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ARTICLE

Interannual variability in the effects of physical habitat and parentage on Chinook salmon egg-to-fry survival

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Abstract: Mortality during incubation is believed to be a major factor limiting the recovery of many salmon populations, though direct field measurements of egg-to-fry survival are rare or small in scale. To determine the effects of physical habitat (river reach, fine sediment intrusion, scour), parentage (mating, source of gametes) on Chinook salmon (*Oncorhynchus tshawytscha*) egg-to-fry survival and developmental stage at emergence across a basin, we constructed 324 artificial redds in nine reaches over 4 years in the Yakima River Basin, Washington, USA. Mean egg-to-fry survival ranged from 49% to 69% annually from 2009 to 2012 brood years. Survival was significantly different among reaches in 2010, but not in 2009, 2011, or 2012, while mating was a significant factor in all years but 2010. In contrast, developmental stage differed significantly among reaches and matings in all 4 years. Percentage of fines, days-in-gravel, and median particle size explained only small (<10%) additional amount of variation in survival or developmental stages. Our results suggest that parentage and reach within a basin are major factors influencing egg-to-fry survival, but their relative influence varies annually, presumably depending on the magnitude of high flows and scour during incubation.

Résumé : S'il est estimé que la mortalité durant l'incubation serait un important facteur limitant du rétablissement de nombreuses populations de saumons, les mesures directes sur le terrain du taux de survie durant la transition œuf-alevin sont rares ou d'ampleur limitée. Afin de déterminer les effets de l'habitat physique (tronçon du cours d'eau, intrusion de sédiments fins, affouillement) et de l'ascendance (croisement, source de gamètes) sur le taux de survie œuf-alevin et le stade de développement au moment de l'émergence à l'échelle d'un bassin chez les saumons quinnats (*Oncorhynchus tshawytscha*), nous avons construit 324 nids de frai artificiels dans neuf tronçons sur une période de 4 ans, dans le bassin versant de la rivière Yakima (État de Washington, États-Unis). Le taux de survie œuf-alevin moyen allait de 49 % à 69 % selon le tronçon pour les années d'éclosion de 2009 à 2012. Le taux de survie variait de manière significative entre les tronçons en 2010, mais non en 2009, 2011 et 2012, alors que le croisement était un facteur significatif pour toutes les années sauf 2010. En revanche, le stade de développement variait de manière significative selon le tronçon et le croisement pour les 4 années. Le pourcentage des sédiments fins, les jours dans le gravier et la taille médiane des particules n'expliquaient qu'une petite partie (<10 %) de la variation du taux de survie ou du stade de développement. Nos résultats donnent à penser que l'ascendance et le tronçon au sein d'un bassin versant sont des facteurs qui exercent une influence majeure sur la survie durant la transition œuf–alevin, mais que leur influence relative varie d'une année à l'autre, vraisemblablement selon la magnitude des crues et de l'affouillement durant l'incubation. [Traduit par la Rédaction]

Introduction

Mortality prior to senescence is typically highest in early life stages for many vertebrates and invertebrates (Caughley 1966). For example, the highest mortality for many viviparous vertebrates such as elephants (*Loxodonta africana* and *Elephas maximus*), gray whales (*Eschrichtius robustus*), marine fishes, and even humans occurs following conception through the first few days or weeks following birth (Levitis 2011). Similarly in aquatic environments, the highest mortality for oviparous vertebrates is during egg deposition, fertilization, development, and shortly after hatching (Bunn et al. 2000; Vonesh and De la Cruz 2002). This is particularly the case for teleost fishes, which often produce thousands of eggs at each spawning (Anderson 1988; Bunn et al. 2000; Duarte and Alcaraz 1989). While fertilization to fry emergence is a critical life stage, it has rarely been studied in most fishes, and even if studies have been conducted, they have been confined to highly controlled laboratory experiments or based on survival at older life stages. Salmonid fishes — despite being one of the most economically important and well-studied of all fish families — are no exception. Numerous studies have examined egg-to-fry survival in the laboratory or focused on counting total adults into a stream and enumerating outmigrating fry or parr several months later rather than direct measuring of egg-to-fry survival (Bradford 1995; Healey 1991; Jensen et al. 2009). This is largely due to the difficulty in conducting field studies to estimate and isolate the variety of environmental factors that may influence survival during development of embryos in a redd and immediately following hatching (Quinn 2005; Sear and DeVries 2008).

Physical factors thought to reduce egg-to-fry survival and limit productivity of salmonid populations including fine sediment,

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dissolved oxygen (DO), gravel size, scour, and fitness of parents and their gametes. Laboratory and field studies have shown a negative relationship between fine sediment levels and salmonid egg-to-fry survival (Chapman et al. 2014; Jensen et al. 2009; Kemp et al. 2011; Levasseur et al. 2006). Fine sediment infiltration into the redd or egg pocket can reduce intergravel flow and DO and suffocate eggs (Chapman 1988; Greig et al. 2005). In other cases it may create a seal above the redd, "entombing" embryos and preventing them from emerging from the gravel (Chapman 1988). The infiltration of low DO groundwater into the egg pocket has been shown to increase egg and embryo mortality in some streams with strong groundwater upwelling (Malcolm et al. 2011; Sowden and Power 1985). In addition to fine sediment, the substrate size in spawning area or redd can influence egg-to-fry survival (Kondolf et al. 2008). Scour of gravels from high flows during egg incubation, which may last several months in colder streams, can also reduce survival (DeVries 1997, 2008). Stream temperature can directly affect survival if it exceeds lethal limits, but can also indirectly influence survival by causing eggs to develop faster or slower and lead to shorter or longer periods in the gravel, resulting in the hatch or emergence of fry when opportunities for growth and development are suboptimal (Murray and McPhail 1988; Quinn 2005; Richter and Kolmes 2005). Moreover, cooler temperatures can lead to longer incubation period, increasing the potential for embryos to be impacted by fine sediment intrusion, scour, predation, or other factors. Biological factors that may influence egg-to-fry survival, which include not only predation, but parental fitness or fitness of their gametes, are also thought to have a strong effect on survival of eggs and embryos (Johnson et al. 2012; Rubin 1995; Young et al. 1990). Studies on Chinook salmon have indicated that parentage or genetic factors can have a strong influence on survival in the hatchery (Evans et al. 2010; Heath et al. 1999), but more recently there is evidence in the natural environment as well (Johnson et al. 2012).

Estimates of life-stage-specific survival are critical for management, recovery, and protection of endangered salmonids such as Chinook salmon (*Oncorhynchus tshawytscha*), which are listed as threatened or endangered under the Endangered Species Act throughout most of their native range in the United States excluding Alaska (Good et al. 2005). Efforts to recover these populations have resulted in hundreds of millions of dollars (US) spent on improving spawning and rearing habitat in streams in the Pacific Northwest and California (Katz et al. 2007). Degradation and loss of spawning habitat is thought to be one of the major factors limiting Chinook salmon populations (Myers et al. 1998). Life-cycle models for some endangered populations of Chinook salmon report egg-to-fry or early life stage survival as one of the main factors limiting population recovery (Kareiva et al. 2000; Honea et al. 2009). However, little data exist on Chinook egg-to-fry survival in the natural environment (Bradford 1995; Healey 1991; but see Merz et al. 2004), and population models rely on combining survival from egg deposition to smolt outmigration or using relationships developed in the laboratory between fine sediment and egg-to-fry survival (Honea et al. 2009; Jensen et al. 2009; Kareiva et al. 2000; Scheuerell et al. 2006). Importantly, there is little information on the temporal and spatial variation in Chinook salmon egg-to-fry survival throughout a watershed. In particular, most field studies on egg-to-fry survival for Chinook and other salmonids have consisted of intensive study in one or a few reaches of a stream or a small number (<15) of artificial redds over a 1- or 2-year period. To provide useful information and data to guide salmon recovery, reintroduction, habitat restoration, and life-cycle modeling efforts, empirical egg-to-fry survival estimates are needed across a basin in multiple years.

