

**Using environmental data to improve wild and hatchery estimates of Chinook and coho
salmon return rates**

**Final Report to Pacific Salmon Commission Southern Fund
February 27, 2009**

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Background

The ability to forecast population-specific returns of salmon is critical to the sound management of individual stocks, and an important function of the Pacific Salmon Commission. A key set of challenges of making these forecasts is relying on exploitation rate and survival estimates from coded-wire-tagged hatchery indicator stocks. For coho salmon, which return at primarily one age, estimating natural mortality and differentiating natural mortality from harvest are important. For Chinook salmon, which return at multiple ages, natural mortality at age is assumed fixed and maturation rates are estimated from hatchery indicator stocks. Harvest rates for specific populations are generally estimated using coded-wire tag groups from hatchery index stocks. However, the application of these harvest rate estimates to wild populations carries the assumption that hatchery and wild fish have similar natural mortality rates and/or maturation rates, or can be accurately corrected for any differences. Both natural mortality and maturation rates in fishes are known to be highly variable in response to environmental fluctuations (Policansky 1983).

Recently, some analyses have questioned the utility of hatchery stocks to represent populations of wild salmon. Because hatchery fish are not naturally reared, they are buffered from freshwater environmental variation. Moreover, because hatchery fish are often reared until they are primed for downstream migration, they exhibit reduced residence in habitats used by wild salmon for rearing. Consequently, a greater proportion of their residence in the wild is associated with marine environments, and individuals may start these stages at larger sizes than their wild counterparts. If return rates of wild fish depend upon residence in freshwater or estuarine habitats, or mortality is size-dependent during these life stages, hatchery groups may be poor indicators of mortality in wild fish. However, it is also possible that high variability in marine mortality could reduce the dependency between return rates and residence or size at earlier life stages, thereby making mortality estimates from hatchery fish a relatively accurate predictor of mortality in wild fish.

Recent research has revealed that mortality of wild fish can be predicted with high precision by using environmental data closely linked to particular salmon life stages (Greene et al. 2005), and in some cases, these data also correlate well with mortality of hatchery stocks (Nickelson 1986). Identifying suites of environmental predictors that closely track return rates in both wild and hatchery fish, and incorporating these predictors into population models therefore holds promise to greatly improve forecasts of salmon. We examined the utility of environmental data to help explain variation in return rates for both wild and hatchery index stocks of Puget Sound Chinook and coho salmon. We utilized environmental correlates measured at different stages of salmon life histories, evaluated their potential for predicting return rates, and developed tools for incorporating these covariates into population models.

Objectives

- 1) Evaluate the utility of index hatchery stocks for predicting return rates of wild Chinook and coho salmon.
- 2) Examine environmental correlates of return rates for hatchery index and wild stocks and their power to forecast future salmon returns.

Methods

We examined environmental predictors of return rates of ocean-type Chinook and coho salmon inhabiting Puget Sound. Including the Straits of Juan de Fuca and San Juan Islands, the entire region has an approximate drainage area of 16,800 km² and presents a variety of physical and environmental conditions which may influence salmon populations. Bathymetric and hydrologic features result in Puget Sound being divided into 7 sub-basins (Appendix 1a). The Strait of Juan de Fuca and San Juan Island sub-basins are primarily influenced by freshwater from the Fraser River in Canada, while Puget Sound freshwater is largely supplied by nineteen major river systems (Burns, 1985). The Whidbey Basin receives 60% of Puget Sound freshwater, while the Main basin receives about 20%, and the South and Hood Canal Basins approximately 10% each. The sub-basins also vary in sedimentation, depth, water circulation and amount of river delta or estuary.

Chinook and coho salmon life cycles

Puget Sound currently supports 22 Chinook populations and 45 coho stocks (WDFW, 2008) which use multiple habitats during their life cycle. Chinook spawn between July and October, with a peak occurring during low freshwater flow in September. Coho spawn between October and January, with peak spawning occurring in November. For both species, eggs incubate in redds for approximately 5 months. After hatching, juvenile Chinook migrate downstream to river deltas to rear for 1 to 2 months before moving to bays and nearshore environments. Although some variation within Puget Sound is likely, in Skagit Bay, extensive field surveys indicate the range of delta habitat use is from February to June and bay habitat, from June through October (E. Beamer, unpublished data). From estuary environments, Puget Sound Chinook migrate out into the Pacific Ocean and remain there three to five years. Coho rear for more than one year in freshwater, and typically migrate in the spring as yearlings, arriving in the estuaries between April and June. There is little research on use of estuarine habitat by coho, but they are believed to be less dependent than Chinook (Duffy et al. 2005). While some male coho do return early to spawn (jacks), the freshwater and estuarine rearing periods are generally followed by 16 months maturing in an ocean environment before returning to spawn. Chinook populations in Puget Sound have been delineated based on genetic analysis by the National Marine Fisheries Service Puget Sound Technical Recovery Team (PSTRT); although no similar comprehensive genetic analysis of coho stocks has been done, for ease of reference in this report both Chinook populations and coho stocks will be referred to as populations.

Although Chinook salmon and coho salmon are noted for their contrasting life cycles, they do share some similarities. Both species deposit eggs in redds that develop over winter, although Chinook salmon tend to spawn much earlier in the season (late spring to early fall) than coho (late fall to early winter). Most Chinook salmon migrate out of rivers in the Puget Sound region as subyearlings, often spending a significant portion of their rearing in estuaries and nearshore habitats. In contrast, most coho salmon rear in streams for over a year, and migrate into Puget Sound as yearlings. Thereafter, most fish migrate out of the Sound within a couple of months. A subset of both Chinook and coho salmon rear for extended periods of time within Puget Sound, and are therefore called “resident” fish. These patterns suggest that both coho might be susceptible to winter incubation floods and conditions within Puget Sound. We would also expect that coho but not Chinook salmon would be sensitive to freshwater discharge during their extended stream rearing. Both species might also exhibit density dependence as they compete for rearing habitat (Greene and Beechie 2004,

Greene et al. 2005). However, the habitats in which each species most experienced density dependence might be expected to differ, with Chinook likely competing in the estuary and nearshore (E. Beamer et al. unpublished data), and coho likely competing in freshwater systems (Grant and Kramer 1990). Given that our data were based on adult returns, we could only examine initial juvenile densities by calculating total egg density from adult returns. Finally, both species might be influenced by conditions experienced in the Puget Sound nearshore (Greene et al. 2005). We examined data from both the natal basin in which salmon migrated into as well as from the nearest nonnatal basin and data from the Straits, the primary route by which most smolts would leave Puget sound. We used these variables as starting points in our analysis linking environmental data to return rates in both species. These models then served as benchmarks to compare with hatchery stocks.

Washington State has a long history of hatchery production and enhancement which have influenced salmon populations. Of the extant Puget Sound populations, approximately half are supported by fully-marked hatchery broodstock programs; only 10 Chinook and 2 coho populations are determined to be native stock with wild production (Salmonscape, SaSI, Duffy et al. 2005). Although ratios of hatchery to wild juveniles are not precisely known, releases of coho and Chinook fry, fingerling, and smolt in Puget Sound have averaged 82 million per year since 1975 (RMIS), and hatchery production accounts for 70% of salmon harvested in the Puget Sound estuary (HSRG 2002).

We tested the relative influence of environmental conditions experienced during the above periods of residency in two habitat classes (freshwater and nearshore) on return rates of 22 wild Chinook and 24 wild coho populations for which population data was available over a sufficient time series. We initially planned to also examine the influence of conditions experienced during estuary rearing, but because of extremely spotty data collection efforts in estuaries across Puget Sound and because we had previously found that approximations of environmental conditions experienced during estuary rearing using nearshore data had little influence on return rates (Greene et al. 2005), we confined our analyses to just freshwater and nearshore periods. We also compared the influence of these conditions on survival of 11 Chinook and 15 coho hatchery stocks corresponding to the wild populations. The longest time series for populations included in our analysis was 30 brood years, and the shortest was 7 (Appendix 1b).

