caspian

terns nesting at the Blalock Island Complex, predation rates were $\leq 1\%$ (Evans et al. 2011), and impacts to the entire ESU would be proportionately less.

Analysis Framework

Our estimates of benefits that might accrue to salmonid populations from reductions in avian predation on the Columbia Plateau were modeled after prior efforts to assess potential benefits from management of avian predation in the Columbia River estuary (Roby et al. 2003, Good et al. 2007, Lyons 2010). It is challenging to project changes in survival at a juvenile life history stage into corresponding changes in recruitment into the adult breeding population (i.e. adult returns). In the Columbia River basin, a common approach to evaluating the relative benefits of a variety of salmon recovery efforts has been to employ the framework of a simple deterministic, age-structured, matrix population growth model (Kareiva et al. 2000). Employing such a demographic model, improvements in survival at a given life history stage can be projected into potential improvements in the average annual population growth rate (percentage changes in λ), using just the change in survival and the population generational time (McClure et al. 2003):

$$\Delta\lambda = \left[\left(\frac{S_f}{S_i} \right)^{1/G} - 1 \right] \cdot 100\%$$

Where S_i is the initial survival rate, S_f is the final survival rate following a recovery action, G is the average generational time, and $\Delta\lambda$ is the percentage change in the average annual population growth rate. This change in λ has been used to compare the potential efficacy of various management actions intended to help recover Columbia River salmonid populations (McClure et al. 2003), and the management objective for reductions in Caspian tern predation in the Columbia River estuary was expressed in the currency of improvements in λ for heavily affected

steelhead ESUs (USFWS 2005). Important assumptions of this approach are that increases in survival at a particular life-history stage are (1) independent of changes in survival elsewhere in the life history and (2) density-independent. We attempt to address the first assumption by presenting results for a range of compensatory mortality if avian predation was reduced (see below). Our ability to assess the possible effects of much higher densities of salmonids (if salmon recovery actions were to significantly enhance salmon populations) on our analyses is limited; this remains an uncertainty in our approach and that of most recovery analyses for Columbia River salmonids (McClure et al. 2003, NOAA 2008).

Using this framework of a matrix population growth rate model relies on the ability to estimate smolt survival rates prior to and following a recovery action. For reductions in avian predation, the effective survival can be considered to be the converse of the mortality due to avian predation (i.e., one minus the mortality), or equivalently, the converse of the predation rate (i.e., one minus the proportion of the smolt population of interest taken by birds from a given colony). Predation rates can be estimated in two ways: either (1) estimating smolt abundance for a given ESU at the life history stage when avian predation occurs and quantifying how many smolts of that ESU are taken, or (2) measuring the predation rate on a representative sample of the given ESU. Estimates of smolts available to avian predators from a given waterbird colony and smolts consumed by birds from that colony have been used to estimate predation rates at the taxonomic level of salmonid species. But due to difficulties in identification of ESU in both the estimation of smolts available and smolts consumed (Roby et al. 2003, Lyons 2010), resolution of avian predation rates to the level of ESU has not yet been accomplished using this approach. The alternative approach, estimating avian predation rates on an ESU using PIT-tagged smolts as the representative sample group, has been the primary means employed to estimate ESU-specific

avian predation rates (Collis et al. 2001, Ryan et al. 2003, Good et al. 2007, Evans et al. 2011). Relying upon predation rates for a sample of smolts does not require estimation of either smolt availability or smolt consumption at the ESU level, for either the baseline or post-management periods. Consequently, benefits accrued to salmonid populations are expressed only as changes in the population trajectory (λ), not in the absolute number of juveniles consumed post-management or as the change in the number of smolts consumed due to management. Additionally, this modeling framework projects changes in juvenile survival to changes in population trajectory and is not capable of estimating a change in the number of adults returning to spawn before and after management.

We defined the stages of the juvenile salmonid life history for this analysis using three primary criteria and described each stage in terms of geographic locations in the outward smolt migration. We first attempted to define each stage as narrowly as possible, covering as short a stretch of the migration corridor as possible, in order to minimize the prevalence of other mortality sources within the given life history stage. Our second criterion was to use a geographic region that approximated the foraging area of birds from each colony. Finally, for the upstream boundary of the region/life history stage, we used sites where it was possible to identify a sample of representative PIT-tagged smolts from the given ESUs that would serve as a pool of available smolts from which predation rates could be estimated. Using these criteria, three distinct life-history stages of juvenile salmonids were defined and matched with the appropriate waterbird breeding colonies for analysis:

1. Upper Columbia Stage: From Rock Island Dam on the upper Columbia River (river km 729) downstream to the upper Hanford Reach (river km 620). This life history stage was used for UCR_{Sp} Chinook and UCR steelhead while

- exposed to predation by Caspian terns nesting at Goose Island, Potholes Reservoir.
2. Confluence Stage: From the upper Hanford Reach on the Columbia River and from Lower Monumental Dam on the Snake River (587 km from the mouth of the Columbia River) downstream to McNary Dam (river km 470). Caspian terns nesting at Crescent Island and double-crested cormorants nesting at Foundation Island preyed upon UCR_{Sp} Chinook, UCR steelhead, Snake River spring/summer-run (SR_{S/S}) Chinook, Snake River fall-run (SR_F) Chinook, Snake River (SR) sockeye and SR steelhead smolts during this life history stage.
 3. Middle Columbia Stage: From McNary Dam downstream to The Dalles Dam (river km 309). UCR_{Sp} Chinook, UCR steelhead, Snake River (SR) spring/summer-run (SR_{S/S}) Chinook, Snake River fall-run (SR_F) Chinook, SR Sockeye and SR steelhead smolts are exposed to Caspian terns nesting in the Blalock Island Complex and gulls nesting on Miller Rocks during this life history stage. A distinct life history stage might have been defined for Miller Rocks gulls beginning at John Day Dam; however gulls forage both in the tailrace and the forebay at John Day Dam. We used McNary Dam as the upper extent so as to not exclude the predation that occurred in the forebay of John Day Dam from the analysis.

Predation Rate Estimates

Samples used for predation rate estimation: As mentioned above, predation rates on a PIT-tagged sample of fish from each ESU were used as the primary input to the demographic analysis. The pool of available smolts for the in-river predation rate calculation varied by ESU and life history stage. Except where noted below, PIT-tagged smolts represented an opportunistic sample of the ESU's smolt population – fish were tagged as part of other studies within the basin. In all cases, we assumed the PIT-tagged sample was representative of the run as a whole. The mean sample size within a pool used to calculate annual PIT tag recovery rates was 14,728 fish per ESU (range: 553 – 74,905 fish). We estimated annual predation rates for each colony/ESU interaction only when at least 500 smolts were enumerated in the available pool. Our study period generally covered the years 2004 – 2010, although data were not available for all ESUs and all colonies in every year. The data used for the ultimate estimation of benefits was from a subset of these years, based on transportation levels for Snake River smolts (see below).

UCR_{Sp} Chinook salmon: The pool of smolts available at the Upper Columbia Stage was those detected at the smolt trap facility at Rock Island Dam. Sufficient PIT-tagged fish to estimate predation rates were available only in 2004, 2009, and 2010. For the Confluence Stage we also started with the pool of smolts interrogated at Rock Island Dam but needed to reduce that pool to account for mortality between Rock Island Dam and the upper Hanford Reach. Survival estimates are not yet available for Chinook salmon smolts through this portion of the upper Columbia River so we instead used sockeye survival rates (measured in 2009 – 2010) from Timko et al. (2011) as a surrogate measure. The pool of smolts available at the Middle Columbia Stage was those detected at McNary Dam.

UCR steelhead: During 2004 – 2010, steelhead smolts tagged at and above Rock Island Dam were used to form the pool of available smolts at each life history stage. During 2008 – 2010, the opportunistic sample of PIT-tagged steelhead smolts coming down the river was supplemented by the capture and tagging of additional smolts at Rock Island Dam, pushing the total pool of available smolts to > 7,000 per year in those years (Allen Evans and Nathan Hostetter, unpublished data). A small proportion of the UCR steelhead ESU is believed to spawn below Rock Island Dam (in the Crab Creek sub-basin) and juveniles from this area were available to avian predators, but were not represented in the tagged sample at Rock Island Dam. We assumed that mortality due to avian predation was similar for this group and fish originating above Rock Island Dam. PIT-tagged smolts interrogated or tagged and released at Rock Island Dam made up the available pool at the Upper Columbia Stage. This pool was reduced by mortality rates measured in steelhead migrating from Rock Island Dam to the upper Hanford Reach (Timko et al. 2011; measured in 2008 – 2010) to form the available pool for the Confluence Stage. The pool of UCR steelhead smolts available at the Middle Columbia Stage consisted of those detected at McNary Dam.

SR_{S/S} Chinook salmon: The available pool of PIT-tagged smolts for the Confluence Stage consisted of those interrogated at Lower Monumental Dam, the lowest dam on the Snake River with adequate interrogation capability across the study period. For the Middle Columbia Stage, the available pool consisted of those detected at McNary Dam. A small portion of the SR_{S/S} Chinook ESU may

spawn below Lower Monumental Dam in the mainstem Snake River, but smolts produced here would be within the foraging area of birds nesting at colonies in the McNary Pool. These fish would not be represented in the sample interrogated at Lower Monumental Dam; we assumed that predation rates on these smolts were similar to those produced higher in the basin and interrogated at Lower Monumental Dam.

SR_F Chinook salmon: The pools for the Confluence Stage and the Middle Columbia Stage consisted of those smolts interrogated at Lower Monumental Dam and McNary Dam, respectively. As with SR_{S/S} Chinook, a small portion of the SR_F Chinook ESU may spawn below Lower Monumental Dam in the mainstem Snake River, but within the foraging area of McNary Pool birds. We assumed that predation rates on these smolts were similar to those interrogated at Lower Monumental.

