Abundance, survival, and life history strategies of juvenile migrant Chinook in the Skagit River, Washington

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Abstract—This study evaluates variables that influence the abundance and diversity of juvenile migrant Chinook from the Skagit River, Washington. Skagit Chinook have at least three freshwater rearing strategies distinguished by the length of time in freshwater – sub-yearling fry, sub-yearling parr, and yearling smolts. We test whether the relationship between spawners and juveniles are best explained by a linear (density-independent survival) or nonlinear (density-dependent survival) model and whether several measures of incubation flow improve models fit to these data. We also test whether each freshwater rearing strategy is a density dependent function of total juvenile abundance. On average, 3.5 million juvenile Chinook emigrate each year with egg-to-migrant survival ranging between 4.5% and 21.5%. Juvenile abundance was best explained by a logarithmic model that included egg deposition and peak incubation flows as explanatory variables. Sub-yearling Chinook represented 96.3 to 99.9% of the migrants. Fry migrants ranged between 34.0 to 84.8% of all sub-yearling migrants and were a positive function of total juvenile abundance. Increased rearing capacity and adequate escapements are needed to maximize the number of juvenile migrants with extended freshwater residency periods. The relative importance of freshwater residency on overall stock productivity will require further study.

In the last decade, salmonid species across the Pacific Northwest have been increasingly protected under the Endangered Species Act. Their protected status reflects the scale of impact and the urgency to identify and implement actions that will rebuild abundance and diversity of existing stocks. In order to successfully rebuild stocks, one must identify bottlenecks to productivity (i.e., spawner per spawner), determine which bottlenecks can be improved through conservation actions, and implement actions of sufficient scale to cause a desired population response. Identifying such bottlenecks is challenging due to the complex life histories and diverse habitat use of salmonid species.

Density-dependence can be a bottleneck to stock productivity even when stock status is depressed (Achord et al. 2003; Copeland and Venditti 2009). Density-dependent responses are evident when fish abundances approach the existing capacity of freshwater habitat for spawning and rearing. Density-dependence can be expressed as changes in per-capita survival or in per-capita migration (Greene and Beechie 2004). Density-dependent survival in freshwater will directly limit overall stock productivity. However, density-dependent migration from freshwater may or may not limit stock productivity depending on survival of migrants in estuary and marine habitats.

Density-independent factors may also impact freshwater survival, irrespective of the number of eggs in the gravel. At least two types of flow impacts may decrease survival during incubation – peak flows and hydraulic work. Peak flow events scour the stream bed to the depth of the egg pocket and remove or damage developing eggs (Holtby and Healey 1986, Montgomery et al. 1996, DeVries 1997). The magnitude of peak flow events determines the area of stream bed that is scoured and filled (LaPointe et al. 2000) and is expected to decrease egg-to-migrant survival proportionately. Hydraulic work is the amount of sediment transported and is the product of the rate of transport at a given flow and the frequency of that flow (Wolman and Miller 1959). Although hydraulic work on a river bed may not mobilize substrate to the depth of the egg pocket, the transport of sediment into redd locations is expected to reduce survival during the intra-gravel life stages (egg or alevin; LaPointe et al. 2000; Lisle 1989). The sediment transport effects may be considerably more frequent than scour effects because maximum sediment transport often occurs at moderate flows (1 or 2 year recurring interval).

The current study is focused on the factors limiting the number of juvenile migrant Chinook in the Skagit River, Washington. The Skagit River is the largest watershed by drainage area in Puget Sound and includes six recognized stocks of Chinook salmon (SRSC and WDFW 2005). Freshwater residency is diverse with respect to timing and duration for both adult and juvenile Chinook. Adults spawn between late July and October and produce juveniles that emigrate between January and August. Juvenile migrants are predominantly sub-yearlings, although some yearlings are observed each year (Kinsel et al. 2008; Seiler et al. 1998). Migration of sub-yearling Chinook is bimodal. Early fry migrants are small and recently emerged (< 45-mm fork length, FL); late parr migrants are large and have reared in freshwater prior to outmigration (50-100 mm FL).

Population models based on spawner-to-spawner recruitment of Skagit Chinook indicate that survival is primarily limited at four life stages – egg deposition, incubation, bay residency, and ocean-age 3 (Greene et al. 2005). This study focuses on the first two of these life stages and examines density-dependent and density-independent mechanisms in freshwater. If the survival of juvenile migrants is limited by egg deposition (i.e., density-dependent survival), we expect that the spawner-juvenile relationship will be better explained by a nonlinear than a linear function. If egg-to-migrant survival is influenced by peak flows or hydraulic work, we expect that the data will be best explained by adding one or more environmental parameters to the spawner-juvenile relationship. If density-independent survival is regionally specific to stock and sub-basin, we expected that the data would be best explained by stock-specific environmental parameters rather than a basin-wide metric.

This study also examined whether freshwater rearing strategies are a density-dependent function of total juvenile abundance. The number of juvenile migrants was partitioned by life history strategy and the proportion of juvenile migrants at a specific life stage was evaluated with respect to total juvenile abundance. If the expression of freshwater rearing strategies is density-dependent, we expected that this proportion will change as a function of total abundance.

Methods

Study Area.—The Skagit River basin includes 3,100 square miles (8,030 square kilometers) of watershed area and 80,728 acres (32,670 hectares) of delta (SRSC and WDFW 2005). The freshwater system includes the main stem and four secondary basins – Baker, Cascade, Sauk, and Suiattle (Figure 1). Peak flows typically occur twice per year. Rain–on-snow events occur between November and February and snow-melt events occur in May and June. A portion of downstream flow has been regulated by hydroelectric dams on Baker River and Skagit River since the 1920s. Hatchery production of tagged Chinook salmon (~750,000/year) is used to measure fisheries exploitation and marine survival. Tagging of all hatchery releases began in 1994 and allows wild and hatchery fish to be differentiated upon capture.

Study Species.—Skagit Chinook spawn between late July and mid-October and include six spawning stocks distinguished by time of river entry and location of spawning (SRSC and WDFW 2005). At least four life history strategies exist for juvenile Chinook in the Skagit River – fry migrants, delta rearing migrants, parr migrants, and yearling migrants (Beamer et al. 2000;

Hayman et al. 1996). Both fry and delta migrants leave freshwater as newly emerged fry and will be referred to as a single group (i.e., "fry migrants") in this manuscript. Fry migrants are assumed to undergo little, if any, rearing in freshwater as their size range is comparable with the lengths of emerging juvenile Chinook (40 to 50-mm FL; Pflug and Mobrand 1989). In comparison, "parr migrants" emerge from egg pockets and rear for several months before migrating to the saltwater at an average size of 75-mm FL (Kinsel et al. 2008; Seiler et al. 1998). Yearling migrants have the longest freshwater rearing period of all juvenile migrants and overwinter in freshwater prior to outmigration. Available scale, otolith, and genetic data suggest that each of the life history strategies are present in each of the six parent stocks (SRSC and WDFW 2005).

Potential Egg Deposition.─Potential egg deposition (*PED*) was based on the female spawner abundance, female body length, and female fecundity. Abundance of Chinook female spawners was derived from surveys on the Skagit River conducted annually by state and tribal biologists. Surveyors enumerate redds and collect biological data from spawners in selected reaches of the river using both ground and aerial surveys. Observed redds are expanded by the ratio of total spawning area to surveyed spawning area (Connor and Pflug 2004; Greene et al. 2005). For each stock, female abundance was the total number of expanded redds (Brett Barkdull, WDFW–Region 4, personal communication).

Length was the average length of female Chinook recovered from spawner surveys each year. For years when less than 10 females were measured for a given stock, length was estimated from an average for all years. Fecundity was predicted from the average length for each stock year. Fecundity-length regressions were derived from Chinook brood stock collected at the WDFW Marblemount Hatchery, which rears spring, summer, and fall-run Chinook. An

ANCOVA model tested whether fecundity was a function of length (covariate) and brood stock. Average fecundity for a given stock and year was estimated based on the selected fecundity-length regression model and the average female length for that stock and year.

PED for each brood year (*i*) was calculated separately for each spawning stock (*s*) and then summed across stocks for a basin-wide estimate. PED was the average fecundity (*F)* multiplied by the female abundance (*A*):

$$(1)\ PED_i = \sum_{s=1}^{s=6} \hat{F}_{is} * \hat{A}_{is}$$

Stream Flow—Stream flow data from five USGS stream gages throughout the Skagit watershed were selected to represent the river flows experienced by the six Skagit Chinook stocks during their corresponding egg incubation period (Table 1, Figure 1). Two of the six stocks, Upper Cascade Springs and Suiattle Springs, do not have a continuous record of stream flow within their spawning area. Therefore, we used results from the Newhalem Creek gage as a surrogate to represent flow conditions for both stocks. This selection was based on the similar hydrograph shape for Chinook spawning areas in these sub basins (Beechie 1992). For example, spawning of Suiattle Springs is known from clear water tributaries which are more similar in size and hydrology to Newhalem Creek than to the main stem Suiattle. Flow data from the Skagit River gage located near Mount Vernon was selected to represent the basin-wide metric because this gage is located downstream of all Chinook spawning.

The incubation period for each stock was defined by the period between Chinook redd deposition each year and the date by which the majority of the population has completed its intra-gravel life stages (egg, alevin). Incubation periods were defined based on results from ongoing spawner surveys and Chinook fry emergence timing assessments. In 1997 and 1998, fry emergence assessments were conducted within the spawning ranges of each Chinook stock using backpack electrofishing methods (SRSC unpublished data).

Peak flows for each brood year were represented by the maximum daily average flow for the stream gage during the incubation period (Table 1). Hydraulic work was represented by the frequency (i.e., proportion) of days within the incubation period that maximum daily flows exceeded recurring flood intervals (RI) of 1 and 2 years. Data were evaluated with respect to both recurring intervals because the flows necessary to move bed load vary among watersheds (Nash 1994; Wolman and Miller 1959) and were not specifically known for the Skagit basin. Flood recurrence intervals were calculated using the annual maximum daily discharge (1954 to 2010) fitted to a log-III Pearson return intervals that included regional skew values (Interagency_Advisory_Committee_on_Water_Data 1982).

Juvenile Fish Collection.─The juvenile trap was located at river mile 17 on the Skagit River (Figure 1). Operation between 1994 and 1996 averaged 97 days per year and reflected the study focus on coho salmon during these years. Beginning in 1997, the trapping season was extended in order to evaluate juvenile Chinook. Between 1997 and 2009, the juvenile trap operated an average of 199 days per year. Two traps were positioned side-by-side on steel pontoon barges and anchored to an upstream railway trestle (Figure 2). The first trap was a 6-foot wide inclined-plane trap that screens a 21-ft^2 rectangular area in cross section (Seiler et al. 1998). The second trap was an 8-foot diameter screw trap that screens a 25-ft^2 cross-sectional area. These traps will hereafter be referred to as "the juvenile trap" because they were operated simultaneously.

The juvenile trap was operated every night and every third day. Captured fish were processed at least two times each day (dusk and dawn). Fish were identified to species and enumerated. A sub-sample of the catch was measured on a daily basis (fork length, FL). Hatchery-origin juveniles were distinguished from wild juveniles by their adipose fin clip or coded-wire tag. Data collected from the trap were divided into day and night trap periods because juvenile migration rates differ between day and night (Reimers 1971; Seiler et al. 1998). Nighttime catches were fish caught between dusk and dawn. Daytime catches were fish caught between dawn and dusk. In addition to the planned daytime trap outages, additional outages occurred due to heavy debris loads, high flows, or equipment malfunction.

Sub-samples of fish were marked and released above the trap. Fish marks included adipose clips, coded-wire tags, Bismarck brown dye (immersed in 14 ppm for 1.5 hours), and a partial caudal fin clip. Recapture rates of released fish were the measure of trap efficiency used to estimate total migrant abundance.

