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Abundance, Survival, and Life History Strategies of Juvenile Chinook Salmon in the Skagit River, Washington

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ARTICLE

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Abstract

To identify potential actions for conserving Chinook Salmon *Oncorhynchus tshawytscha* in the Skagit River, Washington, we used a 16-year time series of streamflow data, adult escapement, and out-migrant abundance to understand how out-migrant abundance and life history diversity were related to spawner abundance and incubation flows. Three freshwater rearing strategies were distinguished based on body size at out-migration: fry (≤ 45 mm FL), subyearling parr (46–100 mm FL), and yearling smolts (> 100 mm FL). Density-independent and density-dependent processes were hypothesized to influence survival in sequence, with density-independent mechanisms operating during incubation and density-dependent mechanisms operating between emergence and out-migration. A model selection process compared spawner–recruit models with and without different incubation flow metrics. Density-independent models that included measures of flow duration and magnitude were strongly supported (Akaike's information criterion [AIC] difference ≤ 3). Sustained flow events of moderate magnitude (1-year recurrence interval) were an equivalent if not better predictor of freshwater survival than short-duration flow events of high magnitude (peak flows). A second model selection process evaluated density dependence of each life history type. The composition of out-migrants (fry, subyearling parr, and yearling smolts) was a density-dependent function of spawner abundance. Fry out-migrant abundance was density independent, and subyearling parr out-migrant abundance was density dependent. Neither model was supported for yearling smolts. At least one out-migrant life history, subyearling parr, should benefit from continued restoration of freshwater habitats in the Skagit River system. Factors contributing to the yearling smolt life history will benefit from additional study.

In the last two decades, salmonid species across the Pacific Northwest have increasingly come under the protection of the Endangered Species Act. Their protected status reflects the scale of impact and the urgency of identifying and implementing actions that may rebuild abundance and life history diversity of existing stocks. To successfully rebuild stocks, it is necessary to identify the bottlenecks to productivity, determine which bottlenecks can be improved through conservation

actions, and implement actions of sufficient scale to result in the desired population response (Gallagher et al. 2012). Identification of such bottlenecks for salmonids is challenging due to their complex life histories and use of both freshwater and saltwater habitats.

Density dependence can be a bottleneck to population productivity even when population abundance is lower than historical levels (Achord et al. 2003; Copeland and Venditti

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2009). Density-dependent responses in the freshwater environment are evident when fish abundances approach the existing capacities for spawning and juvenile rearing and can be expressed as changes in per-capita survival or per-capita migration (Greene and Beechie 2004). Density-dependent survival will directly limit overall population productivity, whereas density-dependent migration from one habitat to another may or may not limit population productivity, depending on survival and growth in the new habitat. The concept of density dependence in multiple connected habitats is highly relevant for anadromous salmonids, which begin their complex life history in freshwater and continue downstream through estuarine and marine habitats.

Density-independent factors, such as streamflows during egg incubation, may also impact freshwater survival. Both infrequent large flow events and frequent moderate peak flows have been demonstrated to move substantial amounts of substrate (Soar and Thorne 2011) and may influence egg and embryo survival. Large peak flow events that scour the streambed to the depth of the egg pocket will displace or damage developing eggs, resulting in egg or embryo mortality (Holtby and Healey 1986; Montgomery et al. 1996; Devries 1997). The magnitude of flow events determines the streambed area and depth that are scoured and filled (LaPointe et al. 2000) and is expected to reduce egg-to-migrant survival proportionately. In comparison, moderate flow events may deposit sediment into redd locations, impacting survival to emergence (Lisle 1989; LaPointe et al. 2000) by reducing interstitial flows and the transport of oxygen and waste products through gravels (Bjornn and Reiser 1991). Transport of sediment resulting from moderate flow events can be substantial. For example, 6.5 million tons of sediment per year are transported from river systems into the marine waters of Puget Sound (Czuba et al. 2011). Flows that maximize sediment movement over time are referred to as effective discharge (Wolman and Miller 1960; Soar and Thorne 2011) and typically occur at bank-full flow (i.e., the largest flow that can be contained within the riverbank; Soar and Thorne 2011). Because effective discharge is difficult to directly estimate, two potential thresholds (1-year and 2-year recurrence intervals [RIs]) were selected for study because they are generally attributed to bank-full flows (Williams 1978; Soar and Thorne 2001).

The purpose of the present study was to understand how the abundance and life history diversity of Chinook Salmon *Oncorhynchus tshawytscha* out-migrants in the Skagit River system, Washington, are related to spawner abundance and incubation flows, as such information would support the identification of potential conservation actions. The Skagit River is the largest watershed (by drainage area) in Puget Sound and includes six recognized populations of Chinook Salmon (SRSC and WDFW 2005; Ruckelshaus et al. 2006). Freshwater residency of both adult and juvenile Chinook Salmon is diverse with respect to timing and duration. Out-migrants are predominantly subyearlings, although some yearlings are observed each year (Seiler

et al. 1998; Kinsel et al. 2008). Early fry migrants are fish that have recently emerged (≤ 45 mm FL), whereas late subyearling parr (46–100 mm FL) and yearling smolts (> 100 mm FL) rear in freshwater prior to out-migration. All of these freshwater rearing strategies are observed in returning spawners from all six populations (Beamer et al. 2005b).

A model selection approach was used to evaluate whether the spawner–out-migrant relationship was better explained by a density-independent or density-dependent relationship and whether a suite of potential flow metrics could help to explain density-independent survival. Both the magnitude of flow events and the duration of moderate flows (RI > 1 year or 2 years) were hypothesized to influence density-independent mortality during egg incubation. Given the diversity in flow patterns among sub-basins of the Skagit River watershed, stock-specific flow metrics may be a better predictor of density-independent mortality than a basinwide flow metric. A second analysis tested whether the relationship between each out-migrant life history (fry, subyearling parr, and yearling smolts) and the number of spawners was density independent or density dependent. The availability of space for juvenile rearing was hypothesized to be a density-dependent mechanism influencing the number of out-migrants. Although density dependence during spawning could also occur, spawning habitat is not considered to be limiting for Chinook Salmon in Puget Sound (Beechie et al. 2006b). Therefore, density-independent and density-dependent processes are hypothesized to occur in sequence for Chinook Salmon in the Skagit River, with density-independent mechanisms occurring during incubation and density-dependent mechanisms operating between emergence and out-migration. The strength of the density-dependent mechanisms is hypothesized to be greater for the subyearling parr and yearling smolt life histories, as they spend longer periods rearing in freshwater than the fry out-migrants. The extent to which the total number of out-migrants is a density-dependent function of spawner abundance will depend on variability in the annual proportions of each out-migrant life history.

METHODS

Study area.—The Skagit River watershed includes 8,030 km² (3,100 mi²) of watershed area and 32,670 ha (80,728 acres) of freshwater tidal delta and estuary (SRSC and WDFW 2005). The freshwater system includes the main-stem Skagit River and four secondary basins: the Baker, Cascade, Sauk, and Suiattle rivers (Figure 1). Peak flows typically occur during two periods of the year: rain-on-snow events between November and February, and snowmelt events typically occurring in May and June (U.S. Geological Survey [USGS], waterdata.usgs.gov/WA/nwis/). The Suiattle and Cascade rivers are dominated by a snowmelt hydrology, whereas the Sauk River and main-stem Skagit River are characterized by a transitional hydrology (combination of rain-on-snow and snowmelt peak flows; Beechie et al. 2006a). Since the 1920s, flows in the main-stem Skagit River downstream of the town of Newhalem