Environmental data

Freshwater data. We determined flood recurrence interval (FRI), the estimated frequency in years at which a flood of a given magnitude will occur, for the single largest peak flow event between September and February of each year. FRI for both average daily maximum and instantaneous peak events were calculated by fitting a log-Pearson Type III distribution to the logarithms of the annual peak flows using PeakFQ software (Version 5.2, U.S. Geological Survey). Annual frequency curve parameters of mean and standard deviation (*SD*) from PeakFQ were used to generate a frequency factor *K* using the following formula.

$$K = [\log(Q) - \log(\text{mean})]/\log(SD) \quad \text{Eq. 1}$$

where *Q* is the peak discharge, in cubic feet per second. Values of *K* can be looked up using the skew coefficient from PeakFQ in Appendix 3 of Bulletin 17B (Interagency Advisory Committee on

Water Data, 1982) or fit to a standard normal distribution to generate an exceedance probability p , inverse of the flood recurrence interval t in years (McCuen, 1989; Berenbrock 2002). It is the convention to calculate recurrence intervals using ten years or more of recent peak data; the minimum number of years used to generate parameters was 13 and the average was 48. If a flow gage was impacted by regulation, peak data prior to regulation was excluded. A small number (< 9%) of instantaneous peaks did not occur during the season of interest; in those cases peak values were interpolated from the generally strong relationship of average daily and instantaneous peaks (average $R^2=0.911$, $n=29$).

For each population, relevant gages were selected based on proximity to spawning and rearing areas based on data from the Washington Lakes and Rivers Information System (WLRIS), published on WDFW's Salmonscape . Matching of gages to spawning and rearing areas was limited for some populations due to lack of gages or continuous time series which matched population data (Appendix 1a). In a very small number of cases, the gage from the nearest watershed was substituted for analysis.

Since coho spend over a year rearing in freshwater, FRI for the largest average daily and instantaneous peak flow event between September and March of the year following incubation was calculated as an overwinter rearing variable. We also used several metrics of stream flow to examine whether discharge during the rearing period explained variation in return rate. We used average and minimum monthly mean discharges for the freshwater rearing period, divided by the annual mean discharge and catchment area to normalize data across river systems. To investigate the impacts of low flow events on coho, we calculated low-flow indices for the summer rearing period of June through September for each brood year. The 3-, 7- and 10-day low-flow series for June through September of each year was computed from the record of rearing gages using SWSTAT (Version 4.1, U.S. Geological Survey) and analyzed by the same program to generate frequency curve parameters (Winterstein et al., 2006). This output from SWSTAT is used exactly the same way as output from PeakFQ to generate a non-exceedance probability, with the exception that SWSTAT does not weight the individual skew coefficient with a regional skew coefficient (Interagency Advisory Committee on Water Data, 1982) and is less precise than PeakFQ output.

Nearshore data. We assembled data describing conditions during nearshore (May-October) residency from several sources, including the Pacific Fisheries Environmental laboratory, University of Hawaii, and the Washington Department of Ecology (Table 1). Data were assembled for all sub-basins across all available years. From these data we used principal components analysis to extract three nearshore factors. We then used factor scores from each sub-basin as environmental correlates. Because use by salmon of different sub-basins will closely depend upon stage of migration, we examined the influence

of the natal sub-basin, the next closest sub-basin along the migration pathways for each population, and data from the Strait of Juan de Fuca (the endpoint of the migration out of Puget Sound). Although principal component scores across all of Puget Sound were uncorrelated, Factor 1 and Factor 3 were correlated within sub-basins. Consequently, we focused our analysis using the first two principal components.

Biological data

Our sample consisted of 22 wild Chinook and 24 wild coho populations (Appendix 1a,b). With some exceptions, complete biological and environmental data for Chinook existed for brood years 1973/1974-2002, and brood years 1986-2003 for coho. We used return rates of both spawners per spawner and recruits per spawner, calculated based on the best escapement, harvest, and age composition estimates available for each spawning population.

For the majority of Puget Sound coho populations, escapement estimates are based on surveys of live fish in index reaches expanded by the ratio of total spawner abundance vs. index abundance for a base year of historical abundance (Cousens et al 1982). The base year estimates of abundance are determined through mark and recapture studies (Eames et al 1983, Conrad et al 1997 and 1998a, 1998b, and 1998c), or expansion of spawning ground survey observations conducted during the base year. Variations on methods of expanding index fish counts to basin or region-total estimates of escapement, while commonly used by management agencies in Oregon, Washington, Alaska and Canada, are subject to the limitations of observer efficiency (Hillborn et al 1999), accuracy of the base year, and/or other assumptions regarding the distribution and density of coho in the index reaches vs. the basin or geographic region (Crain 1996). However, the index-count based method of escapement used for the majority of Puget Sound coho populations is assumed to provide a reasonably consistent index of relative abundance for each population, and are considered to be the best estimates currently available for Puget Sound coho populations located externally to stream reaches located upstream of hatchery and research weirs or dams (Jeffrey Haymes, WDFW, personal communication).

Since coho return to spawn primarily at age 3, we calculated return rates of spawners per spawner based on a particular brood year as:

$$S_t = N_{t+3}/N_t \quad \text{Eq. 2}$$

Where N_t is the wild escapement and N_{t+3} is the escapement three years later. Coho escapement is based on adult returns only, and S_t therefore does not include any estimate of early-returning males or jacks. Although precociousness has been shown to be an important reproductive strategy for coho (Gross, 1985), estimates of jack percentages vary widely between systems and years, and are

Table 1. Factor loadings of nearshore data on three principle components with factors with eigenvalues > 1. These three components explained a total of 68.91% of the variation in the environmental data.

Variable	Factor 1	Factor 2	Factor 3
Sea level ¹	0.248	-0.808	-0.024
Upwelling ²	0.460	0.523	-0.590
Surface NO _x ³	-0.712	-0.192	0.089
Surface salinity ³	-0.679	0.346	-0.051
Surface dissolved O ₂ ³	0.192	0.400	0.822
Surface temperature ³	0.734	-0.025	0.203
Variation explained (%)	30.274	20.706	17.928

¹Pacific Fisheries Environmental Laboratory

²University of Hawaii Sea Level Center

³Washington Department of Ecology marine water quality monitoring data

dependent on genetic and environmental factors (Groot & Margolis, 1991; Quinn, 2005). We determined that the potential error would be greater by attempting to incorporate jacks than by basing analysis on adult returns only.

The primary problem with using S_t is that it does not account for individuals lost to harvest. We therefore calculated a second return rate of recruits per spawner:

$$R_t = [N_{t+3}/(1-H_{t+3})]/N_t \quad \text{Eq. 3}$$

Where H is an exploitation rate applied to that population (Appendix 1) based on historical commercial catches and terminal escapement for five Puget Sound basins available from Pacific Fisheries Marine Council (2008). Rates for the Snohomish/Stillaguamish basin were applied to Central Puget Sound basin populations.

We estimated the number of eggs (E_t) produced by each brood year using a simple proportion of females (0.50) and an average fecundity factor of 2,000 eggs/hen. The fecundity factor was determined from average hatchery eggtakes from 2001-2007 in conjunction with other available estimates for Puget Sound (Groot & Margolis, 1991; P. Topping, WDFW, unpublished data). ArcGIS software (Version 9.2; ESRI, Redlands, California, USA) was used to calculate kilometers of fish distribution for each population using shapefiles available from Salmonscape, and a density variable was calculated by dividing E_t by the kilometers of distribution.