SR sockeye salmon: The pools for the Confluence Stage and the Middle Columbia Stage consisted of those smolts interrogated at Lower Monumental Dam and McNary Dam, respectively. Sufficient numbers of PIT-tagged smolts were available to estimate predation rates in the Confluence Stage during 2006 and 2008 – 2010. Sufficient numbers of PIT-tagged smolts were available to estimate predation rates for the Middle Columbia Stage only during 2009 – 2010.

SR steelhead: The pools for the Confluence Stage and the Middle Columbia Stage consisted of those smolts interrogated at Lower Monumental Dam and McNary Dam, respectively. For the Confluence Stage, the opportunistic sample of PIT-tagged steelhead smolts coming down the river was supplemented

by the capture and tagging of an additional ~7,000 smolts/year at Lower Monumental Dam during 2007 – 2009 (Hostetter et al. 2011).

Smolt PIT-tag recovery at waterbird colonies: To estimate what portion of each PIT-tagged sample of smolts was taken by avian predators, scanning for PIT-tags deposited by birds at their breeding colony sites was conducted using the methods of Ryan et al. (2003), after nesting birds had dispersed following each breeding season (August to November). Not all tags deposited by birds on their colonies are subsequently detected by researchers due to tag erosion, damage to tags, or other factors. Corrections for less than 100% detection efficiency were made using the sown control tag methods of Evans et al. (2011).

Not all colonies were scanned for PIT-tags in all years, nor were control tag data always available to correct for on-colony detection efficiency; thus, the study period for some bird colonies was limited. Data were available for Caspian terns nesting at Goose Island (Potholes Reservoir) during 2006 – 2010 and at the Blalock Island Complex during 2007 – 2010. Data for gulls nesting at Miller Rocks were available during 2007 – 2010. For Crescent Island Caspian terns and Foundation Island double-crested cormorants, data were available for the entire study period of 2004 – 2010.

Annual PIT-tag recovery rates (number present at a given colony after correcting for detection efficiency divided by the number available at that life history stage as defined above) were averaged over the years of the baseline period used when data were available to obtain the baseline PIT-tag recovery rate.

Differences between smolts reared in hatcheries and in the wild: For each ESU and life history stage of available smolts we separately examined the average PIT-tag recovery rate for

tags identified as implanted in hatchery-reared or wild smolts. Wild and hatchery groups were pooled for subsequent analysis unless all of the following three criteria were met:

1. An adequate sample size ($N \geq 500$) of PIT-tagged fish was available for both wild and hatchery rearing types to appropriately estimate independent tag recovery rates for each group,
2. A statistically significant difference in tag recovery rate existed between the two rearing groups. Differences between rearing types were considered significant if the 95% confidence interval for tag recovery rate of each rearing type did not overlap the point estimate of the other rearing type.
3. A biologically significant difference in tag recovery rate existed between the groups. The threshold for biological significance was chosen to be a 0.5 percentage point difference in tag recovery rates between hatchery and wild rearing types.

Three colony/ESU combinations met all three of these criteria, and for those interactions benefits to hatchery and wild rearing types were calculated separately in the subsequent analysis: Goose Island Caspian tern predation on UCR steelhead, Crescent Island Caspian tern predation on UCR steelhead, and Foundation Island double-crested cormorant predation on SR steelhead. In all three cases, PIT tag recovery rates were greater for hatchery-reared smolts.

Converting PIT-tag recovery rates into predation rates: Colony-based PIT tag recovery rates are an excellent indication of the relative impacts of avian predation on the various salmonid ESUs, particularly when comparing the impacts of a single bird colony on the various ESUs that birds from that colony prey upon. Colony-based PIT tag recovery rates do not directly account for all PIT-tagged fish consumed by birds, however, as adult birds may deposit ingested PIT tags (via regurgitation or defecation) at loafing or other sites away from the colony. To

convert on-colony PIT tag recovery rates into estimates of predation rates, a PIT tag deposition rate, or the proportion of ingested PIT tags that are deposited on the colony, is required.

PIT-tag deposition rates have been measured for Caspian terns nesting at the Crescent Island colony using two different methods (Collis et al. 2007). In the first method, PIT-tagged hatchery-reared juvenile rainbow trout (*O. mykiss*) were held in net pens 8 – 11 km from the tern colony during the 2004 – 2006 breeding seasons. These net pens were continuously monitored while uncovered and a count was kept of how many fish were removed by Caspian terns.

Deposition rate was estimated by dividing the number later detected on the colony during normal PIT-tag recovery (after correcting for detection efficiency) by the number removed from the net pens by Caspian terns. A second method was employed during 2005 - 2006, when adult terns were captured on the colony during the late incubation stage of breeding and forcibly fed a PIT-tagged trout by holding the bill open and inserting a fish into the esophagus. Again in this case, deposition rate was estimated by dividing the number later detected on the colony during normal PIT- tag recovery (after correcting for detection efficiency) by the number force-fed to terns.

Of the 265 PIT tags in fish removed from the net pens by terns, 63% were found at the Crescent Island tern colony (mean of annual totals after correcting for detection efficiency). Of the 117 PIT tags in fish force fed to terns, 76% were recovered at the colony (mean of annual totals after correcting for detection efficiency). One possible reason for the observed discrepancy between methods is that for fish removed from the net pen and carried back to the colony in the bill to provision mates or chicks, terns probably experienced some level of kleptoparasitism by the California gulls that also nest on the island. Gull kleptoparasitism rates are particularly high for large salmonids carried back to the colony (e.g., often > 20% of steelhead; Adkins et al. 2011), and a few tags from net pen fish were later detected on the gull colony. Force-fed fish

would not be subject to this loss. Consequently, estimated PIT-tag deposition rates based on the recovery of PIT-tags from net pen fish were considered less biased than those from force-fed fish.

Predation rates can be estimated without bias by dividing the PIT tag recovery rate by the PIT tag deposition rate. For the Crescent Island tern colony, we used the net pen derived deposition rate (63%) to convert PIT tag recovery rates into predation rates for all ESUs. For other colonies and species, PIT tag deposition rates have not been measured. For Caspian terns at Goose Island and the Blalock Island Complex, kleptoparasitism rates are much lower (authors' unpublished data) and so we chose to use the deposition rate measured in force-fed Crescent Island Caspian terns. Deposition rates for other species (cormorants, gulls) have never been measured, and the possible effects of body size, largely non-fish diets for gulls, and poorly known nest attendance rate are difficult to assess. A value similar to that of Caspian terns seemed to be the least arbitrary assumption to make so we chose to use 70% (close to the average of the two results for Crescent Island Caspian terns), until better data become available.

Correction for ESUs that include fish not exposed to avian predation: Portions of all Snake River ESUs are captured at dams and put aboard barges for transportation downstream and release below Bonneville Dam. These transported fish are not exposed to predators during the Confluence and the Middle Columbia life history stages. This has two consequences for the estimation of benefits to ESUs from reduced avian predation. The first consequence of transportation is that only a portion of Snake River ESUs are exposed to predation in the McNary Pool and below. Impacts to each ESU from avian predation are less than suggested by the predation rates on the in-river migrating portion of the ESU. The second consequence of transportation, when levels of transportation vary across years, is a considerable variation in the

number (density) of Snake River smolts that are migrating in-river. Predation *rates* on in-river migrating smolts in the McNary Pool and below are significantly affected by the number of smolts available, especially if the number of smolts consumed each year remains relatively constant (e.g., Table 2).

Snake River transportation rates varied significantly across the study period, with 2004 – 2005 having high transportation rates (80.9 – 97.2 %) and 2007 – 2010 having substantially lower transportation rates (20.5 – 65.4 %; FPC 2011). The 2007 – 2010 period was considered a better predictor of future conditions (Gary Fredericks, NOAA Fisheries, pers. comm.) and that period was used as the baseline period for estimation of predation rates and the ultimate potential benefits to salmonid ESUs. Fortunately, data were available for all five colonies during this period. For comparison purposes, we also calculated benefits using a baseline period of 2004 – 2010 for colonies where data were available (mix of years with high and low transportation rates, Appendix C) and similarly for 2004 – 2005 (years with high transportation rates; Appendix D).

We adjusted the in-river predation rate (PR_{IR}) using the transportation rate (T , the estimated proportion of fish that were transported; FPC 2011) to get the predation rate at the ESU level (PR_{ESU}) after Antolos et al. (2005):

$$PR_{ESU} = PR_{IR} \times (1 - T)$$

The first dam encountered by ESUs from the Upper Columbia River where collection and transportation of smolts occurs is McNary Dam. Consequently, all smolts from these ESUs are exposed to avian predation during the Upper Columbia and Confluence life history stages prior to reaching this point. The Middle Columbia Stage occurs below McNary Dam; if smolts from either the UCR_{Sp} Chinook salmon or UCR steelhead ESUs were collected at McNary Dam then a portion of those ESUs would not be available to Blalock Island Complex Caspian terns or Miller

Rocks gulls. During the baseline period (2004 – 2010), collection and transportation did not occur at McNary Dam until late June or early July. The UCR_{Sp} Chinook and UCR steelhead ESUs have largely left this portion of the river by that time, so a negligible number of smolts from these ESUs were removed from the river and transported. Given this, we assumed that no UCR smolts were transported for the purposes of our analysis.