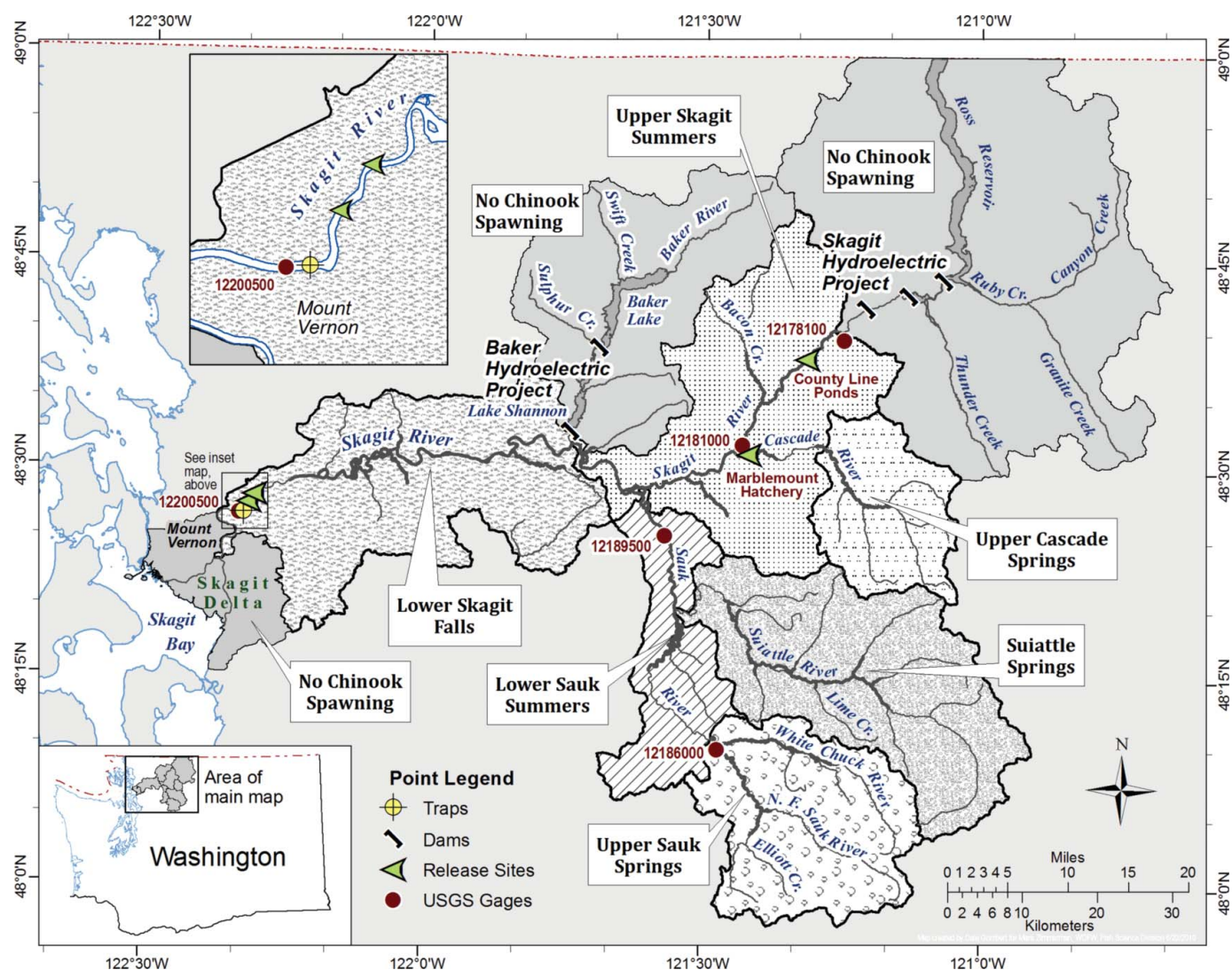


FIGURE 1. Map of the Skagit River basin, Washington, illustrating the spawning distributions of six recognized Chinook Salmon populations, the location of the juvenile trap, and the release sites of marked juvenile Chinook Salmon that were used for trap efficiency trials. Also depicted are the locations of U.S. Geological Survey (USGS) stream gauges selected to represent incubation flows associated with the six stocks (gauge 12200500, Skagit River at Mt. Vernon; 12189500, Sauk River near Sauk; 12186000, Sauk River above Whitechuck; 12181000, Skagit River at Marblemount; 12178100, Newhalem Creek). [Figure available online in color.]

have been regulated by hydroelectric dams located on the upper Skagit River.

Study species.—In the Skagit River, Chinook Salmon spawn between late July and mid-October (SRSC and WDFW 2005; Ruckelshaus et al. 2006). Six spawning populations are named according to the time of river entry (spring, summer, and fall) and the location of spawning (see incubation periods in Table 1). At least three life history strategies are expressed in Chinook Salmon at the time of out-migration from the Skagit River: fry migrants, subyearling parr, and yearling smolts (Hayman et al. 1996; Beamer et al. 2000). Additional diversity of the fry migrants (fry migrants and delta-rearing migrants) is expressed after entry into the estuary but could not be quantified by the methods used in this study. Chinook

Salmon fry out-migrants are assumed to undergo little if any rearing in the main-stem Skagit River, as their size range is comparable with the lengths of emerging fry (40–50 mm FL; Pflug and Mobrand 1989). In comparison, subyearling parr out-migrants rear for several months before migrating to salt-water at an average size of 75 mm FL (Seiler et al. 1998; Kinsel et al. 2008). Yearling smolt out-migrants overwinter in freshwater prior to out-migration at sizes longer than 99 mm FL (Washington Department of Fish and Wildlife [WDFW], unpublished data). Available scale, otolith, and genetic data suggest that each of the life history strategies is present in each of the six Skagit River populations (SRSC and WDFW 2005).

Spawner abundance and potential egg deposition.—Potential egg deposition was derived as the “spawner” variable used

TABLE 1. Flow data selected to represent incubation flows associated with each of the six Chinook Salmon populations in the Skagit River basin, Washington. Flow data were from U.S. Geological Survey (USGS) stream gauges.

Population	USGS gauge (location, gauge number)	Incubation period
Upper Cascade River spring	Newhalem Creek, 12178100	Aug 1–Feb 1
Suiattle River spring	Newhalem Creek, 12178100	Aug 1–Feb 1
Upper Sauk River spring	Sauk River above Whitechuck, 12186000	Aug 15–Feb 1
Lower Sauk River summer	Sauk River near Sauk, 12189500	Aug 25–Mar 1
Upper Skagit River summer	Skagit River at Marblemount, 12181000	Aug 20–Mar 1
Lower Skagit River fall	Skagit River at Mt. Vernon, 12200500	Sep 15–Mar 1
Basinwide	Skagit River at Mt. Vernon, 12200500	Aug 1–Mar 1

in the spawner–out-migrant model. Potential egg deposition (female spawner abundance multiplied by average fecundity) was calculated separately for each spawning population and then was summed across populations for a basinwide estimate. The term “potential” egg deposition reflects the uncertainty in spawning success that inevitably influences the true number of fertilized eggs in the gravel.

Abundance of female spawners was derived from surveys conducted annually on the Skagit River by state and tribal biologists. Surveyors used a combination of aerial and ground surveys to enumerate redds and collect biological data from carcasses in selected reaches of the river. The observed number of redds was expanded by the ratio of surveyed area to total spawning area (Connor and Pflug 2004; Greene et al. 2005) and was converted to the abundance of female spawners in a 1:1 ratio (Brett Barkdull, WDFW, Region 4, personal communication).

Average fecundity for a given population and year was estimated by using a fecundity–length regression model and the average female length for that population and year. Length was the average FL of female Chinook Salmon carcasses recovered during spawner surveys in each year. For years when fewer than 10 females were measured for a given population, the average FL for all years was used. Fecundity–length regressions were derived from Chinook Salmon broodstock (spring, summer, and fall runs) collected at the WDFW Marblemount Hatchery. We used an ANCOVA model to test whether fecundity was a function of length (covariate) and run type. A significant interaction ($P < 0.05$) indicated that separate regression models should be applied to each run type.