Return rates for the 22 Chinook populations were available from historic run reconstructions completed in 2008 by the National Marine Fisheries Service Puget Sound Technical Recovery Team (PSTRT). Abundance and productivity (A&P) tables developed by the multi-disciplinary science team include analyses using annual spawner escapements, hatchery fraction and wild age structure on the spawning grounds, and age-specific harvest data from the State and Tribal co-managers for Chinook Salmon. In order to estimate various population statistics, brood-year run reconstruction was conducted, starting with age specific escapements and applying age specific harvest rates and fixed natural mortality to get age specific standing stock (cohort ocean abundance by age prior to natural and fishing mortality). The method is documented in Ford et al. 2007. Spawners per spawner (S/S) and recruits per spawner (R/S) are calculated for brood years in the A&P spreadsheets similar to Eqs. 2-3, but because Chinook salmon can return at various ages, the calculations integrate age-specific maturation rates to derive metrics of return rate that combine returns at different ages. The number of eggs (E_t) produced by each brood year, and given in the spreadsheets, was based on population-specific estimates of proportion of females and the average fecundity. As with coho salmon, a density variable was calculated by dividing E_t by the area of available freshwater habitat, provided courtesy of Krista Bartz (NOAA's Northwest Fisheries Science Center) as part of a comparison of current and historic Chinook rearing habitat in Puget Sound. Available habitat was determined using a synthetic drainage network with geomorphic attributes combined with natural and anthropogenic barrier data (K. Bartz, unpublished data; Davies et al 2007). Estimates using this method included lake rearing habitat, but did not include off-channel habitat such as side channels or braids.

To compare survival of wild populations with hatchery populations, coho and Chinook hatchery runs were reconstructed based on brood year releases and returns. Brood year releases of hatchery coho

and Chinook were summarized from Regional Mark Information System (2008) data hosted by the Pacific States Marine Fisheries Commission. RMIS serves as the data repository for releases of all hatchery fish (marked, tagged, or unmarked), and recoveries of all tagged fish. In the Puget Sound region, this includes federal, state, tribal, and educational agencies who report release and recovery activities using the guidelines established by the Technical Committee for Joint Data Sharing, Pacific Salmon Commission (PSC, 1989) and mandated by the 1985 Pacific Salmon Treaty. While RMIS data are available as early as 1952, the demarcation point for consistent reporting of hatchery releases for agencies relevant to Puget Sound is considered to be 1975 (G. Nandor, RMPC, personal communication), so release data prior to that time was not considered. Hatchery releases and location coordinates were downloaded for Puget Sound Chinook and coho for brood years 1975-2006. Release locations were mapped in GoogleEarth Pro (Version 4.2) and compared to the hatchery locations where returns would be counted for that brood year; release locations assumed outside of an area of influence on returns were not summarized.

Hatchery brood year returns or escapements were summarized from federal, state, and tribal escapement reports. Unlike coded-wire tag related release and recovery data, there currently exists no inter-agency mandate or guidelines for reporting hatchery returns; records are kept by agencies for management or research purposes and inter-agency procedures and reporting may be less consistent than for releases. Additionally, mass marking of hatchery fish has been used by the Washington State Department of Fish and Wildlife only since 1996; records prior to that time are subject to greater uncertainty as to stock origin. Hatchery escapement of adults and jacks are recorded separately on escapement reports and determined by size at return. Reported coho adults were assumed to be age 1.1 and coho jacks were assumed to be age 1.0. The greater diversity of life history patterns for Chinook resulted in more difficulty assigning hatchery returns to the correct brood year. Age composition data of returning hatchery Chinook based on scale sampling or CWT recovery was available for only a limited number of hatcheries and brood years; given the lack of consistent age data, returning hatchery Chinook were assumed to 0.4 (Baranski, 1979) and Chinook jacks, though reported, were not included in analysis. Return rates by hatchery fish (returns per release) was calculated by dividing the number of brood year releases by the number of brood year returns to the hatchery. Where more than one hatchery existed on a single river system (Appendix 1), releases and returns for both were combined. We also combined all hatchery study types (e.g., experimental, production, indicator releases). Our sensitivity analyses indicated that although return rate estimates are sensitive to the type of study groups included, the conclusions of this study are not. Like return rates of wild populations, hatchery return rates numbers were adjusted for harvest.

Data analysis

For our Sound-wide analyses, we used mixed models to examine the predictive power of hatchery stocks on wild return rates, and of environmental variables on both wild and hatchery return rates. Where possible, we entered sub-basin as a categorical fixed effect and the environmental variables as fixed covariates. Spawning population was entered as a random effect. We examined several possible covariance structures, and selected the structure that resulted in the lowest Akaike Information Criterion (AIC) values (smaller values indicate a more informative model). For Chinook salmon, the best covariance structure was an autoregressive (AR1) structure, while for coho salmon, the best structure was an autoregressive moving average (ARMA) structure. For models that included environmental variables, we tested a number of possible models that included both freshwater and nearshore components, and selected those with the lowest AIC values.

Results

Chinook salmon

Objective 1. Utility of index hatchery stocks for predicting return rates of wild stocks.

To address this objective, we compared wild Chinook salmon return rates with two datasets describing survival of hatchery stocks. Our first metric for hatcheries – hatchery returns per release – was a poor predictor of wild Chinook salmon return rates due to both high variation and an overall negative relationship (Fig 1). For particular spawning populations, the correlations of hatchery and wild return rates ranged from -0.47 to 0.58, with most positive correlations occurring in northern populations (Fig. 2). Only the Skykomish population had a strong positive correlation ($p < 0.05$). When differences among populations and basins were controlled for with a mixed model, the overall effect of hatchery stocks across Puget Sound populations showed a weak negative relationship (Table 3), indicating that hatchery stocks perform poorly as indicators of wild Chinook salmon populations.

Our second hatchery dataset comprised the Pacific Salmon Commission’s marine survival indices for Chinook salmon. We correlated wild and hatchery return rates with the appropriate survival indices based on a wild population’s natal basin in Puget Sound, and found that only 3 of 22 wild spawning populations exhibited strong ($p < 0.05$) positive correlations with a marine survival index (Table 4), and 10 of 29 correlations were negative. In general, correlations of hatchery return rates were better than correlations with wild return rates, but even so, only one hatchery population exhibited a strong positive correlation with any marine survival index.

Objective 2. Environmental correlates of return rates for hatchery index and wild stocks.

Our best model predicting wild return rates from environmental variables was composed of five predictors: a negative effect of rearing density, incubation flood recurrence interval (FRI), and three nearshore factors describing successive phases of migration from natal basin, to the nearest nonnatal basin, to the Strait of Juan de Fuca (Table 5). All variables had negative relationships with wild return rates except the nonnatal and Straits nearshore factor, and some variables

Table 3. Parameter estimates, standard errors (SE), and significance level of variables in mixed model predicting wild recruits per spawner from hatchery returns per release. (R/R).

Variable	Estimate	SE	Sig.
Intercept	-0.308	0.797	0.410
Basin			0.306
South	-0.003	0.292	
Central	0.606	0.417	
Hood	0.178	0.602	
Rosario	1.278	0.573	
Whidbey	0.864	0.340	
Hatchery R/R	-0.181	0.107	0.090