Reductions in predation

In order to offer managers an assessment of a variety of potential management scenarios, we calculated changes in the population trajectory ($\Delta\lambda$) for multiple levels of reduction in avian predation rate. One approach to achieving reductions in avian predation is to reduce the number of birds associated with a given breeding colony (e.g., USFWS 2005), and we opted to describe reductions in predation associated with reductions in colony size of 33%, 67%, and 100% (Table 3). Reductions in colony size would only accrue the below estimated benefits to Columbia River salmonid populations if the birds that are no longer a part of the given colony do not consume salmonids elsewhere within the basin (e.g., as non-breeders). Recent research indicates that for Caspian terns, it may be necessary to relocate the nesting activities of displaced birds to sites outside the Columbia Basin to substantially eliminate consumption of Columbia River salmonids, at least in some years (Maranto et al. 2011). Other means of reducing avian predation can also be analyzed using this approach; however, other management scenarios were not defined at the time of our analysis.

Reductions in avian predation for a given reduction in colony size: To assess what degree of reduction in avian predation would be associated with a given reduction in bird colony size, it is necessary to understand the relationship between colony size and some measure of per capita

(per bird) smolt consumption. C.S. Holling (1965) famously investigated the changes in predator behavior in response to changes in prey abundance or density (“functional response”), but here we are interested in changes in predator behavior as a function of their own abundance, while prey abundance is assumed to be relatively constant. To investigate this relationship, we fitted four different types of functional responses (linear, exponential, logarithmic, and power) to the relationship between colony size (number of breeding pairs) and PIT tag recovery rates for colony-salmonid ESU interactions where data for 2006 – 2010 were available and where PIT tag recovery rates were ≥ 0.5 %. These interactions were Goose Island Caspian tern predation on UCR steelhead; Crescent Island Caspian tern predation on UCR steelhead, SR_{S/S} Chinook, SR_F Chinook, and SR steelhead; and Foundation Island double-crested cormorant predation on SR_{S/S} Chinook and SR steelhead. Data from 2004 – 2005 were not included in the analyses for the Crescent and Foundation island colonies because smolt availability from Snake River ESUs was significantly lower due to high rates of transportation; this confounded the effects of colony size. We used Akaike’s Information Criteria adjusted for small sample sizes (AICc; Burnham and Anderson 2002) to evaluate which type of functional response best fit the data. A linear response would indicate no change in predator behavior (per capita predation rate) as colony size changes. Our datasets do not include the range in colony size that would be included in 33%, 67%, and 100% reductions from the baseline levels, so extrapolation from the range we have seen is necessary. Given the lack of other data, we assumed the functional response indicated over the range of colony sizes we observed is the most defensible approach for extrapolating to smaller colony sizes.

Potential compensatory responses: Avian predation on juvenile salmonids from a given population may be additive mortality, resulting in lowered recruitment into future spawning

cohorts, or may be compensated for by other sources of mortality (e.g., other predators) at other life history stages prior to spawning. The degree to which avian predation on juvenile salmonids in the Columbia River basin is additive versus compensatory is currently unknown. Previous evaluations of avian predation have all acknowledged this uncertainty and dealt with it in different ways. Roby et al. (2003) and Lyons (2010) estimated benefits to salmonids from reductions in losses to avian predators for the range of possible compensation (0% to 100%), while Antolos et al. (2005) and Good et al. (2007) calculated benefits based only on the assumption of 0% compensatory mortality (completely additive mortality) and acknowledged that actual benefits would be less if compensation occurred.

In recent years, evidence has emerged that indicates avian predation is not completely additive or completely compensatory. Preliminary results on a small sample of SR_{S/S} Chinook salmon smolts suggested that fish in poor physical condition, as indicated by bacterial infections and incomplete smoltification, were more susceptible to avian predation in the estuary (Schreck et al. 2006). A more comprehensive study of SR steelhead conducted on the Columbia Plateau indicated that fish in poor condition, as evidenced by external signs of de-scaling, fin damage, disease, and other factors, were significantly more susceptible to avian predation than apparently healthy smolts (Hostetter et al. 2011). This disproportionate consumption of fish in degraded condition suggests that some portion of the smolts consumed by avian predators would likely be compensated for by other mortality factors if avian predation were to be reduced. The Hostetter et al. (2011) study also documented lower, but still substantial, levels of predation on fish seemingly in excellent condition, and noted that fish in poor condition were only a small minority of all fish in-river. These observations suggest that some predation is additive, or not likely to be compensated for by other mortality sources.

We calculated potential benefits to salmonid ESUs for a range of compensation – 0%, 25%, 50%, and 75% (100% compensation would result in zero net benefit from a reduction in avian predation). Recovery efforts for Columbia River salmonids are typically evaluated assuming 0% compensation (NOAA 2008) and results based on that assumption are prioritized for discussion here. Results for 25 – 75% compensation represent a more likely range of potential benefits, however. Considering a range of possible compensatory mortality in this manner avoids the necessity of one of the major assumptions of the modeling framework – that increases in survival at a particular life-history stage are independent of changes in survival elsewhere in the life history.

Estimating Benefits

Changes in λ were calculated using generational times for each ESU from McClure et al. (2003; Table 5), with the exception of SR sockeye salmon, where measuring generational time has been difficult due to the small number of adult returns. For this ESU, we used the age composition of adult sockeye sampled at Bonneville Dam (mean age = 3.0 years; Torbeck et al. 2008), which consists primarily of fish from the Upper Columbia River, as a surrogate measure of generational time.

Benefits were calculated for reductions in predation by birds from each colony independently, assuming reductions at any individual colony would not be compensated for by any of the other analyzed bird colonies. Preliminary analysis suggests little compensation by McNary Pool colonies for variation in predation by Goose Island Caspian terns (Nathan Hostetter, unpublished data); however, a more comprehensive treatment is necessary to confirm this assumption. To consider the potential benefits of reductions in predation by multiple bird

colonies, we simply added benefits derived from reductions at individual colonies, again assuming independence.

Sampling errors were available for some quantities (e.g., PIT tag recovery rates in Evans et al. [2011]) but not others (e.g., generational times) and some quantities were assumed (e.g., PIT tag deposition rates for cormorants and gulls, levels of compensatory mortality), so we did not attempt to estimate confidence intervals for projected improvements in λ , following the lead of earlier efforts (Roby et al. 2003, USFWS 2005, Antolos et al. 2005, Good et al. 2007, USACE et al. 2007).

RESULTS

Baseline avian predation rates (measured during 2007 – 2010) on the in-river migrating portions of each salmonid ESU varied from nearly undetectable levels for some bird colony/ESU combinations (e.g., 0.1% of Chinook and sockeye salmon ESUs consumed by Caspian terns nesting in the Blalock Island Complex) up to 11 – 15% of in-river migrating steelhead from the UCR ESU consumed by Caspian terns from the Goose Island colony (Table 4). Predation rates on steelhead smolts by Caspian terns were the most significant, but gulls and cormorants also took a greater proportion of steelhead than of other ESUs. Adjusting in-river predation rates for the proportion of Snake River ESUs that were transported (FPC 2011) resulted in lower predation rates at the level of the entire population for those ESUs (Table 5). After adjustments for transportation rates were taken into account, predation rates on SR ESUs exceeded 1% for predation by Crescent Island Caspian terns, Foundation Island double-crested cormorants, and

Miller Rocks gulls on steelhead (2.8%, 1.4 – 1.6%, and 1.2%, respectively) and by Foundation Island cormorants on sockeye (1.1%).

A linear functional response fit the available colony size/PIT tag recovery rate data as well ($\Delta AIC_c \leq 2$) or better than the other types of functional response for all interactions examined, so we used a linear functional relationship to estimate the reductions in predation that would occur for 33%, 67%, and 100% colony size reductions. This linear relationship allows the intuitive generalization that for any particular proportional decline in colony size, the proportional decline in predation rate will be the same.

Reductions in predation by Goose Island Caspian terns on UCR hatchery reared steelhead produced the greatest potential increases in average annual population growth rate that might occur from management to reduce predation by a single colony (Tables 6, 7, and 8). For 33% reductions in size of the five study colonies (and predation rates), Goose Island tern predation on UCR steelhead was the only case where benefits exceeded a 0.5% increase in λ , and only if compensatory mortality was 50% or less (Table 6). For a 67% reduction in colony size and assuming no compensatory mortality, benefits from reducing predation by Goose Island terns on steelhead produced a 2.9% increase in λ for UCR hatchery-reared steelhead smolts and a 2.2% increase for wild steelhead smolts (Table 7). For a complete elimination of Goose Island tern predation and no compensatory mortality, benefits for UCR steelhead ($\Delta\lambda$) were 4.2% for hatchery fish and 3.2% for wild fish (Table 8). Additionally, a 0.7% increase in λ for UCR_{Sp} Chinook salmon was also accrued in this scenario. After reductions in predation by Goose Island Caspian terns, the next most significant benefits could be accrued by reductions in predation by Crescent Island terns, with benefits ($\Delta\lambda$) of 0.7% and 0.6% for hatchery and wild UCR steelhead,

respectively, and 0.5% for SR steelhead, based on a complete elimination of predation by Crescent Island terns and no compensation (Table 8).

The hypothetical maximum cumulative potential benefits for particular salmonid ESUs, assuming (1) complete elimination of predation by all five colonies and (2) that none of the reductions in avian predation would be compensated for by other mortality factors, ranged from a low of $\Delta\lambda = 0.4\%$ for SR spring/summer-run and fall-run Chinook salmon up to a high of $\Delta\lambda = 5.0\%$ for UCR steelhead (Table 8). The maximum potential cumulative benefits, based on the two assumptions above, were 0.9% for UCR_{Sp} Chinook salmon, 0.8% for SR sockeye salmon, and 1.0% for SR steelhead.