In 2009, we initiated a 4-year study within the Yakima Basin to quantify Chinook salmon egg-to-fry survival across a basin and examine the effect of river reach, mating (parentage), and the influence of other physical factors (fine sediment intrusion and scour) on Chinook salmon egg-to-fry survival. We reported on the methods and findings from our first year of study in Johnson et al. (2012). The preliminary finding was that the source of gametes or mating appeared to be the major factor driving egg-to-fry survival in upper Yakima Basin. An initial criticism of that study was that it was not replicated through time and only looked at fine sediment intrusion and did not examine other physical metrics such as scour and substrate size. In the following paper, we focus on analysis of the complete data set of all 4 years of the study. Our specific objectives were to

(1) provide overall estimates of the natural range of egg-to-fry survival among reaches across a basin over multiple years;

(2) examine if mating and location (reach) have consistent effects on Chinook egg-to-fry survival across all 4 years; and

(3) examine whether scour, fine sediment intrusion into egg box, days-in-gravel, natural spawner numbers, or prespawning substrate characteristics (fines, D_{50}) help explain any additional variation in egg-to-fry survival or embryo condition among reaches and years.

Methods

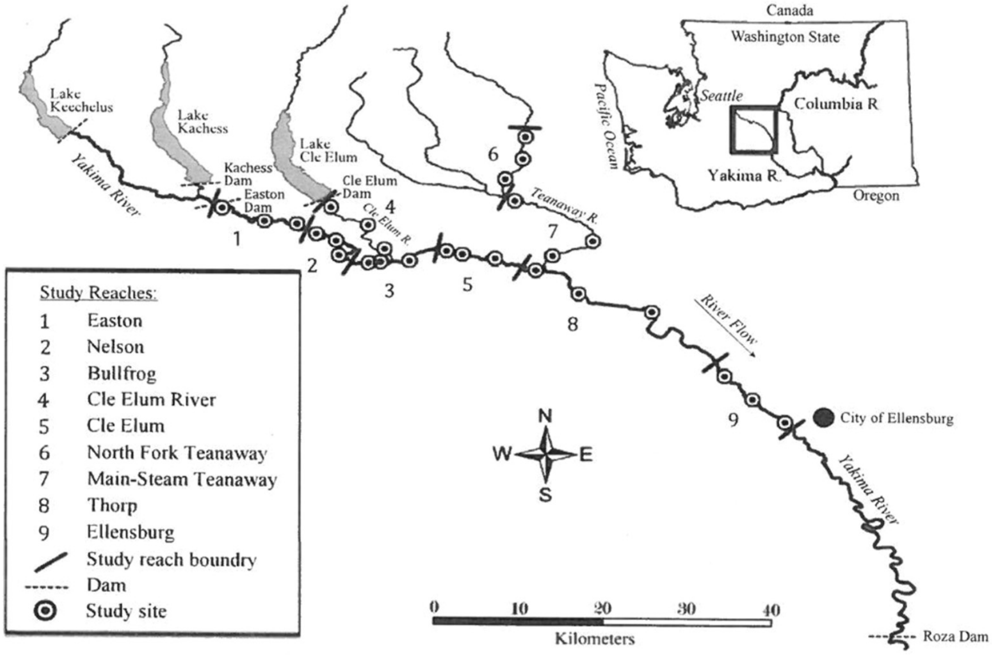
Below we describe the study design and a summary of the methods and refer the reader to Johnson et al. (2012) for additional detail on the study basin, methods of adult and gamete collection, redd construction, and egg fertilization.

Study design

The study area consisted of nine total reaches: six contiguous reaches in the mainstem Yakima River, two in the Teanaway River, and one in the Cle Elum River (Fig. 1). Each of the nine reaches contained three study sites located in the upper, middle, and lower portions of each reach (Fig. 1). Three redds were constructed in each of the study sites over a 3-week period, resulting in a total of 81 artificial redds per year (3 redds per site × 3 sites per reach × 9 reaches). Reaches and reach breaks were defined based on reach morphology (i.e., stream channel gradient and valley confinement) and tributary junctions. They are also different in hydrology and flow and are the reaches used to quantify juvenile and adult salmonid abundance. Reach length varied from 6.8 (Nelson) to 23.3 river kilometers (rkm) (Thorp) (Fig. 1). All reaches were island-braided channel types with the exception of the Thorp reach, which was classified as a confined channel type (Beechie et al. 2006). Slope of reaches was less than 1% and bank-full widths ranged from 20 to 30 m in Easton, Nelson, Bull Frog, and Cle Elum reaches, 10 to 20 m in the North Fork and Mainstem Teanaway, and 30 to 40 m in Celum, Thorp, and Ellensburg reaches. Upper Yakima Basin redd survey GPS coordinates were used to establish areas within each study reach that had been utilized by spring Chinook spawners in previous years (Andrew Dittman, unpublished data). We then divided each reach into upper, middle, and lower segments and selected one accessible study site in each of the three segments. Locations for artificial redd construction in each site were then selected near active, naturally constructed redds or in areas of the channel in which naturally constructed redds had been documented in previous years. Thus, all artificial redds were located in known spawning areas within each reach.

We also constructed artificial redds in a 127 m long by 7.9 m wide artificial spawning channel at the Cle Elum Supplementation and Research Facility (CESRF) to provide an estimate of the upper limit of egg-to-fry survival and condition in a controlled seminatural environment and nearly optimal spawning conditions (i.e., constant flow, temperature, and clean gravels with little or no fine sediment; see Schroder et al. 2010 for details). Only three egg boxes (one for each mating from the first week) were placed in the artificial spawning channel in 2009, but nine (three for each week 1 mating) were placed in all other years. Similar to other sites, 100 fertilized eggs were placed in each egg box.

Fig. 1. Map of the nine contiguous study reaches and three sites per reach in the upper Yakima River Basin (drainage area of 4125 km²). Reach borders are denoted by solid black lines perpendicular to the river channel. Boundaries for lower reaches of the Cle Elum and Teanaway rivers were defined as the area of confluence with the mainstem Yakima River. Each of the nine study reaches contained an upper (most upstream), middle, and lower (farthest downstream) study site.



Gamete collection

Gametes for our experiments were obtained from spring Chinook salmon adults collected annually at Roza Dam (rkm 208; Fig. 1) for use as broodstock in the Yakima Klickitat Fisheries Project (Knudsen et al. 2006; Fast et al. 2008). We used eggs from first-generation hatchery spring Chinook; however, owing to limited availability in the third week, eggs from natural-origin spring Chinook were used in 8 of 81 matings (crosses). Egg-to-fry survival rates from natural-origin and first-generation hatchery adult Yakima Chinook salmon have been the subject of intensive study at CESRF over the last decade and were shown to be similar in both the hatchery and in seminatural stream channels (Knudsen et al. 2008; Schroder et al. 2008, 2010). Postorbit hypural lengths of adults from which gametes were obtained ranged from 52 to 72 cm for females and 54 to 68 cm for males. All fish were 4 years old except two females that were 5 years old.

Gametes were collected each week from three unique male and female pairs over the 3-week study (nine pairs per year, 27 pairs over 4 years). Each mating was given unique alphabetic codes (A through JJ), and gametes from each mating were used to stock each sites (Table 1). A mating consisted of a single male–female pair. Because there were not enough eggs to stock all pairs (matings) at each site and this would have reduced the number of mating used each week, each mating was placed randomly in either the upper, lower, or middle site each week so that each reach received all three mating in any given week. Eggs from each female were individually counted into lots of 100, placed into individual 0.5 L Whirl Pak bags, filled with oxygen, and kept on ice in a large beverage cooler. Approximately 0.3 mL of milt was also collected separately from three males each week and stored in individual 0.1 L bags. Collected gametes were then held overnight in a walk-in cooler at 5 °C. The bags were recharged with fresh oxygen the following morning, sorted by desired mating and stocking order, and transported (still on ice) to their respective sampling reaches.

