Factors Influencing Predation on Juvenile Salmonids by Double-crested Cormorants in the Columbia River Estuary: A Retrospective Analysis

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ABSTRACT

Enhancing the survival of juvenile salmonid (*Oncorhynchus* spp.) is a priority objective to recover populations of Columbia River salmonids listed under the U.S. Endangered Species Act (ESA). In the Columbia River estuary, a significant mortality factor for juvenile salmonids is predation by double-crested cormorants (*Phalacrocorax auritus*) nesting at East Sand Island. The U.S. Army Corps of Engineers is considering management alternatives to reduce this mortality. Understanding the factors that influence cormorant predation is important to understanding the potential consequences of various management strategies. We used principal components regression (PCR) to evaluate the relationship between several annual measures of cormorant predation and a combination of colony size and environmental covariates. The environmental factors considered included large-scale climate indices (Pacific Decadal Oscillation, El Nino/Southern Oscillation Index, North Pacific Gyre Oscillation, Pacific Northwest Index), regional climate measures (sea surface temperature, upwelling strength, upwelling timing), and variables describing conditions during freshwater and estuarine outmigration (river discharge, spill at hydroelectric dams, measures of salmonid smolt survival to the estuary). These covariates potentially influenced both the susceptibility of salmonids to cormorant predation and the abundance and distribution of marine forage fish and their availability as alternative prey for cormorants nesting in the estuary. Measures of cormorant predation spanned a 15-year period (1999 – 2013) and included (1) predation probabilities for multiple steelhead (*O. mykiss*) and Chinook salmon (*O. tshawytscha*) populations derived from recoveries of salmonid passive integrated transponder (PIT) tags at the cormorant colony, (2) estimates of annual consumption of steelhead and yearling Chinook by cormorants derived using bioenergetics modelling, and (3) the observed percentage of the cormorant diet that consisted of salmonids. We also related cormorant diet composition to purse seine catches in the estuary during 2007 – 2012 to assess how predation on salmonids is related to availability of alternative, non-salmonid prey and to examine cormorant selectivity of salmonids relative to other available prey.

PCR analyses indicated that environmental factors explain a substantial proportion of the annual variability seen in several measures of cormorant predation on Columbia River juvenile salmonids. Cormorant colony size was an important explanatory factor in most regressions; however, it never explained more than 17% of the variability in any annual measure of cormorant predation on salmonids. In aggregate, environmental factors explained a greater proportion of the annual variability in cormorant predation than did colony size; in particular, river discharge and the North Pacific Gyre Oscillation (NPGO) were prominent environmental explanatory factors. Based on comparisons to estuary purse seine catches, cormorants appeared to take salmonids in proportion to their relative availability in the Columbia River estuary, not their absolute abundance. Conversely, changes in absolute abundance of alternative prey, both marine and freshwater/estuarine forage fishes, did influence how much cormorants relied on salmonids as prey. While colony size is an important determinant of cormorant impacts on salmonid populations, environmental conditions that regulate the availability of alternative prey might outweigh the effects of changing colony size in any given year. Potential management efforts to reduce the size of the double-crested cormorant colony on East Sand Island to benefit ESA-listed salmonids would best be evaluated in the context of environmental conditions, particularly if evaluation occurs on an annual basis, with special attention given to river discharge and the NPGO. Multiyear data sets following any implementation of management would likely be more useful to evaluate potential benefits.

INTRODUCTION

Increasing salmonid (*Oncorhynchus* spp.) survival at the juvenile life history stage has been proposed as a priority objective to recover Columbia River basin salmonid populations listed under the U.S. Endangered Species Act (ESA; NOAA 2014). In the Columbia River estuary, a significant mortality factor for juvenile salmonids is predation by piscivorous colonial waterbirds (Lyons 2010, Evans et al. 2012). In particular, average annual predation rates on ESA-listed salmonid populations by double-crested cormorants (*Phalacrocorax auritus*) nesting at East Sand Island (river km 8) ranged from 1.9% to 9.8% by population during 2007 – 2012 (Lyons et al. 2014). Total annual salmonid consumption by double-crested cormorants ranged from 9.2 million to 20.5 million smolts during the same interval (BRNW 2014).

While levels of cormorant predation on some populations of juvenile salmonids have been high on average, there has been substantial inter-annual variability. Coefficients of variation (CVs; calculated as the standard deviation divided by the mean value for a given parameter) of annual predation rates (proportion of available smolts that were consumed by cormorants) during 2007 – 2012 ranged from 35% to 89% for Chinook salmon (*O. tshawytscha*) populations and 37% to 63% for steelhead (*O. mykiss*) populations (Lyons et al. 2014). For the total numbers of steelhead and yearling Chinook smolts consumed, CVs were 47% and 50%, respectively, during 2004 – 2012. Similarly, the annual percentage of the cormorant diet that consisted of salmonids varied over an order of magnitude since 2004, ranging from 2% to 20% (CV = 45%) of the diet. While change in the size of the double-crested cormorant colony on East Sand Island may explain some of the annual variability in cormorant predation on salmonids, colony size was relatively stable during 2004 – 2012 (10,950 – 13,800 breeding pairs; CV = 7%).

It is well documented that environmental conditions can play an important role in the survival of juvenile salmonids during outmigration to the ocean and after ocean entry (e.g., Petrosky and Schaller 2010, Burke et al. 2013, Peterson and Burke 2013). Large scale climate indices such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), the El Nino/Southern Oscillation (quantified as the Multivariate ENSO Index, or MEI; Wolter and Timlin 1993, 1998), the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008, Miller et al. 2013), and the Pacific Northwest Index (PNI; Ebbesmeyer and Strickland 1995, Williams et al. 2014), have all been found to relate to juvenile salmonid survival, presumably through the regulation of predators, competitors, and/or food resources (Emmett et al. 2006, Scheuerell et al. 2009, Lyons 2010).

At the regional scale, important factors related to survival of juvenile salmonids include local sea surface temperature (SST; Brosnan et al. 2014) and the strength (Greene et al. 2005) and timing (Logerwell et al. 2003) of coastal upwelling, among others. These conditions probably only weakly regulate conditions in the Columbia River estuary but may play a strong role in the abundance and distribution of marine forage fish and their availability to cormorants nesting in the estuary (Litz et al. 2012). In the estuary, river discharge has been shown to be a factor significantly affecting the composition of the local forage fish community (Weitkamp et al. 2012), presumably by altering salinity distributions, and has been shown to regulate predation on juvenile salmonids by Caspian terns (*Hydroprogne caspia*) nesting at East Sand Island (Lyons 2010).

The conditions that juvenile salmonids experience during their freshwater migration, prior to arrival in the estuary, may also affect their survival in the estuary. The proportion of water passing a dam that flows over the spillway, often the most benign route for a smolt to move past a dam (Muir et al. 2001), can be related to subsequent survival in the estuary or near-shore ocean environments (Petrosky and

Schaller 2010, Haeseker et al. 2012). In addition, river flows experienced by smolts can influence travel times and survival rates during migration through the hydropower system (Scheuerell et al. 2009). Ultimate survival rates of smolts migrating through the Columbia River hydropower system have also been a useful predictor of survival in the estuary and near-shore ocean (Haeseker et al. 2012). Less spill, reduced flows, and/or lower survival through the hydropower system may indicate a rigorous or stressful migration, which may leave smolts more vulnerable to predation in the estuary (the "delayed-mortality hypothesis"; Budy et al. 2002, Schaller and Petrosky 2007).

As a component of a comprehensive strategy for salmonid recovery in the Columbia Basin, management has been proposed to reduce the impacts of East Sand Island double-crested cormorants on juvenile survival of ESA-listed salmonid populations (NOAA 2014). One possible management objective is to reduce the size of the cormorant colony through culling or dispersal of cormorants to areas outside the Columbia River basin. The primary goal of analyses presented here were to provide context for this potential management strategy by assessing the relationship between cormorant colony size and measures of cormorant predation, and identifying important environmental factors that may confound that relationship. The large variability observed in multiple measures of cormorant predation (diet composition, total smolt consumption, and predation rates) that occurred during a period of relatively stable colony size suggests that evaluating the efficacy of colony size reductions requires an understanding of how environmental conditions also influence cormorant predation on juvenile salmonids in the Columbia River estuary.

METHODS

The double-crested cormorant colony on East Sand Island (river km 8) was the largest in western North America during 1998-2013 (Adkins et al. 2014), ranging from 6,300 to 14,900 breeding pairs annually (Appendix C-1, Table C-1.2). We examined predation on juvenile salmonids by cormorants nesting on East Sand Island in the Columbia River estuary using several techniques and datasets during this period, namely by Principal Component Regression (PCR) analysis and by investigating the relationships between the availability of alternative prey and cormorant diet composition.

Principal Components Regression Analysis

To assess the relative importance of colony size and other environmental factors on salmonid predation by cormorants, we used PCR analysis (Koslow et al. 2002, Burke et al. 2013). With this technique, the effects of multiple, sometimes related (i.e., correlated) explanatory factors can be assessed on a given response variable by first transforming the raw explanatory factor data into a set of orthogonal principal components (PCs). Those PCs can then be regressed on the response variable(s) of interest. We conducted this analysis using annual values for both explanatory factors and response variables.

Measures of Cormorant Predation (Response Variables): Two primary measures have been used to assess predation on Columbia River juvenile salmonids by piscivorous waterbirds nesting at colonies in the Columbia River basin: (1) the number of smolts consumed and (2) the percentage of smolts consumed. Each measure is derived using independent techniques.

The number of smolts consumed or *smolt consumption* is estimated using demand-based bioenergetics models, incorporating estimates of waterbird numbers (adults and chicks), energy requirements of individual waterbirds (adults and chicks), diet composition, and energetic content of each prey type

(Roby et al. 2003, Antolos et al. 2005, Lyons 2010, Maranto et al. 2010). The taxonomic resolution of smolt consumption estimates are dictated by the achievable resolution in the data on diet composition. The diet composition of double-crested cormorants nesting on East Sand Island was quantified using identifiable soft tissue from the stomach contents of cormorants collected as they returned to the colony after foraging, with partitioning among prey types by relative identifiable biomass (Collis et al. 2002). In partnership with NOAA Fisheries (D. Kuligowski, Northwest Fisheries Science Center), salmonids from cormorant stomach contents were identified to species using genetic techniques (Lyons 2010, BRNW 2014). In recent years, identification of salmonids to the level of evolutionarily significant unit (ESU) or distinct population segment (DPS) level has been possible due to advancements in genetic stock identification. Sample sizes for each ESU/DPS group have been too small, however, to accurately partition the diet below the level of species on an annual basis. Consequently, estimates of smolt consumption are performed at the species level, with a partition by age class for Chinook salmon. A summary of annual cormorant diet composition (the percentage of the diet that was salmonids) is presented in Appendix C-1 (Table C-1.2) along with smolt consumption results from Lyons (2010) and BRNW (2014; Table C-1.3).

An alternative, and complimentary, measure of cormorant predation is the percent of smolts consumed or *predation probability*, which is the probability of locally available juvenile salmonids being consumed by birds from a particular nesting colony. This measure has been based on detections of smolts tagged with passive integrated transponder (PIT) tags at a point in the river (e.g., a dam) and the subsequent recovery of a portion of those tags at nearby colonies of fish-eating birds (Collis et al. 2001, Ryan et al. 2001, Ryan et al. 2003, Antolos et al. 2005, Good et al. 2007, Evans et al. 2012, Hostetter et al. in-press). Estimates of this measure have been labeled *predation rates* previously in the literature, but *predation probability* is more precise terminology given recent probabilistic modeling approaches to estimation (Appendix C-2; Evans et al. 2012, Osterback et al. 2013, Hostetter et al. in-press). Predation probabilities can be specific to any group of smolts for which there is a representative sample of tagged fish; analyses presented here are conducted at the level of evolutionary significant units (ESUs) or discrete populations segments (DPSs) of smolts following past efforts (Antolos et al. 2005, Good et al. 2007, Evans et al. 2012). We used predation probability estimates for East Sand Island double-crested cormorants that incorporated two significant enhancements over previously available estimates: (1) estimates were calculated using models that accounted for PIT tag detection and deposition probabilities and (2) predation probabilities included the most up to date data available (studies completed in 2013). Further details on predation probability calculations are presented in Appendix C-2 and Hostetter et al. (in-press). The resulting annual estimates of cormorant predation probabilities for all ESA-listed Columbia River DPSs/ESUs originating upstream of Bonneville Dam on the Columbia River and upstream of Sullivan Dam on the Willamette River, where representative samples of PIT-tagged smolts were available, are also presented in Appendix C-2 (Table C-2.1).