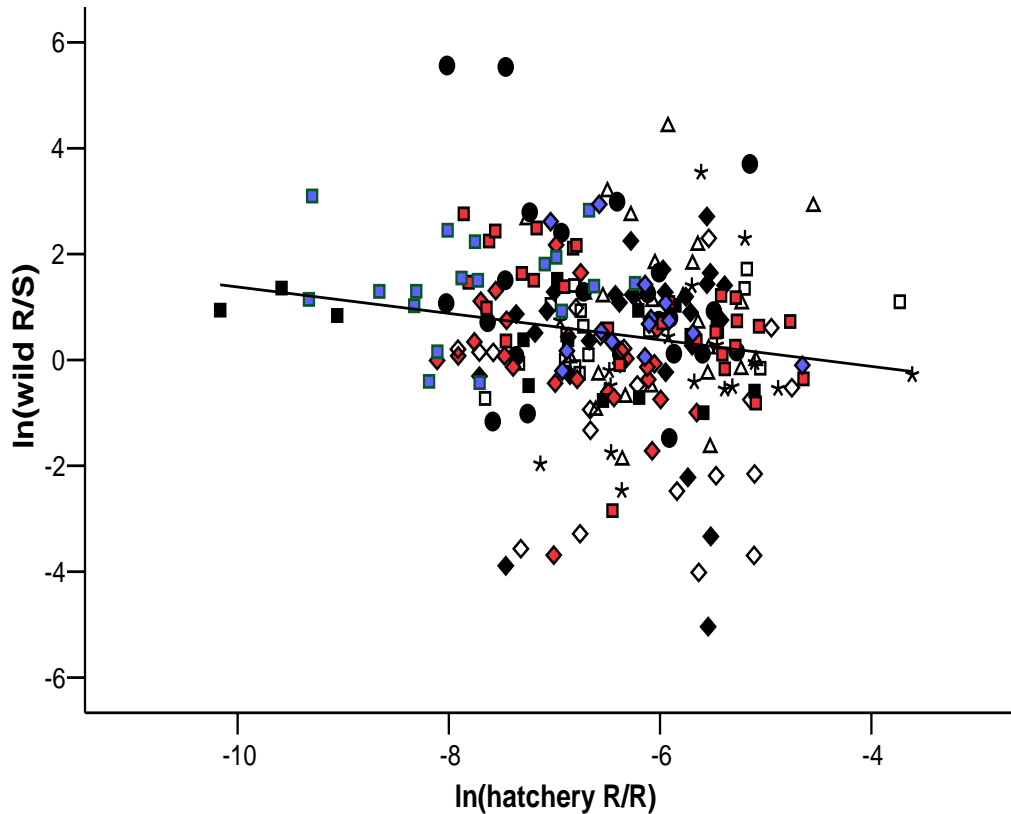


Figure 1. Correlation between wild recruits per spawner (R/S) and hatchery returns per release (R/R). Symbols represent different spawning populations, and similar shapes indicate the same basin in Puget Sound (circles: south Sound, diamonds: central basin, triangles: Hood Canal, squares: Whidbey basin, and stars: Rosario basin)

seemed particularly important for a subset of the populations. For example, the correlation of FRI with wild return rate appears particularly strong for populations in the Whidbey Basin and the Olympic Peninsula, but much less so elsewhere (Fig. 3). Overall, the model explained 25.5% of the variation in wild return rates, a nine-fold improvement in predictive power over hatchery survival metrics.

When we applied this model to hatchery return rates, we found differences with the model for wild returns in the strength and/or sign of most of the environmental variables examined. Some of these are not surprising given that hatchery-reared fish do not experience natural conditions for a large part of their freshwater life stages. Hence, FRI was a strong predictor for wild populations, but did not strongly predict hatchery returns per release. However, unlike wild stocks, hatchery stocks showed no strong relationships with the natal and nonnatal nearshore factors (although the signs of the relationships were the same), and while both showed a strong relationship with the Straits nearshore factor, the direction of the relationship was completely opposite for wild and hatchery returns (Table 5). Both populations exhibited negative effects of wild rearing density, implying that competition occurs in nearshore waters. In total, these variables explained approximately 16% of the variation in hatchery returns per release.

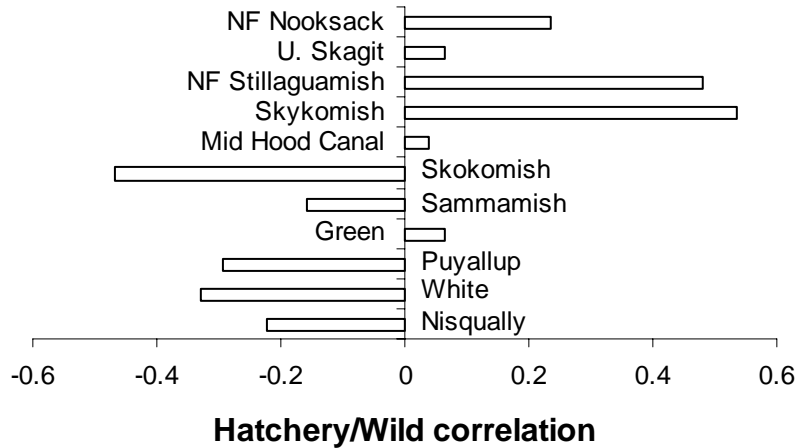


Figure 2. Pearson correlations between hatchery and wild return rates for different populations of Puget Sound Chinook salmon.

Table 4. Pearson correlations of wild and hatchery populations with Pacific Salmon Commission (PSC) survival indices (PSC is summer/fall, PSC Sp. is spring). Strong correlations ($p < 0.05$) are in boldface.

Population	Wild		Hatchery	
	PSC	PSC Sp.	PSC	PSC Sp.
Nisqually	-0.002		0.135	
White	-0.167	0.238	0.587	-0.446
Puyallup	0.016		0.163	
Green	-0.004		0.210	
Cedar	0.208			
Sammamish	-0.038		0.296	
Skokomish	0.227		0.462	
Mid Hood Canal	-0.024		0.087	
Dungeness	-0.111	0.484		
Elwha NOR	0.152			
Snoqualmie	0.178			
Skykomish	0.282		-0.216	
SF Stillaguamish	0.268			
NF Stillaguamish	0.431		-0.133	
U. Sauk	-0.239	0.236		
L. Sauk	0.234			
Suiattle	-0.303	-0.076		
L. Skagit	0.184			
U. Skagit	0.008		0.169	
U. Cascade	0.009	0.432		
SF Nooksack	0.032	0.229		
NF Nooksack	0.136	-0.284	-0.319	0.103

Table 5. Parameter estimates, standard error (SE), and significance level of variables used in mixed models for wild recruits per spawner and hatchery returns per release. FRI = incubation flood recurrence interval. Boldface shows strong effects ($p < 0.05$).

Parameter	Wild Log _e (Recruits/Spawner)			Hatchery Log _e (Returns/Release)		
	Estimate	SE	Sig.	Estimate	SE	Sig.
Intercept	0.566	0.233	0.024	-6.545	0.176	<0.001
Rearing density	-0.600	0.058	<0.001	-0.103	0.050	0.043
FRI	-0.099	0.039	0.013	0.005	0.033	0.870
Natal nearshore factor 2	-0.565	0.566	<0.001	-0.043	0.124	0.730
Nonnatal nearshore factor 2	0.454	-0.600	<0.001	0.145	0.109	0.186
Straits nearshore factor 1	0.398	-0.099	<0.001	-0.289	0.089	0.002