Redd construction, egg fertilization, placement, and recovery

Preconstruction of redds was necessary to allow the stocking of all 27 sites on the same day. Artificial redds were excavated with a shovel at each of the Yakima River Basin sites on Mondays of the last 3 weeks of September, the day before gamete collection. Methods followed those of Johnson et al. (2012), which included standardized egg pocket depth of 30 cm and the use of Whitlock–Vibert egg boxes modified to prevent emerging Chinook alevins from escaping (Johnson et al. 2012; Reiser and White 1983; Wesche et al. 1989). A passive integrated transponder (PIT) tag was glued inside the box and another tethered to a 20 cm nylon string to assist in egg box recovery.

Egg boxes were first filled to within 2 cm of the box lid with clean gravels from the artificial redds. Egg fertilization and stocking of redds followed methods outlined in Johnson et al. (2012) and included submerging the egg box in a tub of water, protecting them from solar radiation, mixing egg in milt in a small 0.5 L bag, pouring fertilized eggs into the egg box, transporting the closed egg box submerged in a tub of water and gently transferred into artificial redd, and filling the redd with clean gravels. Johnson et al. 2012 examined many of the methodological questions associated with this study, including comparing survival of eggs in natural environment with that of eggs held in hatchery, the effect of holding eggs overnight before stocking, the order that reaches were stocked, and the effects of stocking crew on survival. These factors did not to have a significant influence on egg-to-fry survival or developmental stage, and therefore we did not examine those in subsequent years. We assumed 100% fertilization of our eggs with our methodology based on previous unpublished work done at the CESRF, which reported fertilization of rates of >90%.

Egg boxes were recovered between December and June each year, depending on temperature units (TUs). Specific redd excavation recovery dates were determined at each site based on reaching a thermal unit target of 900 TUs, which is the point at which 50% of fry were expected to have emerged from gravel (Johnson

Table 1. Study design showing unique matings (male–female pair that was source of gametes) used in each site and reach in 2009.

		Mating (male–female pair)								
		Week 1			Week 2			Week 3		
Reach	Site	A	B	C	D	E	F	G	H	I
Easton	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Nelson	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Bullfrog	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Cle Elum River	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Celum	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
North Fork Teanaway	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Mainstem Teanaway	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Thorp	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨
Ellensburg	Upper	▨			▨			▨		
	Lower		▨			▨			▨	
	Middle			▨			▨			▨

Note: Other years followed the same design but with different mating (2010 J to R, 2011 S to AZ, and 2012 BB to JJ). Gray boxes indicate which site within a reach received gametes from a specific mating. Each upper, middle, or lower site within a reach received gametes from a unique male–female pair for weeks 1, 2, and 3 each year from 2009 to 2012. For example, in week 1 in 2009, eggs from mating A, B, and C were stocked in upper, lower, and middle reaches, respectively, in each reach. This allowed equal distribution of a specific mating among all reaches for each stocking event. The total study design was composed of nine reaches, each with three study sites and three artificial redds per site (n = 81 artificial redds each year).

et al. 2012). To monitor the accumulation of thermal units at each of the study sites, temperature loggers were deployed at 27 locations throughout the study area. Temperatures during incubation ranged from a high of 17 to near 0 °C (mean = 5 °C) with highest temperatures in September and lowest in December, January, or February. Artificial redd locations were identified by triangulation from the bank and through the use of a handheld PIT tag detector to detect the PIT tag in an egg box. Once located, redds were excavated and the egg box delicately removed to minimize loss of fine sediment and transported to the bank in a small tub of water to enumerate survivors and dead eggs or fry, and the total number of days between stocking of eggs and redd excavation was recorded. A small number of boxes could not be recovered owing to scour greater than the depth of the egg box, large changes in the channel that prevented relocating an artificial redd, or vandalism (one in 2009, ten in 2010, and three in 2011). In cases where the egg box was scoured or of dramatic shifts in channel, survival was assumed to be zero, while egg boxes that were damaged or appeared to have been vandalized were excluded from our analysis. Surviving fry were transported live to the lab where length to the nearest millimetre and wet mass to the nearest milligram were measured on each individual. Measurements were made on sacrificed, unpreserved fry within 5 h following collection in the field. Developmental indices (k_D) were calculated for each of the surviving fry based on Bams (1970). The Bams equation provided a standardized index of alevin developmental stage and is not reflective of alevin condition, but gives insight into the relative stage of development among study reaches.

Spawning substrate, fine sediment infiltration, and natural redds

Wolman pebble counts (Wolman 1954) were used to characterize surface particle size of spawning gravels at each site. Spawning gravels were compared by median particle size (D_{50}), the size at which 84% of the particles are smaller (D_{84}), and the size at which 16% of particles are smaller (D_{16}) (Kondolf et al. 2008). Fine sediment infiltration (percent fines) into artificial redds was estimated from the egg boxes following excavation of artificial redds. In addition, to characterize the surface and subsurface substrate, shovel samples were collected prior to redd construction (Grost et al. 1991). Sediment that had accumulated in the egg boxes and shovel samples were dried at 80° C for 24 h (Johnson et al. 2012). Dried samples were then sieved into 63, 31.5, 16, 8, 4, 2, 1, 0.85, 0.5, 0.25, 0.125, and 0.063 mm size categories and weighed to the nearest 0.01 g. Particles less than 2 mm (2000 μm) in size were considered fines (Fudge et al. 2008; Lisle 1989). Scour chains based on Nawa and Frissell (1993) were installed at each of the study sites: one per site (one per redd in 2011 and 2012) and approximately 0.5 m behind each artificial redd. The scour chains consisted of a 0.8 m length of cable threaded through 30 plastic beads, each 12 mm in diameter (see Johnson et al. 2012 for additional details). As scour occurred throughout the deployment period, beads were exposed to the current and pushed to the end of the cable. Upon egg box retrieval, the scour chain was located and the number of beads that had slid to the end of the cable was recorded, providing an estimate of total scour during the incubation period. Scour chains can also be used to look at subsequent fill or aggradation, but this would require repeated surveys after each flow event, which was not feasible. Scour can influence egg-to-fry survival directly if it is deep enough by scouring the egg pocket and washing eggs or embryos downstream or indirectly by disturbing gravel in the egg pocket or increased infiltration of fines or other material into the redd or egg pocket (DeVries 2008; Sear et al. 2008). Our egg boxes were buried 30 cm in depth, and only scour in excess of this depth led to physical removal of the egg box. Scour to this depth was rare in our study, and we used scour as a measure of disturbance to the redd environment.

To examine whether survival at redds was correlated with the number of nearby redds from naturally spawning fish, we obtained data on location (GPS coordinates) of spring Chinook salmon redds based on annual surveys conducted by NOAA from 2009 to 2012 (see Dittman et al. 2010 for detailed methods). We used these data to calculate the number of natural redds that occurred each year within 100 and 500 m of our artificial redds.

Data analysis

To meet our first study objective (provide range of survival and condition across basin and years), we used summary statistics (mean, standard error of mean) among years, reaches, sites, and matings. To specifically examine the influence of mating and reach (objective 2) on survival and developmental stage, we used analysis of variance (ANOVA) with both reach and mating (male–female pairs or parentage) as fixed factors in the model. Each year was examined separately because matings could not be replicated across years. Tukey multiple comparisons were used to determine differences between pairs of reaches and crosses. An ANOVA was also used to compare physical variables (percent fines, D_{50}, D_{84}, D_{16}, days-in-gravel, natural redds nearby) among reaches and years. A Kruskal–Wallis test was used to compare scour among reaches, as normal probability plots showed that both untransformed and transformed data were highly skewed and not normally distributed. Because the level of fine sediment has been previously reported to be strongly negatively correlated with survival (e.g., Chapman 1988; Sear et al. 2008), we specifically examined the correlation between fine sediment that infiltrated into egg boxes and survival. We used site-level means of fine sediment and survival because replicates within a site were designed to look at variability within a site. This analysis was performed on untransformed data, as the residuals were approximately normal in distribution. We used a 0.05 level of significance for all statistical tests.