DISCUSSION

Interpreting benefits to the population trajectory, or average annual population growth rate (λ), of salmonid ESUs due to reductions in avian predation is not necessarily intuitive and should be considered in a variety of contexts. The potential benefits we describe here are percent increases in λ ; the new value of λ (λ_{new}) can be calculated based on the old value (λ_{old}) and the calculated benefit ($\Delta\lambda$, expressed as a percentage):

$$\lambda_{\text{new}} = \lambda_{\text{old}} \times \left(1 + \frac{\Delta\lambda}{100}\right)$$

For example, if $\lambda_{\text{old}} = 0.93$ and $\Delta\lambda = 3.30\%$, then

$$\lambda_{\text{new}} = 0.93 \times \left(1 + \frac{3.30}{100}\right) = 0.93 \times 1.033 = 0.9607.$$

For a stable population, $\lambda = 1$. When $\lambda > 1$, the population is increasing and for $\lambda < 1$, the population is declining. For salmonid ESUs in decline, the management objective is to increase λ to some level > 1 (McClure 2003, NOAA 2008, 2010).

One important context in which to evaluate the potential benefits of reducing predation on juvenile salmonids by piscivorous waterbirds nesting at colonies on the Columbia Plateau is to compare those benefits to how much improvement in the population growth rate is needed to recover ($\lambda > 1$) the various salmonid ESUs. The most recent λ values calculated for ESA-listed salmonid ESUs from the Columbia Plateau are available in NOAA Fisheries' Biological Opinion (BiOp) and Supplemental Biological Opinion on the proposed operation of the Federal Columbia River Power System (FCRPS; NOAA 2008, 2010), and are provided here in Table 9 (note: estimates presented were calculated using assumptions that produce the most conservative, or lowest, estimates of λ ; see NOAA 2008). Estimates of λ are imprecise and change through time, but if we accept the point estimates averaged across ESU subpopulations as the best and most useful estimate of the population trajectory, then four of the five ESUs where estimating λ is possible need substantial improvements just to restore the population to stability ($\lambda = 1$; $SR_{S/S}$ Chinook $\Delta\lambda = 4\%$, SR_F Chinook 10%, UCR_{Sp} Chinook 15%, and UCR steelhead 42%; NOAA 2010). Given the disparity between needed levels of improvement and maximum potential improvements possible by eliminating all salmonid predation by birds nesting at the five colonies considered here (0.4%, 0.4%, 0.9%, and 5.0%, for the above ESUs respectively), it is apparent that management of Columbia Plateau waterbird colonies cannot, in isolation, restore these salmonid populations to stability ($\lambda = 1$) or a state of growth ($\lambda > 1$). In each of these four cases, eliminating all avian predation considered here would be approximately one tenth of that needed for recovery. Perhaps this should not be a surprising result, however, as salmonid populations suffer from a multitude of deleterious factors (see Lichatowich 1999), and it is the strategy of the involved federal agencies to focus recovery efforts for Columbia River salmonids on a large set of broadly-based recovery actions (Federal Caucus 2000, USACE et al. 2007, NOAA 2008). For

SR steelhead, a population whose current population trajectory is $\lambda > 1$, reduced avian predation on the Columbia Plateau would provide additional, yet modest, benefits to population growth rates.

Another useful context in which to evaluate the benefits calculated here is to compare them to the potential benefits calculated for reductions in predation by Caspian terns nesting at the East Sand Island colony in the Columbia River estuary. In 2005 a management plan and environmental impact statement (EIS) were completed that called for a 66% reduction in the size of that Caspian tern colony (down to approximately 3,125 breeding pairs from a baseline size of 9,150 pairs) to reduce predation on Columbia Basin salmonid populations. Benefits for steelhead ESUs were calculated as part of that plan development using PIT-tag recovery rate data (USFWS 2005, Good et al. 2007). Similar estimates were also produced for the FCRPS management plan and biological assessment, but were based on bioenergetics-based species-level estimates of predation rates (USACE et al. 2007, NOAA 2008). Our estimates of potential benefits from managing some or all five Columbia Plateau waterbird colonies considered here are of a similar order of magnitude to earlier estimates of benefits for dispersing approximately two-thirds of the East Sand Island Caspian tern colony, and are greater for UCR steelhead (Table 10). Potential benefits to ESA-listed ESUs of Columbia Basin salmonids from managing avian predation on the Columbia Plateau are small, however, compared to the cumulative expected benefits projected from all recovery actions included in the FCRPS BiOp (Table 10).

Of the 26 interactions between piscivorous waterbird colonies and salmonid ESUs that were considered in this analysis, the single greatest benefit would be accrued for the Upper Columbia River steelhead ESU by reducing predation by Caspian terns from the Goose Island (Potholes Reservoir) colony. Benefits to this ESU from reducing avian predation by birds from

this one colony would exceed benefits to any other ESU, even for similar reductions in colony size at all five colonies combined. Of the ESA-listed salmonid ESUs considered here, and for which the population trajectory (λ) has recently been quantified, UCR steelhead appear to be in the steepest decline and in the greatest need of targeted recovery actions, with $\lambda = 0.71$ in one estimation (NOAA 2010). Reducing predation by Goose Island Caspian terns, or even all Columbia Plateau piscivorous waterbirds, however, would be only a small step towards recovery.

Management to reduce predation on salmonids by the Goose Island Caspian tern colony would be relatively efficient in terms of benefits per managed bird, as the tern colony there has been relatively small over the baseline period (an average of 350 breeding pairs during 2006 – 2010) and individual Caspian terns from this colony have high per capita impacts (Evans et al. 2011). After reductions in predation by Goose Island terns, reductions at other colonies do not accrue as great a marginal benefit per managed bird. Management to reduce predation by the other two Caspian tern colonies on the mid-Columbia River (Crescent Island and the Blalock Island Complex) would provide the next largest incremental benefit; however, the marginal benefit per managed bird is less than half of that for Goose Island Caspian terns (Table 10). Adding reductions in predation by double-crested cormorants nesting at Foundation Island and gulls nesting at Miller Rocks to reductions in tern predation would add some benefit, but at a much lower marginal benefit per managed bird (Table 10).

Prospective benefits from reduced avian predation on the Columbia Plateau for Snake River ESUs are comparatively less than for Upper Columbia River ESUs. In years when high proportions of Snake River fish are transported, predation rates by McNary Pool birds on the portions of SR ESUs migrating in-river are comparable to those by Goose Island terns on UCR

ESUs. In these years, fewer SR smolts migrate in-river, but the per capita smolt consumption by McNary Pool birds remains relatively consistent with other years (Table 2; Lyons et al. 2011). Consequently, predation *rates* are higher in those years for in-river migrating smolts, even though the number of smolts consumed is similar. These high predation rates are somewhat deceptive, however, when impacts at the ESU level are considered because the majority of the ESU is transported around the Columbia Plateau bird colonies and are not susceptible to predation from birds nesting at these colonies. In these years, transportation significantly reduces the impact of avian predation in the Columbia Plateau region on Snake River ESUs.

In years with less transportation, many more smolts migrate in-river and are available to piscivorous waterbirds nesting on the Columbia Plateau. A degree of predator swamping occurs, as again, per capita consumption does not increase dramatically. In this case, predation *rates* are lower, even though the number of smolts consumed is comparable (Lyons et al. 2011). Upper Columbia River smolts are not transported when in the vicinity of Goose Island, and thus all smolts from Upper Columbia River ESUs are susceptible to predation by Goose Island terns. Apparently, there are too few Upper Columbia smolts to have as significant a swamping effect on Goose Island terns as do Snake River smolts on waterbirds nesting in McNary Pool in years when most SR smolts are migrating in-river. Ultimately, predation rates and potential benefits from reduced avian predation are greater for UCR ESUs preyed upon by Caspian terns nesting at Goose Island.

The results of this analysis of impacts by the Crescent Island Caspian tern colony is in general agreement with those of Antolos et al. (2005) for the years 2000 – 2001. Their estimates of potential benefits for Snake River ESUs, if predation by Crescent Island terns were eliminated, were quite small ($\Delta\lambda \leq 0.05\%$ for all SR ESUs) because a large majority of SR fish

were transported during that period, particularly in the drought year of 2001 ($\geq 98\%$; FPC 2011). The estimate of potential benefit from eliminating predation by Crescent Island terns on UCR steelhead provided by Antolos et al. (2005) ($\Delta\lambda = 1.1\%$) was slightly greater but comparable to ours ($\Delta\lambda = 0.7\%$ for hatchery origin fish, $\Delta\lambda = 0.6\%$ for wild origin). During our baseline period 2007 – 2010, the size of the Crescent Island Caspian tern colony was less than during 2000 – 2001, and a much greater number of Snake River steelhead were migrating in-river than were during 2000 – 2001; this may explain slightly lower impacts to UCR steelhead during the more recent period, and less benefit to be gained for this ESU from reducing by predation by Crescent Island terns.

The PIT-tag-based predation rates that we estimated for the Goose Island Caspian tern colony during 2007 – 2010 were approximately an order of magnitude greater than those estimated by Maranto et al. (2010) for the years 2003 and 2005 – 2006. Consequently, the estimated benefits to UCR salmonids that we calculated from reducing predation by this colony greatly exceed that which would be predicted by the Maranto et al. (2010) analysis. At least two types of methodological differences likely contributed to the differences observed: (1) in this analysis we were able to correct for incomplete PIT-tag detection efficiency and partial deposition rates, which Maranto et al. (2010) were not able to do, and (2) we narrowly defined our pool of available smolts to include only those fish interrogated (or tagged) at Rock Island Dam that were identified to be either UCR steelhead or UCR_{SP} Chinook. Maranto et al. (ibid) defined their available pool as all PIT-tagged smolts within tagged groups that had any individual tag found at the colony. By enumerating tagged fish at Rock Island Dam, we were able to completely rule out mortality between upstream smolt tagging locations and Rock Island

Dam, which is outside the foraging range of Goose Island terns, as well as describe the predation rate for the specific ESA-listed ESUs of interest.