Juvenile fish collection.—Juvenile traps were located at river kilometer 27 on the Skagit River (Figure 1) and consisted of an inclined-plane trap and a 2.44-m-diameter (8-ft-diameter) screw trap, which were positioned side by side on steel pontoon barges (Seiler et al. 1998; Volkhardt et al. 2007). 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. Data collected from the trap were divided into daytime and nighttime trapping periods because out-migration rates differ between day and night (Reimers 1971; Seiler et al. 1998). Captured fish were enumerated at dusk and dawn, and a subsample of the catch was measured (FL) on a daily basis. Adipose fin clips and coded wire tags were used to distinguish hatchery juveniles from wild juveniles. Since 1994, all hatchery releases have been adipose fin clipped, which allows wild and hatchery fish to be differentiated upon capture. Subsamples of juvenile Chinook Salmon were marked and released above the trap at night. Recapture rates of released fish were used as the measure of trap efficiency in estimating total out-migrant abundance.

Subyearling abundance.—Abundance of subyearling Chinook Salmon out-migrants was estimated by expanding the catch in the juvenile trap in a three-step process: (1) missed catch was estimated during trap outages, (2) out-migrant abundance was estimated for the period of trap operation, and (3) out-migration before or after the trapping period was extrapolated. Missed catch was a linear interpolation based on catch rates in the daytime or nighttime strata just prior to and subsequent to the trap outage (Kinsel et al. 2008). Out-migrant abundance during the trapping period was estimated with mark–recapture data and a time-stratified Petersen estimator that accounted for seasonal heterogeneity in capture rates (Carlson et al. 1998; Volkhardt et al. 2007). Strata were assigned after using a G -test (Sokal and Rohlf 1981) to compare the ratio of marked fish that were subsequently seen (i.e., recaptured) or unseen (i.e., not recaptured). Total migration was the sum of out-migrant abundance during the trapping period and linear extrapolation for the periods before and after trapping. The assumed start and end dates of the Chinook Salmon migration were January 1 and August 31 based on observations from expanded trapping seasons early in the study (Seiler et al. 2002). Extrapolation was necessary because the trap typically operated between mid-January and the end of July, but the exact dates varied among years. Additional details of subyearling estimates are provided by Seiler et al. (1998) and Kinsel et al. (2008).

Fry and subyearling parr abundance.—Weekly abundance of subyearlings was divided into fry and subyearling parr life histories. A subsample of Chinook Salmon out-migrants was measured each week, and individual fish were assigned as (1) fry if less than or equal to 45 mm FL or (2) parr if longer than 45 mm FL. Weekly fry and subyearling parr abundance was calculated as the total weekly subyearling abundance

multiplied by the proportions of each life history in the weekly length subsample. Total fry and subyearling parr abundance was the sum of the respective weekly estimates.

Yearling smolt abundance.—The abundance of yearling smolts was estimated by expanding catch in the juvenile trap with a surrogate trap efficiency, as yearling Chinook Salmon were not caught in sufficient numbers to allow for efficiency trials with this life stage. Seasonal trap efficiency for Coho Salmon *O. kisutch* smolts was used as a surrogate because this species is of similar body size and out-migration timing as the yearling Chinook Salmon smolts. Coho Salmon smolts were marked and released from tributary traps above the main-stem trap and were recaptured at the main-stem trap throughout the season (Seiler et al. 1998; Kinsel et al. 2008). Coho Salmon smolt abundance was estimated by using a Petersen estimator with the Chapman modification (Volkhardt et al. 2007). Catch of yearling Chinook Salmon smolts was then expanded by the seasonal trap efficiency for Coho Salmon (i.e., ratio of smolt abundance to smolt catch for Coho Salmon).

Streamflow.—Streamflow data from five USGS stream gauges throughout the Skagit River watershed were selected to represent the river flows experienced by the six Skagit River Chinook Salmon populations during their egg incubation periods (Table 1; Figure 1). Current or long-term continuous records of streamflow within the spawning area were not available for two of the six populations—the upper Cascade River and Suiattle River spring runs. Therefore, we used results from the Newhalem Creek gauge as a surrogate to represent flow conditions for both populations. This selection was based on the similar hydrograph shape for the Chinook Salmon spawning areas in these subbasins (Beechie 1992). For example, spawning of Suiattle River spring Chinook Salmon is largely restricted to the lower sections of clear-water tributaries, which are more similar in size and hydrology to Newhalem Creek than to the turbid main-stem Suiattle River. Flow data from the Skagit River gauge located near Mount Vernon were selected to represent the basinwide metric because this gauge is the downstream-most gaging station in the Skagit River watershed and is located downstream of all Chinook Salmon spawning areas.

The incubation period for each Chinook Salmon stock was defined as the period between redd construction and the date by which the majority of the fry had emerged. Delineation of this period was based on spawner survey observations and fry emergence timing assessments conducted using backpack electrofishing methods in 1997 and 1998 for each Chinook Salmon population in the Skagit River (Skagit River Systems Cooperative, unpublished data).

Peak incubation flows were represented by the maximum daily average flow at the associated stream gauge during the incubation period (Table 1). We also examined the duration of flows exceeding a flood RI of 1 or 2 years. Data were evaluated with respect to both of these RIs because the flows associated with effective discharge (i.e., maximum substrate

mobilization) vary among watersheds (Wolman and Miller 1960; Nash 1994; Soar and Thorne 2011) and were not specifically known for the Skagit River watershed. Flood RIs were calculated using the annual maximum daily discharge (1954–2010) fitted to log Pearson type III return intervals that included regional skew values (IACWD 1982).

Pearson's product-moment correlation (with coefficient r) was used to test whether flow metrics were correlated among years, and a Kruskal–Wallis test was conducted to determine whether flow metrics differed among populations. For both analyses, peak flow RIs were log transformed prior to analysis. A P -value less than 0.05 was considered to indicate statistical significance.

Prior to investigating the contribution of incubation flow to freshwater survival, flow metrics for a given year were calculated as basinwide and stock-specific metrics and then were normalized for input into the spawner–out-migrant models described below. The basinwide metric represented incubation flows with a single flow gauge (Table 1). The stock-specific metric weighted the incubation flows from locations associated with each population by the relative egg deposition for each population and year. Peak flow metrics were log transformed, and all flow metrics were normalized by subtracting the mean value and dividing this difference by the SD among years.

Out-migrant abundance as a function of spawners and flow.—A linear regression model was used to explore how well the individual flow metrics predicted egg-to-out-migrant survival. Egg-to-out-migrant survival (total number of out-migrants divided by potential egg deposition) was log transformed prior to analysis and was regressed on the incubation flow metrics. Models with a P -value less than 0.05 were considered significant, and models with high R^2 values were interpreted as being better predictors of egg-to-out-migrant survival than models with low R^2 values.

A model selection process was used to evaluate whether the abundance of out-migrating Chinook Salmon was better predicted by density-independent or density-dependent survival and whether the inclusion of environmental flow metrics improved these predictions. Spawner data (potential egg deposition) and recruit data (out-migrant abundance) were fitted with linear and nonlinear models. The linear model represented the hypothesis that egg-to-migrant survival rates are independent of spawner abundance (Table 2). The nonlinear Beverton–Holt model represented the hypothesis that egg-to-migrant survival rates decrease with increasing spawner abundance and that the number of out-migrants approaches some asymptotic level as spawner abundance increases. The models were fitted with and without adjustments for the peak incubation flows and the duration of moderate flows ($RI > 1$ year or 2 years). In the Beverton–Holt model, flow parameters were incorporated to modify the productivity parameter (p), consistent with the hypothesis that density-independent mortality due to flow occurs during egg incubation and that density-dependent mortality (i.e., unrelated to flow) occurs after

TABLE 2. Models used to explain the relationship between Chinook Salmon spawners and out-migrants in the Skagit River basin. Parameter m is the slope of the density-independent model; parameters p (productivity) and c (capacity) describe the density-dependent (Beverton–Holt) model. Models were fitted with spawner (S ; potential egg deposition) and recruit (R ; out-migrants) data, with or without flow parameters (a = coefficient of flow peak or duration; F = normalized flow peak or duration).