To examine whether factors other than reach or parentage explained additional variation in survival or developmental stage (objective 3), we used multiple linear regression and models using the independent variables maximum scour depth, number of days-in-gravel, percent egg box fines, percent shovel sample fines, and substrate size (D_{50}). We selected these variables because they represent fine sediment within gravel prior to spawning (shovel fines), fine sediment in egg pocket (egg box fines), and surface particle size measurements often used to characterize spawning habitat (D_{50}). Days-in-gravel is based on accumulated TUs (mean daily temperature), so it was included because it reflects both the temperature and the time eggs were in the gravel. Moreover, other studies have suggested these variables influence egg-to-fry survival, and simple correlation analysis showed they were not correlated with each other. We examined models with all above variables included and then various possible combinations, including just reach or mating. Reach and mating were discrete variables while all others were continuous variables. We also examined whether there was an interaction between reach and fines sediment, as there was some evidence when plotting the data that the relationship varied among reaches. To determine which model best fit the data, we used an information-theoretic approach with Akaike's information criterion, adjusted for small sample sizes ($\mathrm{AIC_c}$) (Burnham and Anderson 2002). The difference between the $\mathrm{AIC_c}$ of a candidate model and the model with the lowest $\mathrm{AIC_c}$ provided the ranking metric $\Delta\mathrm{AIC_c}$. A $\Delta\mathrm{AIC_c}$ between 0 and 3 generally indicates substantial support for a model being as good as the best approximating model, $\Delta\mathrm{AIC_c}$ between 4 and 7 represented less support, and values of greater than 7 indicates very little support for a candidate model relative to the best model (Burnham and Anderson 2002). We also provided our base model that included just reach and mating as a comparison to show additional variation explained by models with additional parameters.

Akaike weights (w_i) were calculated to represent the strength of evidence in favor of model i being the best model and model j being the next best model. The ratio of Akaike weights (w_i/w_j) indicates the plausibility of the best-fitting model compared with other models (Burnham and Anderson 2002). Models with evidence ratios of 10 or less were considered plausible (Burnham and Anderson 2002). Because of the number of potential combination of parameters, we only reported the best-fitting models.

Finally, because several studies have reported on specific correlation between fine sediment and survival, we also looked at simple linear regression analysis to examine potential relationships between survival or developmental stage and fine sediment infiltration. All statistical analyses were performed in R version 3.2.1.

Results

Objective 1: range of egg-to-fry survival in upper Yakima Basin

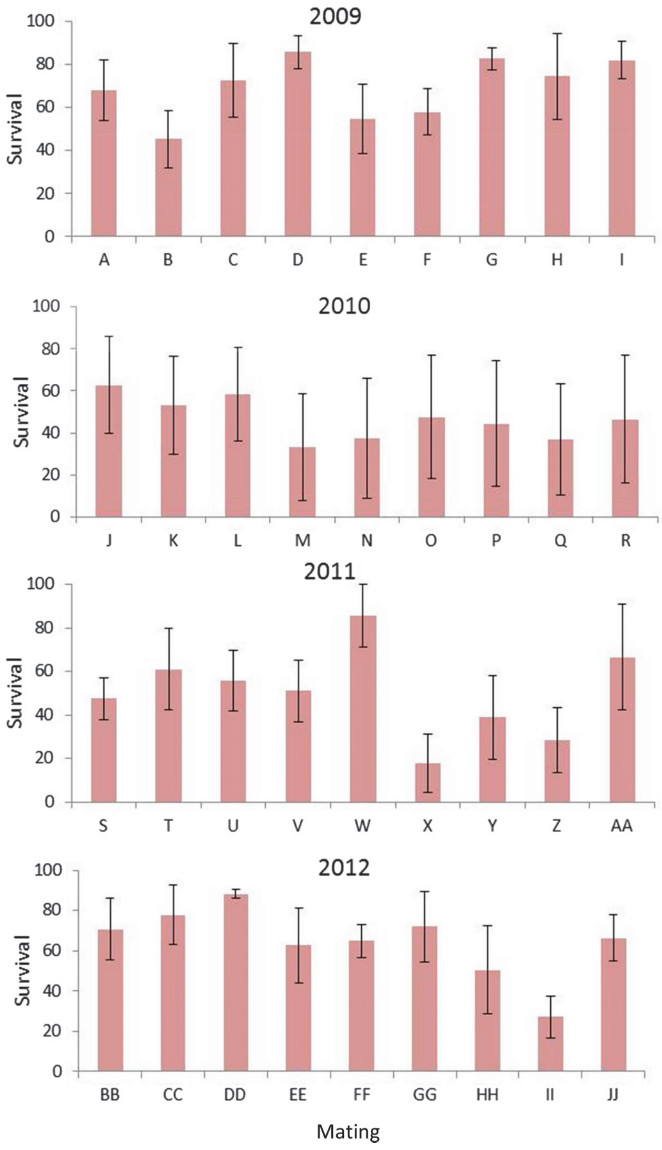
Mean Chinook salmon egg-to-fry survival in individual artificial redds ranged from 0% to 99%, averaged 49% to 69% annually, with reach means ranging from 9% to 91%. Estimated mean survival by mating (cross) ranged from 45% to 86%, 37% to 63%, 18% to 86%, and 27% to 88% in 2009, 2010, 2011, and 2012, respectively (Fig. 2). Mean survival by reach (irrespective of mating) ranged from 58 to 84, 9 to 91, 41 to 60, and 53 to 84 in 2009, 2010, 2011, and 2012, respectively (Table 2).

The median (D_{50}), 84th percentile (D_{84}), and 16th percentile (D_{16}) substrate particle size (estimated from pebble counts of surface substrate prior to spawning) were significantly different among reaches and years ($p < 0.01$). The percent fines in shovel samples less than 2 mm, which represent fines in substrate prior to being disturbed by spawning salmon, differed by reach and year (Table 3; ANOVA; $p < 0.01$). Scour was significantly different among years and reaches (Kruskal–Wallis, $p < 0.01$) with scour in 2009 being considerably lower and scour in 2010 considerably higher than in other years (Table 3). Days-in-gravel was significantly different among reaches for each year (ANOVA, $p < 0.01$; Fig. 3), with the shortest days in the gravel being in the Cle Elum River reach (mean = 114 days) and longest in the North Fork of the Teanaway reach (mean = 246 days). The percent fines in egg boxes, which is a measure of fines infiltrating into redds, was significantly different among years and reaches (ANOVA, $p < 0.01$; Table 3). Natural spawner abundance within 100 m and 500 m of artificial redds was significantly different by year and site nested in reach ($p < 0.01$; Table 3).

Objective 2: influence of reach and parentage

Survival was significantly different among crosses in 2009, 2011, and 2012, but not in 2010 ($p < 0.01$; Table 4), while survival among reaches was only significantly different in 2010 (ANOVA; Table 4). Site location, nested within reach, was a significant factor in 2010 and 2012 ($p < 0.02$; Table 4). Multiple comparisons indicated that the majority of the differences in survival among reaches in 2010 were between the Cle Elum River and other reaches (Table 5).

Fig. 2. Mean survival by mating (parentage or male–female pair) and year for all study reaches combined. Each year had nine unique crosses. Error bars are two standard errors of the mean.



Significant differences in survival among parentage were found among four, seven, and eight different pairs of crosses in 2009, 2011, and 2012, respectively (Table 5).

Mean developmental stage of fry in individual egg boxes ranged from 1.71 to 2.14 and 1.88 to 2.01 when averaged by reach (Table 2). Developmental stage was significantly different among reaches and crosses in all 4 years (ANOVA, $p < 0.01$; Table 4), with differences among site within a reach only significantly different in 2009 ($p = 0.04$ for 2009; $p > 0.10$ for all other years). Tukey honestly significant difference multiple comparisons indicated significant differences in developmental stage of fry in all years among many matings, with differences in reaches being related primarily between Cle Elum River or Teanaway River and other reaches (Table 5).