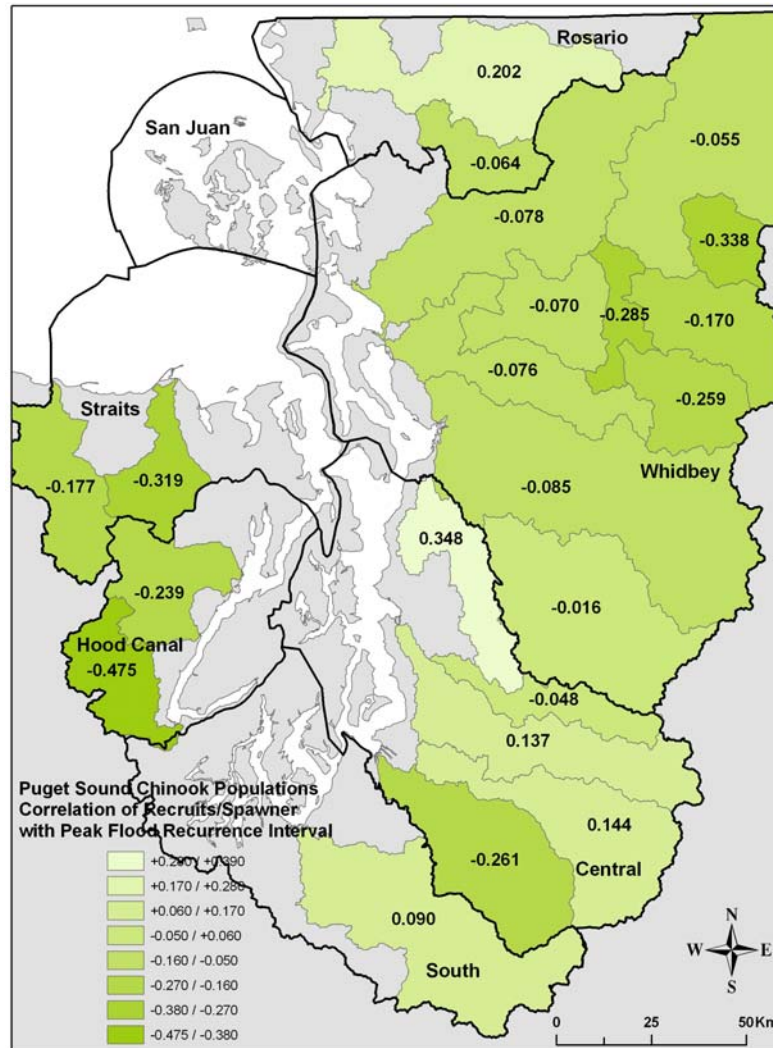


Figure 3. Population-specific correlations of Chinook salmon recruits per spawner data with incubation flood recurrence interval.

Coho salmon

Objective 1. Utility of index hatchery stocks for predicting return rates of wild stocks.

For coho salmon, the utility of index hatchery stocks for predicting wild return rates (Fig 4) was not much more informative than for Chinook salmon. For particular spawning populations, the correlations of hatchery and wild return rates ranged from -0.45 to 0.58. Only two populations – Lake Washington and Puyallup River – had strong correlations ($p < 0.05$, Fig. 5) between hatchery and wild return rates. When differences among populations and basins were controlled for with a mixed model, the overall effect of hatchery stocks across Puget Sound populations showed a weak positive effect (Table 6). The proportion of variation explained by this model (R^2) was 0.059, indicating that hatchery index stocks predict a little over 5% of the variation in wild return rates across all coho salmon stocks. These findings strongly indicate that returns of index stocks are relatively poor predictors of wild returns.

Objective 2. Environmental correlates of return rates for hatchery index and wild stocks.

Our best model of environmental correlates for wild coho salmon populations was a mixed model that included population as a random effect, an autoregressive moving average (ARMA) covariance structure, and five predictors: Puget Sound basin, rearing density, FRI, average annual discharge, and natal nearshore factor (Table 7). With the exception of the nearshore factor, all the effects of predictors upon wild return rate were significantly different from 0. Freshwater variables revealed predictable patterns: a positive effect of average discharge but a negative effect of FRI. However, we also found an extremely strong *positive* effect of rearing density upon return rate. This would not be expected either from the calculation of return rate (rearing density is derived from spawner escapement, so the overall effect of density should be negative), or from previous literature that has focused on competition for space by juvenile coho salmon. The effect of rearing density was by far the strongest of all factors in the model, and was consistent in all populations examined. Despite the strong predictive power of this and the other environmental variables, the overall model explained just 43% of the variation in wild return rates, indicating room for improvement as a predictive tool. Even so, this model was roughly seven times more predictive than a model based solely on index hatchery stocks.

Table 6. Parameter estimates, standard errors (SE), and significance level of variables in mixed model predicting wild recruits per spawner from hatchery returns per release. (R/R).

Variable	Estimate	SE	Sig.
Intercept	0.756	0.327	0.022
Basin			0.095
South	0.867	0.229	
Central	0.177	0.179	
Hood	0.542	0.227	
Rosario	0.763	0.314	
Whidbey	0.221	0.181	
Hatchery R/R	0.117	0.063	0.067

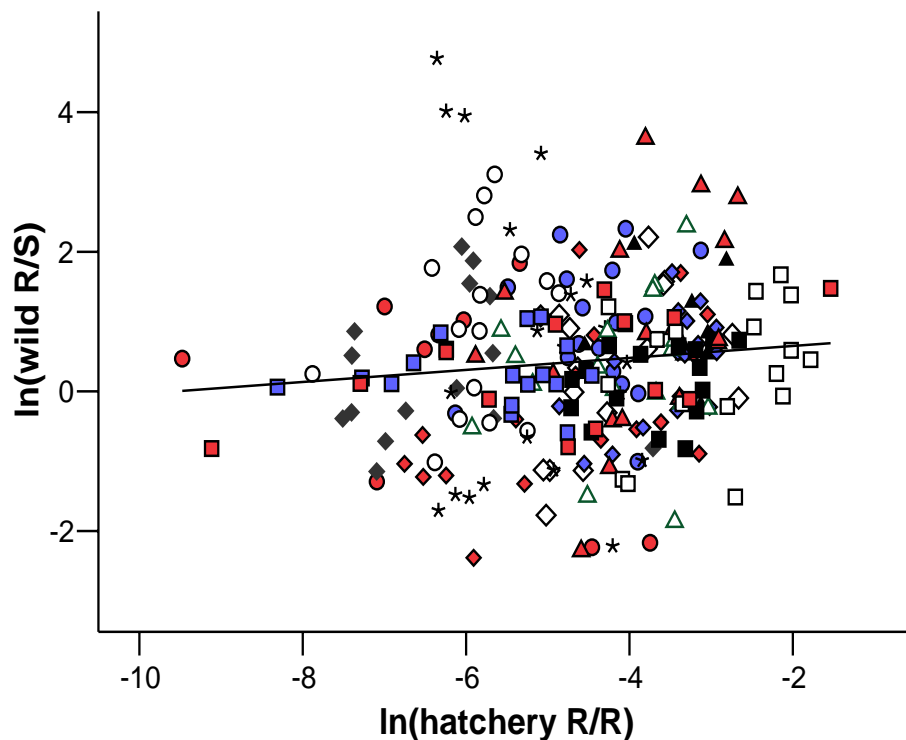


Figure 4. Pearson correlations between wild recruits per spawner (R/S) and hatchery returns per release (R/R). Symbols represent different spawning populations, and similar shapes indicate the same basin in Puget Sound (circles: south Sound, diamonds: central basin, triangles: Hood Canal, squares: Whidbey basin, and stars: Rosario basin)

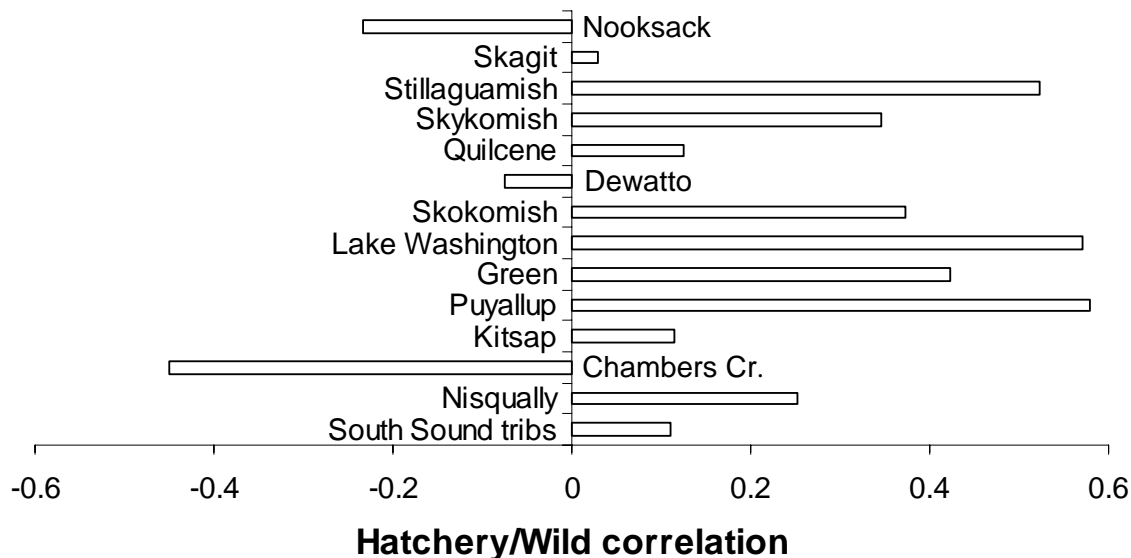


Figure 5. Strength of correlation between hatchery and wild return rates for different populations of Puget Sound coho salmon.