Sub-Yearling Migrant Abundance.—Number of sub yearling Chinook was estimated by expanding Chinook catch in the juvenile trap. The first step in this process was to estimate missed catch due to trap outages. The second step was to estimate total migration during the trapping season. The third step was to estimate migration that occurred before or after the trapping season.

Estimated missed catch ($\hat{n}_i$) for a trap outage period (i) was calculated by applying the average catch rate ($\overline{R}$) of surrounding time periods to the time (T_i) that the trap did not operate. Missed daytime catch was estimated from catch rates of adjacent day time periods. A similar approach was used for missed nighttime catch. Missed catch during the dawn or dusk hours was calculated using the immediately adjacent day and night time periods. Total catch ($\hat{u}$) was the sum of actual (n_i) and estimated missed catch.

$$(2)\quad \hat{n}_i = \overline{R} * T_i$$

$$(3)\ \hat{u} = \sum_{i=1} n_i + \sum_{i=1} \hat{n}_i$$

Migration during the trapping season was based the mark-recapture estimator appropriate for a single partial capture trap (Carlson et al. 1998; Volkhardt et al. 2007). During the outmigration period, a known number of marked fish (*M*) were released upstream of the trap and a portion of these (*m)* were recaptured in the trap. Migrant abundance ($\hat{U}$) was:

$$(4)\ \hat{U} = \frac{\hat{u}(M+1)}{(m+1)}$$

For the purpose of analysis, mark and recapture data were divided into time strata that accounted for seasonal heterogeneity in capture rates (Carlson et al. 1998; Volkhardt et al. 2007). Strata were assigned after comparing the ratio of marked fish that were subsequently seen (i.e., recaptured) or unseen (i.e., not recaptured). The ratio of seen:unseen fish was compared between efficiency trials using a *G*-test (Sokal and Rohlf 1981). If the *G*-test indicated that the ratio differed between two trials ($\alpha = 0.05$), they were considered separate time strata. If the ratio did not differ between trials, trial data were pooled and then compared to the next adjacent trial. This process was repeated until all efficiency strata were identified.

The described analysis approach has evolved over the course of the Skagit juvenile monitoring study. For example, the origin of released fish (hatchery versus wild) as well as the location and timing of releases have changed over time (Table 2). The change in trap calibration methods is problematic for the analysis of long-term data. For example, for migration year 1994 to 1997 the trap was calibrated from the recapture of hatchery Chinook released 60 to 70 miles above the trap. This release was adjusted for anticipated predation between release site and the trap (80%) and for delayed migration of hatchery fish following the completion of trap operations (80%). In addition, various methods were explored in an attempt to "recalibrate" historical data in a consistent way based on environmental variables such as river flows, turbidity, and seasonal date. Unfortunately, correlations between environmental variables and trap efficiency were weak at best. Furthermore, the preferred release and recapture design (2006 to present) occurred simultaneous with a change in river channel configuration that diverted more of the river flow towards the trap and increased average trap efficiency. As a result, the more recent efficiency data are not representative of historical conditions. Therefore, analysis of long-term data was based on the stratification approach described above applied to available data for each year. The drawback of this approach is that seasonal heterogeneity in capture rates are not represented in the earlier years of study.

Total migration was the sum of estimated migration during the trapping season and extrapolated migration before and after trapping. The assumed start and end dates of the Chinook migration were January 1 and August 31. Extrapolation was necessary because the trap typically operated between mid-January and the end of July. Linear extrapolation of pre and post trapping migration ($\hat{N}_{ext}$) was based on the average of daily migrations ($\overline{N}$) for the last (or first) five days of trapping and the number of days (t) between the end (or beginning) of trapping and the assumed end (or beginning) of the migration.

$$(5) \quad \hat{N}_{ext} = \overline{N} * \frac{t}{2}$$

The end date was selected based on extended trapping seasons conducted in four years (1997-2000). Extended trap seasons returned some catch during the month of August but minimal to no catch during the months of September and October. The January 1 start of the Chinook migration was assumed based on the observation that catch in mid-January is nearly zero in most years. The pre-season migration was calculated by linear extrapolation for 1997 to 2008 seasons when the trap season began in mid-January. For 1994 to 1996, the pre-season period was extensive (3 to 3.5 months). This data gap occurred because the target species during these years was coho salmon, which have a shorter migration period that Chinook. For these three years, pre-trapping Chinook migration was extrapolated by applying the average migration timing (1997-2008) to the missed migration periods in 1994 to 1996.

Fry and Parr Sub-Yearlings.—Migration for each statistical week (Monday through Sunday) was divided into "fry" and "parr" components. Weekly fry migration was the total migration multiplied by the proportion fry migrants. For the same period of time, parr migration was the total migration multiplied by the proportion parr migrants. "Fry" were the proportion of measured sub-yearling Chinook on a given statistical week that were less than or equal to 45-mm FL. Parr were the proportion of measured Chinook longer than 45-mm FL.

Yearling Migrant Abundance.—The abundance of yearling Chinook smolts was estimated by expanding the catch by an estimated trap efficiency. Yearling Chinook were not caught in sufficient numbers to allow for mark and release groups. Therefore, the trap was calibrated for coho smolts which are of similar body size and outmigration timing as the yearling Chinook. Coho were marked and released from tributary traps above the main stem trap and recaptured at the main stem trap throughout the season (Kinsel et al. 2008; Seiler et al. 1998). A Peterson estimate with Chapman modification was used to estimate total abundance of coho smolts (Chapman 1951; Volkhardt et al. 2007). Coho were marked continuously throughout the season and therefore stratification of these data was not necessary (Volkhardt et al. 2007). The ratio of coho abundance ($\hat{N}_{coho}$) to coho catch (n_{coho}) was used to expand the yearling Chinook catch (n_{Chin}). The abundance of yearling Chinook ($\hat{N}_{Chin}$) was:

(6) $$\hat{N}_{Chin} = n_{Chin} * \frac{\hat{N}_{coho}}{n_{coho}}$$

Analysis of Freshwater Production and Survival.—Linear and nonlinear models were used to test whether the number of juvenile migrant Chinook (i.e., freshwater production) was best explained by density-independent, density-dependent survival, or a combination of these two mechanisms. Spawner and recruit (juvenile abundance) data were fit with linear, logarithmic and second-order polynomial models. The linear model represents the hypothesis that egg-to-migrant survival rates are independent of spawner abundances whereas the logarithmic and polynomial models represent hypotheses that egg-to-migrant survival rates decrease with increasing spawner abundance. The logarithmic model represents the hypothesis that the number of juvenile migrants approaches some asymptotic level as spawner abundance increases. The second-order polynomial model represents the hypothesis that the maximum number of juvenile migrants is achieved at an intermediate level of spawner abundance.

Models were compared with and without adjustments for the peak incubation flows and hydraulic work (Table 3). Flow adjustments for a given year (i) were represented by basin-wide and stock-specific metrics. The basin-wide metric was a representation of incubation flows from a single flow gage (Table 1). The stock-specific metric was a weighted average of incubation flows from stock-specific locations. Stock-specific flows (E_j) were weighted by the relative *PED* abundance (α_{ij}) for each stock (j) and year (i).

(7) $$E_i = \sum_{j=1}^{j=6} \alpha_{ij} E_{ij}$$

Flow metrics for a given year (i) were normalized by the mean ($\overline{E}$) and standard deviation (SD) among years:

$$(8)\quad E_N = \frac{E_i - \overline{E}}{SD(E)}$$

Thirty-four different models were fit to the data using a likelihood approach (Hilborn and Mangel 1997; Hobbs and Hilborn 2006) and the Solver function in Microsoft Excel. Each model represented alternate hypotheses on how density-dependent and density-independent survival impact the number of juvenile migrant Chinook in the Skagit River and which flow metrics best explained flow-mediated impacts to survival. The best fitting model was selected using Akaike Information Criterion corrected for sample size (n) and the number of parameters (K; Burnham and Anderson 2002).

$$(9)\quad AIC_c = -2\ln[L(\hat{\theta} \mid Y)] + 2K\frac{n}{n-K-1}$$

The strength of evidence (w_r) for a given model r was compared among R models and based on the AIC_c difference (Δ_r) between a given model r and the model with the minimum AIC_c value (Burnham and Anderson 2002).

$$(10)\qquad w_r = \frac{e^{-1/2\Delta_r}}{\sum_{i=1}^{i=R} e^{-1/2\Delta_r}}$$

Analysis of Juvenile Life History Strategies.—The expression of each juvenile freshwater life history (fry, parr, yearling) was considered to be density dependent if the ratio between life history types differed as a function of total juvenile abundance. Specifically, the relative abundance of juvenile migrants at each life stage was considered with respect to all juvenile migrants. A linear regression tested whether the ratio of fry to parr and yearling migrants was a function of total juvenile abundance (fry, parr, and yearling) and whether the ratio of parr to yearling migrants was a function of total parr and yearling migrants. The linear regression was conducted using Sigma Plot software (Systat_Software_Inc. 2008). Data were tested for normality and homogeneity of variance.

Results

Spawner Abundance and Potential Egg Deposition

Escapement of Skagit River Chinook ranged between 2,158 and 10,051 females between 1993 and 2008 (Figure 3*a*). The majority (72%) of all spawners were Upper Skagit Summers (Table 4). Between 1993 and 2008, the number of female spawners increased ($F_{1,14} = 8.9$, $p = 0.01$), but the proportion represented by each stock did not change, with the exception Suiattle Springs which have become proportionately fewer over time ($F_{1,14} = 11.6$, $p = 0.004$).

Over this period, Chinook PED has averaged 32 millions eggs per year and ranged between 12 and 62 million eggs. Average female lengths from the six spawning stocks ranged from 83 to 92-cm FL (Table 4). Estimated average fecundity ranged between 4,949 and 6,218 eggs per female. Fecundity was positively correlated with length ($F_{1,702} = 370.4$, $P < 0.001$) and differed among Springs, Summers, and Falls ($F_{2,702} = 30.4$, $P < 0.001$). Therefore, fecundity of each stock was estimated using run-specific regressions ($F_{spring} = 91*adjL - 2226$, $F_{summer} = 103*adjL - 3272$, $F_{fall} = 110*adjL - 4634$). Female spawner abundance predicted nearly all the variation in potential egg deposition ($PED = 5{,}947*A$; $R^2 = 0.99$).

Flow Metrics

Among all stocks and years, the magnitude of peak flows ranged between a recurring interval of 1 and 206.7 years. The 206.7 year RI corresponded to a daily average flow of 40,000 cfs on the Upper Sauk River in 2003; all other peak flows were below a 60-year recurrence interval. Duration of the incubation period with daily flows exceeding an RI of 1 year ranged between 0%

and 44%. Duration of the incubation period with daily flows exceeding an RI of 2 years ranged between 0% and 11%.

Within each stock, incubation flow metrics (peak and duration) were highly correlated (Table 6). However, the relative values between peak and duration of incubation flows differed among stocks (Figure 4). On average, Lower Sauk Summers had the highest peak flows whereas the Upper Skagit Summers had the longest duration of incubation flows exceeding a 1-year RI.

Juvenile Migrant Production

The number of juvenile migrant Chinook in the Skagit River has averaged 3.5 million Chinook per brood year and ranged nearly 8-fold between the 1993 and 2008 brood years (Table 7). No temporal trend in juvenile production occurred over this time period (Figure 3*b*; $F_{1,14} = 0.55$, $p = 0.47$).

Potential bias of the estimate was assessed with respect to differences in the timing of release groups. The lack of time-stratified data in the earlier years of study violates the assumption that all fish samples have an equal probability of capture (Seber 1973; Volkhardt et al. 2007) because river conditions are known to change trap efficiency over the 8-month migration period. The impact of violating this assumption on the estimate was determined by comparing estimates for the 2006-2009 migration years. The same data were analyzed using stratified mark-recapture data, pooled mark-recapture data, and mark-recapture data from May and June only (the time period of releases in earliest years of study). Estimates were considered different when outside the 95% confidence interval (calculated per Carlson et al. 1998) of that produced by another method. Estimates differed among the methods in some years (Figure 5). When methods differed, pooling the mark-recapture data resulted in a biased low estimate. Pooled data from the entire season versus just the May-June time interval resulted in a different estimate for just one (2009) of the four data sets.