A large and diverse number of measures of double-crested cormorant predation on Columbia River salmonids were available for potential analysis during 1998-2013 (see Appendices C-1 and C-2); for simplicity, we focused on a reasonable, prioritized subset of possible measures. For population-specific measures, we prioritized predation probabilities for ESA-listed populations from the Snake and Upper Columbia rivers that experienced lengthy migrations through the Federal Columbia River Power System (FCRPS). The recovery of these populations was the impetus for management actions, including reductions in cormorant predation, prescribed in the 2014 FRCPS Biological Opinion (NOAA 2014). We also prioritized steelhead and spring/summer (yearling) Chinook salmon, as they were more heavily impacted species/runs and were consistently PIT-tagged during 1999-2013. Estimates of smolt consumption (total numbers consumed) at the species/age-class level were included and offered a more general measure of impacts, complementing the focus on predation probabilities for a few select populations.

By including responses from both methodologies (ESU/DPS-specific predation probabilities and species-specific smolt consumption) our aim was to improve our ability to derive robust results. These criteria resulted in the selection of smolt consumption estimates for steelhead and yearling Chinook (see Appendix C-1), and the predation probabilities for the Snake River (SR) and Upper Columbia River (UCR) steelhead distinct population segments, and the Snake River spring-summer ($SR_{sp/su}$) and Upper Columbia River spring (UCR_{sp}) Chinook salmon evolutionarily significant units as the response variables (see Appendix C-1).

Finally, because it was an important component of the bioenergetics-based smolt consumption estimates and highly variable across the study period, we also included the annual percentage of salmonids in the cormorant diet (% of identifiable prey biomass; see Appendix C-1) as a response measure. We averaged the percent salmonids in the diet across mid-April to mid-June – the major outmigration period for steelhead and yearling Chinook smolts – for each year.

Measures of Biotic and Abiotic Variability (Explanatory Variables): Our analysis focused on explanatory factors that might influence predation on juvenile salmonids by double-crested cormorants in the estuary via four primary mechanisms: (1) by variability in cormorant abundance, (2) by affecting smolt abundance and/or susceptibility to cormorant predation as smolts enter the foraging range of cormorants in the estuary, (3) by influencing the physical environment of the estuary while smolts are migrating through to the ocean, or (4) by affecting the abundance of alternative, non-salmonid prey for cormorants in the estuary. We selected factors demonstrated in the literature to influence smolt survival in the estuary and/or near ocean environment and for which data were likely to be readily available in the future.

Abundance of double-crested cormorants was quantified as the peak colony size observed on East Sand Island each year. High resolution aerial photography was taken at the approximate time of peak colony activity (late May or early June) and three independent counts of cormorant nests in photography were averaged to estimate the number of cormorant breeding pairs present. Because the cormorant breeding colony on East Sand Island is a mixed-species colony, including both double-crested cormorants and Brandt's cormorants (*P. penicillatus*), the number of double-crested cormorant breeding pairs was obtained by subtracting the number of Brandt's cormorant nests from the total number of cormorant nests. Colony size was an input variable in the generation of two response variables, the bioenergetics-based estimates of steelhead and yearling Chinook consumption, so a relationship between these variables was expected; of interest was how much variability was explained by other factors.

We used average monthly values (Jan. – Apr.) of the PDO obtained from the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo). This seasonal metric has been shown to correlate with Caspian tern consumption of smolts in the Columbia River estuary (Lyons 2010). We similarly used average monthly values of the MEI obtained from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory (http://www.cdc.noaa.gov), and the NPGO obtained from Emanuele Di Lorenzo (http://www.o3d.org/npgo). Annual values for the PNI were obtained from the Columbia Basin Research website maintained by the University of Washington (http://www.cbr.washington.edu).

Regional climate conditions were described in three ways. The average daily optimal-interpolated sea surface temperature (SST) was obtained from the International Comprehensive Ocean-Atmospheric Data Set maintained by the University Corporation for Atmospheric Research (http://rda.ucar.edu) and averaged across May and June of each year. Daily upwelling indices were downloaded from NOAA's Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov); daily values were averaged across April through June to describe the strength of upwelling during the period in which steelhead and yearling Chinook salmon smolts were migrating through the estuary. The date of the spring transition to upwelling along the Oregon and Washington coast was obtained from NOAA's Northwest Fisheries Science Center (http://www.nwfsc.noaa.gov).

Several explanatory factors related to physical conditions in the estuary and the freshwater migration conditions that smolts experience prior to arrival in the estuary were evaluated. Values for river discharge at river km 87 (Beaver Army Terminal, site number 14246900) were obtained from the U.S. Geological Survey (http://waterdata.usgs.gov); daily values in May were averaged to represent annual flow, corresponding to the peak outmigration period for steelhead and yearling Chinook (Fish Passage Center 2013). May flows were also highly correlated to the rest of the smolt outmigration period. Annual survival estimates for steelhead and yearling Chinook smolts migrating from Lower Granite Dam on the Snake River to Bonneville Dam on the lower Columbia River were obtained from the Fish Passage Center (http://fpc.org). Daily estimates of spill (% of total water passing through a given dam) were downloaded from the Columbia Basin Research website, averaged over the multiple dams encountered, and temporally averaged across April through June, after Haeseker et al. (2012).

Annual values of all explanatory variables used in the PCR analyses are provided in Appendix C-3 (Table C-3.1).

PCR Analyses: Each explanatory factor was evaluated for normality using Anderson-Darling tests; if data were found to be non-normal or had extreme outliers, a log transformation was performed. For a few variables, outliers were irreconcilable using transformations (normality tests still failed) or the time series included one or more missing values. We consequently conducted two PCR analyses for each response variable. The first PCR included only those variables for which there was a complete (1999-2013) and normally distributed data set (i.e., PDO, MEI, NPGO, SST, upwelling strength, spring transition date to upwelling, river discharge, and colony size). The second PCR included all explanatory variables but excluded years having missing or outlying values for any variable (i.e., PNI, steelhead survival through the hydropower system, Chinook salmon survival through the hydropower system, and average spill). For the second PCR the sample size was reduced from 15 years to 11 years for steelhead and to 13 years for Chinook salmon. In both analyses, all data were scaled to have a mean of zero and a standard deviation of one. A principal component analysis (PCA) was then performed using PC-ORD (MjM Software, Gleneden Beach, Oregon) to transform the explanatory variables into orthogonal principal components (PCs), eliminating the multicolinearity present in the original explanatory variable dataset (Appendix C-3, Table C-3.2).

Response variables were tested for normality and, if found to be non-normal, log-transformed. Multiple linear regression was performed for each response variable initially using the first six principal components generated in the explanatory factor PCA analysis. Model reduction from that initial, full model was performed using backwards stepwise selection and applying Akaike's Information Criterion corrected for small sample sizes (AICc) to prioritize PCs for possible elimination from intermediate models. Model reduction decisions were based on goodness-of-fit F-tests. Model fit was accepted at the level of $P < 0.10$. For responses with acceptable models (i.e. where models including one or more principal components outperformed the null model), we quantified the relative contribution of each of the explanatory factors to the regression by taking the squared loadings of a given factor onto the PCs that remained in the best regression model and multiplying them by the semi-partial correlation coefficient for each remaining PC, then summing across PCs (Burke et al. 2013).

Relationships between Estuary Purse Seine Catches and Cormorant Diet Composition

To assess the relationship between prey availability and cormorant predation on juvenile salmonids, we related the percentage of the cormorant diet (% biomass) identified as salmonids to purse seine catches of both juvenile salmonids and alternative prey. Purse seine sampling was conducted during 2007-2012 as described in Weitkamp et al. (2012). In brief, sampling cruises were conducted approximately every two weeks across the spring and summer at two sites in the estuarine mixing region. Seining was performed during daylight hours on days with early morning low tides using a fine mesh net measuring 10.6 m deep by 155 m long. Sampling was conducted in areas where water depths were approximately 8-10m deep, allowing the net to fish the entire water column. It was possible to estimate catch per unit effort by following a systematic round haul protocol. Using length-weight relationships, purse seine catches were identified as total biomass and the percentage of total biomass for each prey type.

Purse seine catches conducted between 13 April and 21 July overlapped with the collection of data on cormorant diet composition for six to seven sampling cruises per year. Cormorant diet data were partitioned into approximate two-week periods centered on each cruise date. Purse seine and cormorant diet data were averaged across cruises in each year to generate an annual estimate of prey abundance in seine catches and cormorant diet composition. To understand the relationship between cormorant diet and the availability of salmonids and alternative prey, the percentage of the cormorant diet that was observed to be salmonids was related to salmonid biomass in the purse seines, as well as the biomass of marine forage fishes (anchovy, herring, sandlance, and smelts; biomass was log transformed) and freshwater/estuarine resident fish (minnows, flatfish, lamprey, sculpin, stickleback, surfperch, and others). Relationships were evaluated using simple linear regression.

To explore whether double-crested cormorants were feeding selectively on specific types of fish (i.e., eating fish prey types either with greater or lesser frequency than found locally in the estuary), we compared the percent biomass of each prey type in the observed diet with the percent biomass of that fish prey type in the purse seine hauls conducted over the same time period. The selectivity metric we used was the $\log_{10}$ of the odds ratio (LOR; Schabetsberger et al. 2003). The LOR is symmetrical around zero (LOR = 0 indicated no selectivity, or prey eaten in the same proportion as it occurred in the estuary), where positive values mean positive prey selection (prey type found at a higher percentage in the cormorant diet than observed in the purse seine catch) and negative values mean negative prey selection (prey type found at higher percentage in the purse seine catch than in the diet):

$$LOR = log_{10}\left[\frac{d_i(100-e_i)}{e_i(100-d_i)}\right],$$

as calculated from the numerical percentages of fish taxon i in the predator diet (d_i) and local surroundings (e_i). The LOR values were calculated from percent biomass of each prey type in purse seine sampling and cormorant diet over several time periods (April-May, June-July, and April-July). Logarithms to the base 10 of the odds ratios were taken so that odds ratios of + 1 and +2 indicate prey types occurring 10 times or 100 times, respectively, more frequently in the cormorant diet than would be expected given its relative abundance in the estuary as reflected in purse seine catches. Values of - 1 and -2, however, indicate potential prey types avoided by the predator because the species' relative abundance in the purse seine catch was 10 or 100 times greater than its frequency in the diet (Tollitt et al. 1997). This measure of predator selectivity assumes that the purse seine is catching all prey fish species with equal efficiency and accurately represents the prey community from which the cormorants are selecting.

RESULTS

PCR Analyses

The first three principal components explained at least 75% of the variability in the environmental explanatory factors in all iterations of the principal components analysis. Ordination plots of the first two principal component axes for all analyses indicated similar dispersion of the study years, with early years segregated from later years of the study (Figure 1). Cormorant colony size and river discharge (flow) were important drivers of this segregation of years. Interesting outlying years included 2001 (low river discharge), 2005 (delayed spring transition), 2008 (cool and wet spring conditions) and 2011 (high river discharge).