While performing these analyses, we faced a number of critical uncertainties where data were lacking. Perhaps the most critical uncertainty for assessing potential benefits to salmonid populations from reduced predation on juveniles is to what degree other mortality factors later in the life history might compensate for those reductions in predation. Two lines of inquiry are poised to make significant contributions on this issue relatively soon (using fish whose returns to the basin to spawn will be virtually complete in 2012). The first opportunity is a study that examines the outcomes of releasing transported smolts at an alternative site low in the estuary, rather than a short distance below Bonneville Dam, as is currently done (D. Marsh and B. Sandford, NOAA Fisheries, unpublished data). Smolts released low in the estuary experienced lower predation rates by Caspian terns and double-crested cormorants nesting at East Sand Island than did control groups. This differential mortality due to avian predation in the estuary can then be compared to adult return rates (SARs) to examine how much compensatory mortality occurred. The second opportunity is similar, but focuses on avian predation in the Columbia Plateau region (Allen Evans and Nathan Hostetter, unpublished data). In this study, SARs of steelhead that were PIT-tagged as juveniles and experienced differential levels of avian predation in the McNary Pool and elsewhere during their downstream migration will be used to assess compensatory mortality.

Another uncertainty critical to accurately estimating predation rates by double-crested cormorants nesting at Foundation Island is the PIT-tag deposition rate for cormorants. An unknown portion of PIT-tags in fish that are consumed by cormorants are excreted away from the colony and not detected during colony-based PIT tag recovery efforts. Here we assumed a

deposition rate for cormorants based on measurements conducted on Caspian terns. Cormorants are much larger birds and their diet includes larger and heavier-boned fish than that of Caspian terns, so the manner in which they process and excrete PIT-tags from consumed fish may be different than for terns. Experiments were initiated in 2011 at the East Sand Island cormorant colony to attempt to address this unknown and an adequate methodology to quantify deposition rate may be confirmed later this year. PIT-tag deposition rate for gulls nesting at Miller Rocks is also an unknown and we assumed a value based on measurements conducted on Caspian terns. For gulls, however, there is an added complexity. In studies of gulls foraging at John Day Dam, potentially including gulls nesting on Miller Rocks, examination of gull stomach contents have indicated that many PIT tags ingested by gulls are no longer functional (8 of 14 tags found in one study, Zorich et al. 2010). One potential explanation for this is tag damage or breakage while in stomachs of gulls prior to being excreted. Gulls are not strictly piscivorous and they often ingest sand or pebbles to assist in the mastication of hard food items. This grit in the stomach may damage PIT-tags at an appreciable rate, and cause tag recovery efforts, even including a deposition rate correction, to underestimate how many PIT-tagged fish were taken by gulls. It is unclear how important this effect may be across the entire gull population nesting at Miller Rocks, but it is possible that the predation rate estimates we used underestimate smolt predation rates at least to some degree.

Despite these uncertainties, at current bird colony sizes, it is clear that actions to reduce avian predation on juvenile salmonids in the Columbia Plateau region will not by themselves recover ESA-listed anadromous salmonid populations from the Upper Columbia River and Snake River basins. Reductions in avian predation in this region could, however, result in increases in salmonid population growth rates comparable to some other salmonid recovery

efforts in the Columbia Basin, particularly for Upper Columbia River and Snake River steelhead populations. Reducing avian predation might also contribute to broader efforts towards recovery of threatened and endangered stocks, and potentially offer modest benefits for non-listed populations of anadromous salmonids (e.g., coho salmon) or other species of conservation concern that we did not consider (e.g., Pacific lamprey, *Entosphenus tridentatus*).

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Table 1. Matrix of possible interactions between piscivorous waterbird colonies of interest and Columbia River salmonid evolutionarily significant units (ESUs) potentially preyed upon by birds. Interactions included in this analysis are designated by darker, bold font. Darkly shaded ESUs are listed as endangered under the U.S. Endangered Species Act and lightly shaded ESUs are listed as threatened; others are not currently warranted for listing (NOAA 2011). Coho salmon restored to the upper Columbia River and Snake River basins are not recognized as native ESUs (Good et al. 2005) and were not considered for this analysis.

		Chinook ¹					Sockeye ²		Steelhead ³		
		SR _{S/S}	SR _F	UCR _{Sp}	UCR _{Su/F}	MCR _{Sp}	SR	UCR	SR	UCR	MCR
Caspian Terns	Goose Island			X	X			X		X	
	Crescent Island	X	X	X	X		X	X	X	X	
	Blalock Island Complex	X	X	X	X	X	X	X	X	X	X
Double-crested Cormorants	Foundation Island	X	X	X	X		X	X	X	X	
California and Ring-billed Gulls	Miller Rocks	X	X	X	X	X	X	X	X	X	X

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), Upper-Columbia River spring-run (UCR_{Sp}), Upper-Columbia River summer/fall-run (UCR_{Su/F}), and Middle-Columbia River spring-run (MCR_{Sp}).

²Sockeye salmon ESU designations: Snake River (SR) and “Upper-Columbia River (UCR)” which represents both the recognized Okanogan River and Wenatchee Lake ESUs.

³Steelhead trout ESU designations: Snake River (SR), Upper-Columbia River (UCR), and Middle Columbia River (MCR).

Table 2. Effects of transportation rates for Snake River steelhead smolts on total steelhead consumption and Snake River steelhead predation rates by Crescent Island Caspian terns. Proportions of Snake River steelhead transported are from the Fish Passage Center (2011). Number consumed is all steelhead consumed by this colony, irrespective of origin in the Snake or Upper Columbia rivers, derived using bioenergetics methods (Lyons et al. 2011). Predation rates on smolts migrating in-river (PR_{IR}) and at the ESU level (PR_{ESU}) are estimated as described in the text.

Year	Transported (T) ¹	In-river (1 - T)	Number Consumed ²	PR_{IR}	PR_{ESU}
2004	96 %	4 %	58,000	35.2 %	1.3 %
2005	94 %	6 %	46,000	15.9 %	1.0 %
2006	78 %	22 %	56,000	11.0 %	2.4 %
2007	45 %	55 %	74,000	4.4 %	2.4 %
2008	43 %	57 %	64,000	6.5 %	3.7 %
2009	47 %	53 %	55,000	5.1 %	2.7 %
2010	41 %	59 %	55,000	4.4 %	2.6 %

¹Fish Passage Center (2010)

²Lyons et al. (2011)

Table 3. Average colony sizes (numbers of breeding pairs) for selected piscivorous waterbird colonies on the Columbia Plateau, along with colony sizes for 33% and 67% reductions.

Species	Colony	Study Period	Colony Size	33% Smaller Colony	67% Smaller Colony
	Goose Island	2006 – 2010	350	233	117
Caspian Terns	Crescent Island	2004 – 2010	417	278	139
	Blalock Island Complex	2007 – 2010	90	60	30
Double-crested Cormorants	Foundation Island	2004 – 2010	326	217	109
California and Ring-billed Gulls	Miller Rocks	2007 - 2010	3,364 ¹	2,254	1,121

¹Breeding pairs of gulls at Miller Rocks estimated from counts of all individuals on colony using a generic conversion factor of 0.69 pairs per individual on colony typically seen at gull colonies across the Columbia Plateau.

Table 4. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids migrating in-river and belonging to various evolutionarily significant units (ESUs) from the Upper Columbia and Snake rivers. Data are adapted from Evans et al. (2011). For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on fish reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{Sp}	SR	SR	UCR
Caspian Terns	Goose Island	-	-	3.0%	-	-	14.6% 11.4%
	Crescent Island	0.9%	1.2%	0.4%	1.3%	5.1%	2.7% 2.3%
	Blalock Island Complex	0.1%	0.1%	0.1%	0.1%	0.7%	0.7%
Double-crested Cormorants	Foundation Island	1.2%	0.8%	< 0.1%	2.3%	2.9% 2.5%	0.1%
California and Ring-billed Gulls	Miller Rocks	0.4%	0.6%	0.4%	1.4%	2.0%	1.6%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{Sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table 5. Predation rates on juvenile salmonids at the ESU level by birds nesting at selected piscivorous waterbird colonies on the Columbia Plateau. Predation rates on the in-river migrating portion of Snake River ESUs (Table 4) are adjusted here to account for the fractions of those ESUs being transported around Columbia Plateau waterbird colonies (FPC 2011). For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{sp}	SR	SR	UCR
Caspian Terns	Goose Island	-	-	3.0%	-	-	14.6% 11.4%
	Crescent Island	0.6%	0.6%	0.4%	0.6%	2.8%	2.7% 2.3%
	Blalock Island Complex	0.1%	< 0.1%	0.1%	≤ 0.1%	0.4%	0.7%
Double-crested Cormorants	Foundation Island	0.8%	0.4%	< 0.1%	1.1%	1.6% 1.4%	0.1%
California and Ring-billed Gulls	Miller Rocks	0.3%	0.3%	0.4%	0.6%	1.2%	1.6%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table 8. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 100% reductions in piscivorous waterbird colony size, corresponding to 100% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Sockeye	Steelhead	
			SR _{S/S}	SR _F	UCR _{Sp}	SR	SR	UCR
0% Compensation	CATE	GI			0.7%			4.2%
		CI	0.1%	0.2%	0.1%	0.2%	0.5%	3.2%
		BIC	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.1%	0.2%
	DCCO	FI	0.2%	0.1%	< 0.1%	0.4%	0.3% 0.2%	< 0.1%
	Gulls	MR	0.1%	0.1%	0.1%	0.2%	0.2%	0.4%
25% Compensation	CATE	GI			0.5%			3.2%
		CI	0.1%	0.1%	0.1%	0.2%	0.4%	2.5%
		BIC	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%
	DCCO	FI	0.1%	0.1%	< 0.1%	0.3%	0.2% 0.2%	< 0.1%
	Gulls	MR	< 0.1%	0.1%	0.1%	0.2%	0.2%	0.3%
50% Compensation	CATE	GI			0.4%			2.2%
		CI	0.1%	0.1%	< 0.1%	0.1%	0.3%	1.7%
		BIC	< 0.1%	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.1%
	DCCO	FI	0.1%	0.1%	< 0.1%	0.2%	0.2% 0.1%	< 0.1%
	Gulls	MR	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	0.2%
75% Compensation	CATE	GI			0.2%			1.1%
		CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	0.8%
		BIC	< 0.1%	< 0.1%	< 0.1%	< 0.1%	< 0.1%	< 0.1%
	DCCO	FI	0.1%	< 0.1%	< 0.1%	0.1%	0.1% 0.1%	< 0.1%
	Gulls	MR	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	0.1%