Potential bias was also assessed based on the use of hatchery Chinook as surrogates for wild fish in the earlier years of study. This study design may have violated the assumption that marked and unmarked fish have equal catchability (Seber 1973). In 2005, two paired releases of hatchery and wild Chinook did not differ based on a *G*-test comparison of their recapture rates. The first paired release on March 5 had a recapture rate of 4.6% for hatchery Chinook (41 of 895) and 3.7% for wild Chinook (34 of 921, $p = 0.34$). The second paired release on March 31 had a recapture rate of 3.5% for hatchery Chinook (30 of 859) and 3.0% for wild Chinook (22 of 722, $p = 0.62$). Paired releases in other river basins have resulted in non-significant or inconsistent differences between hatchery and wild release groups (Zimmerman, unpublished data).

Juvenile Migrant Survival

Egg-to-migrant survival of Skagit River Chinook ranged from 4.5 to 21.5% or 270 to 1,230 juveniles per female (Table 5). Regressions of survival on individual explanatory variables (*PED*, flows) indicated that egg-to-migrant survival was a negative function of peak flows and the duration of incubation flows exceeding an RI of 2 (Figure 4). However, flow metrics were correlated with each other indicating a lack of independence among the explanatory variables (Table 6).

The relationship among egg deposition, incubation flows, and number of juvenile migrants was best explained by a nonlinear (logarithmic) model that included the basin-wide metric of peak flows during the incubation period (Table 7). This model explained 66% of the inter-annual variation in juvenile migrant Chinook and the weight of evidence supporting this model (w_r =

0.26) was stronger than other models evaluated. Each of the 10 best models all included measures of incubation flow. The second-order polynomial did not improve explanation of the *PED* versus juvenile data with or without flow variables, and stock-specific flow metrics did not improve the ability to explain annual variation in the number of juvenile migrant Chinook.

In general, more eggs deposited in the gravel resulted in more juvenile migrants. A *PED* value adjusted for average egg-to-migrant survival explained 43% of the variation in juvenile production (Figure 7*a*). A *PED* value adjusted for the predicted effect of peak flow on egg-to-migrant survival explained 58% of the variation in juvenile production (Figure 7*b*). A *PED* value further adjusted for the predicted effect of peak flow and spawner abundance on egg-to-migrant survival (best fit model from AIC comparison) explained 66% of the variation in juvenile production (Figure 7*c*). The inclusion of spawners (*PED*) effects on survival in this latter model was needed to linearize the relationship between predicted egg survival and the actual juvenile production estimate.

Juvenile Life History Strategies

Sub-yearling migrants represented 96.3 to 99.9 percent of the total freshwater production of Skagit Chinook for brood years 1993 to 2008 (Table 7). Fry migrants have varied 7-fold among years (905,000 to 6,553,000 fish) and parr migrants have varied 4-fold (537,000 to 2,188,000 fish). Yearling migrants have ranged between 6,000 and 97,000 fish. Migration of sub-yearlings was consistently bi-modal, although the proportion of fry and parr migrants varied from year to year (Figure 6).

Fry abundance increased as total migrant abundance increased (Figure 7). In comparison, the numbers of parr and yearling migrants did not increase with total migrant abundance. The ratio of juveniles that emigrated at the fry stage versus those that emigrated at the parr or yearling stages ranged between 0.7 and 5.6 and was a positive function of total number of juvenile migrants ($F_{1,11} = 11.9$, $R^2 = 0.52$, $p = 0.005$, Figure 8*a*). The ratio of juveniles that emigrated at the parr stage versus those that emigrated at the yearling stage ranged between 12.9 and 156.3 and was not a function of the total abundance for these migrant types ($F_{1,11} = 1.27$, $R^2 = 0.10$, $p = 0.28$, Figure 8*b*).

Discussion

Freshwater Survival

The number of juvenile migrant Chinook in the Skagit River was explained by a combination of density-dependent and density-independent survival. The juvenile-spawner relationship demonstrated that low spawner abundance (below 30 million eggs or 6,000 females) has limited juvenile migrant abundance. The logarithmic function fit to these data suggested that the number of juvenile migrants was approaching some maximum level at high spawner abundances; however, this conclusion was not supported by the lack of relationship between egg-to-migrant survival and potential egg deposition and remains to be validated by future years of high escapement (10,000+ females).

Density-independent survival of Skagit Chinook was a function of incubation flows and indicates that overall survival will fluctuate independently of spawner abundance. The range of egg-to-migrant survival observed for Skagit Chinook was within the egg-to-fry survival range observed for other salmonids (Bradford 1995) and consistent with previous studies demonstrating that egg incubation period is an important bottleneck to freshwater survival (Holtby and Healey 1986; McNeil 1966; Thorne and Ames 1987).

Freshwater production of Skagit Chinook was better explained by the peak flow events than selected metrics of hydraulic work during the incubation period. Unfortunately, correlations among flow variables in this data set meant that the relative impacts of flow metrics on survival could not be distinguished. Peak flows and hydraulic work represent two different mechanisms with potential to influence freshwater survival. Peak flows directly affect salmon eggs by scouring the streambed to the depth of the egg pocket (Devries 1997; Holtby and Healey 1986; Montgomery et al. 1996). Peak flows may also displace recently emerged fry downstream therefore reducing availability of preferred or suitable rearing habitats (Erman et al. 1988; Latterell et al. 1998; Seegrist and Gard 1972). In comparison, hydraulic work may affect freshwater survival by transporting sediments out of or into redd locations. If fine sediments infiltrate around the egg pockets, gravel permeability and dissolved oxygen levels should decrease (Lotspeich and Everest 1981) leading to delayed embryo development, immature emergence, and decreased emergent fry size (Koski 1966; Mason 1969). Sediment transport may also entomb redds and prevent fry from successfully emerging.

The ability to predict the number of juvenile migrants was not improved by incorporating stock-specific flow metrics as compared to basin-wide metrics. Stock-specific differences might be expected due to differences in spawn timing, sub-basin topography, and flow characteristics associated with each of the six spawning stocks. The hydrology of the Skagit basin includes two peak flow periods – one associated with winter precipitation and one with spring snow melt (Beechie 1992). Although this general hydrology occurs across the Skagit basin, maximum flows in the Skagit main stem and lower Sauk occur during the winter storms whereas maximum flows in the upper Sauk, Suiattle, and Cascade regions occur during the spring snow melt (Beechie 1992). Despite these differences, a stock-specific signal may be lacking because peak flows during incubation are correlated in timing and of sufficient magnitude to reduce survival of eggs in the gravel. Alternately, stock-specific effects may exist but were masked due to the majority of egg deposition representing a single stock (Upper Skagit Summers). The current inability to assign captured juvenile migrants to a stock of origin means that variables influencing some of the less abundant stocks can not be distinguished from variables influencing the most abundant Upper Skagit Summers.

Density-Dependent Migration

The occurrence of sub-yearling and yearling migrants from the same brood year of Chinook is widely recognized for Chinook salmon (Healey 1998; Waples et al. 2004), although populations are typically dominated by one strategy (i.e., ocean versus stream type). Alternate life histories of sub-yearling migrants, such as those seen in the Skagit River, are also observed in other Chinook populations (Miller et al. 2010; Reimers 1971; Taylor 1990), including watersheds where Chinook have been introduced (Carl 1984; Davis and Unwin 1989).

Results from this study suggest that juvenile Chinook may be using freshwater rearing habitat in the Skagit River to its capacity. During years when total abundance of juvenile migrants was high, juvenile Chinook were disproportionately fry migrants. A comparable density-dependent migration pattern was also observed in two New Zealand streams where Chinook were introduced (Davis and Unwin 1989). Variation in the percent of fry migrants may occur due to voluntary or involuntary movement associated with higher densities. In one scenario, juvenile Chinook may volitionally swim downstream to the next available rearing habitat. In another scenario, juvenile Chinook that do not secure a sheltered habitat may be involuntarily swept downstream as flows exceed the swimming capacity of 40-50 mm fry. An alternate scenario is that emerging Chinook have a pre-determined fate as a fry or parr migrant but mortality of pre-determined parr migrants is higher in years when total juvenile abundance is higher. With all three mechanisms, the ultimate composition of juvenile Chinook migrants is a density-dependent function. Environmental triggers that determine migration of recently emerged fry should include variables that constrict the available rearing habitat. These variables may include the initial distribution of redds, redistribution of alevin or fry during high flow events, and available rearing habitat downstream of these distributions. Although few studies have addressed freshwater rearing habitats for sub-yearling Chinook, off-channel habitat appears to be important for this life stage in the Skagit River (Hayman et al. 1996) and elsewhere (Limm and Marchetti 2009).

Unlike the analysis of fry migration, parr migrants were not a density-dependent function of juveniles with extended freshwater rearing periods (parr and yearling migrants). This result suggests that either survival from the parr to yearling life stage is too variable to preserve a signal of density-dependent migration or that the parr versus yearling migration strategy is based on genetic predisposition and not environmental capacity.

In the Skagit River, all three freshwater life histories were observed even at the lowest juvenile densities, suggesting that at least some genetic basis exists for each of the life history strategies. Density-dependent migration does not preclude a genetic disposition for life history strategies, rather genetics may help to determine which juveniles are better at securing the existing habitat. Laboratory studies have demonstrated that both aggression (Taylor 1988; Taylor 1990) and dispersal behavior (Bradford and Taylor 1997) of juvenile Chinook have a genetic basis.

Implications for Chinook Recovery

Freshwater survival of Chinook salmon can be expected to vary due to hydrological events. Thus a range in the number of juvenile migrants should be expected from a given escapement of Skagit River Chinook. Although survival was a function of peak incubation flows, current day flow events must be considered with respect to historical events, which were nearly two times the magnitude observed after the water storage projects were implemented (Beamer et al. 2005a). Despite higher incubation flows in some years, historical Chinook salmon populations were self-sustaining at higher abundances. This suggests that variables other than peak flows may currently limit the number of juvenile migrants. One possible explanation is that a given flow event presently has a greater impact on the movement of substrate than a comparable historical flow. Localized changes in land use or channel configurations can change the amount of active bed load movement associated with a given flow event (Hollis 1975; Montgomery et al. 1996), resulting in lower survival during the intra-gravel period without changes in the absolute volume of flowing water.

The density-dependent expression of fry migrants indicates that Chinook salmon currently maximize their use of accessible freshwater rearing habitat in the Skagit River. This conclusion assumes that fry emerge and move in a downstream direction. For example, the majority of spawners are currently Upper Skagit Summer Chinook and fry emerging from this population would not be expected to disperse into the Cascade or Suiattle sub-basins. Without the ability to differentiate juveniles by stock, conclusions regarding habitat capacity are largely influenced by Upper Skagit Summer Chinook. One implication of the density-dependent expression of juvenile migrant types is that stock productivity (recruits per spawner) of Skagit Chinook could be improved by changes to freshwater rearing habitat. Off-channel habitat in the middle and lower portions of the river are of particular importance for Chinook rearing and survival given that the majority of Skagit Chinook spawn in the main stem and all juvenile migrants pass through this region. In some portions of the river, off-channel habitat has been restored to historical levels (Smith 2005); however, floodplain modifications along the main-stem Skagit have reduced the width of flood plain habitat and its connectivity with the river (Beamer et al. 2005b). Increases in freshwater capacity would only translate into increased productivity if downstream habitats (i.e., delta) are currently at capacity and if the life histories with extended freshwater rearing (parr and yearling migrant) have a comparable or higher rate of return than those with extended rearing in the delta or Skagit Bay. Alternately, the lack of density-dependent survival in downstream habitats or relatively poor survival of the parr or yearling migrants would suggest that restoration efforts are best invested in the downstream habitats such as the delta. Relative return rates of juvenile life history strategies will require additional studies for Skagit River Chinook.