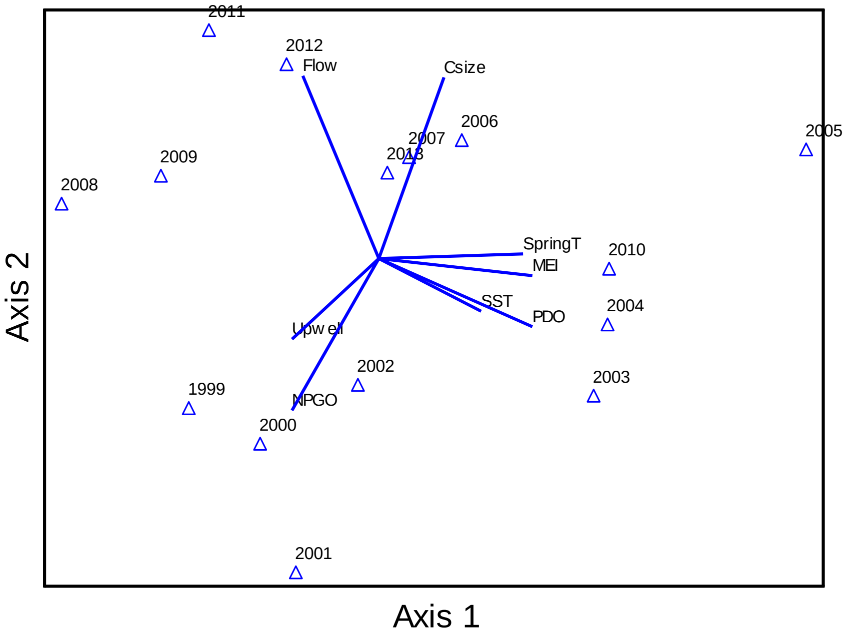

Figure 1. Ordination plot for a principal components analysis of explanatory factors from 1999 to 2013 (all years of the study). Factors included the Pacific Decadal Oscillation (PDO), Multivariate El Nino/Southern Oscillation Index (MEI), North Pacific Gyre Oscillation (NPGO), sea surface temperature (SST), strength of upwelling (Upwell), upwelling spring transition (SpringT), river discharge (Flow), and cormorant colony size (Csize). Outlying years included 2001 (low river discharge), 2005 (delayed spring transition), 2008 (cool and wet spring conditions), and 2011 (high river discharge). The first and second principal components explained 40.3% and 23.3% of the variability in the explanatory factors, respectively.

Reverse stepwise selection of regression models resulted in best fit models that incorporated one or two principal components for most responses; however, in a few cases no model was significantly better than the null model (Tables 1 and 2). For regressions having a model with a good fit, 25-60% of the variability in the response was explained (Table 1 and 2).

Table 1. Best fit Principal Component Regression models resulting from reverse stepwise model selection for the analysis incorporating data from all years of the study period (1999-2013) but a reduced set of explanatory factors. Response variables include cormorant predation on spring (sp) and summer (su) run Chinook salmon and steelhead and Chinook salmon originating from the Snake River (SR) and Upper Columbia River (UCR).

Response Variable	# of Principal Components in best model	F Test P-Value	R^2
Steelhead Consumed	2	0.04	0.42
SR Steelhead Predation Probability	No good fit	NA	NA
UCR Steelhead Predation Probability	2	0.04	0.44
Yearling Chinook Consumed	2	0.04	0.39
$SR_{sp/su}$ Chinook Predation Probability	1	0.06	0.25
UCR_{sp} Chinook Predation Probability	No good fit	NA	NA
Percent Salmonids in Cormorant Diet	2	0.01	0.52

Table 2. Best fit Principal Component Regression models resulting from reverse stepwise model selection for the analysis incorporating data from the complete set of explanatory variables but omitting years with data gaps or extreme outliers. Response variables include cormorant predation on spring (sp) and summer (su) run Chinook salmon and steelhead and Chinook salmon originating from the Snake River (SR) and Upper Columbia River (UCR).

Response Variables	# of Principal Components in best model	F Test P-Value	R^2
Steelhead Consumed	No good fit	NA	NA
SR Steelhead Predation Probability	No good fit	NA	NA
UCR Steelhead Predation Probability	1	0.01	0.50
Yearling Chinook Consumed	2	0.08	0.43
$SR_{sp/su}$ Chinook Predation Probability	No good fit	NA	NA
UCR_{sp} Chinook Predation Probability	2	0.01	0.60
Percent Salmonids in Cormorant Diet	1	0.01	0.52

For the PCR that included a subset of explanatory factors and data from all years of the study, the relative importance of the explanatory factors was consistent across several response variables (Figure 2). Colony size, river discharge, and the NPGO explained more of the variability in each of the predation probability and smolt consumption estimates for which well-fitting PCR models were derived. Cormorant colony size and river discharge explained a similar amount of variability (12-17% and 13-15%, respectively) across these four responses, with the NPGO explaining 6-10%. Large scale (PDO, MEI) and regional (spring transition date, SST) climate factors explained more variability in cormorant diet, with colony size not strongly related to this metric.

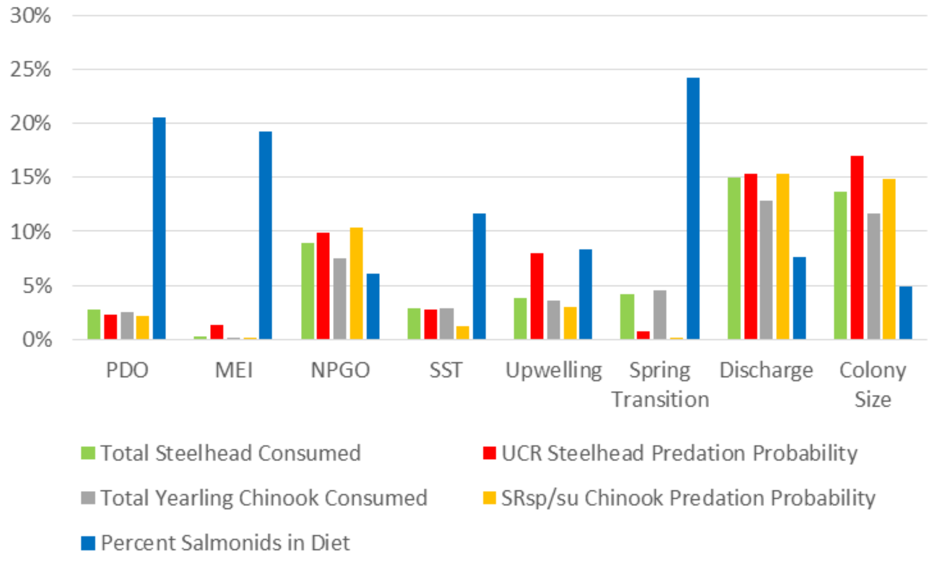

Figure 2. Relative ability of environmental factors to explain inter-annual variability in measures of cormorant predation on juvenile salmonids. Percentages indicate how much of the variability explained by the Principal Component Regression models can be attributed to each particular factor. This analysis included data from the entire study period 1999-2013. Population-specific response variables included cormorant predation probabilities for Upper Columbia River (UCR) steelhead and Snake River spring/summer ($SR_{sp/su}$) Chinook salmon.

In the second set of PCR models, which included the complete set of environmental factors, the effect of individual factors was more dilute (Figure 3). The only prominent exception to this trend was the NPGO, which explained relatively large amounts of variability in both the UCR steelhead and UCR_S Chinook salmon predation probabilities (35% and 22%, respectively). Notably, none of the additional explanatory factors included in this analysis (i.e., PNI, steelhead or Chinook survival through the hydropower system, or average spill conditions) had substantial ability to explain variation in any of the well-modeled responses.

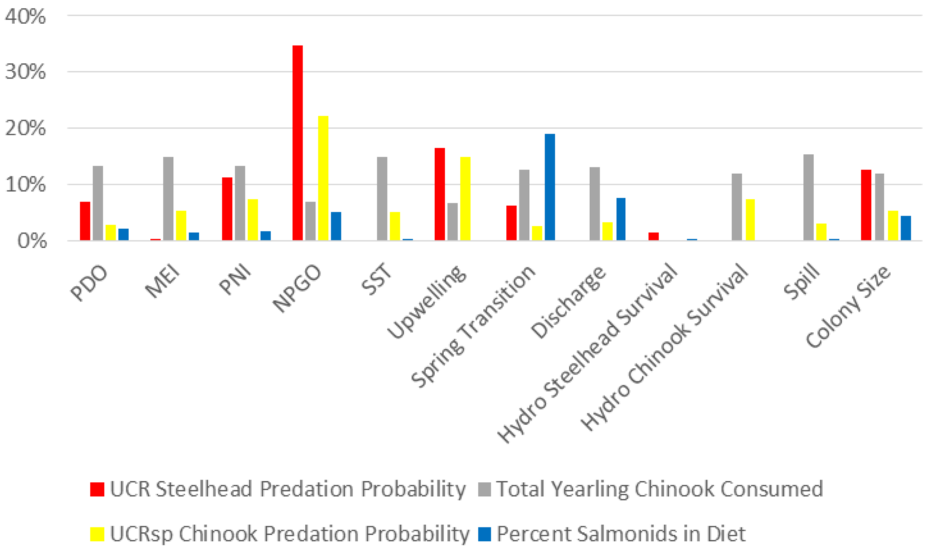

Figure 3. Relative ability of environmental factors to explain inter-annual variability in measures of cormorant predation on juvenile salmonids. Percentages indicate how much of the variability explained by the Principal Component Regression models can be attributed to each particular factor. This analysis omitted data from years when data were unavailable or extreme outliers occurred. Population-specific response variables include cormorant predation probabilities for steelhead and spring (sp) run Chinook salmon originating from the Upper Columbia River (UCR).

Purse Seine Analyses

We found that the annual percentage of salmonids (biomass) in the diet of cormorants was significantly related to the annual percentage of salmonids (biomass) in estuary purse seine (EPS) catches, but not the total annual biomass of salmonids in EPS catches (Figure 4). Consistent with this result, we found that when a greater biomass of alternative forage fish was caught in EPS hauls, the salmonid proportion of the cormorant diet was smaller. This was true for both pooled marine forage fishes and pooled freshwater/estuarine forage fishes (Figure 5).

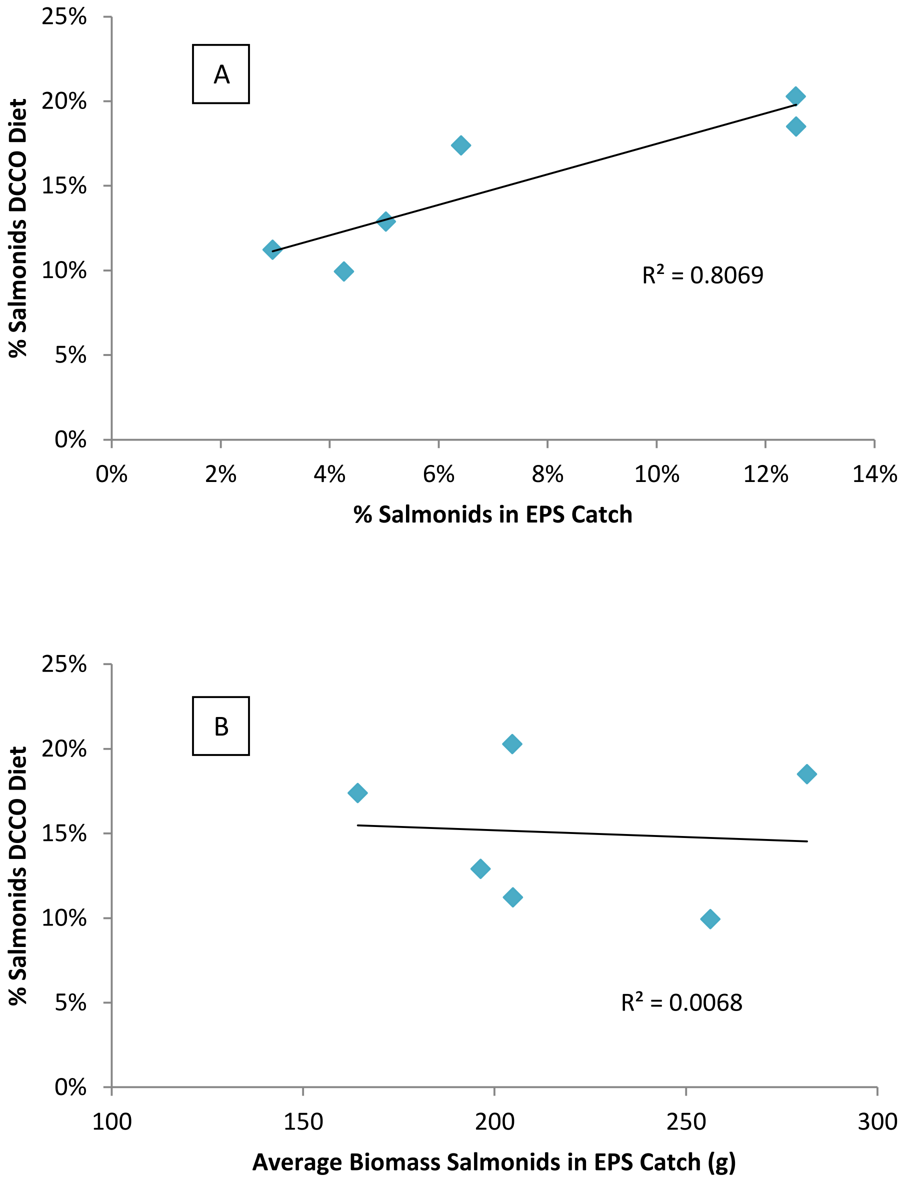

Figure 4. Relationships between the proportion of salmonids (biomass) in the diet of double-crested cormorants (DCCO) nesting on East Sand Island and (A) the proportion of salmonids (biomass) in estuary purse seine (EPS) catches and (B) the average biomass of salmonids caught in EPS hauls. Each data point represents one year of study during 2007-2012. Cormorants appeared to respond to the relative abundance, but not the absolute abundance, of salmonids in the estuary.