Hypothesis	Model
Out-migrants are a density-independent function of spawner abundance	$\log_e(R) = \log_e(m) + \log_e(S)$
Out-migrants are a density-independent function of spawner abundance and incubation flows	$\log_e(R) = \log_e(m) + \log_e(S) + aF$
Out-migrants are a density-dependent function of spawner abundance	$\log_e(R) = \log_e(p \times S) - \log_e\left(1 + \frac{p}{c} \times S\right)$
Out-migrants are a density-dependent function of spawner abundance and are a density-independent function of incubation flows	$\log_e(R) = \left[\log_e\left(p \times e^{aF} \times S\right)\right] - \left[\log_e\left(1 + \frac{p \times e^{aF}}{c} \times S\right)\right]$

emergence. Prior to analysis, both spawner and out-migrant data were log transformed to obtain the additive error structure required for a least-squares model fit (Quinn and Deriso 1999). The two model types are hereafter referred to as the density-independent (linear) and density-dependent (Beverton–Holt) models.

Fourteen different models were fitted to the data by using the least-squares method and the Fisheries Stock Assessment package in R (Ogle 2012; R Development Core Team 2014). The best-fitting model was selected by using Akaike's information criterion corrected for sample size (AIC_c) and number of model parameters using the AICcmodavg package in R (Mazerolle 2014). Support for a given model was evaluated as the difference in AIC_c value (ΔAIC_c) between that model and

the model with the lowest AIC_c (Burnham and Anderson 2002). Models with ΔAIC_c values between 0 and 3 were considered to have substantial support, those with ΔAIC_c values between 4 and 7 were considered to have less support, and those with ΔAIC_c values greater than 7 were considered to have no support (Burnham and Anderson 2002). The AIC weight (w_i) was interpreted as the probability that model i was the best model given all evaluated models and data available (Burnham and Anderson 2002). Nonparametric bootstrapped 95% confidence intervals (CIs) for model parameters were calculated using the nlstools package in R (Baty et al., in press). Overall model fit was evaluated by using an F -test to compare the density-independent and density-dependent models to a null model (average out-migrant abundance). Model comparisons with P -values less than 0.05 were considered to have improved fit over the null model.

Out-migrant life histories as a function of spawners.—A model selection process (AIC_c) was used to compare the fit of density-independent and density-dependent models to spawner–recruit data for each juvenile life stage. Results were interpreted by using the same criteria for evaluating ΔAIC_c and model fit as described above.

RESULTS

Spawner Abundance and Potential Egg Deposition

Escapement of Skagit River Chinook Salmon ranged between 2,158 and 10,051 females between 1993 and 2008, with upper Skagit River summer Chinook Salmon comprising the majority (72%) of all spawners (Table 3). Over the study period, potential egg deposition averaged 32 million eggs/year and ranged between 12 and 62 million eggs/year (Supplementary Table S.1 in the online version of this article). Annual average FL of females from the six spawning populations ranged from 83 to 92 cm. Estimated annual average fecundity ranged between 4,949 and 6,218 eggs/female. Fecundity was positively correlated with FL ($F_{1, 702} = 370.4$, $P < 0.001$) and differed among the spring, summer, and fall runs ($F_{2, 702} = 30.4$, $P < 0.001$). Therefore, the fecundity F of each stock was estimated by using run-specific regressions ($F_{spring} = 91 \cdot FL - 2,226$; $F_{summer} = 103 \cdot FL - 3,272$; $F_{fall} = 110 \cdot FL - 4,634$).

TABLE 3. Average (\pm SD) annual number, FL (cm), and fecundity (eggs per female) of female Chinook Salmon spawners in the Skagit River basin for brood years 1993–2008. Potential egg deposition (PED) was calculated from the number and fecundity of female spawners for each population and brood year.

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

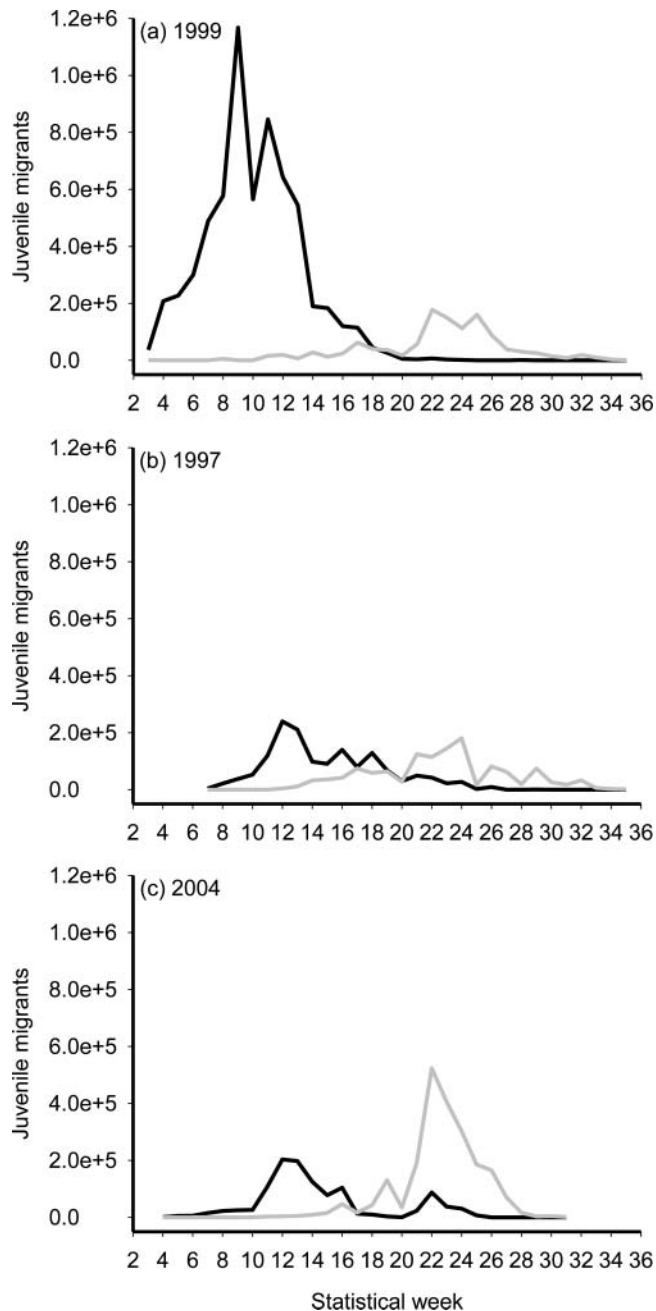


FIGURE 2. Examples of bimodal migration by Skagit River Chinook Salmon subyearling out-migrants partitioned into fry (black lines) and parr (gray lines) life history strategies: (a) migration year 1999, when fry abundance was higher than parr abundance; (b) migration year 1997, when fry and parr abundances were equal; and (c) migration year 2004, when parr abundance was higher than fry abundance.

Out-Migrant Abundance and Survival

The number of Chinook Salmon out-migrants in the Skagit River averaged 3.5 million per brood year and ranged nearly eightfold between the 1993 and 2008 brood years (Table S.1). Egg-to-out-migrant survival ranged from 4.5% to 21.5%, equivalent to 270–1,230 out-migrants/female.

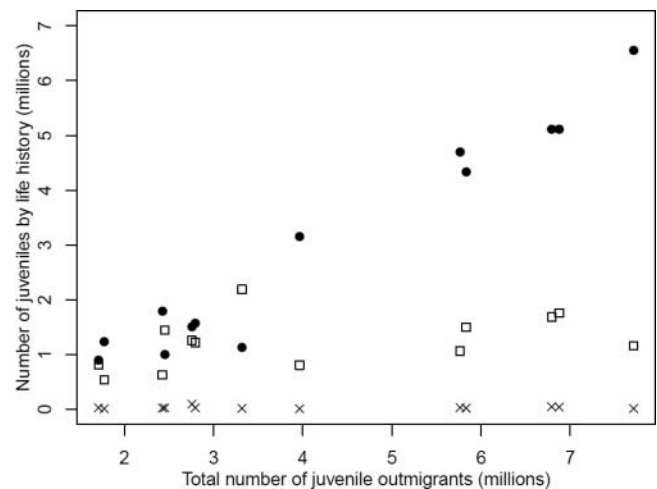


FIGURE 3. Expression of three freshwater life history strategies among out-migrant Chinook Salmon in the Skagit River for brood years 1996–2008. The numbers of fry (black circles), subyearling parr (open squares), and yearling smolts (x-symbols) migrants are shown as a function of total out-migrant abundance for each brood year. Points represent the abundance of each life history strategy for a given brood year.

