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Journal

San Francisco Estuary and Watershed Science, 11(2)

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Publication Date

2013

DOI

<https://doi.org/10.15447/sfew.s.2013v11iss2art2>

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Salmon Life Cycle Considerations to Guide Stream Management: Examples from California's Central Valley

Joseph Merz¹, Michelle Workman², Doug Threlhoff³, and Brad Cavallo⁴

ABSTRACT

A primary goal of the Central Valley Project Improvement Act is to at least double natural production of Chinook salmon (*Oncorhynchus tshawytscha*) in California Central Valley (CV) streams on a sustainable basis. Achievement relies on restoration actions that involve both discharge (e.g., dam releases) and non-discharge (e.g., gravel augmentation, screening) components. Annual adult and juvenile abundance estimates for individual watersheds must be tracked to assess effectiveness of individual actions. However, to date, no substantial efforts have been taken to demonstrate success or deficiencies of their implementations. A major challenge in interpreting time series of counts at any one life stage is that they reflect the cumulative effects of both freshwater and marine factors over the full life cycle. To address this issue, we developed a conceptual framework based on ratios of the abundance of consecutive CV fall-run Chinook salmon life stages and how variation in these ratios tracks key independent variables during the freshwater portion of the life cycle.

Model validation with several case studies shows that estimates of previous stage class production correlate well with estimated individuals produced in the next class, indicating that transition rates tend to vary within a constrained range, and that monitoring programs generate abundance estimates whose errors are small enough not to swamp out the underlying signal. When selected environmental parameters were added to demonstration models, abundance estimates were more closely modeled and several tested relationships between environmental drivers and life-stage transition rates proved consistent across watersheds where data were available. Results from this generalized life-stage conceptual model suggest a potential framework for tracking the success of actions meant to improve survival for a given life stage within an individual stream and for determining how successive stages respond to these changes. Though examples are provided for CV Chinook salmon, these concepts can be applied wherever migratory salmonid populations and associated environmental data are being adequately monitored.

KEY WORDS

Chinook salmon, *Oncorhynchus tshawytscha*, restoration, management, life stage, model

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INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) are an iconic species across the western United States. In response to declines in abundance of once large historical populations, restoration efforts are underway in most regions where the species occurs. Evaluation of the success of those efforts has proven difficult, however.

The Sacramento and San Joaquin river system of the California Central Valley (CV; Figure 1) is an example of this dilemma. The CV supports four races of Chinook salmon: fall run, late-fall run, winter run, and spring run. These races and the large populations they once supported (at least 1 to 2 million adults annually; Yoshiyama et al. 1998, 2000) reflect the diverse and productive habitats that historically existed within the region.

Over the past 180 years anthropogenic effects—including mining, flood protection, power generation, water development, stream and floodplain conver-

sion, water quality degradation, invasive species, harvest, and hatchery management—have stressed, altered, and depleted these resources (Yoshiyama et al. 1998, 2000; Williams 2006; Israel et al. 2011). Global parameters, such as ocean conditions, have also demonstrated a marked effect on adult escapement (Lindley et al. 2007, 2009). In the past 3 decades, the CV spring and winter runs were listed under the United States Endangered Species Act (ESA) of 1973.

In 1998, the United States Fish and Wildlife Service (USFWS) Anadromous Fish Restoration Program (AFRP), under the federal Central Valley Project Improvement Act (CVPIA), was charged with making all reasonable efforts to at least double natural production of CV Chinook salmon (and five other anadromous species) on a sustainable basis. This program identified 172 actions to help meet this goal (USFWS 2001). The Comprehensive Assessment and Monitoring Program (CAMP), also under CVPIA, was tasked with monitoring natural production of adult