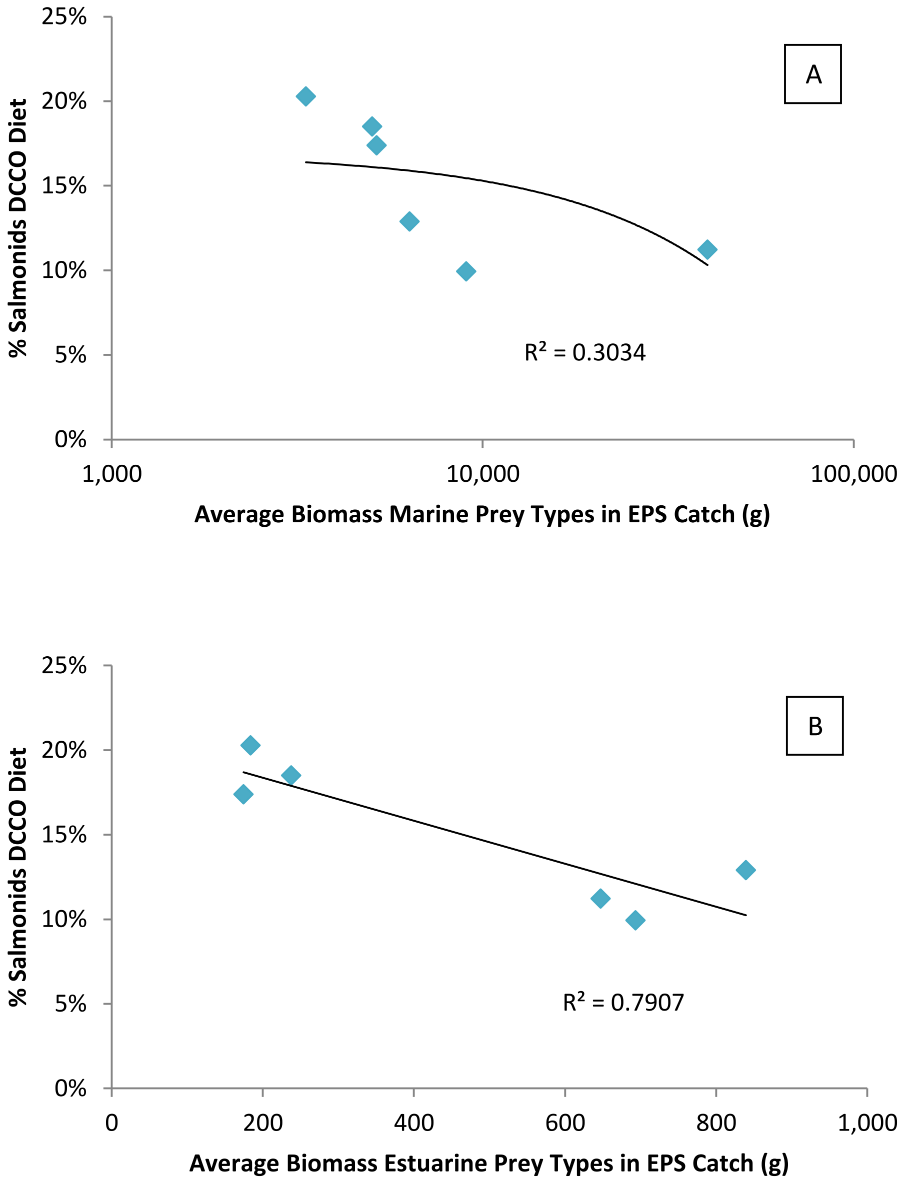

Figure 5. Relationships between the proportion of salmonids in the diet of double-crested cormorants (DCCO) nesting on East Sand Island and (A) average total biomass of marine forage fishes in estuary purse seine (EPS) catches and (B) the average total biomass of estuarine forage fishes in EPS catches. Each data point represents one year of study during 2007-2012. Greater absolute availability of alternative prey was associated with reduced cormorant reliance on juvenile salmonids.

Little evidence of cormorant preference for salmonids was found using log odds ratios of the percent salmonids in the cormorant diet to that in the estuary purse seine catches (Figure 6). Other prey types appeared to be more strongly selected for (anchovy or flatfish) or selected against (clupeids, smelt) by cormorants, but results varied by year and fish family.

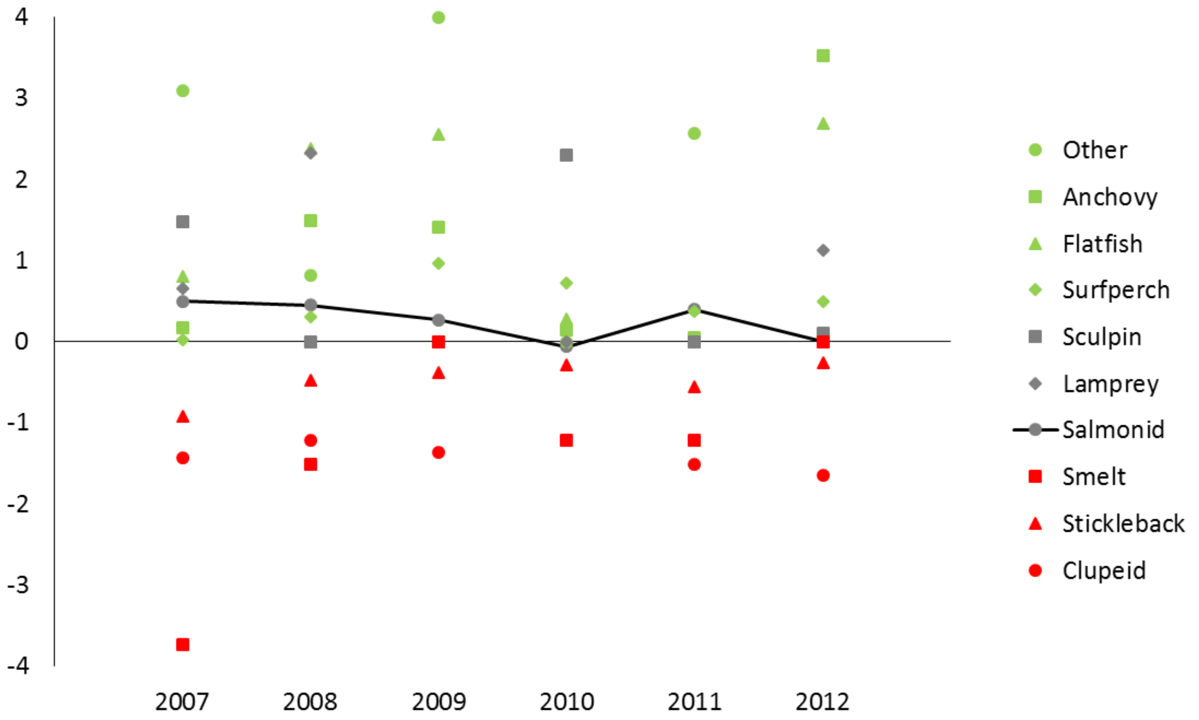

Figure 6. Log odds ratio of the percent of prey types in the diet of double-crested cormorants to the percent of prey types in estuary purse seine catches during April-May. Positive values indicate greater prevalence in the cormorant diet than in seine catches. Compared to values for anchovy, flatfish, and surfperch, selectivity by double-crested cormorants for salmonids (black circles and line) was minimal. The "other" prey type category included several types that were uncommon in both cormorant diets and purse seine catches – gunnels, suckers, gadids, pricklebacks, greenlings, mackerals, lingcod, and crustaceans.

DISCUSSION

Annual measures of cormorant predation impacts on Columbia River juvenile salmonids by double-crested cormorants nesting on East Sand Island derived using two independent methodologies varied substantially across 1999 – 2013. Previous summaries of shorter time periods (2007 – 2012; Evans et al. 2012, Lyons et al. 2014) had indicated substantial inter-annual variation in both smolt consumption and predation probability measures, and that variability was present across the entire extended time period of data summarized for this analysis.

We found that environmental factors explained some of the variability seen in several measures of cormorant predation on salmonids. Many of these same environmental factors have previously been related to variability in survival of juvenile salmonids during freshwater migration, travel through the estuary, or early ocean residency (Petrosky and Schaller 2010, Haeseker et al. 2012). Given the number of potential factors and our relatively short time series (with regards to regression analyses), principal components regression was an effective technique to evaluate the potential importance of many factors simultaneously (Koslow et al. 2002, Burke et al. 2013).

When using all 15 years of our response data sets, the PCR analysis identified a similar set of important explanatory factors, including colony size, river discharge, and the NPGO, for four of the six direct measures of cormorant predation on salmonids. These responses included the number of steelhead and yearling Chinook smolts consumed by cormorants derived using bioenergetics modelling (see Appendix C-1) and predation probabilities derived from PIT tag recoveries (see Appendix C-2) for two ESA-listed populations.

Compared with smolt consumption and predation probabilities, the percentage of salmonids in the cormorant diet was best explained by an alternative set of environmental variables. More variability was explained by the date of spring transition to upwelling and the large-scale climate indices PDO and MEI than by any other factors. The percentage of salmonids in cormorant diets describes predation by cormorants on all species and populations of juvenile salmonids, including coho salmon (*O. kisutch*) and sub-yearling Chinook salmon. In most years, coho salmon have been the salmonid species most frequently consumed by cormorants during the spring outmigration period that was the focus of this analysis (mid-April through mid-June). Often bioenergetics estimates of coho salmon consumption by double-crested cormorants have been greater than those for steelhead and yearling Chinook combined (Appendix C-1, Table C-1.3). This predation on coho salmon masks the contribution of steelhead and yearling Chinook to the percentage of salmonids in the cormorant diet. If the annual susceptibility of coho salmon to cormorant predation responds to a somewhat different set of environmental factors than that of steelhead and yearling Chinook salmon, it would explain the inter-annual differences observed in cormorant diets. Sub-yearling Chinook salmon are typically the smolt type most frequently consumed by cormorants on an annual basis, but most of that predation occurs after mid-June, so is less likely a confounding factor in the analysis presented herein.

When using a subset of our response data set, but including a complete list of environmental factors of interest, the PCR analysis did not reveal strong relationships between any response and the four additional factors added. The NPGO was strongly related to predation probabilities for the UCR steelhead and UCRs Chinook populations, supporting the conclusion from the first PCR that this large scale climate index is an important explanatory factor.