Objective 3: influence of other factors on survival and developmental stage

A large part of the variation in survival and developmental stage was explained by mating and reach (55% and 67% for survival and developmental stage, respectively), with only small amount of additional variation explained by different combinations of physical variables (Table 6). Our model procedure indicated that the most plausible models for survival and developmental stage included site nested within reach, mating, scour, egg box fines, shovel sample fines, D_{50}, and days-in-gravel (Table 6). An interaction between reach and fines added little to the model fit.

When examined separately, mean percent fines (<2 mm) was not significantly correlated with mean survival in 2009, 2011, or 2012 ($p > 0.07$); it was significantly correlated with survival in 2010 ($p < 0.01$), explaining 35% of the variation in mean survival among sites. Similarly, developmental stage was negatively correlated with fine sediment in 2010 ($p = 0.03$, adjusted $r^2 = 0.22$), but not in other years ($p > 0.09$). As lower developmental index value indicates a more progressed developmental stage, a negative correlation with fine sediment suggests that as fine sediment increases, fry are more developed (smaller yolk sac).

Discussion

Our results from more than 320 artificial redds constructed over 4 years suggest four major findings related to Chinook salmon egg-to-fry survival, including (1) egg-to-fry survival in Chinook salmon in the Yakima Basin is relatively high compared with that reported for other salmonids; (2) parentage and reach within a basin are major factors influencing Chinook egg-to-fry survival and developmental stage; (3) site-specific physical variables (e.g., percent of fines, days-in-gravel, and median particle size) explained little additional variation in egg-to-fry survival; and (4) interannual variation in egg-to-fry survival appears to be driven by scour and high flows during incubation.

Variation in egg-to-fry survival

Egg-to-fry survival across all reaches and sites in our study averaged 44.8% to 68.9% each year, which is relatively high compared with other studies on egg-to-fry survival for other species of salmon (Bradford 1995). While our estimates of survival are higher than that for other salmonids, they appear to be within the range of limited field studies done on Chinook salmon (Fast et al. 1991; Gangmark and Bakkala 1960; Healey 1991; Merz et al. 2004). Chinook embryos appear to be less negatively influenced by fine sediment and low DO during incubation than other salmonid species (Chapman et al. 2014; Sternecker et al. 2014), and under ideal conditions, egg-to-fry survival is thought to approach that found in hatchery environment (Bams 1985). Our estimates are also within the range estimated previously in the Yakima Basin from capping of a small number of natural redds (Fast et al. 1991). While life-cycle models such as that of Kareiva et al. (2000) have suggested that egg-to-fry survival is a major factor limiting survival in Columbia River Chinook salmon populations, it does not appear to be the case in the upper Yakima Basin.

Influence of reach and parentage on survival

Our results indicate that variation in Chinook salmon egg-to-fry survival in the Yakima Basin is driven by both mating and physical factors at the reach and site scale. While our results on parentage (matings) confirm findings in our pilot study (Johnson et al. 2012), they indicate that it is not a major factor in all years. Moreover, the influence of reach varies greatly from year to year, most likely because of differences in incubation conditions likely resulting from high flow events that scour or lead to physical disturbance of gravels or higher infiltration of fine sediment in the egg pocket. For example, there was a strong reach effect and no parental effect for only the 2010 brood year, when there were several high flow events (Fig. 4). Rather than something unique about the nine matings used in 2010, it appears that variability in survival within matings across reaches was very high in 2010, which suggests factors other than mating or parental effect are influencing survival in that year (see Fig. 2).

Table 2. Mean Chinook salmon egg-to-fry survival (percent), developmental stage, and number of natural redds located within 100 and 500 m of each artificial redd for each study reach and year.

				Percent survival		Developmental stage		No. of natural redds within:	
Reach	rkm	Year	*N*	Mean	SD	Mean	SD	100 m	500 m
Easton	11.7	2009	9	63	20	1.92	0.04	14	30
		2010	8	52	34	1.91	0.10	25	47
		2011	7	45	24	1.91	0.08	13	28
		2012	9	61	18	1.93	0.03	12	26
Nelson	6.8	2009	9	61	32	1.93	0.05	14	31
		2010	5	55	50	1.98	0.04	23	46
		2011	9	59	34	1.95	0.04	18	42
		2012	9	59	39	1.95	0.04	11	17
Bullfrog	12.9	2009	9	80	16	1.93	0.03	22	46
		2010	9	56	37	1.96	0.03	39	82
		2011	9	42	38	1.93	0.06	23	31
		2012	9	53	42	1.97	0.05	18	40
Cle Elum River	12.9	2009	9	78	12	1.93	0.05	16	26
		2010	9	91	3	2.01	0.07	13	36
		2011	9	60	28	1.99	0.06	4	14
		2012	9	73	23	2.00	0.07	2	9
Celum	11.3	2009	9	84	16	1.94	0.04	3	19
		2010	9	57	35	1.95	0.03	3	26
		2011	8	52	33	1.96	0.03	8	27
		2012	9	75	18	1.97	0.04	3	21
North Fork Teanaway	10.5	2009	8	60	35	1.91	0.03	2	1
		2010	9	22	33	1.91	0.05	4	8
		2011	9	43	27	1.90	0.04	1	2
		2012	9	60	30	1.94	0.02	1	2
Mainstem Teanaway	19.3	2009	9	64	31	1.88	0.04	1	1
		2010	8	9	23	1.92	0.03	2	4
		2011	9	53	30	1.91	0.04	0	2
		2012	9	58	25	1.93	0.04	0	1
Thorp	23.3	2009	9	73	17	1.93	0.05	7	14
		2010	9	33	35	1.96	0.05	7	16
		2011	9	41	35	1.93	0.06	9	4
		2012	9	65	23	1.94	0.05	8	14
Ellensburg	13.7	2009	9	58	24	1.94	0.04	2	4
		2010	8	15	23	1.96	0.04	1	8
		2011	9	53	33	1.93	0.02	2	3
		2012	9	70	25	1.96	0.02	2	2
Spawning channel	NA	2009	3	59	26	1.92	0.02	NA	NA
		2010	9	80	13	2.00	0.04	NA	NA
		2011	9	55	21	1.97	0.06	NA	NA
		2012	9	84	11	1.99	0.01	NA	NA

Note: Means are averages of data from all three sites in each reach. *N* = number of artificial egg boxes that were recovered. Natural redds represent mean number that were located within 100 and 500 m of an artificial redd. Sites are in order from upstream to downstream. "rkm" refers to length of reach in river kilometres; NA, not applicable.

Developmental stage appears to be influenced by both parentage and reach across all years. While parental fitness or fitness of gametes was thought to play a role in egg-to-fry survival in the natural environment (Johnson et al. 2012; Rubin 1995; Young et al. 1990) and has been well-documented in the hatchery environment (Burt et al. 2011; Knudsen et al. 2008; Schroder et al. 2008, 2010), our study supports our initial findings (Johnson et al. 2012) and is the first to document a parentage effect on egg-to-fry survival across multiple years in the natural environment. The exact source of the parental effect is unclear and beyond the scope of our study. Survival among families can vary greatly in the hatchery environment (Knudsen et al. 2008; Schroder et al. 2008, 2010), and different thermal regimes can lead to differences in emergence timing and fry condition within and among families (Steel et al. 2012; Whitney et al. 2014). We assume the parental effect observed is due to differences in gamete fitness, which may be a genetic or phenotypic, or is an indication of parental condition during development of gametes prior to or during spawning. Previous studies on Chinook salmon have indicated that differences in egg-to-alevin survival among families are largely due to maternal effects, with additive genetic effects influencing survival and growth at later life stages (Evans et al. 2010; Heath et al. 1999). Thus, it is likely that differences we saw in egg-to-fry survival were largely maternal, though it would require a study with additional replication of all possible matings, similar to that done by Heath et al. (1999) to confirm.