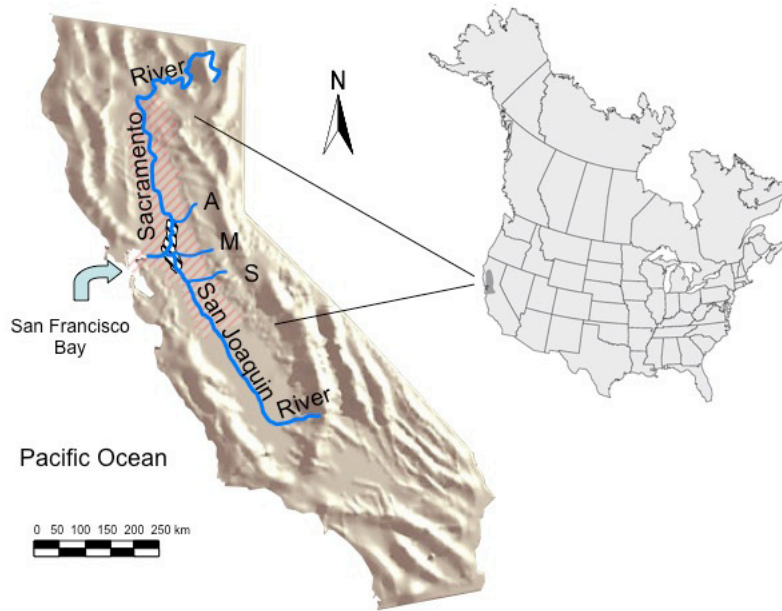


Figure 1 Present distribution of California Central Valley fall-run Chinook salmon (denoted by red and white area) in relationship to the Sacramento and San Joaquin rivers and three study tributaries (blue line), Sacramento San Joaquin Delta (black and white area), San Francisco Bay, California Central Valley, and the continental United States and Canada (inset). A = American River; M = Mokelumne River; S = Stanislaus River

CV salmon, assessing progress toward fish production targets established by the AFRP, and evaluating the effectiveness of Chinook salmon restoration projects (e.g., water management and structural modifications, habitat restoration, fish screens) in specified watersheds.

Despite the need to evaluate restoration actions, it has been difficult to assess their effectiveness at the population level. This difficulty arises from several factors. First, the Chinook salmon life cycle is complex because it encompasses both freshwater and ocean ecosystems (Figure 2). Second, from a monitoring perspective, time series of counts at any one life stage reflect the cumulative effects of both freshwater and marine factors over the full life cycle, thereby complicating the ability to measure population responses to specific actions. Third, complex interactions of factors that range from stream flow and temperature to large-scale and long-term shifts in marine conditions (Botsford et al. 1997; Bisbal and McConnaha 1998; Beamish and Noakes 2002). Fourth, large inputs of hatchery production and fluctuating harvest rates also obscure the ability to identify the factors that affect population trends in naturally spawned salmon (Ricker 1981; Johnson et al. 2012).

Because of these confounding factors, resource managers have not been successful in evaluating the effectiveness of freshwater restoration actions that use the traditional method of quantifying abundance at single life stages in isolation. An alternative is to consider survival rates, life history variability, and the individual quality of salmon that transition between each freshwater life stage within individual watersheds. Placing these elements in an appropriate analytical context could facilitate our understanding of how freshwater habitats contribute to different life cycle stages and, thus, the effectiveness of restoration actions in improving population performance in the face of extrinsic constraints.

The purpose of this paper is to provide salmon managers with such an evaluation framework. To accomplish this goal we address the following question: within a watershed, can we detect the effects of environmental variables on individual life cycle

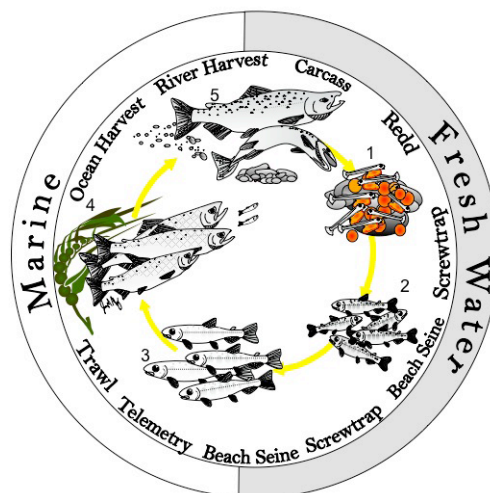


Figure 2 Generalized life-cycle and examples of associated Central Valley monitoring for Chinook salmon; (1) hyporheic development of embryo and pre-emergent fry; (2) fry and parr rearing; (3) smolt rearing and emigration; (4) ocean development and return immigration to natal streams; (5) adult stream maturation and spawning.