When we applied this model to hatchery stocks, we found that differences among most of the variables in the strength and/or sign of most of the environmental variables examined. Some of these are not surprising given that hatchery-reared fish do not experience natural conditions for a large part of their freshwater life stages. Hence, while freshwater variables strongly predicted wild return rates, they did not strongly predict hatchery returns per release. Other differences were more surprising. Strong differences existed in wild return rates among the basins of Puget Sound, but not for hatchery return rates, and the ordering of basins was different. In addition, hatchery but not wild stocks showed a strong relationship with the natal nearshore factor, and the influence of this factor was positive for wild fish but negative for hatchery fish. The only variable that maintained a consistent effect was wild rearing density: this was positive for both wild and hatchery fish. The variables explained approximately 56% of the variation in hatchery returns per release.

Conclusions

While hatcheries can function for a number of purposes, including production of harvestable fish and supplementation of poorly performing wild stocks, a basic role most hatcheries play is to provide information on harvest rates. The validity of this “indicator” role of hatchery stocks depends upon the assumption that hatchery and wild stocks behave similarly during their migrations. However, several fundamental differences between hatchery and wild stocks challenge this assumption: 1) releases of hatchery stocks are intentionally delayed to reduce impacts of freshwater environmental variation, 2) hatchery fish are raised to a relatively large size before being released, thereby insuring a rapid outmigration, 3) hatchery fish are generally released at one time within a river, while wild stocks migrate downstream over a longer time period. While we could not isolate which of these issues is most important for improving hatchery stocks as indicators, we could examine the fundamental issue directly: are hatchery stocks good indicators, and are environmental correlates better predictors than the indicator stocks themselves?

Table 7. Parameter estimates, standard error (SE), and significance level of variables used in mixed models for wild recruits per spawner and hatchery returns per release. FRI = incubation flood recurrence interval. Boldface shows strong effects ($p < 0.05$).

Parameter	Wild			Hatchery		
	Log _e (Recruits/Spawner)			Log _e (Returns/Release)		
	Estimate	SE	Sig.	Estimate	SE	Sig.
Intercept	-8.188	1.157	<0.001	-5.893	1.774	<0.001
Basin			0.008			0.469
South	1.110	0.443		-4.841	.563	
Central	0.748	0.370		-3.801	.664	
Hood	-0.004	0.301		-4.156	1.162	
Whidbey	-0.314	0.345		-5.506	.654	
Rosario	2.549	0.646		-4.388	.570	
Rearing density	0.573	0.042	<0.001	0.149	0.061	0.015
FRI	-0.141	0.036	<0.001	-0.045	0.054	0.400
Avg discharge	0.688	0.227	0.003	0.080	0.354	0.823
Natal nearshore factor 1	0.080	0.093	0.387	-0.227	0.098	0.025

Our analyses indicated that for both Chinook and coho salmon, return rates (returns per release) of hatchery stocks were poor predictors of return rates of wild stocks, and that environmental indicators show much greater promise of predicting returns of wild stocks than hatchery stock data. These results suggest that large differences in biological responses to environmental conditions experienced during juvenile stages confound the covariation of returns of hatchery and wild stocks. A remaining question concerns whether adult stages of hatchery and wild stocks are sufficiently similar that hatchery data adequately represent wild stocks. For example, estimates of harvest rates determined from coded wire tag expansions might be validly applied to adult wild salmon if these expansions did not depend upon natural juvenile mortality described by our environmental correlates. Because harvest rate estimates derived from coded-wire tags can rely on assumptions about mortality at other stages, we believe this question deserves careful examination.

Effects of rearing density

Our results shed some interesting light on patterns of density dependence across Puget Sound. On one hand, we would expect from theory that populations compete with each other in habitats that are limiting (Greene and Beechie 2004). On the other hand, both Chinook salmon and coho salmon are now at low abundances than they were historically, reducing the potential for negative density-dependent interactions and increasing the likelihood of Allee effects at low densities (Greene 2008, Greene and Guilbault 2008). We found evidence that negative density dependence influences Chinook salmon and that Allee effects influence coho salmon across most wild populations in Puget Sound, as well as for many hatchery stocks. The results for Chinook salmon corroborate previous analyses (Greene et al. 2005) and suggest that density dependence often occurs in estuarine environments where many juvenile Chinook salmon rear, as well as nearshore environments where Chinook salmon are most likely to interact with hatchery stocks. The different effects we found of nearshore environmental correlates on wild and hatchery fish might reflect to some degree where juvenile fish of different sizes are most likely experiencing density dependence. The strongest environmental correlates of wild return rates were those associated with natal nearshore environments, while the only strong correlate of hatchery return rates was with environmental conditions in the Strait of Juan de Fuca.

Our findings of strong positive effects of rearing density upon most stocks of wild coho salmon are surprising given that much literature has focused on competitive aspects of juvenile rearing and adult spawning in coho salmon (Gross 1985, van den Berghe and Gross 1989, Grant and Kramer 1990, Sabo and Pauley 1997). Assuming our findings are not spurious relationships, these results are interesting from a biological standpoint because they suggest that benefits to coho salmon from marine derived nutrients (Reichert et al. 2008) or benefits from migrating in groups may trump density-dependent effects of territoriality so well documented in other populations of coho salmon (Grant and Kramer 1990). These findings are also worrisome in that populations subject to demographically-detectable Allee effects are often at an elevated risk of collapse (Dennis 1989, Greene 2008).

Effects of freshwater conditions

We found effects on wild return rates of freshwater conditions in both wild Chinook and coho salmon populations. Return rates of both species were negatively correlated with incubation flood recurrence interval (FRI), and return rates of coho salmon positively correlated with mean discharge during the first year of rearing. These findings make sense biologically, and are bolstered in part by the absence of these effects in hatchery stocks, which are not exposed to these conditions. From a

management standpoint, these patterns are important in that both FRI and average discharge can be directly influenced by human activities and have been predicted to change in negative ways as a consequence of climate change (Mantua et al. 2009). Hence our findings may be useful in predicting long term hydrographic changes on salmon stocks.

Effects of nearshore conditions

We also found evidence that conditions experienced by juvenile salmon in the nearshore influence return rates. A priori, we would predict that fish that enter as smaller individuals and hence rear for longer time periods would be more sensitive to nearshore variation than larger fish, and this finding was largely born out in our analysis of Chinook salmon. We found strong correlations of nearshore predictors for wild stocks, as opposed to a single correlation with one parameter in hatchery stocks. However, this same pattern did not hold for coho salmon. Hatchery individuals are generally larger than wild individuals, but only hatchery stocks showed an effect of nearshore conditions. These findings deserve more analysis in terms of determining what aspects of the nearshore environment (e.g., abiotic conditions like temperature and salinity, biotic conditions like food availability) most strongly affect these species.

Limitations and Future Directions

Our findings may depend to varying degrees on several data limitations. First, our analyses depend upon the quality of biological data for both wild and hatchery populations. Wild population estimates based on adult counts are often criticized for their variation and low accuracy. This problem could confound some of our conclusions, particularly for coho salmon which often spawn during the fall and winter rainy season. In addition, we have found some discrepancies in return rate estimates using Chinook salmon run reconstructions by the Technical Recovery Team (TRT) and simpler reconstructions developed for seven populations in the Whidbey Basin. The primary difference in the two sets of reconstructions is that the TRT outputs have formalized corrections for influence of hatchery fish on spawning grounds, while the simpler reconstructions do not. However, both sets of estimates are correlated with each other, so the estimates we used for Chinook salmon are probably not seriously compromised. Similar problems exist with the returns per release data for hatchery stocks: estimates of returns are complicated by straying, and data quality for returns of released can vary across hatcheries. In particular, we found fairly strongly relationships between the correlation of hatchery and wild returns and the percentage of hatchery study types designated as production or experimental releases or a combination. Nevertheless, we made extensive efforts to check data quality, and we believe our conclusions will stand up despite some uncertainty in the biological data.