Out-Migrant Life History Strategies

Subyearling out-migrants represented 96.3–99.9% of the total freshwater production of Skagit River Chinook Salmon for brood years 1993–2008 (Table S.1). Over this time period, fry migrants varied sevenfold (905,000–6,553,000 fish) and parr migrants varied fourfold (537,000–2,188,000 fish). Yearling migrants ranged between 6,000 and 97,000 fish and varied 16-fold. Out-migration of subyearlings was consistently bimodal (Figure 2). The proportion of fry and parr migrants varied from year to year, and the proportion of fry increased as the number of out-migrants increased (Figure 3).

Flow Metrics

Among all stocks and years, the magnitude of peak flows ranged between an RI of 1 year and an RI of 207 years. The 207-year RI corresponded to an estimated daily average flow of 1,132.68 m³/s (40,000 ft³/s) in the upper Sauk River during 2003. All other annual peak flows in the time series were below a 60-year RI. Duration of daily flows exceeding an RI of 1 year ranged between 0% and 44% of the incubation period. Duration of daily flows exceeding an RI of 2 years ranged between 0% and 11% of the incubation period. Annual flow metrics are provided in Table S.1.

Incubation flow metrics (peak and duration) were highly correlated within each population. Pearson's *r*-values ranged between 0.60 and 0.94, and all but one comparison (pairwise comparison of RI > 1 year versus RI > 2 years for upper Sauk River spring Chinook Salmon) had a slope that was significantly different from zero ($P < 0.05$).

The proportion of the incubation period with flows exceeding a 1-year flood RI differed among populations

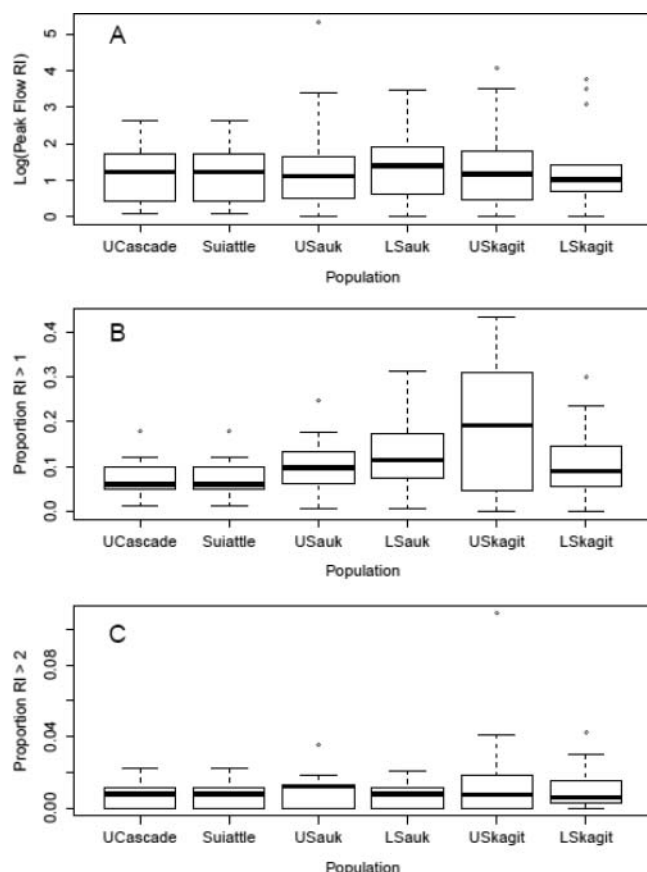


FIGURE 4. Box plot of streamflow metrics during the egg incubation period for Chinook Salmon in the Skagit River between 1993 and 2008: (a) peak flow, which is the maximum daily average flow converted to a flood recurrence interval (RI) and \log_e transformed; (b) proportion of the incubation period with flows exceeding a flood RI of 1 year ($RI > 1$); and (c) proportion of the incubation period with flows exceeding a flood RI of 2 years ($RI > 2$). The bold horizontal line denotes the median value, boxes frame the middle 50% of the values, whiskers represent the range of values (excluding outliers), and points represent outliers that are more than 1.5 times the upper or lower quartile (top or bottom of the box).

(Kruskal–Wallis $\chi^2 = 2.4$, $df = 5$, $P = 0.03$). Upper Skagit River summer Chinook Salmon experienced the longest duration of flows above this threshold (Figure 4b). In comparison, the magnitude of peak flows (Figure 4a) and flow durations above a 2-year RI (Figure 4c) did not differ among populations ($P > 0.70$).

Total Out-Migrant Abundance as a Function of Spawners and Flow

Egg-to-out-migrant survival was negatively correlated with four of the six flow metrics (Figure 5). Two of the individual survival–flow regressions (basinwide flow duration greater than a 1-year RI; and stock-specific flow durations greater than a 2-year RI) were not significantly different from the null

model. Stock-specific incubation flow durations exceeding a 1-year RI explained 48% of the variation in survival, more than any of the other individual flow regressions.

Two of the 14 spawner–out-migrant models had substantial support ($\Delta AIC_c \leq 3$), and both were density-independent models (Tables 4, 5). The top models included a stock-specific metric of flow duration exceeding a 1-year RI and a basinwide metric of peak flow magnitude. Based on w_i values, there was (1) a 47% probability that the best of the selected models was a density-independent model with stock-specific flow durations greater than a 1-year RI; and (2) a 14% probability that the best of the selected models was a density-independent model with a basinwide metric of peak flow. The density-dependent model that included these same two flow metrics received less support than the density-dependent model with these flow metrics, suggesting that the additional parameter in the density-dependent model did not improve fit to the data. The F -tests used to evaluate model fit indicated that both the density-independent and density-dependent models improved fit to the data over the null model alone ($P < 0.001$).

Out-Migrant Life Histories as a Function of Spawners

Support for density-independent versus density-dependent models differed among rearing strategies. When fitted to the fry data, the density-independent model was more strongly supported than the density-dependent model ($\Delta AIC_c > 3$; Figure 6b; Tables 6, 7). Based on w_i , there was an 85% probability that the density-independent model was the better of the two models for predicting fry abundance. In comparison, when fitted to the subyearling parr data, the density-dependent model was more strongly supported than the density-independent model ($\Delta AIC_c > 7$; Figure 6c; Tables 6, 7). Akaike weights indicated a 98% probability that the density-dependent model was the better of the two models for predicting subyearling parr abundance. Based on the Beverton–Holt model, freshwater capacity (i.e., parameter c) was approximately 1.4 million ($\pm 95\%$ CI = 692,000) subyearling parr of Chinook Salmon. The productivity parameter (p) value of 0.245 had an unrealistically high upper 95% confidence limit (> 1.0), indicating imprecision in this parameter estimate given the available data. Density-independent and density-dependent models had similar support when fitted to the yearling smolt data ($\Delta AIC_c = 1.76$; Figure 6d; Table 6). The yearling smolt analysis yielded similar results when conducted with versus without one outlier (brood year 1996; 97,000 yearlings). This data point was two times greater than the next-highest annual estimate and four times greater than the average annual number of yearling smolts. The F -tests for evaluating model fit indicated that use of the density-independent and density-dependent models improved the fit to the fry and subyearling parr data relative to the null