Juvenile life history diversity and the habitats supporting this diversity should be important for the long-term resilience of Skagit Chinook stocks. The link between diversity and resilience has been described as a "portfolio effect" where long-term growth is supported by short-term, non-synchronous fluctuations among its components (Greene et al. 2009; Schindler et al. 2010). Such diversity may buffer fisheries and minimize species extinction rates (Schindler et al. 2010). In the Skagit River, the Chinook portfolio includes six adult spawning stocks and at least four juvenile life histories (three of which are distinguishable in freshwater). As a result, survival risk of adults is spread over both space and time. Survival risk of juveniles is distributed among four different rearing habitats linked in a "downstream" direction (tributary and spawning area, off-channel habitat, delta, bay and pocket estuaries). The portfolio concept leads to the conclusion that recovery of Skagit Chinook will depend on the quality of rearing habitats that support currently successful juvenile life histories and well as sustained protection of habitats that support the currently subordinate life history strategies.

Understanding the population dynamics of Skagit Chinook will involve understanding mechanisms operating in freshwater and estuary habitats. In addition, studies in the Skagit system would be well complemented by a comparison with other Puget Sound populations that have varying degrees of freshwater and estuary rearing habitats. Estuary habitat available to Skagit River Chinook has been greatly reduced and yet is still one of the best available for the Puget Sound Chinook Evolutionary Significant Unit. For Puget Sound populations where little or no estuary remains, freshwater diversity may be even more important for the long-term resilience of Chinook populations.

Acknowledgements

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TABLE 1.─Flow data selected to represent incubation flows associated with each of the six Skagit River Chinook stocks. Flow data were collected from United State Geological Survey (USGS) stream gages.

Stock	USGS Gage	Incubation period
Upper Cascade Springs	Newhalem Creek, #12178100	August 1 – February 1
Suiattle Springs	Newhalem Creek, #12178100	August 1 – February 1
Upper Sauk Springs	Sauk River above Whitechuck, #12186000	August 15 – February 1
Lower Sauk Summers	Sauk River below Suiattle, #12189500	August 25 – March 1
Upper Skagit Summers	Skagit River at Marblemount, #12181000	August 20 – March 1
Lower Skagit Falls	Skagit River at Mt Vernon, #12200500	September 15 – March 1
Basin-wide	Skagit River at Mt. Vernon, #12200500	August 1 – March 1

TABLE 2.─Release and recapture of marked sub yearling Chinook used to calibrate Skagit River trap efficiency. Over time, releases have differed in fish origin, release dates, and release location. Marblemount Hatchery (61.5 river miles, rM, above trap) and Countyline Ponds (72 rM above trap) were release sites for migration years 1994 to 1997.

Migration Year	Number of Trials		Release Dates		Seasonal Efficiency			
	Hatchery	Wild	First	Last	Marks	Recaptures	Efficiency	Release Site
1994	1	0	6/6	6/15	160,000	3,418	2.1%	61.5 rM
1995	2	0	6/16	8/3	326,229	6,575	2.0%	61.5 rM, 72 rM
1996	2	0	6/1	7/8	390,109	7,793	2.0%	61.5 rM, 72 rM
1997	2	0	5/15	6/1	154,000	4,959	3.2%	61.5 rM, 72 rM
1998	4	0	5/22	6/4	9,412	271	2.9%	1.89 rM
1999	4	0	5/13	6/3	10,087	169	1.7%	1.89 rM
2000	3	0	5/8	5/24	7,543	214	2.8%	1.89 rM
2001	4	0	5/9	6/19	10,185	196	1.9%	1.89 rM
2002	4	1	3/28	7/16	2,920	45	1.5%	1.89 rM
2003	1	4	2/27	5/8	3,430	73	2.1%	1.89 rM
2004	4	0	3/23	5/20	3,383	42	1.2%	1.89 rM
2005	4	3	2/23	6/9	5,797	207	3.6%	1.03 rM
2006	0	49	1/18	7/31	17,973	464	2.6%	1.03 rM
2007	0	26	1/19	7/25	15,808	839	5.3%	1.03 rM
2008	0	25	2/1	7/13	14,018	819	5.8%	1.03 rM
2009	0	24	2/8	6/27	16,294	1,176	7.2%	1.03rM

TABLE 3.─Linear and nonlinear models used to explain the relationship between spawners and juvenile migrants of Skagit River Chinook. Models were fit spawner (*S*, potential egg deposition) and recruit (*R*, juvenile production) data, with and without flow parameters. Basin-wide and stock-specific values were used to derive flow parameters.

Hypothesis	Model	Parameters
Juvenile production is a density-independent function of spawner abundance	$R = b * S + a$	a = intercept b = slope (first-order) c = slope (second-order) f_P = coefficient peak flows E_P = normalized peak flow f_D = coefficient flow duration E_D = normalized flow duration
Juvenile production is a density-dependent and infinitely increasing function of spawner abundance.	$R = b * \ln(S) + a$	
Juvenile production is a density-dependent function of spawner abundance and a density-independent function of incubation flows.	$R = [b * \ln(S) + a] * e^{(f_P E_P + f_D E_D)}$	
Juvenile production is a density-dependent function of spawner abundance with a maximum number of juveniles produced by a finite number of spawners.	$R = c * S^2 + b * S + a$	
Juvenile production is a density-dependent function of spawner abundance and a density-independent function of incubation flows.	$R = c * S^2 + b * S + a + f_P E_P + f_D E_D$	

TABLE 4.─Number, fork length (cm) and fecundity (eggs per female) of female spawners of Skagit River Chinook salmon, brood years 1993 to 2008. Potential egg deposition (PED) is calculated from the number and fecundity of female spawners for each stock and brood year. Data are average ± 1 standard deviation.

Stock	Females	Length	Fecundity	PED
Upper Cascade Springs	121 ±55	86.2 ±3.3	5,611 ±262	680,783 ±310,067
Suiattle Springs	149 ±60	83.0 ±4.9	5,297 ±378	789,092 ±319,554
Upper Sauk Springs	153 ±94	85.7 ±3.2	5,548 ±230	857,149 ±546,537
Lower Sauk Summers	256 ±169	92.1 ±4.8	6,218 ±186	1,588,228 ±1,040,729
Upper Skagit Summers	3,985 ±2,061	89.6 ±4.8	5,950 ±513	24,199,637 ±13,494,972
Lower Skagit Falls	819 ±533	86.9 ±5.3	4,947 ±523	4,124,263 ±2,877,948

TABLE 5.—Juvenile migrant abundance (*J*), egg-to-migrant survival (*S*), and juveniles per female spawner (*J/F*) of Skagit River Chinook, brood years 1993-2008. Fry and parr components of sub-yearling migrants were not estimated for the 1993 to 1995 brood years due to data limitations in these years.

Brood	All Juveniles			Sub yearlings (*i* +1)		Yearlings
Year (*i*)	*J*	*S*	*J/F*	Fry	Parr	(*i* +2)
1993	2,132,000	14.7%	810	2,071,000		61,000
1994	1,939,000	15.7%	805	1,933,000		6,000
1995	1,009,000	6.5%	326	1,000,000		9,000
1996	2,855,000	11.9%	612	1,504,000	1,254,000	97,000
1997	2,478,000	18.6%	1,048	1,009,000	1,445,000	24,000
1998	7,725,000	21.5%	1,230	6,553,000	1,159,000	13,000
1999	1,783,000	13.6%	826	1,238,000	537,000	8,000
2000	6,837,000	16.0%	952	5,111,000	1,682,000	44,000
2001	5,853,000	15.9%	935	4,338,000	1,496,000	19,000
2002	5,793,000	11.4%	701	4,703,000	1,062,000	28,000
2003	3,334,000	12.6%	785	1,132,000	2,188,000	14,000
2004	3,972,000	6.4%	395	3,160,000	805,000	7,000
2005	6,914,000	13.0%	784	5,117,000	1,759,000	38,000
2006	2,447,000	4.5%	270	1,799,000	629,000	19,000
2007	1,735,000	6.1%	365	905,000	806,000	24,000
2008	2,821,000	9.3%	537	1,580,000	1,216,000	25,000

TABLE 6.─Pearson correlations among incubation period flow metrics of Skagit Chinook. Flow metrics include maximum daily flow (Peak) and duration of incubation period exceeding flows with recurrence intervals of 1 and 2 years (RI 1, RI 2). Correlations are for basin-wide and stock specific flow metrics. Peak flow RI were log transformed prior to analysis. Asterisk (*) indicates a significant correlation ($\alpha < 0.05$).

Stock	Peak vs. RI 2	Peak vs. RI 1	RI 2 vs. RI 1
Upper Cascade Springs	*0.86	*0.62	*0.62
Suiattle Springs	*0.86	*0.62	*0.62
Upper Sauk Springs	*0.91	*0.62	0.49
Lower Sauk Summers	*0.83	*0.85	*0.60
Upper Skagit Summers	*0.87	*0.67	*0.50
Lower Skagit Falls	*0.94	*0.85	*0.79
Pooled	*0.94	*0.85	*0.79

TABLE 7.─Akaike Information Criteria (AIC_c) and weight of evidence (w_r) for 10 best models fit to egg deposition (*PED*) and juvenile migrant data for Skagit River Chinook salmon. Models were fit to PED and juvenile data for brood years 1993 to 2008 and included three metrics of incubation flows – peak flow (Peak) and duration of time exceeding a recurring flood level of 1 and 2 years (RI > 1 and RI > 2 respectively). Flood variables were either a basin-wide (Basin) or stock-specific (Stock) values.

Rank	Model	Environmental	Specificity	$AICc$	w_r	$adjR^2$
1	Logarithmic	Peak	Pooled	19.8	0.26	0.66
2	Logarithmic	RI > 1	Stock Specific	20.9	0.15	0.68
3	Logarithmic	RI > 2	Pooled	21.4	0.11	0.64
4	Logarithmic	Peak	Stock Specific	22.8	0.06	0.62
5	Linear	Peak	Pooled	23.0	0.05	0.51
6	Logarithmic	Peak + RI > 1	Pooled	23.2	0.05	0.50
7	Linear	RI > 2	Pooled	23.8	0.03	0.45
8	Logarithmic	Peak + RI > 2	Pooled	24.1	0.03	0.48
9	Logarithmic	Peak + RI > 1	Stock Specific	24.2	0.03	0.70
10	Logarithmic	RI > 2	Stock Specific	24.2	0.03	0.52

Figures

FIGURE 1.─Map shows spawning distributions of six recognized stocks of Skagit River Chinook, location of juvenile trap, and release sites of marked juvenile Chinook used for trap efficiency trials. Map also shows locations of USGS gages selected to represent incubation flows associated with the six different stocks (#12200500 Skagit River at Mt Vernon, #12189500 Sauk River near Sauk, WA, #12186000 Sauk River above Whitechuck, #12181000 Skagit River at Marblemount, #12178100 Newhalem Creek).

FIGURE 2.─Aerial photograph of Skagit River juvenile trap. Trap is operated along the left bank and anchored to the Burlington Northern railroad trestle in Mt. Vernon, Washington.

FIGURE 3.─Female spawner abundance (*a*) and juvenile migrant abundance (*b*) of Skagit River Chinook, brood year 1993-2008. Spawner abundance is partitioned among the six recognized stocks. Juvenile migrant abundance is partitioned among the three freshwater life history types. Sub yearling migrants from the 1993-1995 brood years were not be partitioned into fry and parr migrants due to data limitations.

FIGURE 4.─Flow metrics representing the incubation period of six Chinook salmon stocks in the Skagit River. The peak flow metric is the recurrence interval of instantaneous peak flows during the incubation period for each stock. Index of hydraulic work is the proportion of the incubation period with flows exceeding a 1-year recurrence interval. Data are median values for the 1993-2008 brood years.