Our models examining effects of environmental variables have other limitations. One of our biggest challenges was that freshwater and nearshore data were much easier to collect than data in estuaries, where spatially comprehensive data collection efforts are absent. As a consequence we dropped estuary environmental data from our analysis. In addition, time series of both environmental and biological data are relatively short, and correlations between the two datasets are subject to the variability exhibited in this time period. Even so, we still found some strong correlations that bear merit for future analysis. Of course, it can be difficult to make strong conclusions about correlations between environmental data and adult return rates, simply because these correlations may not reflect causal relationships, and may be indicators of causal relationships with other variables. We hope our

findings can help guide more direct studies on how freshwater or nearshore data affect juvenile fish, and note that outmigrant trapping data are invaluable for both detecting freshwater effects on juvenile stages and for calibrating population sizes in subsequent stages. However, even if the correlations we detected are not causal, they can still be valuable as indicators of productivity and be useful forecasting tools. Our findings support the argument that environmental correlates can be fairly good indicators to forecast salmon returns. In the future, we will focus on improving the predictive power by selecting indicators for other life stages, and evaluating better indicators during juvenile stages.

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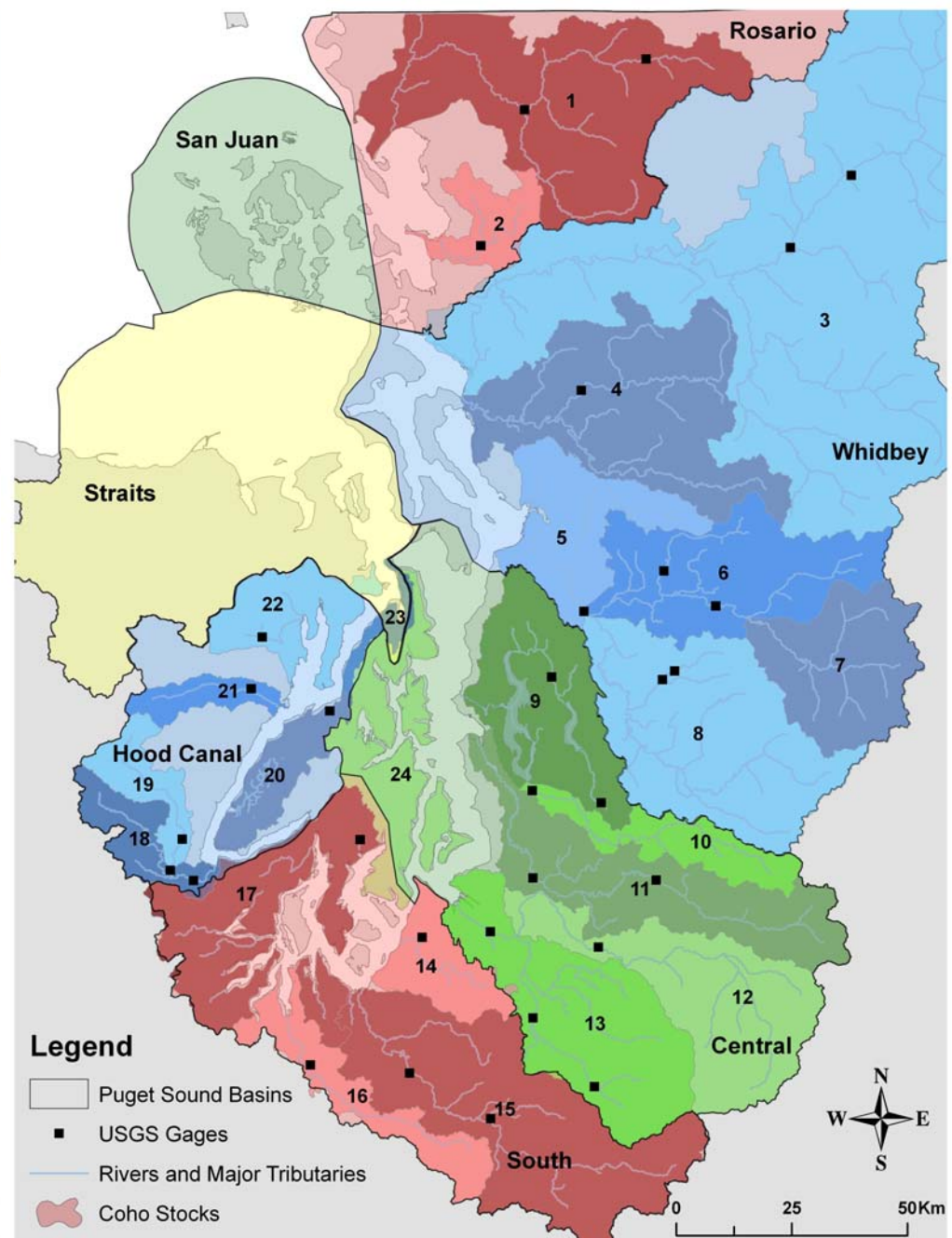
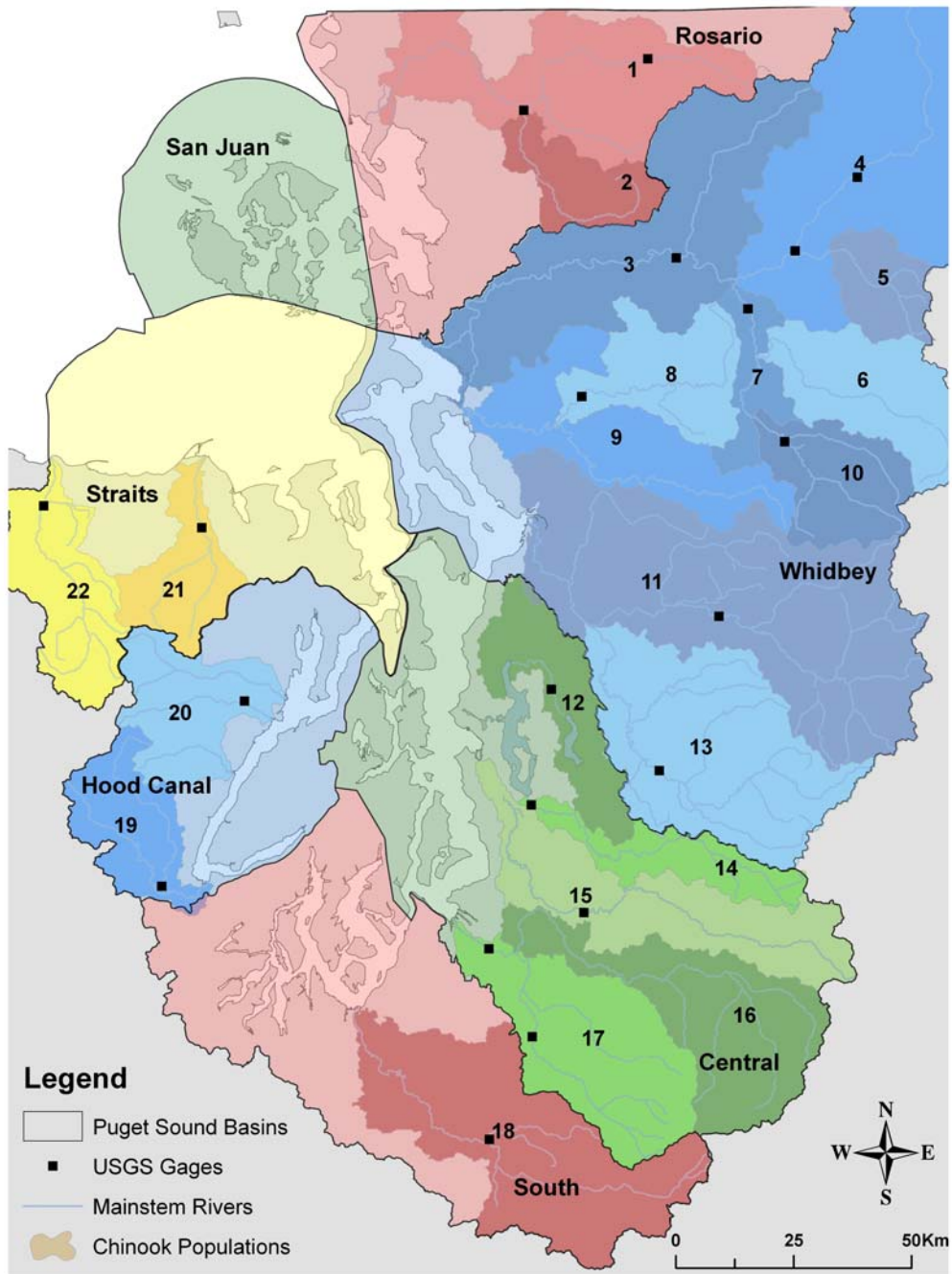
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Appendix 1a. Puget Sound Chinook (left) and coho (right) populations across seven sub-basin of the Puget Sound region. Map numbers reference populations listed in Appendix 1b. Locations of USGS gages used in analysis are shown.