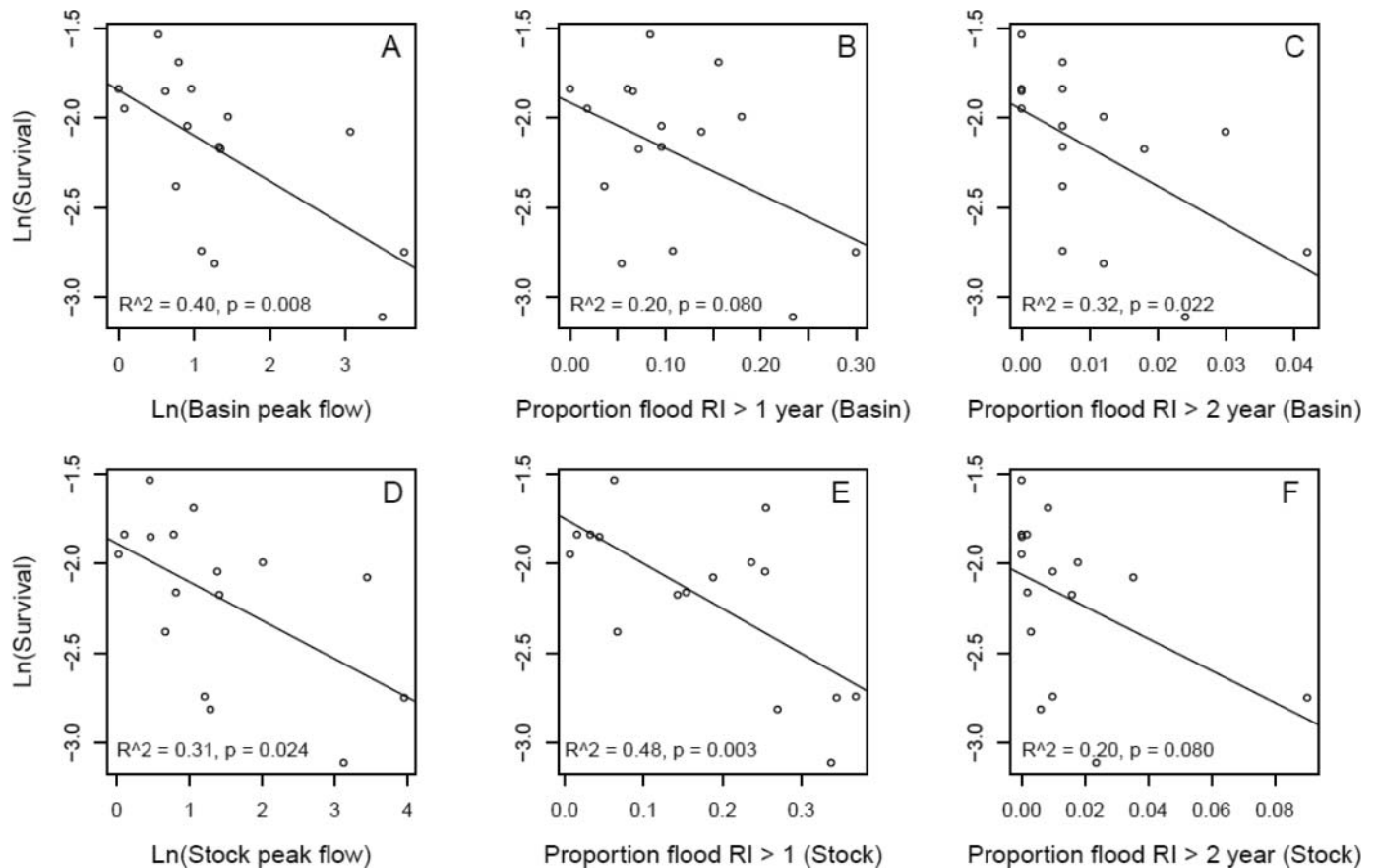


FIGURE 5. Freshwater survival (log transformed) of Chinook Salmon (brood years 1993–2008) as predicted by different incubation flow metrics for the Skagit River: (a) basinwide peak flow recurrence interval (RI; \log_e transformed) during the incubation period; (b) basinwide proportion of the incubation period with flows exceeding a 1-year flood RI ($RI > 1$); (c) basinwide proportion of the incubation period with flows exceeding a 2-year flood RI ($RI > 2$); (d) stock-specific peak flow RI (\log_e transformed) during the incubation period; (e) stock-specific proportion of the incubation period with flows exceeding a 1-year flood RI; and (f) stock-specific proportion of the incubation period with flows exceeding a 2-year flood RI.

model ($P \leq 0.01$) but did not improve the model fit to the yearling smolt data ($P > 0.06$).

DISCUSSION

The abundance of Chinook Salmon out-migrants in the Skagit River was best explained by a combination of density-dependent and density-independent factors. Overall freshwater survival was density independent and influenced by two flow metrics: stock-specific duration of flows exceeding a 1-year RI and a basinwide metric of flow magnitude. A previous study of Chinook Salmon in the Skagit River showed that the magnitude of peak flow events was an important predictor of survival (Greene et al. 2005). The current study explored a broader range of flow metrics and showed that the duration of moderate flows ($RI > 1$ year) was an equivalent if not better predictor of freshwater survival than the magnitude of peak flows. In addition, although overall survival was density independent, the composition of out-migrants (fry, subyearling parr, and yearlings) was a density-dependent function of spawner abundance.

Density-Independent Survival Mediated by Incubation Flows

Density-independent survival resulting from flow events during the egg incubation period means that overall survival will fluctuate independently of spawner abundance. The range of freshwater survival observed for Chinook Salmon in the Skagit River was within the egg-to-fry survival range observed for other salmonid species (Bradford 1995) and was consistent with previous studies demonstrating that the egg incubation period is an important bottleneck to freshwater survival (McNeil 1966; Holtby and Healey 1986; Thorne and Ames 1987; Greene et al. 2005). Estimates of egg-to-out-migrant survival from the Skagit River were much lower than the 60–87% egg-to-fry survival observed for spring Chinook Salmon in the Yakima River (Johnson et al. 2012). However, the Yakima River study was conducted under benign flow conditions, and survival was measured while fry were still in the gravel. Nevertheless, if egg-to-fry survival in the Skagit River is even half that measured by Johnson et al. (2012), a substantial amount of mortality must occur after emergence in order to result in the 4.5–21.5% egg-to-migrant survival we estimated over a 16-year time frame.

TABLE 4. Model selection for predicting the total number of Chinook Salmon out-migrants in the Skagit River (k = number of parameters; LL = log likelihood; AIC_c = Akaike's information criterion corrected for small sample sizes; ΔAIC_c = AIC_c difference between the given model and the best model; w_i = Akaike weight, indicating weight of evidence for model i ; SER = standard error of the regression). Density-independent (DI) and density-dependent (DD) models were fitted to potential egg deposition and out-migrant data (all life histories combined) for brood years 1993–2008 and three metrics of incubation flow: peak flow (Peak), duration of time for which flows exceeded a flood recurrence interval (RI) of 1 year ($RI > 1$), and duration of time for which flows exceeded a flood RI of 2 years ($RI > 2$). Flood variables were either basinwide (Basin) or stock-specific (Stock) values.

Model	k	LL	AIC_c	ΔAIC_c	w_i	SER	df
DI, $RI > 1$, Stock	3	−4.19	16.39	0.00	0.47	0.336	14
DI, Peak, Basin	3	−5.37	18.75	2.36	0.14	0.362	14
DD, $RI > 1$, Stock	4	−3.88	19.40	3.01	0.10	0.342	13
DD, Peak, Basin	4	−4.28	20.20	3.81	0.07	0.351	13
DI, $RI > 2$, Basin	3	−6.39	20.78	4.39	0.05	0.386	14
DI, Peak, Stock	3	−6.47	20.94	4.55	0.05	0.388	14
DD, $RI > 2$, Basin	4	−5.14	21.92	5.54	0.03	0.370	13
DD, Peak, Stock	4	−5.44	22.51	6.12	0.02	0.377	13
DI, $RI > 1$, Basin	3	−7.68	23.35	6.97	0.01	0.418	14
DI, $RI > 2$, Stock	3	−7.68	23.37	6.98	0.01	0.418	14
DD, $RI > 2$, Stock	4	−6.05	23.73	7.34	0.01	0.391	13
DI, No Flow	2	−9.49	23.90	7.51	0.01	0.452	15
DD, $RI > 1$, Basin	4	−6.20	24.05	7.66	0.01	0.396	13
DD, No Flow	3	−8.53	25.06	8.67	0.01	0.441	14

Among the selected flow metrics, the magnitude and duration of flow events represent two different mechanisms. Flow events of large magnitudes will directly affect salmon eggs and alevins by scouring the streambed to the depth of the egg pocket (Holtby and Healey 1986; Montgomery et al. 1996; Devries 1997). Large flow events may also displace recently emerged fry downstream, thus reducing availability of preferred or suitable rearing habitats (Seegrist and Gard 1972; Erman et al. 1988; Latterell et al. 1998). In comparison, sustained flows of moderate magnitude ($RI > 1$ year) 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, premature emergence, and decreased emergent fry size (Koski 1966; Mason 1969). Sediment transport may also entomb the redds and prevent the fry from successfully emerging.