FIGURE 5.─Comparison of methods used to derive the number of sub-yearling Chinook migrants in the Skagit River, 2006 to 2009. Bars represent time-stratified mark-recapture data

(open), pooled mark-recapture data (light gray), and modified pooled mark-recapture data (dark gray, May and June releases only). Data are abundance estimate with 95% confidence intervals.

FIGURE 6.─Egg-to-migrant survival of Skagit Chinook (brood year 1993-2008) as a function of potential egg deposition (*a*), peak incubation flows (*b*), duration of incubation flows exceeding a 2-year flood interval (*c*), and duration of incubation flows exceeding a 1-year flood interval (*d*). Flow data were measured at the Mt. Vernon USGS gage #12200500.

FIGURE 7.─Number of juvenile migrant Chinook in the Skagit River, brood year 1993 to 2008. Correlation between potential egg deposition (*PED*) and number of juvenile migrants is shown as a function of average survival (*a*), survival predicted from flow regression (*b*), and survival predicted from best fit flow and *PED* model (*c*, see Table 7). Each data point represents an individual year.

FIGURE 6.─Bimodal migration of sub yearling Skagit Chinook partitioned into fry and parr life history strategies. Migration year 1999 (*a*) is an example of well-defined fry and parr migrations with higher fry abundance. Migration year 1997 (*b*) is an example of overlapping fry and parr migrations with equivalent fry and parr abundance. Migration year 2004 (*c*) is an example of well-defined fry and parr migrations with higher parr abundance.

FIGURE 7.─Relative expression of three freshwater life history strategies for juvenile Chinook in the Skagit River, brood year 1993-2008. Graph shows the number of fry (black circle), parr (gray square), and yearling (open diamond) migrants as a function of total abundance.

FIGURE 8.─Ratio of juvenile life history strategies as a function of number of juvenile Chinook migrants. Ratio of fry to parr and yearlings from the same brood year is shown as a function of all juvenile migrants (*a*). Ratio of parr to yearlings from the same brood year is shown as a function of parr and yearling migrants (*b*).

Figure 1.

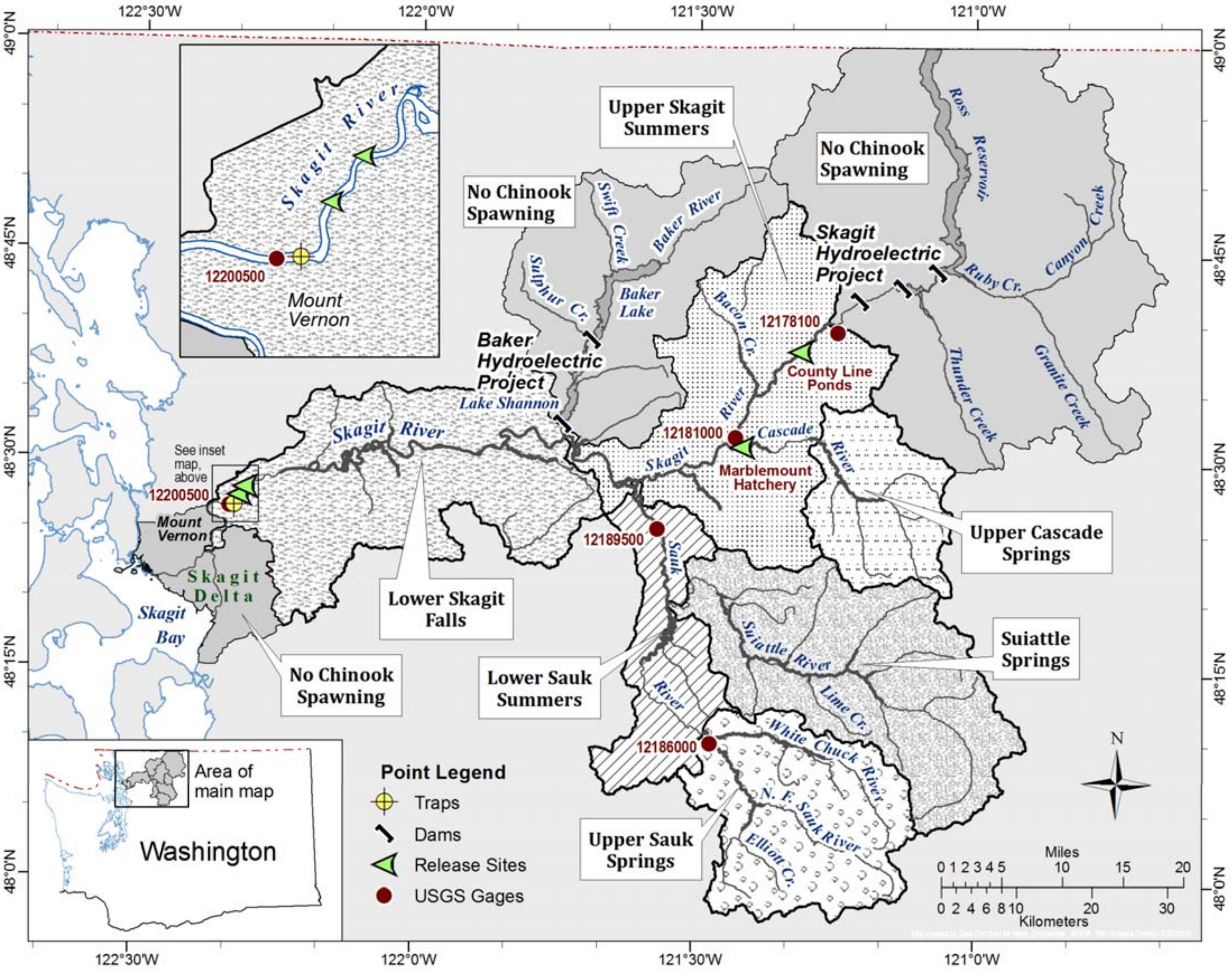

122°30'W
122°0'W
121°30'W
121°0'W
49°0'N
48°45'N
48°30'N
48°15'N
48°0'N
Skagit River
12200500
Mount Vernon
See inset map, above
Skagit Delta
Skagit Bay
No Chinook Spawning
Lower Skagit Falls
Skagit River
Lake Shannon
Baker Hydroelectric Project
No Chinook Spawning
Swift Creek
Baker River
Sulphur Cr.
Baker Lake
Upper Skagit Summers
No Chinook Spawning
Skagit Hydroelectric Project
Ross Reservoir
Ruby Cr.
Canyon Creek
Thunder Creek
Granite Creek
Bacon Cr.
12178100
County Line Ponds
River
12181000
Cascade
Skagit
Marblemount Hatchery
River
Upper Cascade Springs
12189500
Sauk
Lower Sauk Summers
River
Suiattle River
Suiattle Springs
Lime Cr.
12186000
White Chuck River
N. F. Sauk River
Elliott Cr.
Upper Sauk Springs
N
Miles
0 1 2 3 4 5 10 15 20
0 2 4 6 8 10 20 30
Kilometers
Area of main map
Washington
Point Legend
Traps
Dams
Release Sites
USGS Gages

Figure 2.

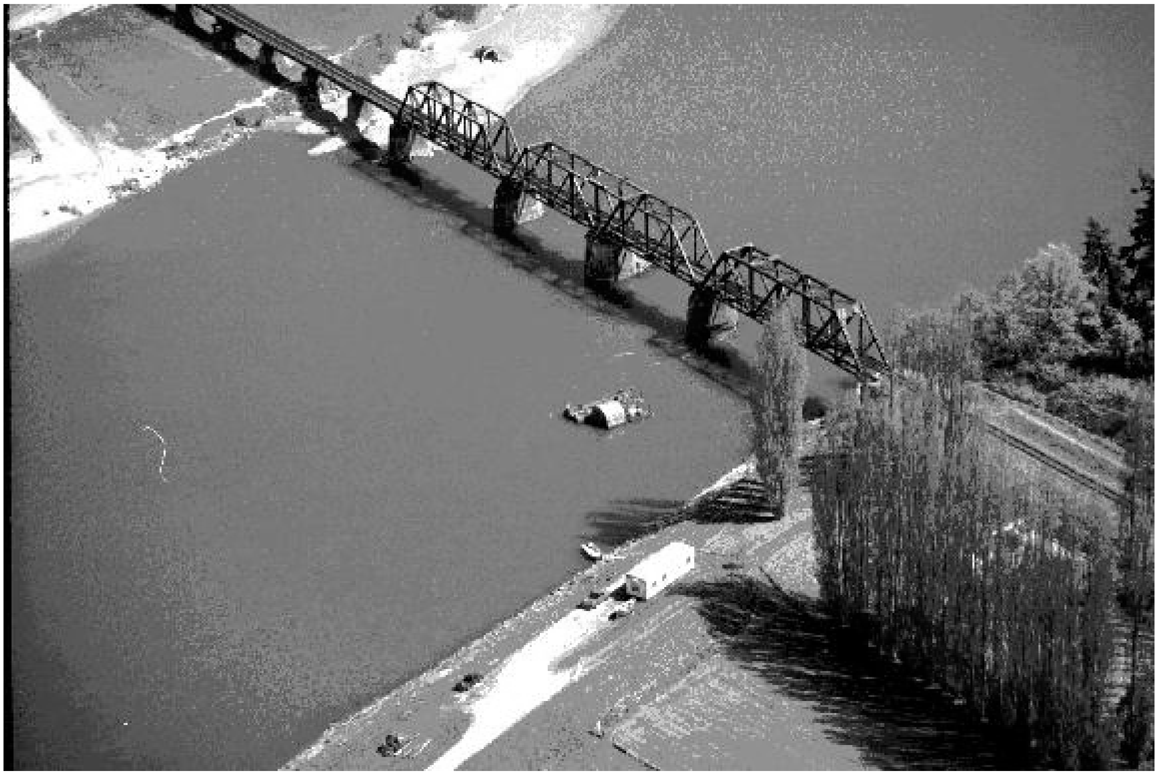
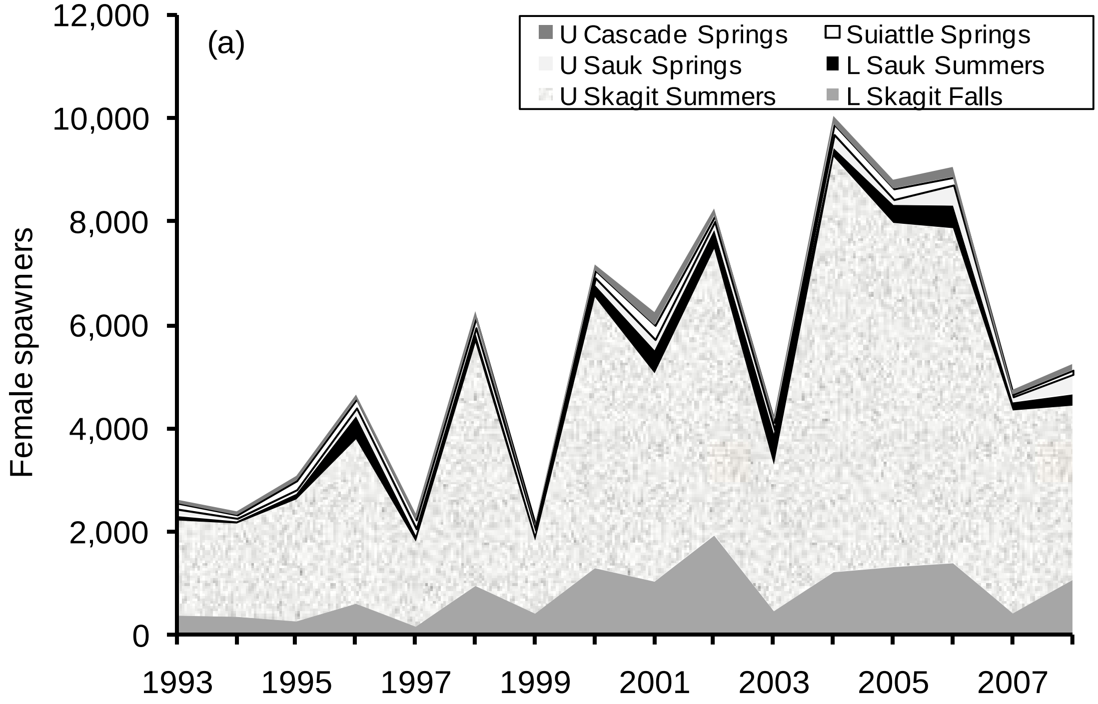
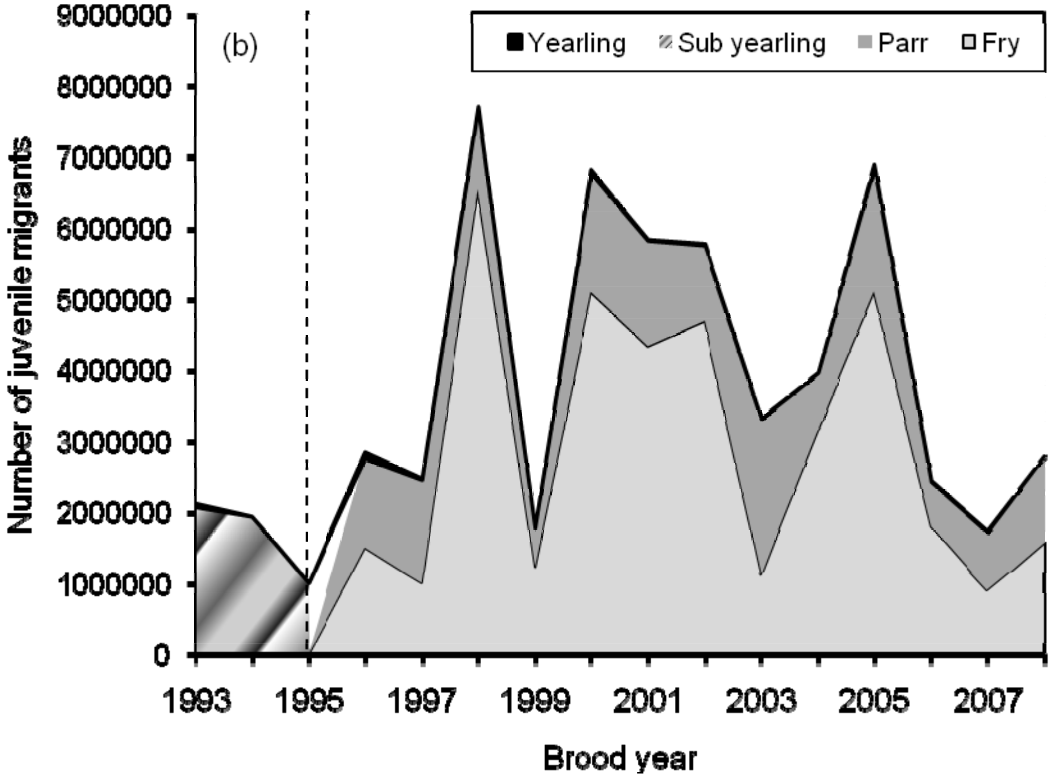