Table 9. Recent estimates (and 95% confidence intervals) of the average annual population growth rate (λ) for Columbia Plateau salmonid ESUs (NOAA 2010), and for declining populations, the percentage improvement needed (percentage change from current value) to achieve population stability ($\lambda = 1$). Cited lambda values use pessimistic assumptions about the spawning contribution of hatchery origin fish (NOAA 2008). Averages are unweighted means of the sub-population values. Due to the small size of the population, λ estimates for Snake River sockeye salmon are not available.

Species	ESU	Sub-population	λ Point Estimate	95% CI	% Gain Needed
Chinook	SR _{S/S}	Tucannon	0.86	0.66 – 1.44	16%
		Upper Grande Ronde ¹	0.85	0.67 – 1.09	18%
		Catherine Creek ¹	0.81	0.53 – 1.26	23%
		Lostine/Wallowa Rivers ¹	0.82	0.59 – 1.13	22%
		Minam River ¹	0.98	0.71 – 1.36	2%
		Imnaha River ¹	0.93	0.65 – 1.33	8%
		Wenaha River ¹	0.94	0.68 – 1.32	6%
		Secesh R	1.02	0.82 – 1.27	-
		South Fork Salmon East Fork ¹	1.05	0.87 – 1.26	-
		Big Creek	1.01	0.74 – 1.39	-
		Loon Creek	0.99	0.67 – 1.44	1%
		Sulphur Creek	1.03	0.77 – 1.38	-
		Bear Valley Creek	1.04	0.80 – 1.35	-
		Marsh Creek	1.01	0.77 – 1.33	-
		Lemhi R	0.96	0.67 – 1.35	4%
		Lower Mainstem Salmon River	0.99	0.75 – 1.31	1%
		Yankee Fork Salmon River ¹	1.06	0.67 – 1.68	-
	Valley Creek	1.02	0.76 – 1.38	-	
	Average	.97		4%	
		SR _F	NA	0.91	0.75 – 1.12
	UCR _{Sp}	Wenatchee R	0.86	0.67 – 1.11	16%
		Entiat R	0.90	0.73 – 1.11	11%
		Methow R	0.85	0.60 – 1.21	18%
		Average	0.87		15%
Steelhead	SR	Average “A-Run” ¹	1.05	0.50 – 2.23	-
		Average “B-Run” ¹	1.00	0.63 – 1.58	-
		Average	1.03		-
	UCR	Wenatchee R	0.79	0.64 – 0.96	27%
		Entiat R	0.80	0.66 – 0.96	25%
		Methow R	0.67	0.57 – 0.77	49%
		Okanogon R	0.56	0.48 – 0.66	79%
	Average	0.71		42%	

¹No updated data included in NOAA (2010) so data drawn from NOAA (2008).

Table 10. Hypothetical maximum cumulative potential benefit to each salmonid ESU resulting from complete elimination of predation by all five analyzed piscivorous waterbird colonies on the Columbia Plateau, only the three Caspian tern colonies analyzed, or just the Goose Island Caspian tern colony (assuming 0% compensation). For comparison, potential benefits from management to reduce Caspian tern predation in the Columbia River estuary (calculated different ways in USFWS 2005 and USACE et al. 2007), and for the cumulative total of all recovery actions in the 2008 Federal Columbia River Power System Biological Opinion (BiOp; NOAA 2008) are presented below. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others. The number of birds projected to be managed and the marginal benefit per managed bird are also provided for comparative purposes.

Action	Chinook			Steelhead		Number of Birds Managed (Individuals) ⁴	Marginal Benefit (UCR Steelhead) per Managed Bird ⁵
	SR _{S/S}	SR _F	UCR _{Sp}	SR	UCR		
Complete Elimination of Predation by Goose Island Caspian Terns	NA	NA	0.7%	NA	3.7%	700	6.4E-5
Complete Elimination of Predation by Columbia Plateau Caspian Tern Colonies	0.2%	0.2%	0.8%	0.6%	4.6%	1,700	1.8E-5
Complete Elimination of Predation by all five Columbia Plateau Waterbird Colonies	0.4%	0.4%	0.9%	1.0%	5.0%	9,100	2.0E-6
Partial Dispersal of Caspian Terns from Columbia River Estuary (CATE EIS) ¹	-	-	-	1.5%	1.7%	12,100	-
Partial Dispersal of Caspian Terns from Columbia River Estuary (2008 FCRPS BiOp) ²	0.5%	0.2%	0.5%	0.8%	0.8%	12,100	1.6E-6
All Actions of 2008 FCRPS BiOp ³	10%	2-6%	14%	4%	18-24%	12,100	-

¹Based on PIT tag recovery rates (no deposition rate correction) during 1999 – 2003 (USFWS 2005, Good et al. 2007).

²Based on bioenergetics-based predation rates at the species level during 1997 – 2006 (USACE et al. 2007).

³From NOAA (2008). Ranges represent differing assumptions used to calculate λ values. Includes Caspian tern management in the Columbia River estuary.

⁴Based on intended reductions from baseline conditions; estuary Caspian tern baseline taken from USACE et al. (2007).

⁵Marginal benefit is computed as (% benefit/managed birds) for Goose Island terns, then (additional % benefit/additional birds managed) for scenarios of adding reductions in predation by other tern colonies and then by adding predation reductions by cormorants and gulls. % benefit is benefits for all five salmonid ESUs added together.



Figure 1. Map of Caspian tern (CATE), double-crested cormorant (DCCO) and California and ring-billed gull colony sites considered in this document. The geographic boundaries of the salmonid life history stages outlined in the text are shaded and labeled.

APPENDIX A

COMPARISON OF PIT-TAG BASED PREDATION RATE ESTIMATES TO THOSE BASED ON BIOENERGETICS TECHNIQUES

In the Columbia River basin, management decisions to promote salmon recovery have been made at the level of distinct population segment (DPS) or evolutionarily significant unit (ESU; e.g., NOAA 2008, 2010). To consider the potential benefits from reducing avian predation by colonial nesting waterbirds, the important metric is the baseline predation rate by birds from a given breeding colony on a given salmonid DPS/ESU. For most salmonid DPSs/ESUs, a sample group has been tagged using passive integrated transponder (PIT) tags and data from the recovery of PIT-tags at bird colonies has been used to derive these DPS/ESU-specific predation rates (USFWS 2005, Antolos et al. 2005, Good et al. 2007, Evans et al. 2011, this document). PIT-tag recovery rates, once corrected for detection efficiency and deposition rate, are unbiased estimates of predation rates.

In some analyses of the impacts of avian predation impacts on salmonid populations, demand-based bioenergetics techniques have been used to estimate numbers of juvenile salmonids consumed (Roby et al. 2003, Antolos et al. 2005, Lyons 2010, Maranto 2010). Predation rate estimates are possible based on these consumption estimates when the number of smolts available to bird colonies can also be estimated. The ability of these bioenergetics-derived estimates of predation rate to resolve between categories of salmonids (e.g., species, DPSs/ESUs, hatchery/wild) are limited by the ability to distinguish between salmonid groups of interest

during the bioenergetics data collection process. For Caspian tern colonies, diet composition is typically determined by observing fish carried back to the colony by adult terns to provision mates and/or chicks (“bill-load” fish), with fish identified by observers stationed in blinds at the colony perimeter using binoculars or spotting scopes (Collis et al. 2002). Using this method, juvenile salmonids can be identified to the level of family and to species for steelhead/rainbow trout (*Oncorhynchus mykiss*). Other salmonid species (Chinook, coho, and sockeye salmon) and age classes (yearling and sub-yearling Chinook salmon) cannot be distinguished from one another and so are pooled. In some cases, additional datasets are available to breakdown salmonid consumption at a finer resolution (e.g., when either salmonid bill-loads or salmonid tissue recovered from the guts of collected birds are available for either morphological or genetic identification to species; Roby et al. 2003, Lyons 2010, Maranto et al. 2010). For colonies of other species of piscivorous birds, resolution beyond the level of Salmonidae has been dependent on identification of salmonid tissue from the guts of collected adult birds, and sufficient samples sizes have seldom been achieved (but see Lyons 2010).