Multiple comparisons indicate that reach-scale differences in developmental stage and survival (2010 only) are largely due to differences between reaches of Cle Elum River, North Fork Teanaway, and Mainstem Teanaway and all other reaches in mainstem Yakima. In fact, reanalysis of our survival data categorizing sites simply as mainstem Yakima, Cle Elum, and Teanaway produced nearly identical results to our classification as nine reaches (i.e., reach and parentage were significantly different in 2009 and 2012, reach in 2010, parentage in 2011). Differences among these portions of the basin are probably related to large differences in hydrology and temperature regimes of these sub-basins. While the Teanaway is unregulated, the Cle Elum reach is located imme-

Table 3. Mean levels of fine sediment less than 2 mm (proportion) that was measured in shovel samples, infiltrating into egg boxes, and mean particle size (in mm; 16th and 50th, and 84th percentiles: D_{16}, D_{50}, and D_{84}) from pebble counts for each reach and year.

		Proportion fine		Pebble count			
Reach	Year	Egg box	Shovel	D_{16}	D_{50}	D_{84}	Scour (mm)
Easton	2009	0.14	0.10	28	57	101	0
	2010	0.18	0.08	17	45	83	6
	2011	0.17	0.14	28	49	74	1
	2012	0.13	0.09	15	41	81	0
Nelson	2009	0.06	0.10	20	45	81	1
	2010	0.14	0.08	17	38	70	2
	2011	0.12	0.17	25	40	68	2
	2012	0.07	0.12	25	53	77	0
Bullfrog	2009	0.04	0.00	30	61	100	1
	2010	0.14	0.16	17	40	77	3
	2011	0.14	0.13	30	47	74	0
	2012	0.10	0.24	27	55	82	−1
Cle Elum River	2009	0.01	—	23	45	77	0
	2010	0.05	0.14	12	37	76	1
	2011	0.05	0.16	25	40	57	0
	2012	0.09	0.16	15	37	64	0
Celum	2009	0.03	0.09	24	49	88	1
	2010	0.13	0.15	17	40	74	1
	2011	0.03	0.15	25	48	81	0
	2012	0.03	0.13	24	52	83	1
North Fork Teanaway	2009	0.14	0.09	27	58	137	7
	2010	0.14	0.09	24	51	107	27
	2011	0.16	0.10	26	46	84	8
	2012	0.18	0.11	21	77	169	4
Mainstem Teanaway	2009	0.16	0.11	35	62	119	0
	2010	0.25	0.10	15	43	87	42
	2011	0.12	0.14	30	54	96	5
	2012	0.14	0.10	28	54	97	6
Thorp	2009	0.04	0.09	31	54	86	2
	2010	0.12	0.09	26	51	89	20
	2011	0.13	0.08	26	41	61	2
	2012	0.05	0.12	21	41	68	0
Ellensburg	2009	0.07	—	31	51	80	2
	2010	0.14	0.09	22	43	72	−1
	2011	0.11	0.15	30	57	88	1
	2012	0.15	0.19	20	45	85	0
Spawning channel	2009	0.02	0.00	31	48	62	0
	2010	0.00	0.00	31	48	62	0
	2011	0.01	0.00	31	48	62	0
	2012	0.02	0.00	31	48	62	0

Note: Means are averages of data from all three sites in each reach. Sites are in order from upstream to downstream.

Table 4. Summary of results (p values) of significant factors in nested ANOVA examining the influence of mating (cross or male–female pair) and study reach on egg-to-fry survival and developmental stage (k_D) measured at 27 sites in Yakima River from 2009 to 2013.

Year	Mating	Reach	Reach–site
Survival			
2009	<0.01	0.06	0.40
2010	0.73	<0.01	0.02
2011	<0.01	0.65	0.09
2012	0.01	0.11	0.01
Developmental stage			
2009	<0.01	<0.01	0.04
2010	<0.01	<0.01	0.85
2011	<0.01	<0.01	0.10
2012	<0.01	<0.01	0.54

diately below Cle Elum Dam and Reservoir, is ideal spawning habitat (i.e., stable flow, coarse gravel, and high natural spawner abundance), and survival in the Cle Elum reach in many years was as high or higher than that found in the spawning channel. Not only do the flow regimes differ among these three major areas of the basin, but the temperature regimes are very different, with the Teanaway being much colder and the Cle Elum being much warmer than other reaches. All our artificial redds were stocked on the same day each week, yet alevins accumulated 900 TUs in the Cle Elum River in December and January (as little as 83 days-in-gravel), while most of mainstem Yakima reaches achieved 900 accumulated TUs in February or March. Our egg boxes in the much colder Teanaway reaches did not accumulate the same TUs until April or even June in some cases (up to 267 days-in-gravel). In short, the Cle Elum reach is warmer and experiences few high flows and little scour during incubation because it is highly regulated, while the Teanaway River is unregulated, much flashier, and colder than other reaches. The Yakima reaches above the Teanaway are also buffered from high flows and scour because of the presence of multiple dams and reservoirs, but is not as warm as the Cle Elum River (Fig. 1). These differences in flow and temperature regimes appear to be driving differences in scour, fine sediment, and observed reach-scale developmental stage and survival.

Influence of other physical variables on survival

Factors other than parentage or reach explained little additional variation in survival or developmental stage. Previous studies on egg-to-fry survival have focused on DO, fine sediment infiltration, or scour as factors limiting survival (e.g., Chapman 1988; DeVries 2008; Jensen et al. 2009; Sear et al. 2012). The fact that egg-to-fry survival in some years and reaches was similar to that found in a near-ideal seminatural environment in the CSERF spawning channel (mean survival of 55% to 84%; Table 2) suggests that DO or fine sediment are not major factors impacting egg-to-fry survival at many locations in the upper Yakima Basin during years with limited or moderate peak flows. However, the relationship among DO, fine sediment, and egg-to-fry survival is complex, and some evidence exists that they act independently on egg-to-fry survival (Peterson and Quinn 1996; Yamada and Nakamura 2009). Laboratory studies on fine sediment and survival have generally indicated that survival decreases when the level of fines exceeds 10% and drops drastically when levels exceed 25% to 30% (Chapman 1988; Jensen et al. 2009). The levels of fine sediment in the gravel prior to spawning and that infiltrated into our egg boxes or from surrounding spawning gravel rarely exceeded 20% (Table 5). This may explain why we found only weak correlations between mean percent fines (<2 mm) and egg-to-fry survival at a site except in 2010, the only year where mean fine sediment levels in egg boxes approached 30% at a handful of sites. Mean developmental stage at a site was also negatively correlated with mean percent fines only in 2010, which is contrary to most literature, which shows decreased growth or development with increasing fines or reduced DO (Chapman 1988). However, this relationship was driven by one point, the upper North Fork Teanaway site (30% fines), where eggs had been in the gravel much longer than other sites (252 days). This would explain why fry from this site would be more well-developed and have a lower developmental index (lower k_D = more developed). In addition, when this one data point was removed, the correlation between developmental stage and fine sediment was no longer significant. In addition, we sampled many sites across a basin, while most studies that have reported a strong relationship between DO or fines and survival have intensively sampled one or a few sites. It is possible that the

Fig. 3. Box plot showing days-in-gravel (median and interquartile range of) for egg boxes in artificial redds by reach and year. The date of excavation of each artificial redd was based on temperatures at each site needed to reach 900 temperature units, and thus days-in-gravel reflect accumulated thermal units. Reach abbreviations: BF = Bullfrog, CER = Cle Elum River, NFT = North Fork Teanaway, MST = Mainstem Teanaway, Eburg = Ellensburg, and SC = Spawning channel. See Fig. 1 for location of reaches.