transition rates? Specifically, by looking at each life stage transition within fresh water, can we detect how a specific independent variable that is hypothesized to affect a particular stage in the life cycle influences the ratio of the number of fish transitioning out of the life stage relative to the number coming in? For illustration purposes, we use models to demonstrate the influence of flow on redd production success (superimposition), fry production, emigrants per fry produced, and the ratio of smolt to fry emigrants for several populations within the CV. This last analysis is motivated by an interest in the relationship between environmental variables and life history diversity rather than a specific transition rate *per se*, because the smolt:fry ratio depends on several interacting factors we do not attempt to separate in this analysis.

STUDY SITE

The Sacramento and San Joaquin river basins form the Sacramento–San Joaquin river system (SSJRS), which drains approximately 100,000 km² (40% of California area) (Gleick and Chalecki 1999; Kimmerer 2002). As discharge from the two basins converges and moves west, it passes through the Sacramento–

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San Joaquin Delta (Delta), enters San Francisco Bay (Bay), and then the Pacific Ocean. Similar to many watersheds throughout the Pacific United States, large-scale CV monitoring efforts have been underway for periods that range from years to decades. Population estimates for various Chinook salmon freshwater life stages are available from 22 watersheds (see Williams 2006 for discussion). These monitoring efforts include counts of immigrating adult salmon at weirs or ladders, adult carcass surveys, pre-spawn mortality estimates, angler surveys, snorkel surveys, redd surveys, rotary screw trap operations that monitor fry and smolt production, various tracking methodologies of individuals and cohorts (e.g., passive integrated transponders, acoustic transmitters, coded-wire tags) and trawling efforts to estimate emigration survival from freshwater to the marine environment. In many cases (e.g., carcass surveys), populations of each life stage are estimated through mark-recapture models (e.g., Cormack-Jolly-Seber model). Although methods vary, typically an estimate of the number of life stage-specific fish residing in, or passing through, a given stretch of river, is estimated, as is the uncertainty resulting from sampling efficiency and error (Roper and Scarnecchia 1996). Quality of fish within each life stage is also assessed in many situations as a further indicator of population response to environmental conditions and overall health (e.g., juvenile life stage, condition factor, egg retention, disease) (Whalen et al. 1999; Quinn et al. 2007). Although considerable monitoring and research has been devoted to CV salmonids, those activities have not been coordinated well. According to Brown (2005), this lack of coordination results in methods that may not always provide robust population estimates, and much of the metadata on methods are not readily available to scientists and managers (McDonald and Banach 2010).

CENTRAL VALLEY FALL-RUN CHINOOK SALMON LIFE CYCLE

Central Valley Chinook salmon spend most of their life cycle in the coastal ocean waters of the Pacific United States, but must return to freshwater to reproduce (anadromy). For many anadromous salmonids, in particular CV fall-run Chinook salmon, distinct life

stages occur during specific time periods (Table 1). Comprehensive descriptions of CV Chinook salmon life stages are given by Moyle (2002) and Williams (2006). For the purpose of our analysis, we summarize aspects of only a subset of freshwater life stages and related environmental metrics.