For the waterbird colonies examined in this document, suitable bioenergetics estimates of juvenile salmonid consumption to the level of species exist only for the case of Crescent Island Caspian tern predation on juvenile steelhead (Lyons et al. 2011). Recently, the annual abundance of juvenile salmonids arriving at the forebay of McNary Dam has also been estimated (Allen Evans, Real Time Research, and Ben Sandford, NOAA Fisheries, unpublished data), providing smolt availability data that can be used to estimate predation rates. Management decisions will be made based on analyses conducted at the level of DPSs/ESUs and thus reliant on PIT-tag-based predation rates; however, bioenergetics-based predation rates at the species level, while

not a true apples-to-apples comparison, can provide a qualitative corroboration of the PIT-tag methodology (e.g., USFWS 2005).

For predation by Crescent Island Caspian terns on steelhead, the annual trends in bioenergetics-based predation rates on steelhead at the species level (includes all steelhead that were available in the McNary Pool) and the PIT-tag based predation rates specifically for the Snake River (SR) and Upper Columbia River (UCR) DPSs are qualitatively similar (Table A1). For all three measures, the maximum predation rates were estimated in 2004 with a downward trend over the study period to a minimum in 2010. In absolute terms, the PIT-tag based estimates for SR steelhead are substantially greater than the bioenergetics-based estimates; however, the estimates based on PIT-tags from UCR smolts are strikingly similar to the generic bioenergetics estimates. Relatively good correspondence between methodologies was present during the period of moderate transportation levels (2007 – 2010), from which the baseline estimation of benefits were produced.

Again, it should be noted that the measures from the different methodologies do not represent predation rates on the same groups of fish. The bioenergetics-based predation rates are for a composite of all steelhead – those produced above Rock Island Dam on the Upper Columbia River (the UCR ESU), above Lower Monumental Dam on the Snake River (the SR ESU), and all other steelhead that originate below these points and enter the McNary Pool (not covered by any PIT-tag based predation rate discussed in this document). In general, given the overall qualitative agreement between the methodologies, particularly during the baseline period of moderate transportation, the bioenergetics-based results corroborate the use of PIT-tag based predation rates for the larger analysis of potential benefits for salmonids if avian predation were to be reduced, at least for Crescent Island Caspian tern predation on steelhead.

Table A1. Comparison of annual estimates of predation rates on steelhead by Crescent Island Caspian terns derived using bioenergetics estimates of smolt consumption and PIT-tag recoveries.

Year	Steelhead Consumed ¹	Steelhead Arriving to McNary Dam Forebay ²	Bioenergetics Predation Rate on All Steelhead ³	PIT-tag Predation Rate on SR Steelhead ⁴	PIT-tag Predation Rate on UCR Steelhead ⁴
2004	58,000	802,000	6.7 %	35.0 %	5.2 %
2005	46,000	1,032,000	4.2 %	15.8 %	3.3 %
2006	56,000	2,038,000	2.7 %	10.9 %	2.2 %
2007	74,000	3,116,000	2.3 %	4.4 %	3.0 %
2008	64,000	3,417,000	1.8 %	6.5 %	2.2 %
2009	55,000	4,054,000	1.3 %	5.0 %	2.5 %
2010	55,000	4,421,000	1.2 %	4.4 %	1.4 %
Average			2.9 %	11.7 %	2.8 %

¹From Lyons et al. (2011).

²Allen Evans, Real Time Research, and Ben Sandford, NOAA Fisheries, unpublished data.

³Calculated as Predation Rate = (# Consumed)/(# Consumed + # Arriving to McNary Dam Forebay).

⁴On-colony PIT-tag recoveries corrected for detection efficiency and deposition rate.

APPENDIX B

CALCULATION OF BENEFITS WITHOUT DEPOSITION RATE CORRECTION

In past publications and reports, PIT-tag recovery rates at piscivorous waterbird colonies in the Columbia Plateau region (with and without detection efficiency correction) have been used as minimum estimates of predation rates, without correcting for birds depositing (excreting) some proportion of ingested tags away from the colony (Collis et al. 2001, Ryan et al. 2003, Antolos et al. 2005, Maranto et al. 2010, Evans et al. 2011). This has been in part due to lack of appropriate data on deposition rates, but also has not been necessary to assess relative susceptibility of different salmonid species and stocks to avian predation. In the main text of this document our objective was to estimate the absolute benefits that might be accrued by salmonids for reductions in avian predation. In order to achieve unbiased estimates of benefits, we incorporated what information was available on PIT-tag deposition rate in those calculations, making explicitly stated assumptions when necessary (see Methods in main text for details).

For comparison purposes, in this appendix we present estimates of benefits ($\Delta\lambda$ values) calculated without the deposition rate correction to predation rates. These estimates are biased low for predation rates (Tables B1 and B2) and for potential increases in λ (Tables B3, B4, and B5) derived from reductions in predation rates.

Table B1. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids migrating in-river and belonging to various evolutionarily significant units (ESUs) from the Upper Columbia and Snake rivers. Data are adapted from Evans et al. (2011). For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{Sp}	SR	SR	UCR
	Goose Island	-	-	2.3%	-	-	11.1% 8.7%
Caspian Terns	Crescent Island	0.6%	0.8%	0.2%	0.8%	3.2%	1.7% 1.5%
	Blalock Island Complex	0.1%	< 0.1%	0.1%	< 0.1%	0.5%	0.5%
Double-crested Cormorants	Foundation Island	0.9%	0.6%	< 0.1%	1.6%	2.0% 1.7%	0.1%
California and Ring-billed Gulls	Miller Rocks	0.3%	0.4%	0.3%	1.0%	1.4%	1.1%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{Sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table B2. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids at the ESU level. Predation rates on the in-river migrating portion of Snake River ESUs (Table B1) are adjusted here to account for significant fractions of those ESUs being transported around Columbia Plateau waterbird colonies (FPC 2011). For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{sp}	SR	SR	UCR
Caspian Terns	Goose Island	-	-	2.3%	-	-	11.1% 8.7%
	Crescent Island	0.4%	0.4%	0.2%	0.4%	1.8%	1.7% 1.4%
	Blalock Island Complex	0.1%	< 0.1%	0.1%	≤ 0.1%	0.3%	0.5%
Double-crested Cormorants	Foundation Island	0.6%	0.3%	< 0.1%	0.8%	1.1% 1.0%	0.1%
California and Ring-billed Gulls	Miller Rocks	0.2%	0.2%	0.3%	0.4%	0.8%	1.1%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

APPENDIX C

CALCULATION OF BENEFITS USING A BASELINE PERIOD INCLUDING HIGH AND MODERATE TRANSPORTATION CONDITIONS (2004 – 2010)

The analyses included in the main body of this document are based on data collected during a period with moderate rates of transportation for smolts from the Snake River (2007 – 2010). These conditions were deemed to be most likely representative of future conditions (Gary Fredericks, NOAA Fisheries). Predation rate data by birds from some colonies on some salmonid ESUs extends back as far as 2004, however. For comparison purposes, we present estimates of predation rates and benefits to salmonid ESUs ($\Delta\lambda_s$) for the 2004 – 2010 period here, for the colonies and salmonid ESUs where additional data are available. This period corresponds to a mix of high transportation rates (2004 – 2005), moderate transportation rates (2007 – 2010) and an intermediate year (2006; Table C1).

For Crescent Island Caspian terns and Foundation Island double-crested cormorants, PIT-tag recovery was performed and deposition rate corrections were available in all the additional years (2004 – 2006). For Goose Island Caspian terns, one additional year of PIT-tag data was available (2006). For Snake River salmonid ESUs, sufficient Chinook salmon and steelhead smolts were interrogated at Lower Monumental Dam ($N > 500$) to generate predation rate estimates in all three additional years (2004 – 2006). Sufficient Snake River sockeye salmon were interrogated in 2006. For Upper Columbia River ESUs, sufficient steelhead smolts were interrogated at Rock Island Dam in all three years to generate predation rates for Goose Island

terns (in 2006, when PIT-tag recovery data were available) and for Foundation Island cormorants and Crescent Island terns (in all three years). There were sufficient UCR_{Sp} Chinook smolts interrogated in 2004 to generate predation rates for Foundation Island cormorants and Crescent Island terns (suitable PIT-tag recovery data were not available for Goose Island terns in that year). PIT-tag recovery did not occur at the Blalock Island Complex nor at Miller Rocks during 2004 – 2006, so no revisions to the calculations in the main text were possible.

Compared to the shorter, moderate transportation baseline period, predation rates on smolts migrating in-river averaged across the 2004 – 2010 period were generally greater (Table C2), primarily because predation rates on in-river migrating smolts during 2004 – 2005 were very high. ESU-level predation rates (including both in-river and transported smolts) were generally lower for Snake River fish, due to the substantially greater levels of transportation during 2004 – 2005, when the overwhelming majority of Snake River smolts were not exposed to avian predation in the Columbia Plateau region. It is noteworthy, that while predation rates by Crescent Island terns on Snake River steelhead went down in years of high transportation, and thus drove the average predation rate down compared to the 2007 – 2010 baseline period, predation rates by this colony on Upper Columbia River steelhead were *greater* during high transportation years. It appears that transportation of Snake River steelhead smolts serves to protect the transported fish, but may increase the impacts of avian predators on non-transported steelhead smolts, including those from the Upper Columbia River.

Using a baseline period spanning 2004 – 2010, which included the high transportation years of 2004 – 2005, changed some of the point estimates of potential benefits from reduced avian predation; however, the qualitative conclusions closely mirrored those based on the 2007 – 2010 baseline period in the main text.