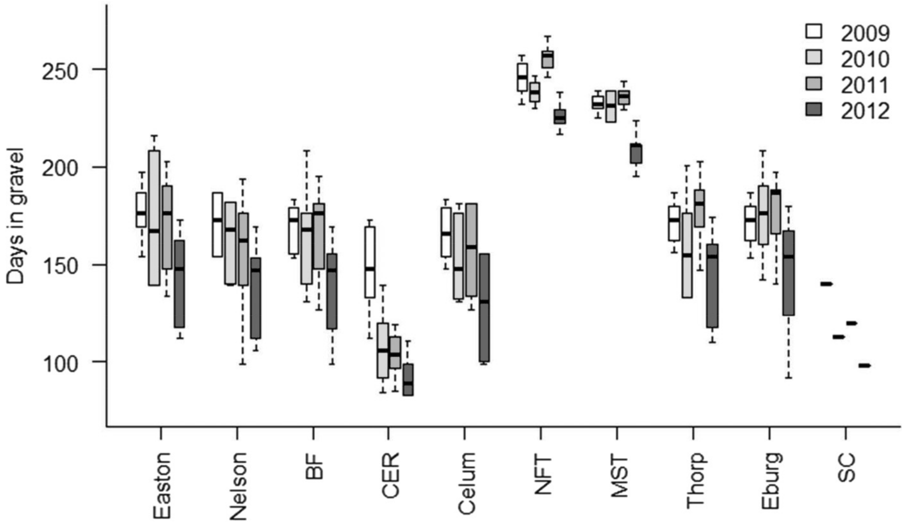


Table 5. Results of pairwise multiple comparisons (Tukey's HSD) of reaches and matings in years when these where significant factors ($p < 0.05$) in ANOVA model (see Table 4).

	Survival		Developmental stage	
Year	Mating	Reach	Mating	Reach
2009	B vs D, B vs G, B vs H, B vs I	No significant difference for any comparison	F vs D, G vs F, A vs F, B vs E, B vs F, B vs A, C vs F, C vs B, H vs F, J vs B, I vs F, I vs B	MST vs Bullfrog, MST vs Celum, MST vs Cle Elum River, MST vs Ellensburg, Nelson vs MST, Thorp vs MST
2010	No significant difference	Ellensburg vs Cle Elum River, MST vs Cle Elum River, NFT vs Cle Elum River, Thorp vs Cle Elum River	L vs K, P vs M, P vs N, P vs O, P vs J, P vs L, Q vs L, R vs L	Cle Elum River vs Celum, Easton vs Cle Elum River, NFT vs Cle Elum River
2011	X vs W, X vs AA, X vs T, X vs Y, Y vs W, Z vs AA, Z vs WW	No significant difference for any comparison	Z vs Y, T vs V, T vs Y, T vs S, U vs V, U vs Y, U vs AA, U vs S	Cle Elum River vs Bull Frog, Easton vs Cle Elum River, Ellensburg vs Cle Elum River, MST vs Cle Elum River, NFT vs Cle Elum River
2012	II vs BB, II vs CC, II vs DD, II vs EE, II vs FF, II vs GG, II vs JJ, DD vs HH	No significant difference for any comparison	JJ vs HH, CC vs JJ, DD vs JJ	Easton vs Cle Elum River, MST vs Cle Elum River, NFT vs Cle Elum River, Thorp vs Cle Elum River

Note: For mating, letter represents male–female pair that was source of gametes. For example, in 2009, B vs D indicates a significant difference in survival between these two matings. Similarly for comparison of reach, MST vs Bullfrog under developmental stage indicates that multiple comparisons were significantly different between the MST and Bullfrog reaches. If a pairing is not listed, no significant differences were detected. NFT, North Fork Teanaway; MST, Mainstem Teanaway.

broad spatial scale of our sampling masked relationships that occur within a site. However, while there were only three sites per reach, within a reach there appears to be a similar negative trend between survival and fine sediment seen across all reaches and sites. This suggests that a negative relationship between fine sediment and egg-to-fry survival exists at all sites in the Yakima, but it is only a factor in years when fine sediment intrusion is very high (>20%). Finally, it is possible that had we sampled in a basin or a reach where fine sediment levels regularly exceeded threshold of 25% to 30% identified in laboratory studies, we may have seen a stronger relationship between survival or developmental stage and fine sediment.

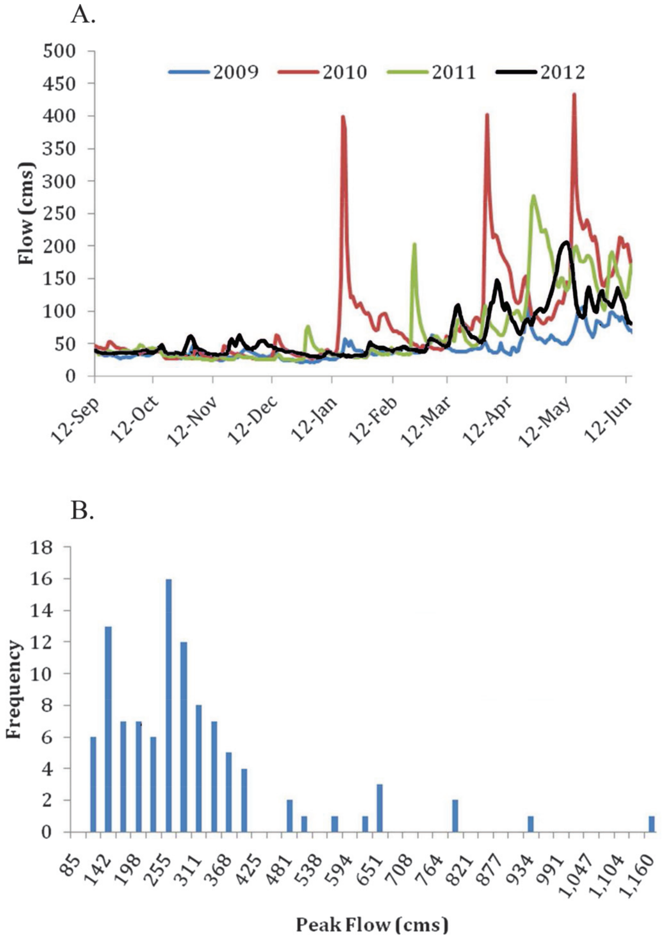
Previous studies have shown that monitoring DO requires continuous data loggers (Malcolm et al. 2006), which was not possible at all 27 locations in our study. Although not representative of our entire study area, we installed continuous data DO loggers (YSI 600OMS) at egg pocket depth at one site in the Bull Frog reach (2010), the Cle Elum River reach (2011 and 2012), and Mainstem Teanaway reach (2012). Oxygen saturation levels remained above 7.3 and 9.0 $mg \cdot L^{-1}$ in the Bull Frog and Cle Elum River reaches, respectively (all years), but below published critical values for Chinook (2.5 $mg \cdot L^{-1}$; Silver et al. 1963) through late December in the Mainstem Teanaway site, seemingly in response to seasonal flow increases in late October. Despite the apparent decline in available oxygen, 2012 survival in the Mainstem Teanaway was not significantly lower in comparison with Celum, Cle Elum, or other study reaches. Because oxygen demands are lowest during earlier stages of alevin development (Alderdice and Velsen 1978; Quinn 2005), it is possible that the timing of the decrease within the period of incubation buffered the effects of low oxygenation to the eggs. Moreover, our limited data on DO and relatively high egg-to-fry survival in most reaches and years suggest that low DO

Table 6. Results of selection procedure for models of egg-to-fry survival and developmental stage, including r^2, AIC, ΔAIC, and total number of parameters in model.

Model	r^2	Parameters	AIC	ΔAIC
Survival				
Survival ~ Reach(Site) + Mating + Box fines + Shovel fines	0.58	63	2357	0
Survival ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines	0.58	64	2358	2
Survival ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines + D_{50}	0.58	65	2360	3
Survival ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines + D_{50} + Days-in-gravel	0.59	66	2362	5
Survival ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines + D_{50} + Days-in-gravel × Box fines	0.59	66	2364	7
Survival ~ Reach(Site) + Mating	**0.54**	**60**	**2380**	**23**
Developmental stage				
Avg_k_D ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines + D_{50} + Days-in-gravel	0.76	65	−901	0
Avg_k_D ~ Reach(Site) + Mating + Scour + Box fines + Shovel fines + D_{50} + Days-in-gravel + Reach × Box fines	0.76	72	−892	9
Avg_k_D ~ Reach(Site) + Mating	**0.62**	**60**	**−783**	**118**

Note: Only models with a ΔAIC > 10 are reported. Box fines and shovel fines represent fine sediment less than 2 mm. Also presented are base model including just reach and mating, shown in bold font. Site is nested in reach in all models.