Use of a basinwide metric of flow magnitude but a stock-specific metric of flow duration improved the fit of the

spawner–out-migrant model. Large storms are likely to cause synchronous changes in the magnitude of flows across the watershed, whereas moderate flows ($RI > 1$ year) may be more heterogeneous among subbasins due to differences in spawn timing, subbasin topography, and subbasin hydrology. The hydrology of the Skagit River watershed includes two peak flow periods—one associated with winter precipitation and the other associated with spring snowmelt (Beechie 1992; Beechie et al. 2006a). In the Sauk River and main-stem Skagit River, the highest flows occur during the winter storms and correspond with the egg incubation period. In the Suiattle River and Cascade River subbasins, the highest flows occur during the spring snowmelt and correspond to the early summer rearing period for recently emerged juveniles. Despite these differences, a population-specific influence of peak flow magnitude on survival had the potential to be masked in our analysis because a majority of the egg deposition was represented by a single population (the upper Skagit River summer run), and the peak flows associated with this population are commonly dampened by the storage capabilities of the hydroelectric project located directly upstream (Connor and Pflug 2004). Improved resolution of population-specific responses to flow and spawner abundance may be possible if genetic tools are identified to discriminate the less-abundant Chinook Salmon populations from the most abundant population, the upper Skagit River summer run.

Density-Dependent Out-Migrant Life Histories

The occurrence of subyearling and yearling out-migrants from the same brood year in Chinook Salmon is widely

TABLE 5. Nonparametric bootstrapped coefficients (95% confidence interval in parentheses) for the top models predicting the total number of Chinook Salmon out-migrants in the Skagit River for brood years 1993–2008 (m = slope; a = flow coefficient). See Table 4 for model definitions.

Model	m	a
DI, $RI > 1$, Stock	0.113 (0.098–0.133)	−0.319 (−0.469 to −0.149)
DI, Peak, Basin	0.112 (0.095–0.133)	−0.283 (−0.458 to −0.113)

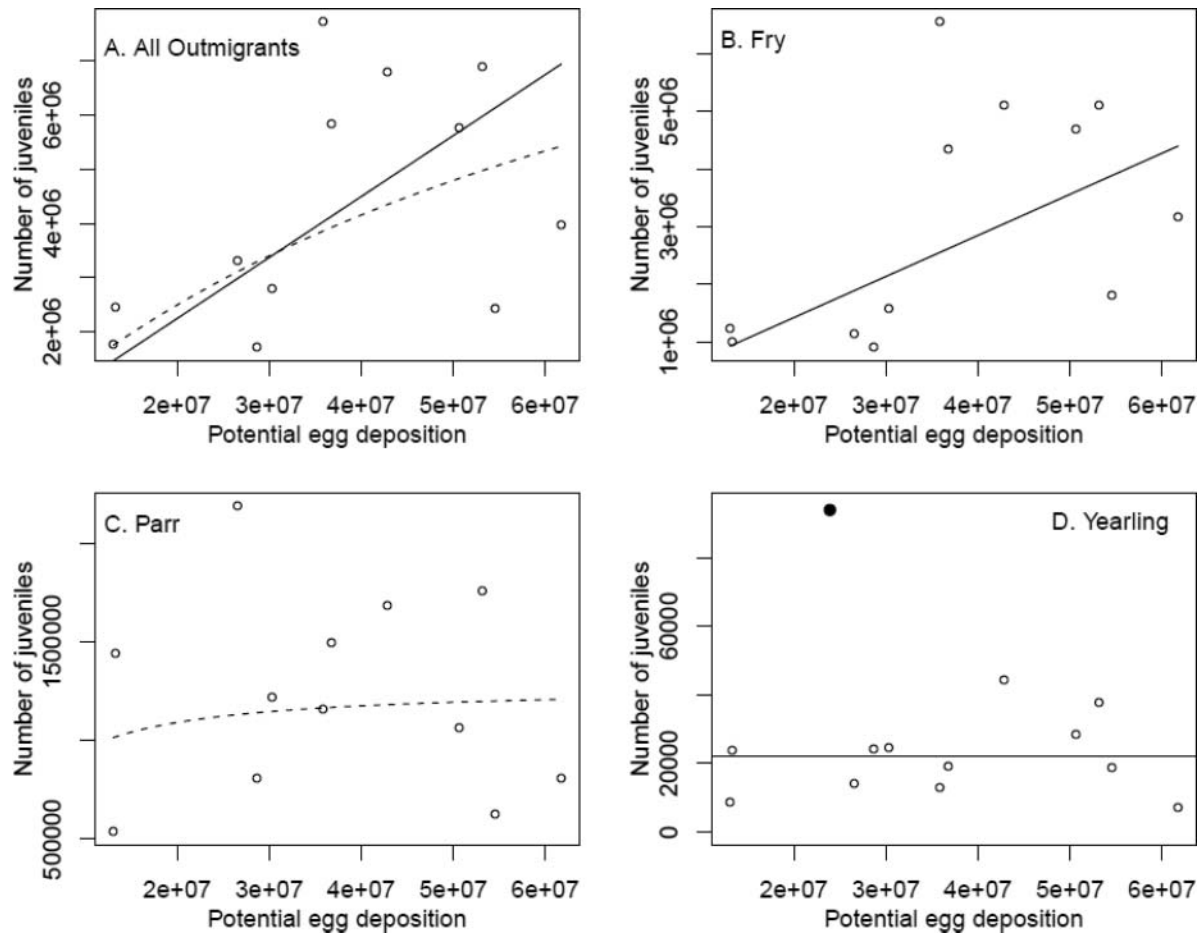


FIGURE 6. Freshwater life history strategies of Chinook Salmon as a function of potential egg deposition in the Skagit River basin. Points represent annual estimates of (a) all out-migrants, (b) subyearling fry out-migrants, (c) subyearling parr out-migrants, and (d) yearling smolt out-migrants. Lines represent the best-fit density-independent (solid line) and density-dependent (dashed line) models for each data set. The outlier (shaded circle) in panel d was not used in the model.

recognized (Healey 1998; Waples et al. 2004), although one of these life history types is typically more abundant than another within a given population. In the Skagit River watershed, individuals that out-migrated as subyearlings and yearlings are observed among the returning spawners for all six populations, but the annual contributions of yearling out-migrants to returning spawners are highest (44–51%) in the upper Cascade River spring, upper Sauk River spring, and Suiattle River spring populations, which spawn in basins with snow-dominant hydrology (Beamer et al. 2005b). Alternate life histories of subyearling migrants, such as those observed in this study, are also found in other Chinook Salmon populations (Reimers 1971; Taylor 1990; Miller et al. 2010), including watersheds where Chinook Salmon have been introduced (Carl 1984; Davis and Unwin 1989).