Table C1. Estimated transportation rates of Snake River juvenile salmonids separated by evolutionarily significant unit. Data are from the Fish Passage Center (2011). Values from 2006 – 2010 for Chinook salmon and steelhead are means of separately estimated rates for hatchery-reared and wild groups, equally weighted. Yearling Chinook are assumed to belong to the spring/summer-run (SR_{S/S}) and sub-yearling Chinook to the fall-run (SR_F).

Year	SR _{S/S} Chinook	SR _F Chinook	SR Sockeye	SR Steelhead
2004	87.0 %	97.2 %	95.2 %	96.4 %
2005	92.0 %	80.9 %	85.9 %	94.0 %
2006	59.5 %	54.2 %	59.2 %	77.7 %
2007	20.5 %	35.8 %	53.2 %	45.4 %
2008	49.1 %	52.2 %	62.0 %	42.9 %
2009	38.0 %	48.0 %	65.4 %	47.0 %
2010	32.0 %	52.5 %	33.0 %	40.5 %
Average	54.0 %	60.1 %	64.8 %	63.5 %

Table C2. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids migrating in-river and belonging to various evolutionarily significant units (ESUs) from the Upper Columbia and Snake rivers. Data are adapted from Evans et al. (2011). For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{Sp}	SR	SR	UCR
Caspian Terns	Goose Island	-	-	3.0%	-	-	13.4%
	Crescent Island	1.5%	1.8%	0.2%	2.1%	11.7%	9.9%
Double-crested Cormorants	Foundation Island	1.1%	0.5%	0.1%	2.0%	3.0% 2.3%	0.1%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{Sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table C3. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids at the ESU level. Predation rates on the in-river migrating portion of Snake River ESUs (Table C2) are adjusted here to account for significant fractions of those ESUs being transported around Columbia Plateau waterbird colonies (FPC 2011). For three colony/year interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Sockeye ²	Steelhead ³	
		SR _{S/S}	SR _F	UCR _{sp}	SR	SR	UCR
Caspian Terns	Goose Island	-	-	3.0%	-	-	13.4%
	Crescent Island	0.5%	0.6%	0.2%	0.9%	2.3%	9.9%
Double-crested Cormorants	Foundation Island	0.5%	0.3%	0.1%	0.9%	1.1%	3.6%
						0.9%	2.8%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table C5. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 67% reductions in piscivorous waterbird colony size, corresponding to 67% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Sockeye	Steelhead	
			$SR_{S/S}$	SR_F	UCR_{Sp}	SR	SR	UCR
0% Compensation	CATE	GI			0.5%			2.6%
		CI	0.1%	0.1%	< 0.1%	0.2%	0.3%	1.9%
		FI						0.6%
	DCCO	CI						0.5%
		FI	0.1%	0.1%	< 0.1%	0.2%	0.1%	< 0.1%
		FI					0.1%	< 0.1%
25% Compensation	CATE	GI			0.4%			2.0%
		CI	0.1%	0.1%	< 0.1%	0.2%	0.2%	1.4%
		FI						0.5%
	DCCO	CI						0.4%
		FI	0.1%	< 0.1%	< 0.1%	0.2%	0.1%	< 0.1%
		FI					0.1%	< 0.1%
50% Compensation	CATE	GI			0.2%			1.3%
		CI	< 0.1%	0.1%	< 0.1%	0.1%	0.1%	1.0%
		FI						0.3%
	DCCO	CI						0.3%
		FI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	< 0.1%
		FI					0.1%	< 0.1%
75% Compensation	CATE	GI			0.1%			0.7%
		CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	0.5%
		FI						0.2%
	DCCO	CI						0.1%
		FI	< 0.1%	< 0.1%	< 0.1%	0.1%	< 0.1%	< 0.1%
		FI					< 0.1%	< 0.1%

Table C6. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 100% reductions in piscivorous waterbird colony size, corresponding to 100% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Sockeye	Steelhead	
			SR _{S/S}	SR _F	UCR _{Sp}	SR	SR	UCR
0% Compensation	CATE	GI			0.7%			3.8%
		CI	0.1%	0.2%	0.1%	0.3%	0.4%	1.0%
	DCCO	FI	0.1%	0.1%	< 0.1%	0.3%	0.2% 0.2%	< 0.1%
25% Compensation	CATE	GI			0.5%			2.9%
		CI	0.1%	0.1%	< 0.1%	0.2%	0.3%	0.7%
	DCCO	FI	0.1%	0.1%	< 0.1%	0.2%	0.2% 0.1%	< 0.1%
50% Compensation	CATE	GI			0.4%			2.0%
		CI	0.1%	0.1%	< 0.1%	0.2%	0.2%	0.5%
	DCCO	FI	0.1%	< 0.1%	< 0.1%	0.2%	0.1% 0.1%	< 0.1%
75% Compensation	CATE	GI			0.2%			1.0%
		CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1%	0.2% 0.2%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.1% < 0.1%	< 0.1%

APPENDIX D

CALCULATION OF BENEFITS USING A BASELINE PERIOD INCLUDING ONLY HIGH TRANSPORTATION CONDITIONS (2004 – 2005)

The analyses included in the main body of this document are based on data collected during a period with moderate rates of transportation of smolts from the Snake River (2007 – 2010). These conditions were deemed to be most likely representative of future conditions (Gary Fredericks, NOAA Fisheries). Predation rate data by birds from some colonies on some salmonid ESUs extends back as far as 2004, however, which includes the high transportation years of 2004 and 2005 (see Table C1 in Appendix C). For comparison purposes, we present estimates of predation rates and benefits to salmonid ESUs ($\Delta\lambda$ s) for the 2004 – 2005 period here, for the colonies and salmonid ESUs where additional data are available: Foundation Island double-crested cormorants and Crescent Island Caspian terns. Note: insufficient Snake River sockeye were interrogated at Lower Monumental Dam in 2004 – 2005, so sockeye are excluded from this analysis.

ESU-level predation rates, and the potential benefits if predation were reduced, are substantially lower for Snake River ESUs in this high transportation scenario than for the moderate transportation conditions considered in the main body of this document (Tables D1 – D5). Predation rates on Upper Columbia River steelhead by Crescent Island Caspian terns is

higher under the high transportation scenario, however, with potential benefits also correspondingly greater.

Table D1. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids migrating in-river and belonging to various evolutionarily significant units from the Upper Columbia and Snake rivers. Data are adapted from Evans et al. (2011). For two colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Steelhead ³	
		SR _{S/S}	SR _F	UCR _{Sp}	SR	UCR
Caspian Terns	Crescent Island	2.4%	2.9%	< 0.1%	25.4%	5.3% 4.3%
Double-crested Cormorants	Foundation Island	0.9%	0.2%	0.4%	2.8% 2.1%	0.1%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{Sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table D2. Predation rates by birds nesting at selected piscivorous waterbird colonies on juvenile salmonids at the ESU level. Predation rates on the in-river migrating portion of Snake River ESUs (Table D1) are adjusted here to account for significant fractions of those ESUs being transported around Columbia Plateau waterbird colonies (FPC 2011). For two colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W).

		Chinook ¹			Steelhead ³	
		SR _{S/S}	SR _F	UCR _{sp}	SR	UCR
Caspian Terns	Crescent Island	0.3%	0.3%	< 0.1%	1.1%	5.3% 4.3%
Double-crested Cormorants	Foundation Island	0.1%	< 0.1%	0.4%	0.1% 0.1%	0.1%

¹Chinook salmon ESU designations: Snake River spring/summer run (SR_{S/S}), Snake River fall-run (SR_F), and Upper Columbia River spring-run (UCR_{sp})

²Sockeye salmon ESU designation: Snake River (SR)

³Steelhead trout ESU designations: Snake River (SR), and Upper Columbia River (UCR)

Table D3. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 33% reductions in piscivorous waterbird colony size, corresponding to 33% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Steelhead	
			SR _{S/S}	SR _F	UCR _{Sp}	SR	UCR
0% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.5% 0.4%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
25% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.4% 0.3%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
50% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.2% 0.2%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
75% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.1% 0.1%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%

Table D4. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 67% reductions in piscivorous waterbird colony size, corresponding to 67% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Steelhead	
			SR _{S/S}	SR _F	UCR _{Sp}	SR	UCR
0% Compensation	CATE	CI	< 0.1%	0.1%	< 0.1%	0.1%	1.0% 0.8%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
25% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.7% 0.6%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
50% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.5% 0.4%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
75% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	< 0.1%	0.2% 0.2%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%

Table D5. Percentage increases in the average annual population growth rate (λ) of selected salmonid ESUs for 100% reductions in piscivorous waterbird colony size, corresponding to 100% reductions in predation by birds from those colonies. For three colony/ESU interactions, predation rates on smolts reared in hatcheries significantly exceeded those on smolts reared in the wild; for those interactions, both predation rates are listed (H/W). $\Delta\lambda$ values are provided for three levels of compensatory mortality that may result from these reductions in mortality due to avian predation. Bold, black font is used for all interactions with $\Delta\lambda \geq 1\%$, black font for $\Delta\lambda \geq 0.5\%$, and gray font for all others.

			Chinook			Steelhead	
			SR _{S/S}	SR _F	UCR _{Sp}	SR	UCR
0% Compensation	CATE	CI	0.1%	0.1%	< 0.1%	0.2%	1.4% 1.2%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
25% Compensation	CATE	CI	0.1%	0.1%	< 0.1%	0.1%	1.1% 0.9%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
50% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.7% 0.6%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%
75% Compensation	CATE	CI	< 0.1%	< 0.1%	< 0.1%	0.1%	0.4% 0.3%
	DCCO	FI	< 0.1%	< 0.1%	< 0.1%	< 0.1% < 0.1%	< 0.1%