Fig. 4. Mean flows (m³·s⁻¹) in Yakima River from USGS stream gage at Umtanum, Washington, from 12 September to 21 June from 2009 to 2013 (A) and annual peak flows from 1906 to 2013 (B).



or intrusion of low DO groundwater is not likely limiting Chinook survival in most reaches in the upper Yakima River basin. We also examined differences in temperature between surface water and within artificial redds at a depth of 30 cm at a selected number of sites and found no difference between surface and subsurface temperatures. This lack of difference between subsurface and surface temperatures also suggests little groundwater intrusion into our redds.

The amount of fine sediment infiltration is related to scour and high flow events (Acornley and Sear 1999; Sear et al. 2008). Scour was typically 1 or 2 cm at most of our study reaches in most years, but higher in 2010 particularly in the Teanaway River and Thorp reaches. Three separate high flows events in 2010 exceeded 400 m³·s⁻¹ — which has a reoccurrence interval of about 25 years — while high flow events were rare or did not occur until spring in other years (Fig. 4). This may explain, in part, why fine sediment levels were both higher and negatively correlated with survival and developmental stage only in 2010. Scour in all years was consistently highest in the North Fork and Mainstem Teanaway reaches, which were the only reaches in our study where flow is not regulated by storage reservoirs. The regulated nature of the flows on much of the upper Yakima River may buffer some scouring flows and partially explain why survival is lower in unregulated Teanaway than in other reaches. While scour can increase fine sediment infiltration and indirectly influence survival, scour can also cause direct mortality if it scours to the depth of the top of the egg pocket (~20 cm in our study; DeVries 1997). This rarely occurred in our study, with the exception of 2010 when scour at some sites in the Teanaway and Thorp reaches approached or exceeded 30 cm.

Implications for salmon recovery and restoration

The large differences in number of days needed to reach 900 TUs among sites can influence postemergence survival and have direct implications for attempts to recover Yakima River spring Chinook and increase the numbers of returning adults in the Teanaway and other tributaries. The developmental stage, condition, and timing of emergence influence the survival of fry upon emergence (Quinn 2005). Earlier emergence timing can result in increased growth and a competitive advantage, as small size differences can influence agonistic behavior, food acquisition, and susceptibility to predation following emergence (Crozier et al. 2008; Quinn 2005; Murray and McPhail 1988). Conversely, emerging earlier or later than when food resources are available can lead to decreased growth and survival. Small differences in spawning and emergence timing in pink salmon (*Oncorhynchus gorbuscha*) have been shown to lead to differences in either freshwater or marine survival, with diverse emergence timing resulting in increased overall survivorship and long-term population resilience (Gharrett et al. 2013). Such differences in emergence timing also allow for a reduction in density-dependent effects to a population that may be limited in spawning habitat (Gharrett et al. 2013). Protracted emergence timing has also been identified as a potentially important buffer against the impacts of climate change (Shanley and Albert 2014). Spring Chinook in the upper Yakima are a mix of natural origin and hatchery production. Outplanting of first-generation hatchery smolts occurs annually in several locations, including the Teanaway River, in an attempt to rebuild the spring Chinook salmon population in the upper Yakima. Spawning density within the Teanaway River is low compared with the Cle Elum and other reaches in the Yakima River above the confluence of the Teanaway River. Moreover, most of the spawning Chinook salmon in the Teanaway are thought to be the product of hatchery smolts released from the Teanaway acclimation site (Dittman et al. 2010), with little natural production occurring there. Given the differences we found in emergence timing (time to reach 900 TUs ranged from 114 to 246 days) and developmental stage, it may be that the current Chinook stock being used for supplementation, which is derived from fish spawning in upper Yakima basin above the confluence with the Teanaway, is ill-suited to the cool temperature regime in the Teanaway, spawning too late to allow fry to emerge at the optimal time for growth. It is also possible that fry in the Cle Elum River reach, which consistently demonstrated high egg-to-fry survival and the shortest time for redds to reach 900 TUs, emerge too early or at a suboptimal time. However, accelerated development and early emergence timing, even prior to optimal growing conditions, has been shown to lead to increased survival for Atlantic salmon (*Salmo salar*) and reduces exposure to harsh conditions (Skoglund et al. 2011; Sternecker et al. 2014). Moreover, every year the Cle Elum River has some of the highest relative densities of natural spawners of any upper Yakima River reach or tributary; this suggests offspring from this reach are successful or natural spawners are consistently attracted to that reach (Dittman et al. 2010). Regardless, our results on differences in incubation time across a basin and those of Dittman et al. (2010) suggests that choosing a donor stock or parents that are suited to the unique temperature regime of a tributary or reach is an important factor for successful reintroduction of Chinook salmon.

We used a traditional degree-day accumulation model based on daily mean temperature above gravel to estimate TUs and predict emergence timing (Alderdice and Velsen 1978). While our estimates of accumulated TUs were based on temperature loggers in water just above the gravel adjacent to artificial redds, we monitored temperatures both above and within artificial redds at several sites and found no differences. Recent evidence suggests that TU models may be insufficient to accurately predict emergence timing, particularly under highly variable thermal regimes or temperatures that are above or below those optimal for incubation (Steel et al. 2012). Thermal regimes that appear similar in mean daily temperature can produce very different fry emergence timing or condition (Steel et al. 2012). It is possible that some of the differences we saw in developmental stage among some reaches were from our inability to accurately predict time of emergence (and date to excavate our artificial redds) using a simple degree-day model. However, the differences we observed in egg-to-fry survival, environmental conditions, and returning adults among reaches in the Teanaway, Cle Elum, and mainstem Yakima suggest real differences in spawner success among these reaches.

Implementing a study such as ours over a large basin and multiple years is a daunting task requiring consistent methods and extensive coordination. Differences in survival and developmental stage we observed could have been influenced by holding gametes overnight, differences in handling by crews among weeks and years, or handling during excavation. However, this is unlikely for two major reasons. First, we took great care in making sure that procedures were consistent among crews and years. Second, we examined these factors in detail in our methods study (Johnson et al. 2012) and found no effect of holding eggs overnight, crew, or stocking date on survival. We may have found different results had we compared areas currently utilized by spawning Chinook with those areas that appeared suitable but were not currently used by spawning Chinook. However, understanding why Chinook use some areas and not others was not the focus of our study. Moreover, if there were large differences in survival based on whether natural spawners preferred a site or not, we would have expected that the distance of artificial redds to natural redds to be negatively correlated with survival or developmental stage or help explain some of the variation in survival, which it did not.

Future research

All methods for measuring egg-to-fry survival in the field are known to have limitations (Rubin 1995; Kondolf et al. 2008). Our methods, which allowed us to control for many factors, including mating (source of gametes) and accurately enumerate the number of eggs that survived at many locations, do not allow measurement of mortality that may occur when fry swim up through gravel (Johnson et al. 2012). There is also evidence that increased fines or early emergence can lead to increased risk of predation (Louhi et al. 2011). Measuring "swim-up" and survival postemergence is much more difficult and an area that needs additional research. Climate change is expected to lead to changes in temperature and timing and magnitude of peak and low flows in most Pacific salmon streams, factors that influence egg-to-fry survival and timing of fry emergence (Crozier et al. 2008; Beechie et al. 2013; Shanley and Albert 2014). Thus, measuring egg-to-fry survival, scour, and fine sediment infiltration over several years using methods similar to ours may be a suitable approach to assessing the projected impacts of climate change on salmonid spawning and reproductive success. Finally, our results indicate that in absence of extreme flow and scour events, parentage rather than physical variables are a primary factor influencing egg-to-fry survival. This emphasizes the need to account for parentage when examining influence of physical factors on egg-to-fry survival and the need for research to understand what factors are influencing fitness of parents and their gametes.

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