Figure 3.


12,000
10,000
8,000
6,000
4,000
2,000
0
Female spawners
(a)
U Cascade Springs
Suiattle Springs
U Sauk Springs
L Sauk Summers
U Skagit Summers
L Skagit Falls
1993
1995
1997
1999
2001
2003
2005
2007


(b)
■ Yearling
▨ Sub yearling
■ Parr
☐ Fry
Number of juvenile migrants
9000000
8000000
7000000
6000000
5000000
4000000
3000000
2000000
1000000
0
1993
1995
1997
1999
2001
2003
2005
2007
Brood year

626

Figure 4.

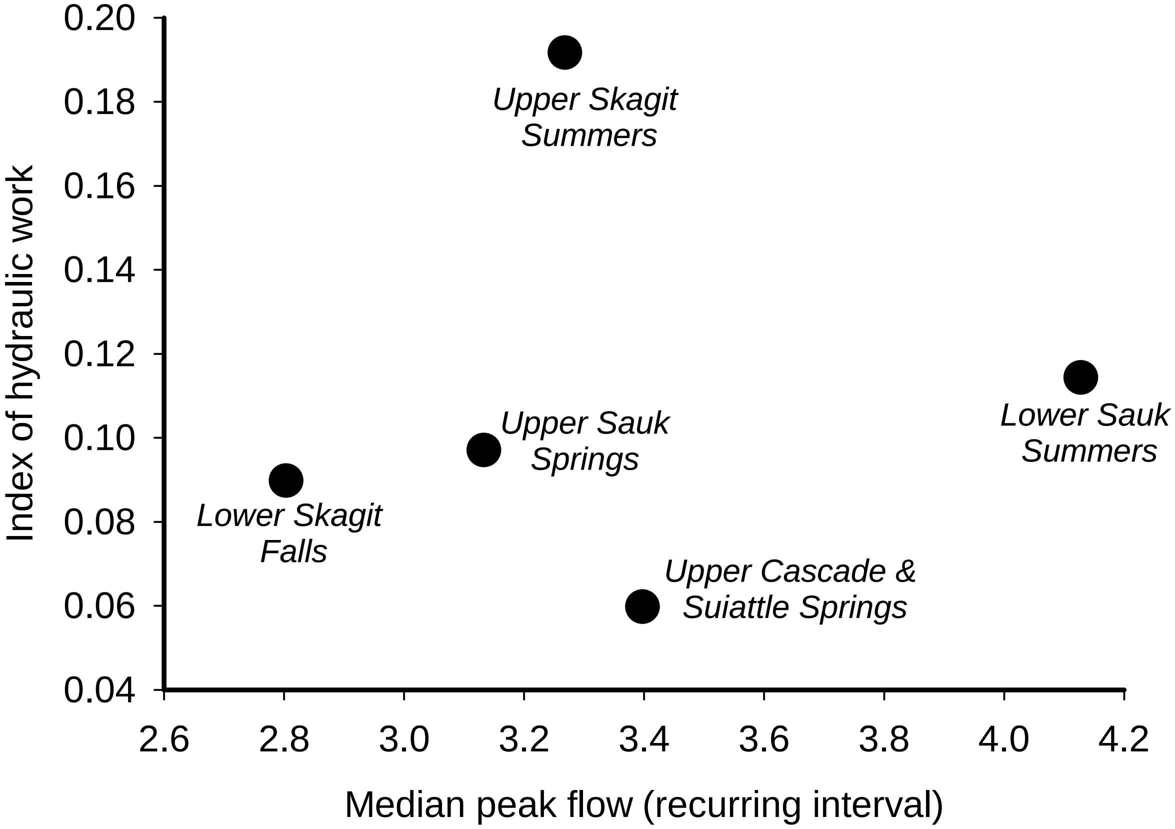

0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
Index of hydraulic work
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
Median peak flow (recurring interval)
Upper Skagit Summers
Upper Sauk Springs
Lower Skagit Falls
Upper Cascade & Suiattle Springs
Lower Sauk Summers

Figure 5.

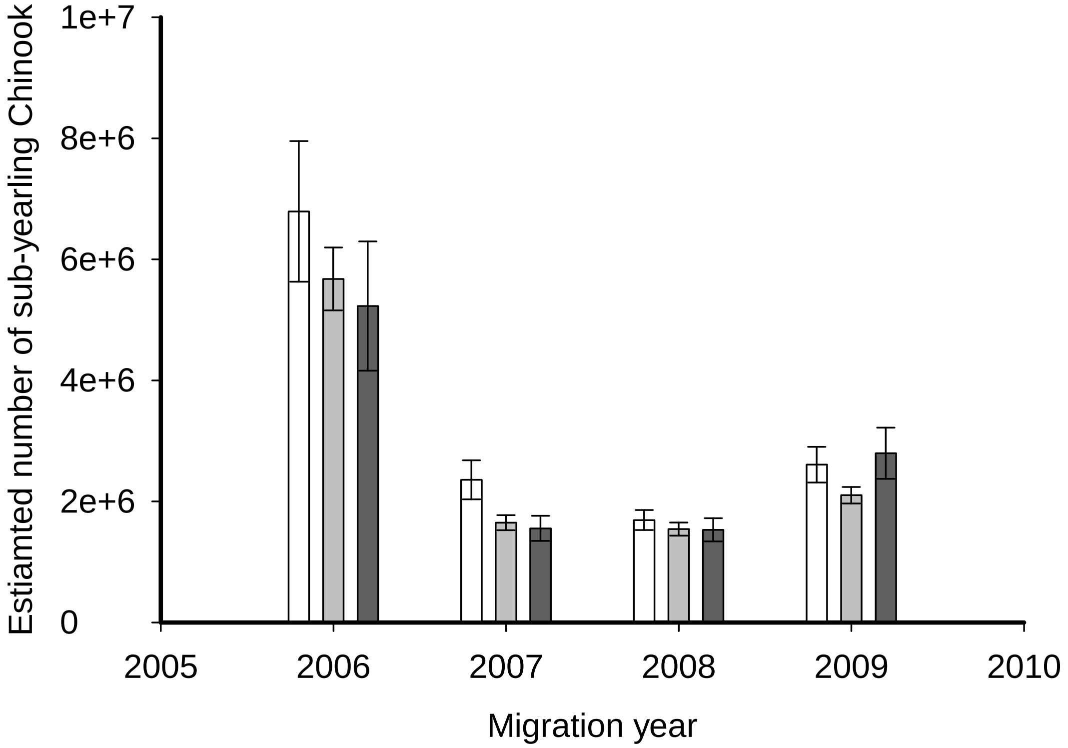

Estiamted number of sub-yearling Chinook
1e+7
8e+6
6e+6
4e+6
2e+6
0
2005
2006
2007
2008
2009
2010
Migration year

Figure 6.