The PCR models sought to explain variability in both predation probabilities derived from PIT tag recoveries and estimates of smolt consumption derived from bioenergetics models. These two independent measures of cormorant predation on salmonids are not directly comparable, but each offers useful and complimentary information about cormorant impacts on survival of juvenile salmonids. Predation probabilities offer a direct measure of cormorant impacts on specific salmonid conservation units: ESA-listed ESUs and DPSs. In addition, predation probability is more easily interpreted in the context of juvenile salmonid survival, a priority metric of broader salmon recovery efforts in the Columbia River Basin (NOAA 2014). Smolt consumption estimates, conducted at the species level (and age-class level for Chinook salmon), offer a more general or inclusive measure of cormorant predation, and do not rely on representative PIT tag sampling of smolts but rather a representative sample of the birds diet. Demand-based bioenergetics calculations of smolts consumed also offer a cormorant-centric mechanistic understanding of factors influencing smolt consumption levels – factors such as cormorant colony size, diet, and productivity (number of young produced), as well as prey fish nutritional quality (energy content) – all of which are important input parameters in the estimation process. Species-specific estimates of salmonid consumption integrate consumption of all Columbia River populations, both ESA-listed and non-listed. Such integrated measures are useful to interpret large-scale salmonid conservation and management issues; however, they cannot be directly related to specific population recovery objectives under the ESA.

Another measure of predation impact is *consumption rate* (the analog of predation probability) at the species level, which can be estimated by dividing species-specific smolt consumption estimates by estimates of the species-specific number of smolts available to cormorants in the estuary (e.g., see Appendix E of NOAA [2014]). We did not choose to calculate consumption rates in this manner for our analyses because our objective was to explore the ability of colony size and environmental factors to explain variability in cormorant predation. Uncertainty in annual estimates of smolt availability in the estuary (Burke et al. 2013) could confound such relationships. Furthermore, consumption rates, are not directly comparable to ESU/DPS-specific predation probabilities, as they describe predation on multiple ESUs/DPSs. Significant differences between predation probabilities on different ESUs/DPSs of the same species (see Appendix C-2, Table C-2.1) indicate that an integrated measure of consumption rate at the species level may be substantially different from the predation probability for any particular component ESU/DPS.

River discharge and the large scale climate index, the North Pacific Gyre Oscillation, were the most important environmental factors in PCR models. Varying levels of river discharge significantly influences the distribution of freshwater within the estuary, particularly at the surface and in shallower areas (Fox et al. 1984). At high flows, saltwater intrusion into the estuary is greatly reduced and marine forage fish are substantially less abundant (Weitkamp et al. 2012). In such cases, alternative prey for cormorants are reduced and reliance on salmonids may be greater. High discharge may also speed the arrival of juvenile salmonids into the estuary, perhaps before some are physiologically ready to enter saltwater, thereby increasing the residence time of juvenile salmonids in the estuary. These extended estuary residence times presumably prolong exposure to predation by cormorants nesting on East Sand Island (Schreck et al. 2006). Our results suggest that predation impacts on salmonids by cormorants were elevated during high flow years. Smolt survival through the FCRPS is typically highest in years of high river flow, however (Petrosky and Schaller 2010, Haeseker et al. 2012). Thus the benefits of higher smolt survival to the estuary in years having higher river flows may be offset to some degree by increased predation by double-crested cormorants in the estuary.

The NPGO is calculated monthly as the second principal component of sea surface height across the Northeast Pacific Ocean. This derived index of climate variability has tracked well with salinity, chlorophyll, nitrates, and upwelling winds in the California Current along the North American Pacific Coast (Di Lorenzo et al. 2008). Our result that cormorant predation in the estuary was related to the NPGO is consistent with recent studies that have seen relationships between the NPGO and, for example, Snake River spring/summer Chinook salmon smolt-to-adult return rates (Miller et al. 2013). Exact mechanisms of how large scale climate indices influence survival of Columbia Basin salmonids at specific life history stages are challenging to identify; however, cormorant predation in the estuary is one possible mechanism. Presumably the NPGO regulates cormorant predation on smolts indirectly by regulating alternative prey that may enter the estuary and be available for cormorants to consume instead of salmonids.

Both cormorant diets and estuary purse seine catches were highly variable within seasons and between sampling cruises, suggesting that prey resources in the estuary are highly dynamic on short time scales (e.g., tidal cycles, daily, weekly, and monthly time scales). Relationships between purse seine catches and cormorant diets were more consistent at annual scales, so we focused on those comparisons. Correlations at the annual scale, however, rely on a small sample size of purse seine catch data (n = 6 years), so results should be viewed as suggestive.

Based on the comparisons to the purse seine catches, double-crested cormorants nesting on East Sand Island appeared to take salmonids (all species combined) in proportion to their relative availability in the Columbia River estuary, not their absolute abundance. In years when more salmonids were caught in purse seine hauls, cormorants did not necessarily respond by consuming a higher proportion of salmonids in the diet. Instead, when salmonids were a greater proportion of the total catch (greater proportion of biomass caught), salmonids made up a greater proportion of cormorant diets as well. Changes in absolute abundance of alternative prey, both marine and freshwater/estuarine forage fishes, did influence how much cormorants relied on salmonids as prey. This provided strong evidence that double-crested cormorants respond to changes in the availability of alternative prey within the estuary, and suggests that in years when alternative prey (marine and estuarine forage fishes) are relatively abundant, cormorant predation on salmonids will be reduced. The log odds ratio calculations also suggested that cormorants did not exhibit selectivity for salmonids relative to their relative availability in the estuary. Taken together, these results suggest that cormorants are foraging on smolts opportunistically in the Columbia River estuary. The degree to which cormorants make use of salmonids as prey is thus very likely dependent on environmental factors that influence the availability of alternative prey.

In summary, double-crested cormorants consumed a substantial number and percentage of juvenile salmonids in the Columbia River estuary during 1999-2013, and colony size was an important explanatory factor in most models. Environmental factors were as or more important in explaining the variability in cormorant predation than colony size, however. In aggregate, environmental factors explained a greater portion of variability in cormorant predation, and at least one other factor (river discharge) appears to be as important as colony size in determining levels of cormorant predation on smolts. While colony size is an important determinant of cormorant impacts on salmonid populations, environmental conditions that regulate the availability of alternative prey could outweigh the effects of changes in colony size in any given year. Consequently, management efforts to reduce the size of the East Sand Island cormorant colony to benefit ESA-listed salmonids would best be evaluated in the context of environmental conditions, particularly if evaluation occurs on an annual basis, and with specific attention given to river discharge and the NPGO. Multiyear data sets following any implementation of management would likely be more useful to evaluate potential benefits.

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APPENDIX C-1: Estimates of colony size, diet composition, and smolt consumption of East Sand Island double-crested cormorants.

Estimates of colony size, diet composition, and smolt consumption used in this report are based on methods previously developed by Collis et al. (2002), Roby et al. (2003), and Lyons (2010).

Colony Size: The number of adults breeding at each colony during late incubation (peak colony size usually occurred in late May or early June) was precisely estimated using high-resolution aerial photographs (see Collis et al. 2002). Counts of occupied nests in aerial photographs were interpreted as the peak number of breeding pairs for a given colony in a given year. Multiple counts of occupied nests by independent observers varied with a SE ≤ 3% of the mean count.

Diet Composition: Cormorant diet data were obtained from stomach contents of cormorants collected during the breeding season. Five to fifteen samples per week were collected for approximately 10 weeks from late April until the end of July; 125 – 140 samples were available for analysis in each year (Collis et al. 2002). Diet composition, in percent biomass, was taken from the identification to prey family (or genus and species, when possible) of all undigested soft tissue present in the fore-gut. Stomachs lacking any soft tissue (but possibly containing bones), and portions of gastro-intestinal tracts lacking any undigested soft tissue (e.g., bones in intestines), were excluded from the quantitative diet composition analysis. Soft tissue was identified to family using external features when possible or, when necessary, using diagnostic bones following artificial digestion of soft tissue. Unidentifiable soft tissue lacking diagnostic bones was excluded from analysis. From 21 – 25 kg of prey soft tissue biomass was identified in diet analyses each year, which represented >90% of total prey soft tissue mass. Salmonids were identified to species using morphology of external soft tissue when possible or, more frequently, using PCR amplified genetic material (extracted from intact soft tissue or bone) after Purcell et al. (2004).

Smolt Consumption: Smolt consumption estimates were derived using a bioenergetics model based on cormorant abundance, diet composition, energy requirements, and prey energy content (Roby et al. 2003, Lyons 2010, Figure C-1.1). Calculations were performed using a Monte Carlo technique to produce “best” estimates and corresponding 95% confidence intervals (after Furness 1978).

Cormorant Abundance: Peak colony size during each breeding season was estimated as described above. Data were collected on the abundance of cormorants across each breeding season using a combination of aerial photographs and direct counts from boats or blinds within the cormorant colony. Counts of nests in aerial photographs were used to estimate colony size from mid-May until early July during 2008 – 2013. These colony size estimates excluded any non-breeding cormorants using East Sand Island during this period. Counts from boats or blinds conducted at other times (early season, late season, and years prior to 2008) included all birds using East Sand Island and included any non-breeding cormorants present.

For simplicity, chicks were assumed to hatch synchronously in early June and achieve independence eight weeks later. The initial number of chicks present was taken to be the average initial brood size observed in representative focal nests (in sample plots monitored from observation blinds) multiplied by the peak colony size (measured as the number of breeding pairs). The number of chicks present 28 days later was taken to be the average brood size at 28 days post-hatch seen in focal nests, again multiplied by the peak colony size. To quantify the number of chicks present at other times during the chick rearing period an exponential decay function was fit to these two datapoints (total number of chicks present 1 day and 28 days post-hatch). The number of chicks present following the chick rearing period (i.e. > 8 weeks following the early June hatch date) were directly enumerated in counts from boats or blinds.

Diet Composition: Diet samples were pooled across 4-week periods spanning the period when cormorant nesting overlapped with smolt outmigration (mid-April through the end of July). For periods before and after this sampling period, the diet was assumed to be equivalent to the nearest period sampled. If a prey type was not detected during any given period, it was presumed to be absent from the diet during that time and was not incorporated into the consumption calculations for the given period.

Because the cormorant stomach sample is the independent sampling unit for diet composition, multiple salmonid samples identified from the same stomach are not independent samples of salmonid composition. The breakdown of each stomach sample containing salmonids identified to species is compiled by frequency (e.g., 100% coho salmon, 50% yearling Chinook salmon and 50% steelhead, etc.), averaged across the available samples, and then translated into proportional biomass using the average masses of each salmonid species/type. Because of limited clean tissue samples in any given year, samples are pooled across years. Data through 2013 are summarized in Table C-1.1. Seasonal trends in salmonid species breakdown data are consistent with nearby purse seine sampling of salmonids in the Columbia River estuary (Weitkamp et al. 2012) and salmonid species identified in the diet of Caspian terns also nesting on East Sand Island (Lyons 2010).

Sensitivity analysis has shown that for cormorants, the uncertainty in characterizing diet composition due to small sample sizes was the leading factor causing uncertainty in the subsequent smolt consumption estimates (Lyons 2010). Diet sampling of cormorants was constrained by practical and ethical considerations, however. Non-lethal sampling (e.g., collection of regurgitated stomach samples from adults and/or chicks) was not feasible on a larger scale without inducing significant disturbance to a large portion of the breeding colony, which might have had significant impacts to reproductive success or fidelity to the breeding site. Larger scale lethal sampling (greater collection of adult cormorants) could have caused a reduction in the East Sand Island adult breeding population. Either of these results would have been an inappropriate outcome of scientific research and counter to protections offered cormorants under the Migratory Bird Treaty Act. Consequently, diet sample sizes were limited to levels that would avoid a colony-level impact. Use of the Monte Carlo calculation technique described below allows for estimation of uncertainty in consumption irrespective of sample size for estimating the input parameter distributions.

Energy Requirements: Adult energy expenditures were measured using the doubly-labeled water technique during chick-rearing and chick energy requirements were derived from published values for cormorants and other birds (Lyons 2010). Measurements on breeding adults were conducted in 2001, 2003, and 2006 (total n = 10). A mean daily energy expenditure (DEE) for the adult population was derived by averaging the measured DEE for males and females, each calculated separately. This value was used during the chick rearing period. During other portions of the breeding season (pre-breeding, incubation, and post-breeding), DEE was scaled using data on daily activity budgets after Gremillet et al. (2000, 2003).