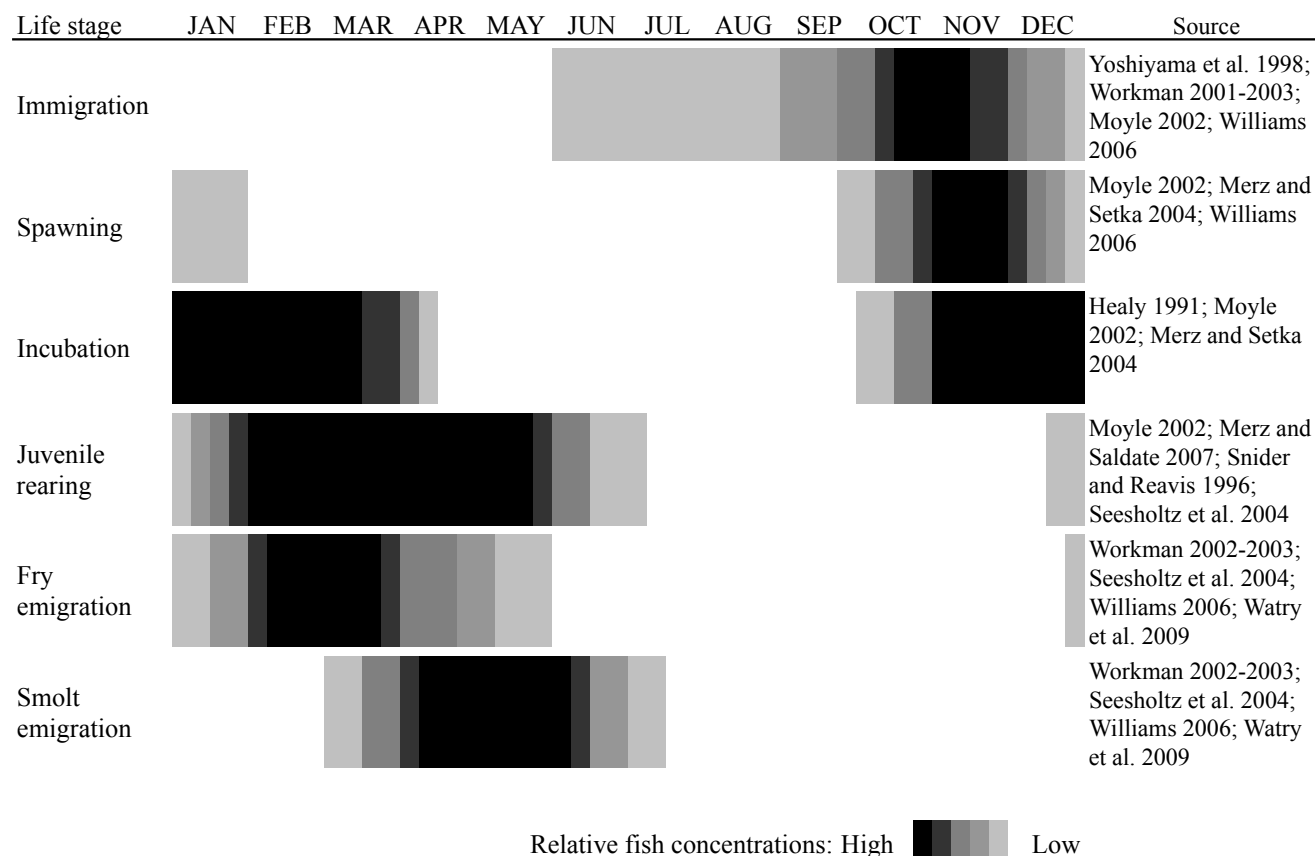
Upstream Adults

During immigration, adults stop feeding and subsist on body fat reserves. Although cues that trigger adults to return to spawning grounds are not well understood, it is thought that the ability to find their way is related mainly to long-term olfaction memory (Dittman and Quinn 1996). Homing ability within fresh water also may be aided by vision (Healey 1991), and by celestial and magnetic compass orientation (Quinn 1980) and may be stimulated by changes in streamflow, turbidity, temperature, and oxygen content (Allen and Hassler 1986). Migratory routes must be free of barriers that impede movement upstream and downstream. Numerous factors, such as predation, harvest, and water quality affect an adult's ability to reach spawning areas and spawn successfully (Hillemeier 1999; Beamesderfer 2000; Goniea et al. 2006). The ability to return to natal watersheds is further affected by anthropogenic effects such as water diversion structures, channel modification, and water quality (Fisher et al. 1991).