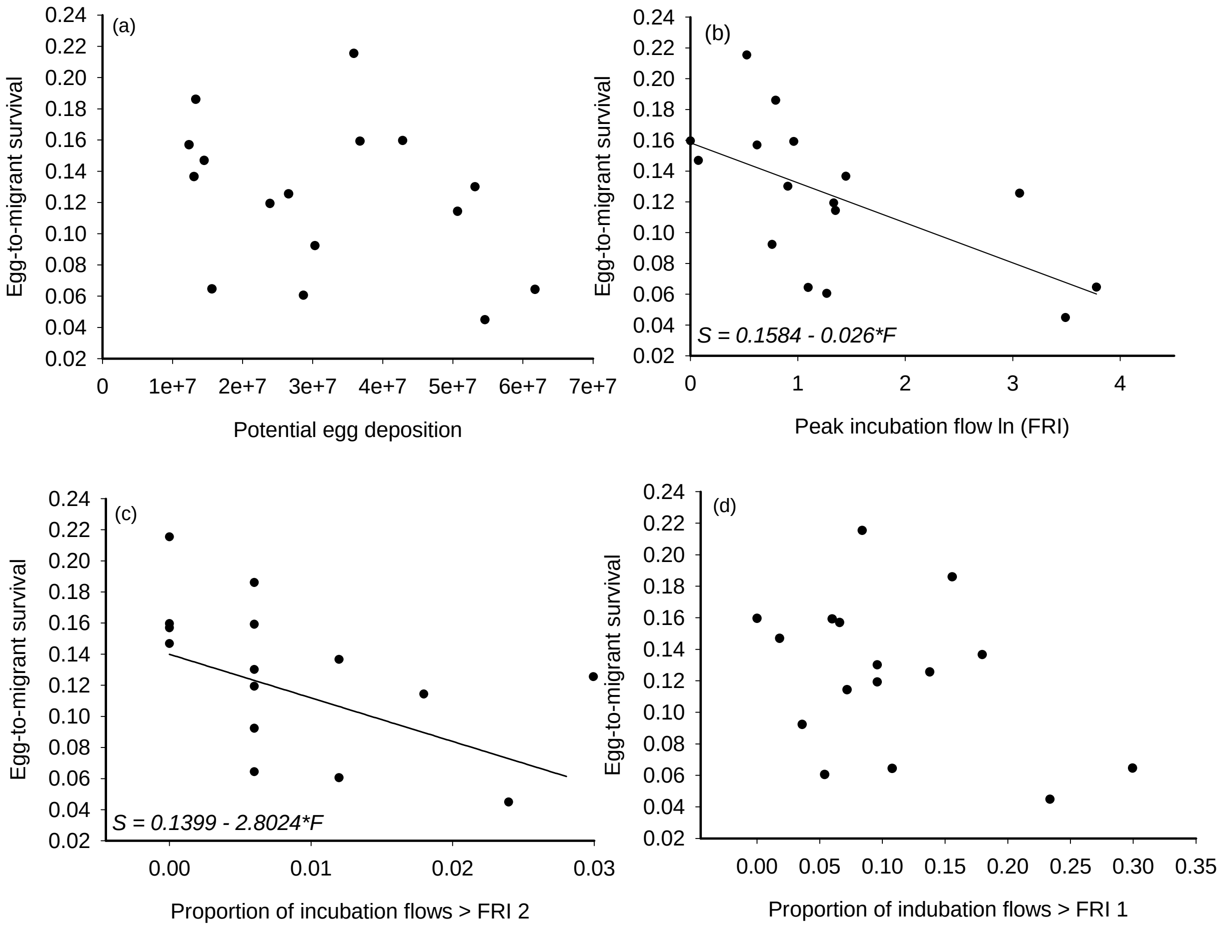

(a)
Egg-to-migrant survival
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0
1e+7
2e+7
3e+7
4e+7
5e+7
6e+7
7e+7
Potential egg deposition
(b)
S = 0.1584 - 0.026*F
0
1
2
3
4
Peak incubation flow ln (FRI)
(c)
S = 0.1399 - 2.8024*F
0.00
0.01
0.02
0.03
Proportion of incubation flows > FRI 2
(d)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Proportion of indubation flows > FRI 1

Figure 7.

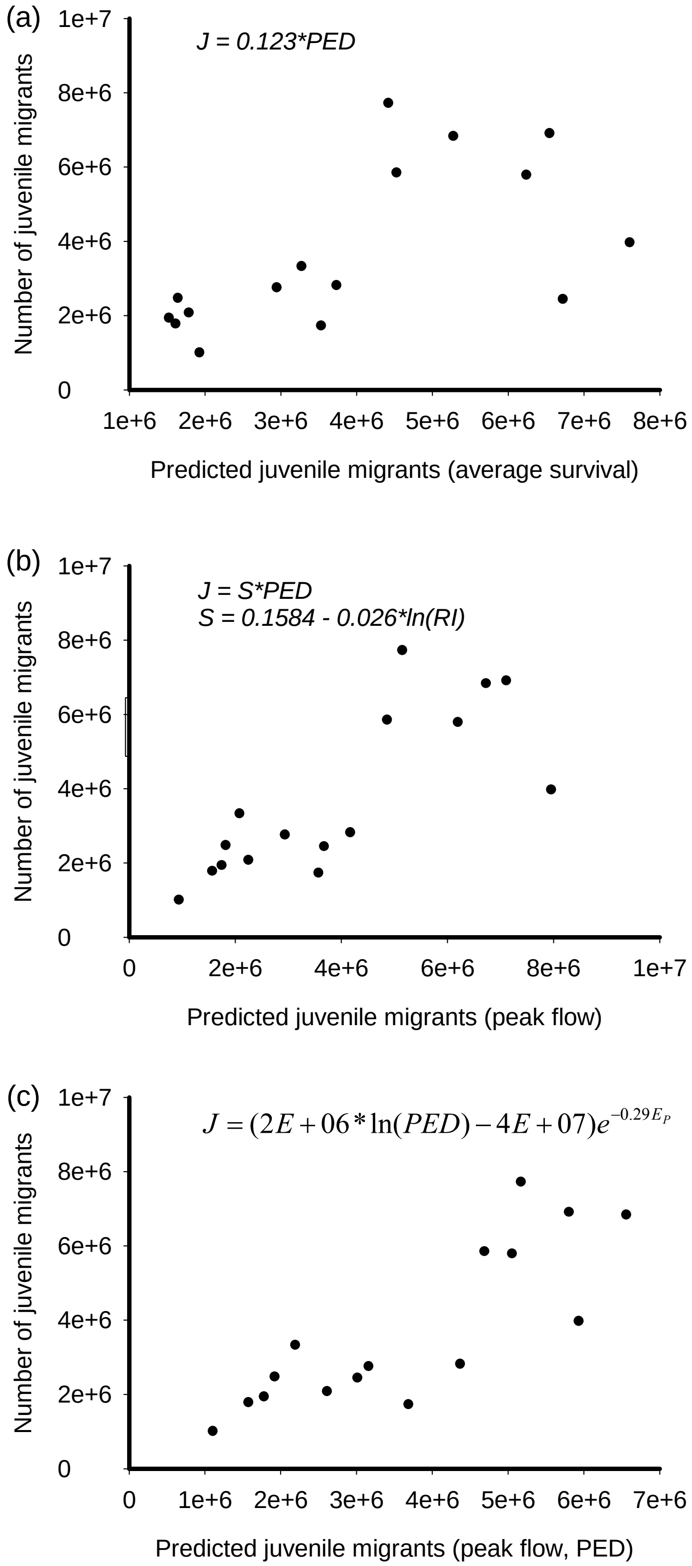

(a)
J = 0.123*PED
Number of juvenile migrants
0
2e+6
4e+6
6e+6
8e+6
1e+7
1e+6
2e+6
3e+6
4e+6
5e+6
6e+6
7e+6
8e+6
Predicted juvenile migrants (average survival)
(b)
J = S*PED
S = 0.1584 - 0.026*ln(RI)
Number of juvenile migrants
0
2e+6
4e+6
6e+6
8e+6
1e+7
0
2e+6
4e+6
6e+6
8e+6
1e+7
Predicted juvenile migrants (peak flow)
(c)
$J = (2E + 06 * \ln(PED) - 4E + 07)e^{-0.29E_P}$
Number of juvenile migrants
0
2e+6
4e+6
6e+6
8e+6
1e+7
0
1e+6
2e+6
3e+6
4e+6
5e+6
6e+6
7e+6
Predicted juvenile migrants (peak flow, PED)

Figure 6.

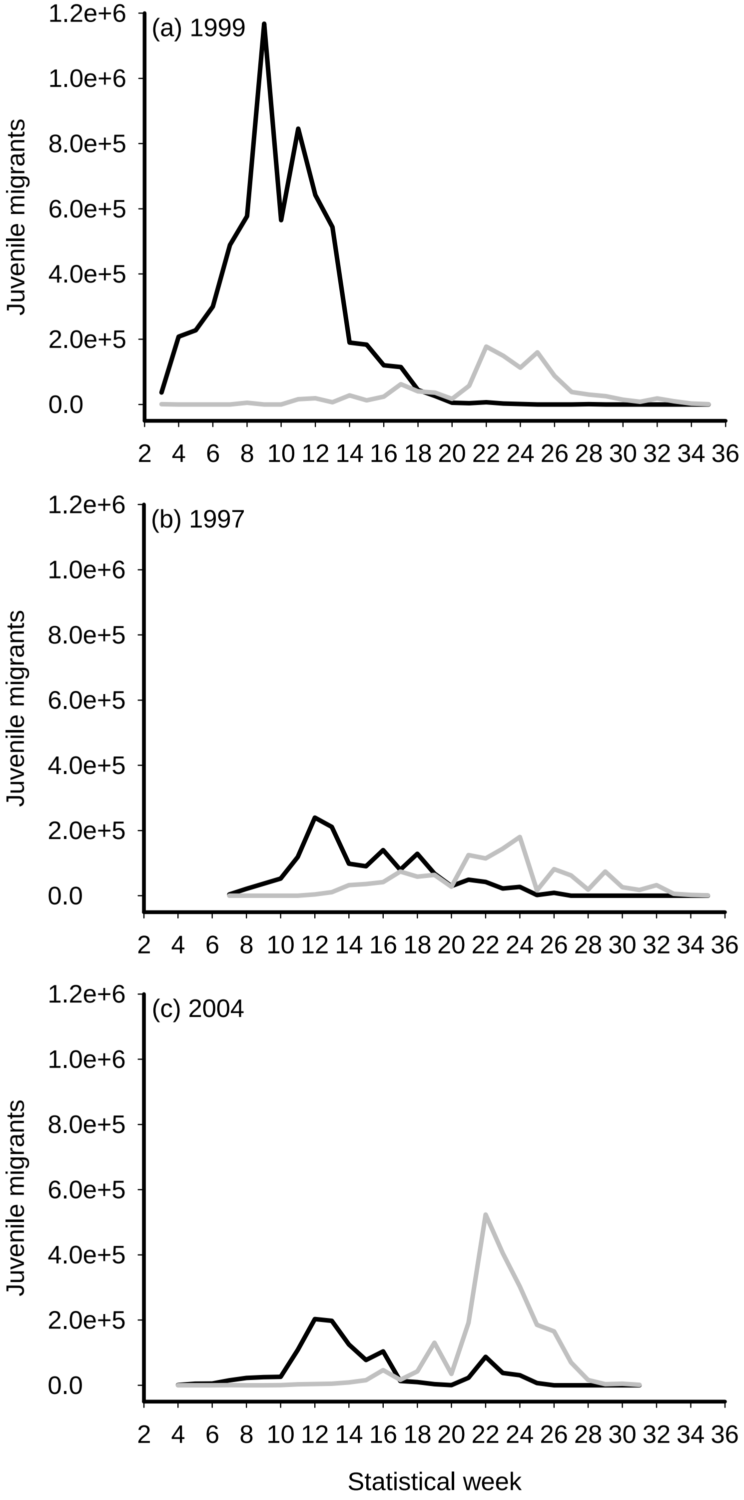

(a) 1999
(b) 1997
(c) 2004
Juvenile migrants
1.2e+6
1.0e+6
8.0e+5
6.0e+5
4.0e+5
2.0e+5
0.0
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36
Statistical week

Figure 7.