Chick energy expenditures were derived from allometric predictions of total energy requirements during the entire chick rearing period (Weathers 1992). Total energy requirements were partitioned into daily requirements using the trend in daily chick requirements observed by Dunn (1975) for developing double-crested cormorant chicks. Energy requirements for chicks following the rearing period were assumed to be equivalent to post-breeding adults.

Assimilation efficiencies of consumed food were assumed to be 77.3% after Brugger (1993), for both adults and chicks.

Prey Energy Content: Prey energy densities were obtained from a parallel study on the bioenergetics of Caspian terns in the Columbia River estuary (Roby et al. 2003, Lyons 2010), where energy densities were measured using proximate composition analysis. Energy densities were assumed to be constant across seasons and years. Prey mass data were obtained from whole fish captured by terns and, for larger prey types, from minimally digested samples removed from the stomachs of collected cormorants. Prey masses were assumed to be constant across seasons, but were varied across years if significant differences were observed (tested using Kruskal-Wallace one-way ANOVA, $\alpha = 0.05$).

Monte Carlo Calculation Technique: Estimates of prey consumption were calculated for discrete 2-week periods across each cormorant breeding season and summed to get annual totals. A Monte Carlo process was used to generate a "best estimate" of smolt consumption for each salmonid species/type and to describe the uncertainty in those estimates (after Furness 1978). The calculations were performed 1000 times using a routine written in Visual Basic 6.0 (Microsoft Corporation, Redmond, WA). In each iteration, a "random" value was drawn from the empirically measured or assumed (obtained from published literature) sampling distribution of each input parameter and used collectively in the calculations. For parameters other than diet proportions, random values were drawn from a normal distribution with the measured (or assumed) mean and standard error. Sampling errors in these input parameters were assumed to be uncorrelated. For diet proportions, random values were drawn from a normal distribution with a mean equal to the empirically measured value and a standard error determined using the proportional standard deviation and diet sample size. If the random value generated was < 0, the diet proportion for that prey type and simulation were set to 0, thus truncating the distribution of values used. This truncated normal distribution effectively approximated a one-sided distribution for small diet proportions, avoiding false negatives, which was appropriate given positive detection of a particular prey type, even if in small proportions. Each diet proportion was generated from an assumed normal or truncated normal distribution without constraint initially, but after proportions were generated for all detected prey types in a given period, the values were normalized to sum to a value of 1. This approach was taken because diet proportions are not entirely independent - if cormorants consume more of any given prey type, they will inevitably consume less of all other prey types combined.

The median of the 1000 calculated values of smolts consumed was used to describe the most likely or central value. A 95% confidence interval for that "best estimate" was defined by the 2.5th percentile value as the lower confidence limit and the 97.5th percentile value as the upper confidence limit.

Key assumptions of the bioenergetics methodology include:

A1. There are relatively few non-breeding cormorants associated with East Sand Island during the peak breeding period (mid-May to early July).

A2. Chick abundance is well estimated by assuming complete hatching synchrony in early June.

A3. The seasonal pattern in salmonid breakdown in the cormorant diet is consistent across years.

A4. The energy expenditure of adult cormorants is consistent across years.

A5. Energy requirements of independent (post-fledging) cormorant chicks is equivalent to post-breeding adults.

A6. Annual differences in prey energy content are adequately represented by differences in prey mass. Energy density is assumed to be similar across seasons and years. Prey mass is assumed to be constant across seasons.

Observations of cormorants on East Sand Island during the peak breeding season suggest that a strong majority (>95%) of cormorants have active nests during the period of peak breeding (A1). Additionally, observations of cormorants throughout the Columbia River estuary at these times have never suggested a surplus of individuals significantly greater than the number of cormorants nesting at East Sand Island. While cormorant chick hatching synchrony vary to some extent from one year to the next, in most years median hatch date of nests in observation plots has been within 1-2 weeks of June 1st (A2). No independent measure of smolt availability in the estuary is available to test assumption A3, that the seasonal pattern in the salmonid breakdown of cormorant diets is consistent across years (A3). There are likely differences in arrival times of naturally-spawned groups/species of smolts between years, but hatchery production may dampen this variability. The seasonal pattern of salmonid breakdown in the diet of Caspian terns nesting at East Sand Island has been characterized with sufficient sample sizes to test for interannual differences in some years. Differences have been detected in a few years, but for most, no difference from the overall pattern is detectable. Adult cormorant energy expenditure may vary between years of high and low prey availability, or cormorants may put forth a consistent energy expenditure in order to maximize productivity (i.e. the number of chicks fledged) in good years. In either case, the interannual variability in energy expenditure is likely less than the individual variability characterized by studies of cormorants at East Sand and Rice islands (A4). There are no studies that characterize the energy expenditure of recently fledged cormorants, so an empirical comparison to adult energy expenditures is not possible (A5). Body mass and daily activity budgets of recent fledglings and post-breeding adults are similar, however, suggesting energy expenditures may also be similar. Annual differences in the energy (lipid) content of marine forage fish have been observed in the California Current ecosystem (Litz et al. 2010); however, differences in total energy content have not (A6). Differences in fish mass have been characterized, and are likely a good surrogate measure of total prey energy content. Additional information on assumptions and caveats for these bioenergetics methods can be found in Roby et al. (2003) and Lyons (2010).

Elasticity analysis performed for the cormorant bioenergetics model in Lyons (2010) indicated that colony size across the season and the salmonid proportion of the diet were the two input variables with the most potential to influence the estimates of the number of smolts consumed. Since the time of that analysis, colony size has been more precisely quantified by counting active nests or individual cormorants in a series of aerial photographs of the East Sand Island colony taken across the breeding season. This methodological improvement left diet composition – the proportion of the diet that is salmonids – as the factor having the most leverage on the calculated smolt consumption. Because sample sizes were relatively small for cormorant diet, the uncertainty in that proportion salmonids parameter propagates into substantial uncertainty in the estimated number of smolts consumed. Other factors contributing to uncertainty in smolt consumption estimates were (in rank order beginning with the most influential after the salmonid proportion of the diet) the total energy required by chicks, energy densities of non-salmonid prey types, average mass of salmonid prey types, average mass of non-salmonid prey types, daily energy expenditure of adult cormorants, and the assimilation efficiency.

Table C-1.1: Proportional breakdown (by frequency) of salmonids by species/type in stomachs of double-crested cormorants collected near East Sand Island, during 2000 – 2013.

Species/type	Time Period			
	3/27 – 5/7	5/8 – 6/4	6/5 – 7/2	7/3 – 7/30
Chinook, sub-yearling	0.03	0.18	0.87	0.91
Chinook, yearling	0.10	0.19	0.03	0.00
Coho	0.54	0.32	0.83	0.01
Sockeye	0.00	0.02	0.00	0.00
Steelhead	0.33	0.29	0.07	0.08
N	68	94	35	25

Table C-1.2: Estimated peak colony size (95% confidence interval) and the percentage of salmonids (% salmonids) in diet samples of double-crested cormorants nesting on East Sand Island in the Columbia River estuary during 1998-2013 (Lyons 2010, BRNW 2014, Adkins et al. 2014).

Year	Peak Colony Size (breeding pairs)	% Salmonids (all species)	
		April-June	April-July
1998	6,300 (5,900 - 6,700)	12%	15%
1999	6,600 (6,200 - 7,000)	33%	28%
2000	7,200 (6,700 - 7,600)	21%	17%
2001	8,100 (7,600 - 8,600)	12%	9%
2002	10,200 (9,600 - 10,800)	6%	5%
2003	10,600 (10,000 - 11,300)	10%	8%
2004	12,500 (11,700 - 13,200)	7%	6%
2005	12,300 (11,500 - 13,000)	2%	2%
2006	13,700 (12,900 - 14,600)	19%	14%
2007	13,800 (12,900 - 14,600)	14%	11%
2008	11,000 (10,600 - 11,300)	15%	12%
2009	12,100 (11.900 - 12,200)	12%	9%
2010	13,600 (13,100 - 14,100)	22%	17%
2011	13,000 (12,900 - 13,200)	22%	18%
2012	12,300 (11,900 - 12,700)	27%	20%
2013	14,900 (14,500 - 15,300)	14%	11%

Table C-1.3: Estimated annual consumption numbers (95% confidence interval) of juvenile salmonid smolts by double-crested cormorants nesting on East Sand Island in the Columbia River estuary during 1998-2013. Smolt consumption estimates are based on the percentage of salmonids (% salmonids) found in cormorant diet samples and bioenergetics modeling (Lyons 2010, BRNW 2014).

	Consumption Estimates (millions)				
Year	Yearling Chinook	Sub-yearling Chinook	Coho	Sockeye	Steelhead
1998	0.5 (0.1 – 1.2)	10.3 (5.7 – 19.8)	0.9 (0.3 – 2.0)	<0.1 (0.0 - 0.2)	0.6 (0.2 – 1.2)
1999	0.9 (0.3 – 2.1)	8.3 (4.3 – 16.4)	1.6 (0.8 – 3.5)	<0.1 (0.0 - 0.3)	1.0 (0.5 – 2.1)
2000	0.8 (0.2 – 2.1)	4.4 (2.2 – 9.4)	1.3 (0.5 - 2.9)	<0.1 (0.0 - 0.3)	0.9 (0.4 – 2.2)
2001	0.4 (0.1 – 1.3)	5.0 (2.3 – 11.1)	0.8 (0.2 – 2.1)	<0.1 (0.0 - 0.2)	0.5 (0.2 – 1.3)
2002	0.1 (0.0 - 0.3)	4.1 (1.6 – 8.9)	0.3 (0.1 - 0.8)	<0.1 (0.0 - 0.0)	0.1 (0.0 - 0.4)
2003	0.7 (0.1 – 2.2)	1.4 (0.4 – 3.9)	0.9 (0.3 – 2.5)	<0.1 (0.0 - 0.4)	0.7 (0.2 - 1.7)
2004	0.5 (0.1 – 1.4)	5.3 (1.9 – 11.8)	1.0 (0.3 – 2.4)	<0.1 (0.0 - 0.3)	0.6 (0.2 – 1.4)
2005	0.1 (0.0 - 0.4)	2.2 (0.5 – 6.3)	0.4 (0.1 – 1.0)	<0.1 (0.0 - 0.1)	0.2 (0.0 - 0.6)
2006	1.6 (0.5 – 4.1)	2.7 (0.9 – 6..3)	3.3 (1.6 – 7.0)	<0.1 (0.0 - 0.6)	1.7 (0.8 – 3.7)
2007	1.0 (0.3 – 2.7)	5.0 (1.7 – 11.9)	2.5 (1.2 – 5.6)	<0.1 (0.0 - 0.4)	1.3 (0.5 - 2.9)
2008	0.9 (0.3 - 1.8)	5.8 (2.6 – 10.7)	1.8 (0.9 - 2.8)	<0.1 (0.0 - 0.3)	0.9 (0.4 - 1.6)
2009	0.7 (0.1 – 1.4)	8.7 (3.7 – 17.0)	1.4 (0.6 – 2.6)	<0.1 (0.0 - 0.3)	0.8 (0.3 – 1.4)
2010	1.2 (0.3 – 2.4)	13.8 (6.8 – 24.2)	3.0 (1.6 – 4.6)	<0.1 (0.0 - 0.4)	1.5 (0.7 – 2.4)
2011	0.9 (0.2 - 1.6)	15.7 (9.1 – 25.5)	2.9 (1.5 – 4.3)	0.1 (0.0 - 0.9)	1.3 (0.6 – 2.1)
2012	1.5 (0.5 – 2.7)	11.1 (5.9 – 17.4)	4.8 (3.0 – 7.2)	0.2 (0.0 – 1.1)	1.8 (1.0 - 2.7)
2013	1.0 (0.3 – 2.0)	11.9 (6.0 – 21.3)	2.8 (1.3 – 4.6)	0.3 (0.0 – 1.2)	1.1 (0.5 – 1.9)