Spawning

In general, Chinook salmon spawn in stream substrates with a median particle diameter up to about 10% of their body length (Kondolf and Wolman 1993). Proximity to cover and flow shear zones provides important refuge from predation and resting zones for energy conservation (Merz 2001; Wheaton et al. 2004). During spawning, the female makes a redd (an area containing several individual nests) by turning on her side and repeatedly flexing her body to force gravel and fine sediment into the water column; this action coarsens the spawning substrate, forming an oval depression with a mound of bed material located immediately downstream (Crisp and Carling 1989). Often, several males will court and fertilize the eggs of a single female. Chinook salmon

Table 1 Generalized life-history timing for Central Valley fall-run Chinook salmon



spawn once and then die (semelparity) although individuals may survive for days to weeks after spawning.

Fecundity and egg size differ among salmon stocks that inhabit different geographic areas (Fleming and Gross 1990; Meyers et al. 1998). For example, the average number of eggs per female fall-run Chinook salmon from the Mokelumne River is 5,423 (range: 2,132 to 9,492) while the historic average for the Sacramento River has been as high as 7,423 eggs (range: 4,795 to 11,012) (Healey and Heard 1984; Kaufman et al. 2009). Density-dependent (e.g., disease, redd superimposition) and independent variables (e.g., temperature, flow) can affect spawning success and the health of gametes released to the stream (Patterson 2004; Tierney et al. 2009). Since available spawning areas are limited, late spawners may superimpose their redds on previously constructed redds of

other females. Superimposition can be a major mortality factor for incubating embryos causing a density-dependent relationship in which fry production is inversely related to adult spawner numbers (McNeil 1964; Heard 1978; Buklis and Barton 1984; Parneskiy 1990; Chebanov 1991).

Incubation

The female salmon buries in her redd fertilized eggs (embryos) that will develop in gravel interstices. Incubation generally lasts from 40 to 90 days at water temperatures of 4.4 °C to 12.2 °C (Bams 1970; Heming 1982; Bjornn and Reiser 1991; Geist et al. 2006). Alevins may remain in the gravel for 4 to 6 weeks after hatching, receiving nutrients and energy from their yolk sac before emerging to the water column (Moyle 2002). Incubation is highly dependent on water temperature, dissolved oxygen (DO) and

substrate permeability (Merz et al. 2004). For successful incubation, gravel must be sufficiently free of fine sediment to facilitate DO supplied to embryos, transport metabolic wastes away, and not hinder emergence of fry from the gravel (Tappel and Bjornn 1983; and see discussions in Chevalier et al. 1984 and Groot and Margolis 1991). Other water quality-related parameters (e.g., disease, contaminants) can further affect embryo development and survival (Merz et al. 2006).

Juvenile Rearing

Newly emerged young are often found in shallow, slow-moving water and transition to deeper, faster water as they increase in size (see Cramer and Ackerman 2009). Habitat complexity (e.g., woody debris, overhanging vegetation, seasonally inundated areas) provides juvenile hiding, resting, and feeding habitat, increasing their ability to grow, develop, and survive emigration. Juvenile diets often vary by habitat type, but terrestrial and aquatic invertebrates, and larval fish and eggs are important prey for juvenile salmon upstream of the Delta (Sasaki 1966; Merz and Vanicek 1996; Sommer et al. 2001). Prey size and ingestion rates are affected by juvenile size and water temperature (Merz 2002). At times, floodplains may provide better juvenile rearing opportunities because they often create optimum temperatures, offer habitats rich in prey items and away from salmon predators, and provide refuge from high flows (Sommer et al. 2001; Jeffres et al. 2008). Habitat availability, water quality, and predation are examples of environmental parameters that can affect successful rearing (Lindley and Mohr 2003).

Emigration

The timing and stimuli for emigrants to leave a natal stream depends on individual genetics, social cues, and the environmental factors to which individuals are exposed as they emerge, rear, and migrate downstream. Within the CV, Chinook salmon emigration size varies widely. For example, juvenile fall-run emigrate as fry (<55 mm fork length [FL]), parr (≥55 mm FL and <75 mm FL), or smolts (≥75 mm FL) (Brandes and McLain 2001; Williams

2001). In some systems, the proportion of salmon leaving as fry, parr, or smolts may shift from year to year (Figure 3). Though several researchers have questioned if fry migrants make a significant contribution to adult populations (Brandes and McLain 2001; Williams 2001), Miller et al. (2010) empirically demonstrated that CV fry-sized emigrants represent a viable life history strategy. Flow, temperature, water quality, diversion, and predation have been implicated as key parameters that affect successful emigration (Cavallo et al. 2012).