Annual variation in the proportions of out-migrant life histories may occur due to voluntary or involuntary instream movement associated with higher densities. In one scenario, juvenile Chinook Salmon swim volitionally downstream to the next available rearing habitat. Dispersal from the natal

habitat during the freshwater rearing period and prior to out-migration has been observed for Chinook Salmon in multiple watersheds (Hamann and Kennedy 2012; Shrimpton et al. 2014), including the Skagit River (Pflug and Mobernd 1989). In a second scenario, juvenile Chinook Salmon that do not secure a suitable sheltered habitat may be involuntarily swept downstream as flows exceed the swimming capacity of 45-mm fry. A third potential scenario is that emerging Chinook Salmon are predetermined to be fry or parr migrants, but the mortality of parr migrants is higher when total juvenile abundance is higher because all of the suitable habitats are already filled. Survival in each of these scenarios may have some genetic basis, as genetics may help to determine which juveniles survive (Johnson et al. 2012), which juveniles disperse (Bradford and Taylor 1997), and which juveniles are better able to secure existing habitat.

Results from this study suggest that subyearling Chinook Salmon may be using the current freshwater rearing habitat of the Skagit River in its entirety. Variables that provide or limit available rearing habitat include the initial distribution of

TABLE 6. Model selection for predicting out-migrant life histories of Chinook Salmon in the Skagit River. Model selection statistics are defined in Table 4.

Model	k	LL	AIC _c	Δ AIC _c	w_i	SER	df
Fry							
Density independent	2	−9.72	24.65	0.00	0.85	0.532	12
Density dependent	3	−9.71	28.09	3.45	0.15	0.555	11
Subyearling parr							
Density dependent	3	−6.37	21.41	0.00	0.98	0.430	11
Density independent	2	−11.95	29.10	7.69	0.02	0.632	12
Yearling smolts							
Density dependent	3	−10.96	30.11	0.00	0.71	0.540	13
Density independent	2	−13.43	31.87	1.76	0.29	0.613	14

redds, the available rearing habitat downstream of spawner locations, and the redistribution of alevins or fry during spring flow events. For example, the majority of annual egg deposition is derived from upper Skagit River summer Chinook Salmon, all of which spawn within a short reach of main-stem channel characterized by regulated flows that dampen the magnitude of peak flow events. This population may have a lower proportion of subyearling parr relative to other populations due to habitat capacity limitations within and downstream of this spawning area. Although few studies have addressed freshwater rearing habitats for Chinook Salmon subyearling parr, low-velocity edge and backwater habitats along the banks of the river, off-channel habitat, and large log-jams appear to be important for this life stage in the Skagit River (Hayman et al. 1996; Beechie et al. 2005; Lowery et al. 2013) and elsewhere (Limm and Marchetti 2009).

Our analysis could not distinguish between either density independence or density dependence of yearling smolts. The poor model fit for the yearling smolts likely resulted from several sources of data uncertainty. The mark–recapture estimate of yearling smolts relied on a surrogate trap efficiency derived from Coho Salmon smolts, which added unknown bias to the estimate. In addition, the yearling smolt life history is primarily expressed in the spring-run populations of the upper Sauk, Suiattle, and Cascade River subbasins (Beamer et al. 2005b; Beechie et al. 2006a), and these populations represented an

average of just 8% of the total spawners in the Skagit River watershed (Table 3). Variation in spawner abundance for these populations was likely obscured by the more abundant populations in our analysis. To more fully understand the expression of the yearling smolt life history, additional study of targeted spawning populations will be needed.

Implications for Chinook Salmon Recovery

Variability in freshwater survival of Chinook Salmon may be reduced in areas of the watershed where variation in flows has been dampened by dam operation. Flow regulations for the Skagit River Hydroelectric Project have been modified in order to minimize impacts to salmon and steelhead *O. mykiss*. A reduction in maximum spawning flows and an increase in minimum incubation flows were implemented in the early 1980s and formalized in the 1990s during Federal Energy Regulatory Commission relicensing. Due to their spawning location, the upper Skagit River summer Chinook Salmon are most directly influenced by regulated flows. This population has represented an increasing proportion of all Chinook Salmon from the Skagit River over a 30-year period—a result that is attributed to changes in regulated flow management (Conner and Pflug 2004). Results from the current study suggest that the survival benefit of dampened flow magnitudes could be offset if the

TABLE 7. Nonparametric bootstrapped coefficients (95% confidence interval in parentheses) for the top models predicting out-migrant life histories of Chinook Salmon in the Skagit River for brood years 1993–2008 (m = slope in the density-independent model; p = productivity parameter in the density-dependent model; c = capacity in the density-dependent model). A null model (average abundance) coefficient is provided for the yearling smolt life history because the spawner–recruit model did not improve the fit relative to that of the null model.

Model	Intercept	m or p	c ($\times 10^6$)
Fry			
Density independent		0.071 (0.052–0.098)	
Subyearling parr			
Density dependent		0.245 (0.065–4.560)	1.39 (1.04–2.64)
Yearling smolt			
Null model	24,076 (12,582–35,569)		

duration of more moderate flows ($RI > 1$ year) increases in the process. Indeed, upper Skagit River summer Chinook Salmon experienced the highest flow durations (Figure 4b) of all populations in the Skagit River watershed. Therefore, our results indicate that freshwater survival of this population may increase if the duration of moderate flows is reduced to levels more similar to those in the other subbasins.

Although we demonstrated that survival in the Skagit River is a function of the magnitude of incubation flows, examination of these results in a historical context is important. Disturbance regimes are characteristic of the Pacific Northwest region, where Chinook Salmon have persisted for thousands of years (Waples et al. 2008). As one example, the magnitude of flows in the Skagit River prior to the water storage projects was nearly two times the magnitude observed after the river was dammed (Beamer et al. 2005a). Despite higher incubation flows in some years, Chinook Salmon populations were self-sustaining during the period prior to dam construction. This suggests that while the magnitude of peak flows contributes to annual freshwater productivity (Greene et al. 2005; Waples et al. 2008), variables in addition to peak flows are needed to explain the low present-day abundance of Chinook Salmon in the Skagit River basin.

One implication of the density-dependent expression of juvenile life history strategies is that freshwater productivity of Chinook Salmon could be improved by increases in the quality and quantity of freshwater rearing habitat. Backwater areas, natural banks, and off-channel habitat in the middle and lower portions of the Skagit River are of particular importance for Chinook Salmon rearing and survival given that the majority of spawning occurs in the main stem and all out-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 River have reduced the width of floodplain habitat and the floodplain's connectivity with the river (Beamer et al. 2005b). In addition, freshwater rearing habitat in the Cascade, Suiattle, and Sauk rivers appears to be particularly important for the yearling smolt life history (Beamer et al. 2005b). Although understanding the density dependence of the yearling smolt life history will require additional work beyond this study, habitat protection and restoration that target these subbasins will also target this out-migrant life history (Beechie et al. 2006a).

Out-migrant life history diversity and supporting habitats, as well as overall genetic diversity (Ozerov et al. 2012; Gharrett et al. 2013), are important for the long-term resilience of Chinook Salmon populations in the Skagit River. The link between diversity and resilience has been described as a "portfolio effect" wherein long-term growth is supported by short-term, nonsynchronous fluctuations among its components (Greene et al. 2009; Schindler et al. 2010). Such diversity may buffer fisheries and minimize rates of species

extinction (Schindler et al. 2010). In the Skagit River, the Chinook Salmon "portfolio" includes six adult spawning populations and at least three juvenile life histories in freshwater (one additional juvenile life history is expressed after marine entry). In addition to freshwater capacity, the population productivity of Chinook Salmon depends on the capacity of downstream delta or estuarine habitats (e.g., Beamer et al. 2005c), the relative return rates of different life history strategies, and overall survival in the marine environment.

Management of Chinook Salmon in the Skagit River will require an understanding of both density-independent and density-dependent mechanisms operating in freshwater and estuarine habitats. Our results show that freshwater survival is density independent and that sustained flow events of moderate magnitude (1-year RI) may have as large an impact on freshwater survival as short-duration flow events of high magnitude (peak flows). Furthermore, our results demonstrate that the expression of juvenile life histories is density dependent and that life history types with extended freshwater rearing will benefit from continued restoration of freshwater rearing habitats.

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