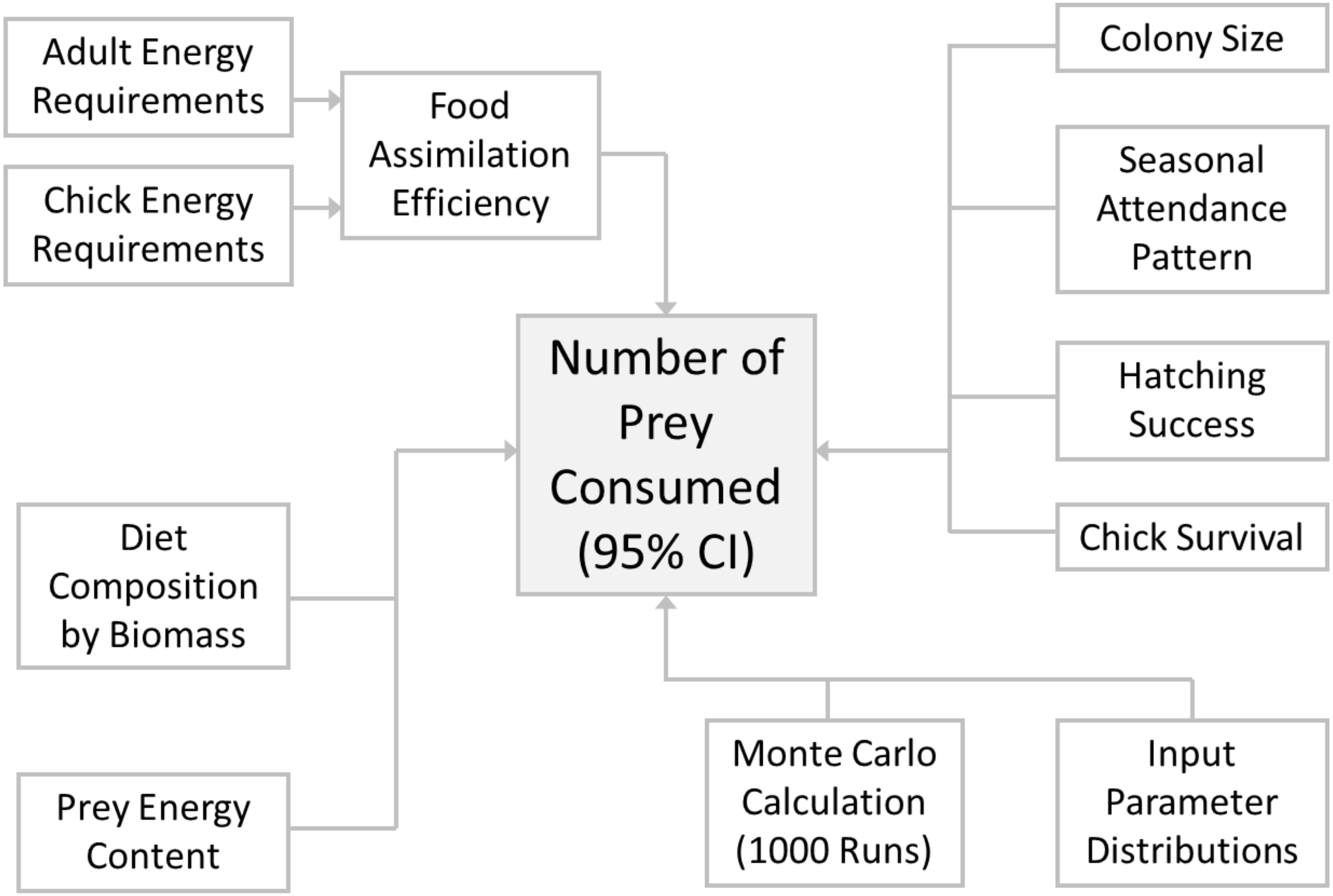

Figure C-1.1. Conceptual framework of the bioenergetics model used to estimate smolt consumption by East Sand Island double-crested cormorants after Lyons (2010), showing important input variables and methodology.

APPENDIX C-2: Estimates of Smolt Predation Probabilities by East Sand Island Double-crested Cormorants

Capture-recapture methods are commonly used to estimate fish mortality due to avian predation (Ryan et al. 2001; Boström et al. 2009; Jepsen et al. 2010; Evans et al. 2012; Sebring et al. 2013; Hostetter et al. in-press). In these studies samples of fish are captured and tagged to identify individuals or groups, and then returned to mix with the rest of the population of interest. Nearby bird colonies are then searched to detect tags from fish consumed by birds that were subsequently deposited at the bird colony. The recovery of tags on bird colonies, however, is not a direct measure of predation impacts because some proportion of consumed tags are deposited off-colony or damaged during digestion (deposition probability; Hostetter et al. in-press) or the tag is deposited on-colony but missed during the recovery process (detection probability; Evans et al. 2012). Statistical models have been applied to address the challenge of imperfect recovery of PIT tags deposited on bird colonies (Evans et al. 2012; Osterback et al. 2013; Hostetter et al. in-press). These models can then be used to generate best or absolute measures of predation on groups of tagged fish. PIT tag predation probabilities presented herein and those presented in the Double-crested Cormorant Management Plan to Reduce Predation on Juvenile Salmonids in the Columbia River Estuary were derived using modeling techniques published in Evans et al. (2012) and Hostetter et al. (in-press) and are summarized below, with results presented in Table C-2.1.

Availability of PIT-tagged Smolts to Double-crested Cormorants Nesting on East Sand Island: Following the methods of Evans et al. (2012) and Hostetter et al. (in-press), PIT-tagged salmonid smolts last detected passing Bonneville Dam on the lower Columbia River or Sullivan Dam on the lower Willamette River during March-August provide data on the number of smolts available to cormorants nesting on East Sand Island each year (1999-2013). PIT-tagged fish were grouped by evolutionary significant unit (ESU) or distinct population segment (DPS), with each ESU/DPS representing a unique combination of species (Chinook salmon, sockeye salmon, or steelhead trout), run-type (spring, summer, fall, or winter), and river-of-origin (Columbia, Snake, or Willamette). The designation of ESU/DPSs follows that of NOAA (2011), which includes both wild and hatchery-reared fish, depending on the ESU/DPS.

PIT tag Recovery on East Sand Island: Recovery of smolt PIT tags on the East Sand Island double-crested cormorant colony following methods of Ryan et al. (2001) and Evans et al. (2012). Briefly, scanning for PIT tags was conducted after birds dispersed from the breeding colony following the nesting season (September - November). The colony areas was scanned using pole-mounted PIT tag antennas. The area scanned was determined based on year-specific aerial photography and colony visits during the nesting season.

PIT tag Detection Probability on East Sand Island: The probability that a PIT tag was detected by researchers given that the tag was deposited on-colony (i.e., detection probability) required surveys of tags known to have been deposited on-colony (see Evans et al. 2012). Studies estimating PIT tag detection probability at the East Sand Island cormorant colony were conducted during 2000-2013, with detection probability data provided by NOAA fisheries (Ryan et al. 2002, Sebring et al. 2013) and BRNW (BRNW 2005-2007; Evans et al. 2012, Hostetter et al. in-press). Briefly, PIT tags with known tag codes were sown on the East Sand Island cormorant colony during 1-2 occasions prior to and after the nesting season (hereafter "test tags") and the proportion subsequently recovered after the nesting season was used to model detection efficiency during the nesting season via logistic regression per Evans et al. (2012). In years when zero (1999) or just one (2000-2006) release of test tags occurred, release and recovery values for the missing occasion were averaged across the nearest years with adequate data.

PIT Tag Deposition Probability on East Sand Island: Studies estimating PIT tag deposition probability (i.e., the probability a tag was deposited on-colony after it was consumed) were conducted on the East Sand Island cormorant colony in 2012 and 2013 (Hostetter et al. in-press). Briefly, fish with known tag codes were consumed by double-crested cormorant nesting on East Sand Island at different times of the day (morning, evening) and throughout the nesting season. The proportion of consumed tags subsequently deposited on-colony was then used to estimate deposition probability. The distribution of the mean deposition probability derived from these studies (0.51; 95% confidence interval 0.34-0.70; Hostetter et al. in-press) was applied across all years (1999-2013). This distribution was used as (i) data on cormorant deposition probabilities in other years (1999-2011) were unavailable and (ii) results from 2012-2013 indicated cormorant deposition probabilities did not significantly differ by consumption time, consumption day, or year.

Cormorant Predation probability: Predation probabilities were modeled independently for each year and each salmonid ESU/DPS. The probability of recovering a PIT-tagged smolt on the cormorant colony was the product of the three probabilities described above: the probability that the fish was consumed (θ), deposited (μ_{ϕ}), and detected (ψ) on-colony

$$k_i \sim Binomial(n_i, \theta_i * \mu_{\phi} * \psi_i)$$

where k_i is the number of smolt PIT tags recovered from the number available (n_i) in week *i*. Detection probability (ψ_i) was modeled as a logistic function as described above, the distribution of the mean cormorant deposition probability (μ_{ϕ}) was applied across all weeks, and θ_i is the predation probability for week *i*. We used an informative prior (beta [15.98, 15.29]; Hostetter et al. in-press) for the mean deposition probability as deposition probability data were not available in all years. We ascribed a hyperdistribution for weekly predation probabilities ($\boldsymbol{\theta}$):

$$logit(\theta_i) \sim Normal\left(\mu_{\theta}, \sigma_{\theta}^2\right)$$

This allowed each week (*i*) to have a unique predation probability (θ_i), but information was shared among weeks (*i*) to improve precision. Annual predation probabilities were derived as the sum of the estimated number of PIT-tagged smolts consumed each week divided by the total number of individuals last detected passing Bonneville or Sullivan dams that year.

$$\sum\nolimits_{all\ i}(\theta_i * n_i) \Big/ \sum\nolimits_{all\ i}(n_i)$$

The derived annual predation probability constitutes the estimated proportion of available PIT-tagged smolts consumed by DCCO nesting at East Sand Island in a given year.

We implemented all predation probability models in a Bayesian framework using the software JAGS (Plummer 2003) accessed through R version 3.0.1 (R Core Team 2014). We ran three parallel chains for 50,000 iterations each and a burn-in of 5,000 iterations. Chains were thinned by 20 to reduce autocorrelation of successive Markov chain Monte Carlo samples, resulting in 6750 saved iterations. Chain convergence was tested using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004). We report results as posterior medians as well as 2.5 and 97.5 percentiles, which represent the Bayesian equivalent to 95% Confidence Intervals (95CRI). Predation probabilities were only calculated for ESUs/DPSs when ≥ 500 PIT-tagged salmonids were interrogated passing Bonneville or Sullivan dams in a given year to control for imprecise results that might arise from small annual sample sizes of available PIT-tagged smolts (Evans et al. 2012).

Results from this predation modeling procedure were based on the following assumptions:

A1. PIT-tag salmonid release and interrogation information obtained from Bonneville and Sullivan dams were complete and accurate.

A2. PIT-tagged smolts last detected passing Bonneville and Sullivan dams were available to cormorants nesting downstream on East Sand Island.

A3. The detection probabilities of test PIT tags sown on-colony was equal to that of PIT tags naturally deposited by cormorants on-colony in each study year.

A4. The deposition probabilities of PIT tags (those used in deposition studies; see Hostetter et al. in-press) during 2012-2013 were equal to that of fish consumed and deposited by birds in all years (1999-2013).

A5. PIT tags from consumed fish were deposited on a bird colony within a short time period (weeks) of the fish being detected passing an upstream dam.

A6. PIT-tagged fish, by species, ESU, rear-type, and detection site (dam), were representative of non-tagged fish.