FRESHWATER MONITORING TECHNIQUES

Adult Escapement

A variety of methods is used to estimate CV adult escapement including hatchery returns and direct counts at fish ladders and weir facilities (Williams 2006). However, the most consistently used method to generate escapement estimates involves mark-recapture techniques applied to carcasses (Williams 2001). Since 1976, the California Department of Fish and Wildlife (DFW) has used a modified Schaefer method but recently has reported estimates based on the Jolly-Seber method (e.g., Snider and Reavis 1996), and the agency has developed procedures for calculating adult escapement estimates using a superpopulation modification to the Cormack-Jolly-Seber model. This effort has been expanded and significant work has been performed to compare and contrast various escapement estimates on specific systems including video, infrared imaging, DIDSON, carcass, and hatchery escapement estimates (Merz and Merz 2004; Workman 2004b; Holmes et al. 2005).

Spawning

Redd counts are commonly used to index adult escapement and assess population trends (Beland 1996; Rieman and Myers 1997; Isaac et al. 2003). As the product of reproductive females only, redd counts provide an index of effective population size (Meffe 1986). The use of redd counts for population monitoring may be complicated by superimposition

or if females produce false, “test” redds (Crisp and Carling 1989; Gallagher and Gallagher 2005). Redd enumeration errors must be identified and reduced before this method can be useful for long-term monitoring (Maxell 1999; Dunham et al. 2001).

Chinook salmon redds are typically monitored by two methods: direct count by wading and boat on smaller streams (Merz and Setka 2004) and aerial photographs on larger streams where water quality is clear enough to identify where female salmon have disturbed the gravel substrate (Williams 2001). Egg

retention, identified in post-spawn females collected during carcass surveys, is often used as an indicator of spawning success and has been correlated with stream temperature and predation in other systems (Quinn et al. 2007).

Incubation and Emergence

According to Williams (2006), no regular CV programs that monitor redd conditions or survival of eggs and alevins are conducted in the Central Valley,