Appendix 1b. Biological data used in the analyses.

Map ID	Population	First Brood Year	Last Brood Year	Brood Years in Analysis	Escapement Estimate Method *	PFMC Harvest Rate for r/s (Basin) **	Associated Hatchery Run(s)
<i>Chinook</i>							
14	Cedar	1973	2002	30	Live Spawner	Stillaguamish-Snohomish	
21	Dungeness	1986	2002	17	Redd Count	Strait of Juan de Fuca	
22	Elwha	1986	2002	17	Redd Count	Strait of Juan de Fuca	
15	Green	1973	2000	28	Redd Count	Stillaguamish-Snohomish	Soos Creek, Keta Creek
7	Lower Sauk	1973	2000	28	Redd Count	Skagit	
3	Lower Skagit	1973	2002	30	Redd Count	Skagit	
20	Mid Hood Canal	1974	2002	29	Live Spawner + Redd	Hood Canal	Hoodsport
18	Nisqually	1978	2002	25	Redd Count	South Puget Sound	Kalama Creek, Clear Creek
1	North Fork Nooksack	1984	1998	15	Redd Count	Nooksack-Samish	Kendall Creek, Lummi Sea Ponds
8	North Fork Stillaguamish	1974	2000	27	Redd Count	Stillaguamish-Snohomish	
17	Puyallup	1973	2002	30	Exp. Redd Count	Stillaguamish-Snohomish	Voights Creek, Diru Creek
12	Sammamish	1983	2000	18	Escapement Est (Live)	Stillaguamish-Snohomish	Issaquah Creek
19	Skokomish	1987	2001	15	Live Spawner + Redd	Hood Canal	George Adams
11	Skykomish	1973	2002	30	Redd Count + Trap	Stillaguamish-Snohomish	Wallace River
13	Snoqualmie	1973	2002	30	Redd Count	Stillaguamish-Snohomish	
2	South Fork Nooksack	1984	2000	17	Redd Count	Nooksack-Samish	Skookum Creek
9	South Fork Stillaguamish	1974	2000	27	Redd Count	Stillaguamish-Snohomish	
6	Suiattle	1973	2002	30	Exp. Redd Count	Skagit	
5	Upper Cascade	1981	2000	20	Exp. Redd Count	Skagit	
10	Upper Sauk	1973	2000	28	Exp. Redd Count	Skagit	
4	Upper Skagit	1973	2000	28	Redd Count	Skagit	Marblemount
16	White	1973	2000	28	Trap	Stillaguamish-Snohomish	White River
<i>Coho</i>							
10	Cedar	1986	2003	18	CFD	Stillaguamish-Snohomish	
14	Chambers Creek	1986	2003	18	Rack Passage	South Puget Sound	
17	Deep South Sound Tribs	1986	2003	18	CFD	South Puget Sound	Minter Creek
16	Deschutes	1987	2003	16	Trap	South Puget Sound	
20	Dewatto	1986	2003	18	CFD	Hood Canal	
21	Duckabush	1986	2003	12	CFD	Hood Canal	
24	East Kitsap	1986	2002	17	CFD	Hood Canal	Grovers Creek, Cowling Creek
11	Green River	1986	2003	18	CFD	Stillaguamish-Snohomish	Soos Creek, Keta Creek
9	Lake Washington	1986	2003	17	CFD	Stillaguamish-Snohomish	Issaquah Creek
15	Nisqually	1986	2003	18	CFD	South Puget Sound	Kalama and Clear Creek

1	Nooksack	1976	2003	24	Spawner survey	Nooksack-Samish	Kendall Creek, Lummi Ponds
19	North Fork Skokomish	1991	2003	13	CFD	Hood Canal	
23	Northeast Hood Canal	1986	2003	18	Escapement Est. (Trap)	Hood Canal	
13	Puyallup	1986	2003	18	CFD	Stillaguamish-Snohomish	Voights Creek, Diru Creek
22	Quilcene/Dabob Bays	1986	2003	11	Escapement Est. (Redd)	Hood Canal	Quilcene NFH
2	Samish †	1996	2002	7	Escapement Est. (Rack)	Nooksack-Samish	Samish
3	Skagit	1986	2003	18	CFD	Skagit	Marblemount
18	Skokomish Tributaries	1986	2003	18	CFD	Hood Canal	George Adams
6	Skykomish	1986	2003	18	CFD	Stillaguamish-Snohomish	Wallace River Hatchery
5	Snohomish	1986	2003	18	CFD	Stillaguamish-Snohomish	Bernai Kai Kai Gobin
8	Snoqualmie	1986	2003	18	CFD	Stillaguamish-Snohomish	
7	South Fork Skykomish	1986	2003	18	Trap	Stillaguamish-Snohomish	
4	Stillaguamish	1986	2003	18	CFD	Stillaguamish-Snohomish	Stillaguamish
12	White River	1986	2003	18	Trap	Stillaguamish-Snohomish	

CFD = Cumulative Fish Days

**Basin-scale harvest rates determined by Pacific Fishery Marine Count

†Not included in analysis due to small number of years of complete data

Appendix 2. Financial Statement of Expenditures

Below is a summary of our proposed and final expenditures for the project. By and large, we followed our planned budget. The principal differences occurred in our subcontracts and capital costs. We decided to hire two technicians and employ them for a longer period of time rather than a postdoctoral researcher and a technician for a shorter period of time. This difference worked out well, and resulted in a net savings for that component of the budget. The second major difference was in capital expenditures. This difference occurred due to a need for additional software and a replacement computer that failed during the time of this project. Due to savings in subcontracts and travel, we were easily able to adjust for this difference. The final difference was the increased in-kind costs by the PI, which was necessary to help with training of technicians.

Budget	Proposed		Actual	
	In-kind	PSC	In-kind	PSC
Labor				
Wages and salaries	17,280	17,280	22,480	17,292
Subcontractors				
Postdoc		65,000		0
Technicians (2)		8,976		68,891
Site/Project costs				
Travel		2,000		0
Capital costs	8,000	2,000	8,000	8,565
Total overhead	22,304	22,304	29,016	22,812
Total	47,584	117,560	59,496	117,560

This budget accurately reflects expenses incurred during the course of this project.


 Cindy Masada, Environmental Conservation Division Coordinator

07/18/2009
 Date