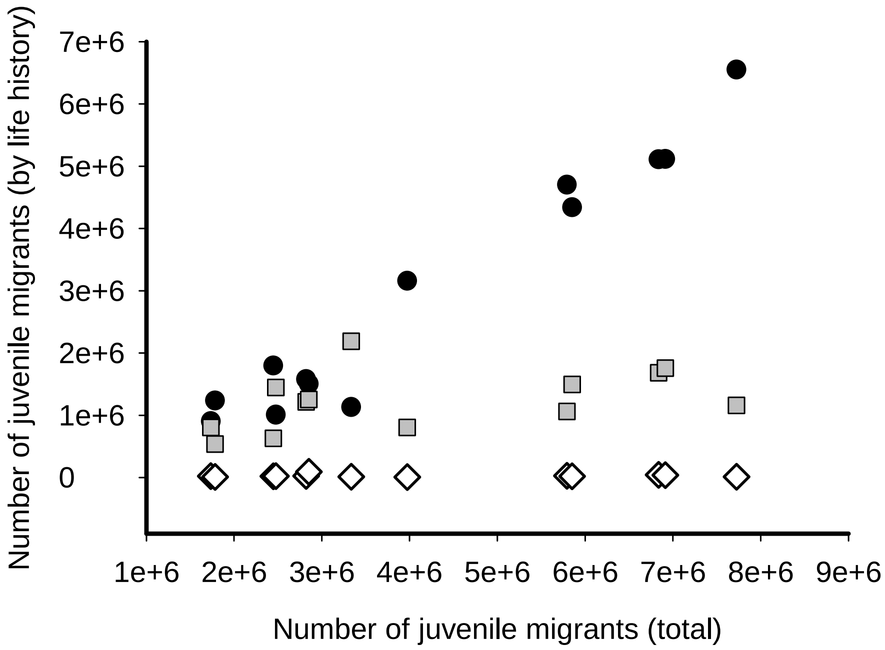
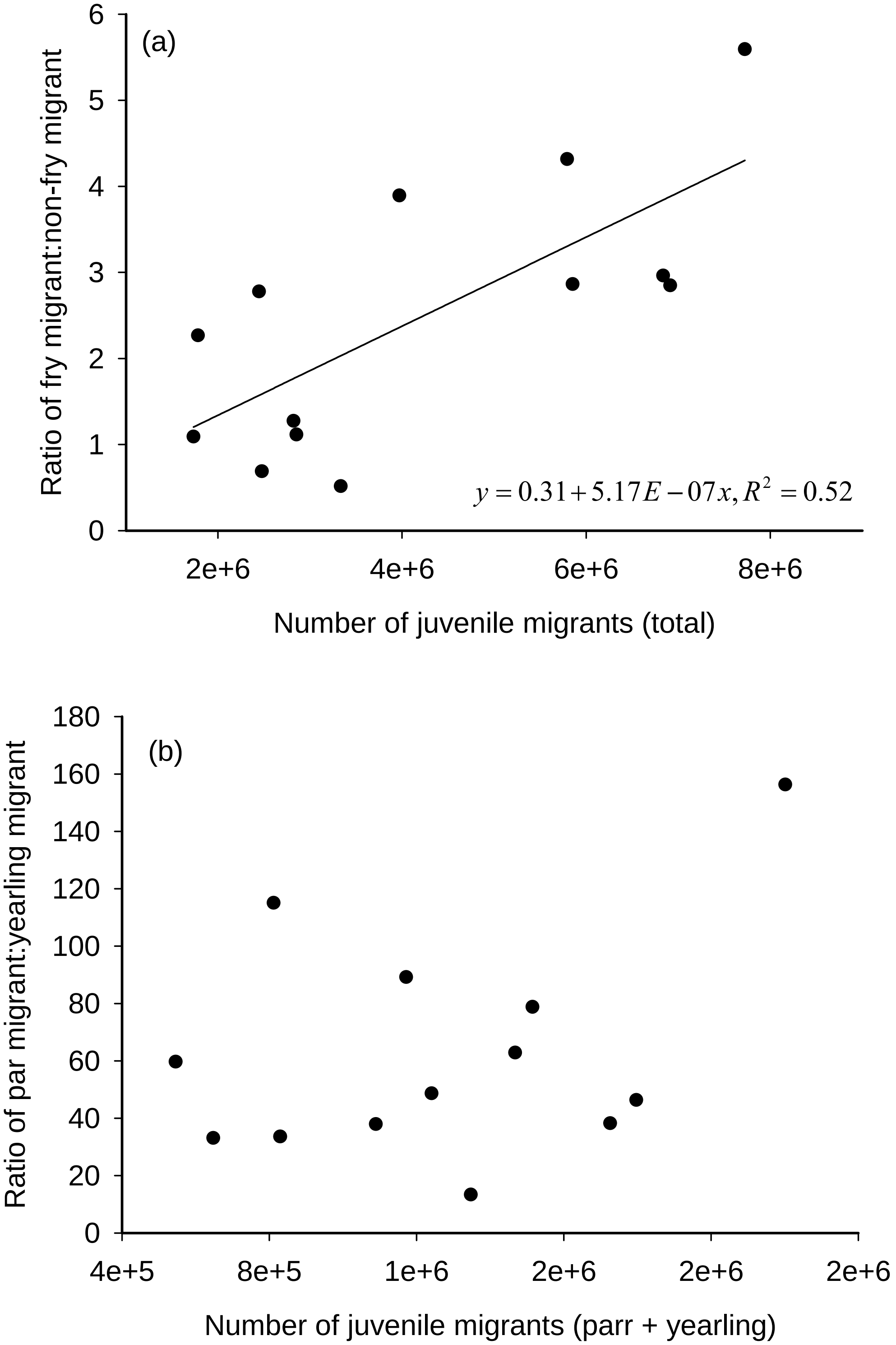

Number of juvenile migrants (by life history)
7e+6
6e+6
5e+6
4e+6
3e+6
2e+6
1e+6
0
1e+6
2e+6
3e+6
4e+6
5e+6
6e+6
7e+6
8e+6
9e+6
Number of juvenile migrants (total)

Figure 8.


(a)
Ratio of fry migrant:non-fry migrant
0
1
2
3
4
5
6
$y = 0.31 + 5.17E - 07x, R^2 = 0.52$
2e+6
4e+6
6e+6
8e+6
Number of juvenile migrants (total)
(b)
Ratio of par migrant:yearling migrant
0
20
40
60
80
100
120
140
160
180
4e+5
8e+5
1e+6
2e+6
2e+6
2e+6
Number of juvenile migrants (parr + yearling)

References

Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: The ghost of impacts past? Ecology Letters 6(4):335-342.

Beamer, E., B. Hayman, and S. Hinton. 2005a. Appendix B. Linking watershed conditions to egg-to-fry survival of Skagit Chinook salmon, http://www.skagitcoop.org/index.php/documents/.

Beamer, E. M., B. Hayman, and D. Smith. 2005b. Appendix C. Linking freshwater rearing habitat to Skagit Chinook salmon recovery, http://www.skagitcoop.org/index.php/documents/.

Beamer, E. M., J. C. Sartori, and K. A. Larsen. 2000. Skagit Chinook life history study progress report number 3. Federal Energy regulatory Commission Project Number 553., http://www.skagitcoop.org/index.php/documents/.

Beechie, T. J. 1992. Delineation of hydrologic regions in the Skagit River Basin. Report to Skagit Systems Cooperative, LaConnor, Washington.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52(6):1327-1338.

Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behaviour of newly emerged chinook salmon (Oncorhynchus tshawytscha) from the upper Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 54(7):1585-1592.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carl, L. M. 1984. Chinook salmon (*Oncorhynchus tshawutscha*) density, growth, mortality, and movement in two Lake Michigan tributaries. Canadian Journal of Zoology 62:65-71.

Carlson, S. R., L. G. Coggins, and C. O. Swanton. 1998. A simple stratified design for mark-recapture estimation of salmon smolt abundance. Alaska Fishery Research Bulletin 5:88-102.

Chapman, D. 1951. Some properties of the hypergeometric distribution with applications to zoological census. University of California Publications of Statistics 1:131-160.

Copeland, T., and D. A. Venditti. 2009. Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. Canadian Journal of Fisheries and Aquatic Sciences 66(10):1658-1665.

Davis, S. F., and M. J. Unwin. 1989. Freshwater life history of chinook salmon (*Oncorhynchus tshawytcha*) in the Rangitata River catchment, New Zealand. New Zealand Journal of Marine and Freshwater Research 23:311-319.

Devries, P. 1997. Riverine salmonid egg burial depths: Review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54(8):1685-1698.

Erman, D. C., E. D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. Canadian Journal of Fisheries and Aquatic Sciences 45:2195-2200.

Greene, C. M., and T. J. Beechie. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61(4):590-602.

Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2009. Improved viability of populations with diverse life-history portfolios. Biology Letters doi:10.1098/rsbl.2009.0780

Greene, C. M., D. W. Jensen, G. R. Pess, E. A. Steel, and E. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. Transactions of the American Fisheries Society 134(6):1562-1581.

Hayman, R. A., E. M. Beamer, and R. E. McClure. 1996. FY 1995 Skagit River Chinook restoration research. Final project performance report for NWIFC contract #3311 for FY95. Skagit System Cooperative, LaConner, Washington.

Healey, M. C. 1998. Life history of Chinook salmon (*Onchorhynchus tshawytscha*). C. Groot, and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver.

Hilborn, R., and M. Mangel. 1997. Ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

Hobbs, N. T., and R. Hilborn. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. Ecological Applications 16:5-19.

Hollis, G. E. 1975. The effect of urbanization on floods of difference recurrence interval. Water Resources Research 11:431-435.

Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho slamon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:1946-1959.

Interagency_Advisory_Committee_on_Water_Data. 1982. Guidelines for determining flood flow frequency: Bulletin 17B of the Hydrology SubCOmmittee. Office of Water Data Coordination, U.S. Geological Survey, Reston, Virginia.

Kinsel, C., M. S. Zimmerman, L. Kishimoto, and P. Topping. 2008. 2007 Skagit River salmon production evaluation, FPA 08-08. Washington Department of Fish and Wildlife, Olympia, Washington.

Koski, K. V. 1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three oregon coastal streams. M. Sc. thesis, Oregon State University, Corvallis, Oregon.

LaPointe, M., B. Eaton, S. Driscoll, and C. Latulippe. 2000. Modelling the probability of salmonid egg pocket scour due to floods. Canadian Journal of Fisheries and Aquatic Sciences 57:1120-1130.

Latterell, J. L., K. D. Fausch, C. Gowan, and S. C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. Rivers 6:240-250.

Limm, M. P., and M. P. Marchetti. 2009. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environmental Biology of Fishes 85(2):141-151.

Lisle, T. E. 1989. Sediment transport and resulting deposition in spawning gravels, north Coastal California. Water Resources Research 25(6):1303-1319.

Lotspeich, F. B., and F. H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. Pacific Northwest Forecast and Range Experiment Station, Research note PNW-369, Corvallis, Oregon.

Mason, J. C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26:63-91.

McNeil, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. Fishery Bulletin 65:495-523.

Miller, J. A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Marine Ecology Progress Series 408:227-240.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53(5):1061-1070.

Nash, D. B. 1994. Effective sediment-transporting discharge from magnitude frequency analysis. The Journal of Geology 102:79-95.

Pflug, D., and L. Mobrand. 1989. Skagit River salmon and steelhead fry stranding studies. Prepared by R. W. Beck Associates for the Seattle City Light Environmental Affairs Division, March 1989, Seattle, Washington, 300 pp.

Reimers, P. E. 1971. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Ph. D. thesis, Oregon State University, Corvallis, Oregon.

Schindler, D. E., and coauthors. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465(3):609-612.

Seber, G. A. F. 1973. The estimation of animal abundance. Charles Griffin and Company Limited, London.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478-482.

Seiler, D. E., L. Kishimoto, and S. Neuhauser. 1998. 1997 Skagit River wild 0+ Chinook production evaluation. Washington Department of Fish and Wildlife, Olympia, WA.

Smith, D. 2005. Off-channel habitat inventory and assessment for the Upper Skagit River basin. Report to Non-flow Coordinating Committee Skagit River Hydroelectric Project (FERC No. 553). Skagit River Systems Cooperative, La Conner, Washington.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd edition. W.H. Freeman and Company, New York.

SRSC, and WDFW. 2005. Skagit Chinook Recovery Plan. Skagit River Systems Cooperative and Washington Department of Fish and Wildlife, http://www.skagitcoop.org/.

Systat_Software_Inc. 2008. SigmaPlot for Windows, Version 11.

Taylor, E. B. 1988. Adaptive variation in rheotactic and agnostic behavior in newly emerged fry of Chinok salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. Canadian Journal of Fisheries and Aquatic Sciences 45:237-243.

Taylor, E. B. 1990. Phenotypic correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. Journal of Animal Ecology 59:455-468.

Thorne, R. E., and J. J. Ames. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Canadian Journal of Fisheries and Aquatic Sciences 44:1791-1795.

Volkhardt, G. C., S. L. Johnson, B. A. Miller, T. E. Nickelson, and D. E. Seiler. 2007. Rotary screw traps and inclined plane screen traps. Pages 235-266 *in* D. H. Johnson, and coeditors, editors. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland.

Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution 58:386-403.

Wolman, M. G., and J. P. Miller. 1959. Magnitude and frequency of forces in geomorphic processes. Journal of Geology 68:54-74.