To verify the first assumption (A1), irregular entries were either validated by the respective coordinator of the PIT-tagging effort or eliminated from the analysis. Detections of PIT-tagged salmonids at dams upstream of bird colonies were deemed the most appropriate measure of fish availability given the downstream movement of juvenile salmonids, the ability to standardize data across sites, and the ability to define unique groups of salmonids by a known location and passage date (Assumption A2). Assumption A2 assumes all PIT tagged fish last detected passing Bonneville or Sullivan dams were alive and available to cormorant predation in the estuary. If large numbers of fish died immediately following passage and prior to reaching the foraging range of cormorants, however, predation probabilities would underestimate impacts. Detection efficiency estimates (A3) were generally high (ca. 70%, depending on year; see Evans et al. 2012 and Hostetter et al. in-press), suggesting possible violations of assumption A3 would have little effect on estimates of predation. Data collected during 2012-2013 (where multiple measures of deposition were estimated in each year) showed no evidence of a within season temporal trend in deposition probabilities (Assumption A4). Assumption A5 relates to the use of the last date of live detection as a proxy for the date a PIT tag was deposited on a bird colony and needs to be only roughly true because detection efficiency did not change dramatically on a weekly bases (see Evans et al. 2012; Hostetter et al. in-press). Assumption A6 relates to inference regarding the consumption of PIT-tagged fish last detected passing Bonneville and Sullivan dams to all fish (tagged and untagged) of the same ESU/DPS susceptible to cormorant predation in the estuary.

There are few empirical data to support or refute assumption A6, other than to note that the run-timing and abundance of PIT-tagged fish is often in agreement with the run-timing and abundance of non-tagged fish passing dams on the Columbia and Willamette rivers and that differences in fish vulnerability to cormorant predation based on a fish's passage route or migration history (in-river or transported) tend to be small and inconsistent from year-to-year (Ryan et al. 2003; Lyons et al. 2014). Finally, sample sizes of PIT-tagged fish varied considerably by year and ESU/DPS but were generally in the thousands, minimizing the potential risk for bias or spurious results that could emerge with small numbers of tagged fish. These and other assumptions, caveats, and discussion points are presented in more detail in Evans et al. (2012), Lyons et al. (2014), and Hostetter et al. (in-press).

Table C-2.1: Estimated annual predation probabilities (95% credible interval) of PIT-tagged, ESA-listed salmonid smolts by double-crested cormorants nesting on East Sand Island in the Columbia River estuary during 1999-2013. Predation probabilities are based on numbers of PIT-tagged fish (N) interrogated passing Bonneville Dam on the Columbia River or Sullivan Dam on the Willamette River, and subsequently consumed by cormorants in the estuary. Only salmonid populations with ≥ 500 PIT-tagged smolts interrogated passing a dam were evaluated in any given year. Dashes denote populations with < 500 PIT-tagged fish available. Salmonid populations originating from the Snake River (SR), Upper Columbia River (UCR), Middle Columbia River (MCR) and Upper Willamette River (UWR) were evaluated, with runs of spring (Sp), summer (Su), and fall (Fa) fish included, where applicable.

	ESU/DPS-specific Predation Probabilities							
Year	SR Sp/Su Chinook (Threatened)	SR Fa Chinook (Threatened)	UCR Sp Chinook (Endangered)	UWR Sp Chinook (Threatened)	SR Sockeye (Endangered)	MCR Steelhead (Threatened)	SR Steelhead (Threatened)	UCR Steelhead (Threatened)
1999	.009 (.006-.015) N=18,558	.015 (.006-.030) N=1,987	.007 (.002-.020) N=1,325	-	-	.010 (.001-.035) N=632	.024 (.017-.039) N=12,287	.020 (.013-.032) N=12,123
2000	.033 (.023-.053) N=11,810	.051 (.029-.093) N=1,323	.034 (.016-.068) N=1,123	-	-	-	.106 (.075-0.168) N=10,356	.060 (.039-.100) N=3,100
2001	.022 (.014-.035) N=8,845	.055 (.029-.104) N=807	.033 (.017-.063) N=1,230	-	-	.025 (.010-.057) N=872	.028 (.011-.061) N=774	-
2002	.018 (.013-.030) N=30,617	.014 (.008-.026) N=4,899	.022 (.016-.036) N=20,493	-	-	-	.031 (.020-.051) N=7,331	.037 (.014-.086) N=561
2003	.017 (.012-.027) N=28,150	.011 (.007-.020) N=6,234	.014 (.009-.021) N=30,723	-	-	-	.019 (.012-.030) N=8,553	.015 (.010-.024) N=27,918
2004	.051 (.033-.085) N=4,816	.019 (.006-.047) N=929	.047 (.032-.076) N=9,533	-	-	-	.036 (.014-.080) N=803	.074 (.051-.118) N=6,040
2005	.048 (.032-.079) N=5,935	.036 (.018-.069) N=1,121	.045 (.028-.078) N=2,518	-	-	-	.043 (.020-.086) N=753	.055 (.037-.088) N=5610
2006	.052 (.035-.085) N=5,570	.027 (.016-.046) N=4,057	.047 (.022-.095) N=731	-	-	-	.131 (.082-.227) N=1,100	.047 (.028-.082) N=2,064
2007	.017 (.011-.027) N=23,830	.016 (.007-.033) N=2,005	.027 (.015-.051) N=2,268	.010 (.003-.026) N=1,505	-	.028 (.015-.052) N=2,234	.035 (.023-.058) N=6,391	.034 (.021-.061) N=3,042
2008	.035 (.024-.055) N=11,425	.026 (.019-.042) N=24,136	.036 (.020-.066) N=1,662	.033 (.019-.058) N=2,509	-	.140 (.095-.232) N=2,291	.147 (.106-.232) N=19,572	.062 (.040-.104) N=2,513
2009	.068 (.049-.107) N=17,396	.045 (.032-.071) N=16,314	.027 (.015-.049) N=2,064	.014 (.008-.024) N=5,573	.057 (.035-.098) N=1,845	.149 (.103-.238) N=2,700	.166 (.120-.257) N=23,311	.072 (.047-.120) N=2,265
2010	.053 (.039-.084) N=38,441	.039 (.027-.061) N=17,974	.033 (.023-.054) N=5,972	.042 (.016-.092) N=510	.026 (.013-.049) N=1,382	.082 (.058-.131) N=8,515	.075 (.055-0.121) N=40,024	.068 (.049-.106) N=12,284
2011	.043 (.029-.069) N=6,557	.019 (.013-.031) N=12,327	.056 (.029-.108) N=704	.004 (.001-.015) N=1,119	.048 (.024-.091) N=826	.078 (.046-.140) N=865	.053 (.037-.085) N=7,028	.114 (.078-.186) N=2,419
2012	.037 (.026-.060) N=17,929	.026 (.018-.042) N=10,742	.021 (.012-.037) N=3,227	.006 (.003-.013) N=3,731	.037 (.020-.069) N=1,457	.033 (.017-.064) N=1,084	.049 (.032-.081) N=4,768	.065 (.043-.108) N=3,357
2013	.036 (.025-.057) N=16,167	.022 (.013-.037) N=4,465	.030 (.018-.053) N=3,112	.010 (.004-.020) N=2,629	.033 (.018-.062) N=1,454	.021 (.010-.041) N=1,865	.025 (.017-.040) N=8,516	.034 (.022-.057) N=4,473

APPENDIX C-3: Summary of explanatory factors used in Principal Components Regression analysis.

Table C-3.1: Annual values of explanatory variables used in the Principal Components Regression analysis. Variables included the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), the El Nino/Southern Oscillation (MEI; Wolter and Timlin 1993, 1998), the Pacific Northwest Index (PNI; Ebbesmeyer and Strickland 1995), the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), local sea surface temperature (SST; Brosnan et al. 2014), the strength (Upwelling; Greene et al. 2005) and timing (Spring Transition; Logerwell et al. 2003) of coastal upwelling, river discharge (Scheuerell et al. 2009), survival of Snake River spring-summer (sp/su) Chinook and steelhead through the hydropower system (Hydro Chinook Survival, Hydro Steelhead Survival; Haeseker et al. 2012), the proportion of water passing through a dam that passes over the spillway (Spill; Muir et al. 2001), and the size of the East Sand Island double-crested cormorant colony (BRNW 2014, Adkins et al. 2014).

Year	PDO	MEI	PNI	NPGO	SST (°C)	Upwelling	Spring Transition (Julian Day)	River Discharge (cfm/day)	Hydro Chinook Survival	Hydro Steelhead Survival	Spill	Colony Size (breeding pairs)
1999	-0.43	-1.11	-0.54	1.75	12.4	33	134	361355	0.52	0.40	0.34	6561
2000	-0.55	-0.97	0.45	2.01	14.2	19	97	305871	0.45	0.38	0.35	7162
2001	0.26	-0.49	0.88	2.60	12.7	23	79	174742	0.27	0.04	0.03	8120
2002	-0.28	-0.02	0.10	1.71	13.1	23	108	271903	0.55	0.23	0.34	10230
2003	1.63	0.68	0.77	1.39	13.4	22	156	300613	0.53	0.29	0.32	10646
2004	0.52	0.14	0.96	0.36	15.6	18	132	253452	0.35	NA	0.26	12480
2005	0.91	0.79	0.92	-1.48	14.5	-2	230	295000	0.53	NA	0.27	12287
2006	0.54	-0.58	-0.70	-0.59	13.2	37	180	388645	0.61	0.42	0.36	13738
2007	-0.04	0.18	0.10	-0.13	12.3	19	81	309258	0.56	0.37	0.38	13771
2008	-1.00	-1.33	-0.98	1.21	11.4	30	64	390226	0.46	0.48	0.40	10950
2009	-1.55	-0.53	-0.08	0.61	12.3	27	65	354065	0.53	0.68	0.34	12087
2010	0.72	1.26	0.60	1.75	12.0	8	177	285871	0.55	0.62	0.39	13596
2011	-0.72	-1.54	0.05	0.73	12.8	9	82	474161	0.48	0.59	0.44	13045
2012	-0.89	-0.36	0.18	1.30	11.4	4	126	453516	0.59	0.60	0.40	12301
2013	-0.34	-0.11	NA	1.13	13.9	22	91	358226	0.52	0.50	0.39	14916
Mean	0.01	-0.08	0.20	0.96	13.1	20	129	334185	0.50	0.43	0.33	11136
St. Dev.	0.87	1.04	0.58	1.00	1.1	10	57	72963	0.09	0.16	0.09	2664

Table C-3.2: Correlations between transformed and normalized explanatory variables used in the Principal Components Regression analysis. Variables included the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), the El Nino/Southern Oscillation (MEI; Wolter and Timlin 1993, 1998), the Pacific Northwest Index (PNI; Ebbesmeyer and Strickland 1995), the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), local sea surface temperature (SST; Brosnan et al. 2014), the strength (Upwelling; Greene et al. 2005) and timing (Spring Transition; Logerwell et al. 2003) of coastal upwelling, river discharge (Scheuerell et al. 2009), survival of Snake River spring-summer (sp/su) Chinook and steelhead through the hydropower system (Hydro Chinook Survival, Hydro Steelhead Survival; Haeseker et al. 2012), the proportion of water passing through a dam that passes over the spillway (Spill; Muir et al. 2001), and the size of the East Sand Island double-crested cormorant colony (BRNW 2014, Adkins et al. 2014).

	PDO	MEI	PNI	NPGO	SST	Upwelling	Spring Transition	River Discharge	Hydro Chinook Survival	Hydro Steelhead Survival	Spill	Colony Size
PDO	1.00											
MEI	0.75	1.00										
PNI	0.53	0.50	1.00									
NPGO	-0.19	-0.16	0.04	1.00								
SST	0.50	0.35	0.56	-0.30	1.00							
Upwelling	-0.07	-0.15	-0.59	0.22	-0.06	1.00						
Spring Transition	0.77	0.77	0.29	-0.38	0.42	-0.14	1.00					
River Discharge	-0.40	-0.27	-0.61	-0.23	-0.35	-0.02	-0.02	1.00				
Hydro Chinook Survival	-0.05	0.20	-0.42	-0.40	-0.32	-0.05	0.35	0.56	1.00			
Hydro Steelhead Survival	-0.38	0.00	-0.32	-0.40	-0.27	-0.32	0.06	0.73	0.56	1.00		
Spill	-0.31	-0.11	-0.53	-0.21	-0.29	-0.07	-0.04	0.77	0.76	0.76	1.00	
Colony Size	-0.11	-0.09	-0.03	-0.52	-0.11	-0.36	-0.18	0.22	0.42	0.45	0.39	1.00