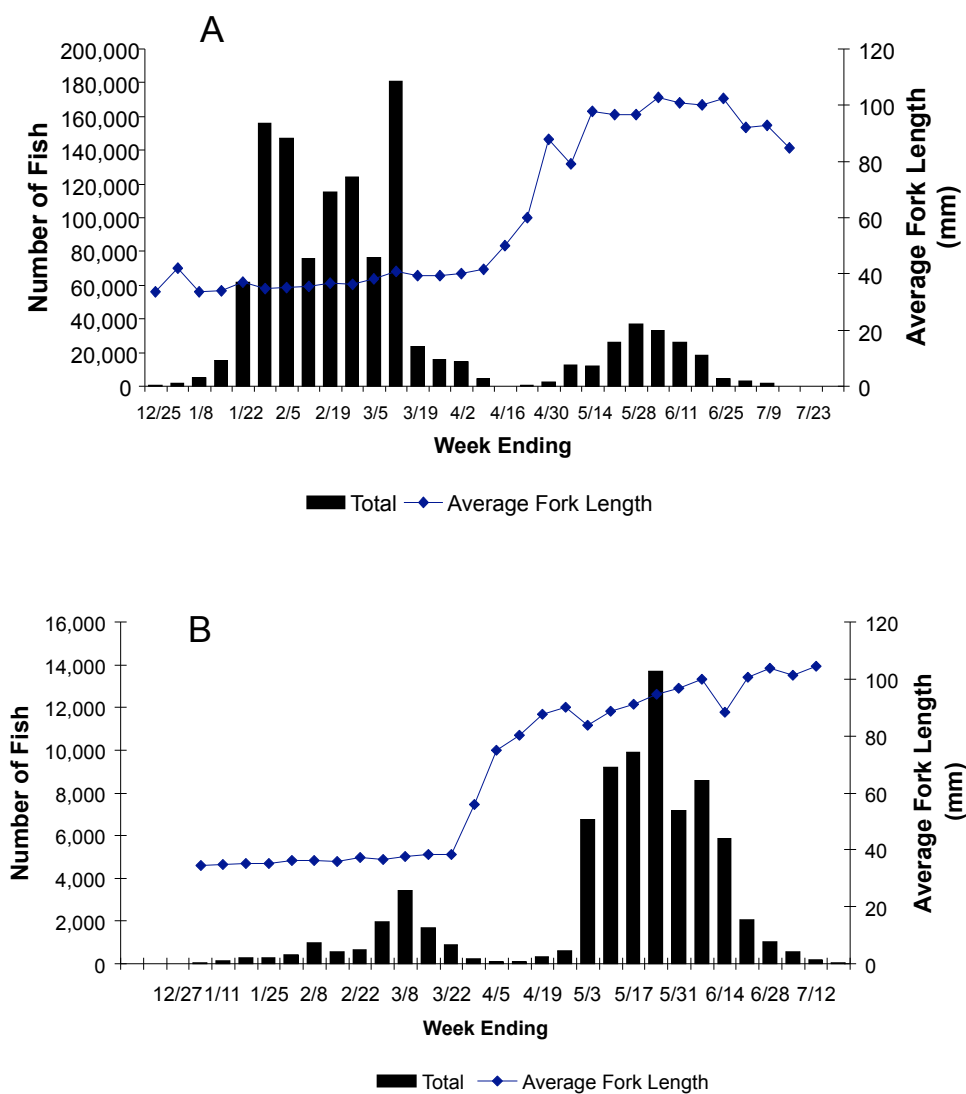


Figure 3 Examples of variable timing for fry and smolt emigrant pulses estimated from daily catch estimates at two rotary screw traps on the lower Mokelumne River, California: (A) 2005–2006 emigration period, (B) 2001–2002 emigration period

but such assessments have been done in various short-term CV studies (e.g., Vyverberg et al. 1997; Merz et al. 2004). Modeling exercises have been suggested to assess or predict embryo survival as a function of sediment deposition (Tappel and Bjorn 1983; Wu 2000).

Rearing

Various traps, including incline plane and rotary screw traps (RSTs), have been used throughout the Pacific Northwest to estimate juvenile salmon rearing characteristics, such as:

- Emigration abundance (Tsumura and Hume 1986; Baranski 1989; Orciari et al. 1994; Thedinga et al. 1994; Letcher et al. 2002; Johnson et al. 2005);
- Outmigration timing (Wagner et al. 1963; Hartman et al. 1982);
- Outmigrant body size (Orciari et al. 1994; Olsson et al. 2001; Workman 2003, 2004a);
- Survival (Schoeneman et al. 1961; Wagner et al. 1963; Tsumura and Hume 1986; Thedinga et al. 1994; Olsson et al. 2001; Letcher et al. 2002); and
- Behavior (Brown and Hartman 1988; Roper and Scarnecchia 1996).

Juvenile salmon are also assessed in CV waters with beach seines (e.g., Brandes and McClain 2001). Juvenile abundance monitoring during each life stage (e.g., fry, parr, smolt) enables mortality to be partitioned between freshwater (emergence-to-migration) and marine (smolt-to-adult) life stages (Volkhardt et al. 2007).

Emigration

Emigrant survival estimates from natal streams to the Pacific Ocean can be calculated for various populations by fin clipping and inserting coded-wire tags (CWTs) in juvenile salmon captured in migrant traps (Workman et al. 2007). Since 1978, as part of the Interagency Ecological Program (IEP), the USFWS

has monitored the relative abundance of Chinook salmon smolts that emigrate from the CV with mid-water trawl net surveys at Chipps Island (Baker and Morhardt 2001; Brandes and McLain 2001). Adipose fin-clipped smolts are sacrificed and their CWTs are read. To form an estimate of absolute abundance, the number of smolts captured is expanded to account for the amount of time spent sampling and the ratio of sampling net width-to-channel width. For CWT-bearing smolts, the expanded recovery for each tag group is divided by the number of smolts originally released and reported as a smolt survival index (SSI). Baker and Morhardt (2001), Newman and Rice (2002), Newman (2003), and Newman and Brandes (2010) have analyzed and reported relative survival rates from these experiments. More recently, researchers are using acoustic telemetry methods to estimate emigration survival (e.g., Perry et al. 2010).

Comparability of Sampling Methods

Juvenile salmon abundance is used by the AFRP and CAMP as a measurement of salmonid production and survival attributable to AFRP habitat restoration actions. When normalized for the number of adult females, relative changes in numbers of juvenile salmon should serve as a primary indicator of habitat conditions in natal streams. Here we suggest that a focus on juvenile salmon could avoid the need to account for many variables not related to AFRP actions, including ocean conditions, ocean sport and commercial harvest, habitat conditions and water quality outside of natal streams, in-river sport harvest, adult predation, and water project operations in the Delta and Bay.

METHODS

General Stage Class Model

The reproduction stage (or redd construction) involves multiplicative processes where one reproductive individual can give rise to multiple offspring. The proportion of fry versus smolts represents the combined effects of multiple life cycle transitions. All other stages of the life cycle involve survival until

Table 2 Data used in model validation for fall-run Chinook salmon in the California Central Valley

Lifestage	Watershed	Data	Sampling techniques	Sample year used	Source
Adult escapement and spawning	American River	Adult escapement	Carcass surveys	1991–1995 2004–2009	http://www.fws.gov/stockton/afrp/Documents/GrandTab_020111.pdf
		Redds	Aerial photos and sub-sample groundtruthing	1991–1995 2004–2009	Snider and Vyverberg 1995 Snider and Reavis 1996 Hannon, unpublished
		Flow	Calibrated station	1991–1995 2004–2009	<a ;"="" href="http://waterdata.usgs.gov/ca/nwis/inventory/?site_no=11446500&agency_cd=USGS&">http://waterdata.usgs.gov/ca/nwis/inventory/?site_no=11446500&agency_cd=USGS&";
	Mokelumne River	Adult escapement	Fish ladder video and trapping	1990–2006	Marine and Vogel 1994, 1996, 2000 Vogel and Marine 1998, 1999 Workman 2001–2007
		Adult sex ratios	Fish ladder video and trapping	1990–2006	Merz and Merz 2002
		Redds	Roving surveys	1990–2006	Hagar 1991 Hartwell 1992–1996 Mulchaey and Setka 2007 Setka 2004
Incubation and emergence	Mokelumne River	Redds	Roving surveys	1990–2006	Hagar 1991 Hartwell 1992–1996 Mulchaey and Setka 2007 Setka 2004
		Emergence and emigration	Rotary screw trap	1992–1997 2000–2006	Marine and Vogel 1994, 1996, 2000 Vogel and Marine 1998, 1999 Workman 2001–2007
		Fecundity	Necropsy	NA	Kaufman et al. 2009
Juvenile emigration	Stanislaus	Emigration	Rotary screwtrap	1996–2009	Watry et al. 2007; Tri-Dam Fishbio
		Flow	Calibrated station	1996–2009	<a ;"="" href="http://waterdata.usgs.gov/ca/nwis/inventory/?site_no=11303000&agency_cd=USGS&">http://waterdata.usgs.gov/ca/nwis/inventory/?site_no=11303000&agency_cd=USGS&";
	Mokelumne River	Emigration	Rotary screwtrap	1992–1997 2000–2006	Marine and Vogel 1994, 1996, 2000 Vogel and Marine 1998, 1999 Workman 2001–2007
		Flow	Calibrated station	1992–1997 2000–2006	http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=CMN

the next stage, thus, we assume that the expected number of individuals leaving a stage class can be predicted as a multiple (≤ 1.0) of the number entering the stage class:

$$E(F_{LS}) = QF_{LS-1} \quad (1)$$

where $E()$ denotes expectation, F is the number of fish at a given life stage LS , F_{LS-1} is the number of fish at the previous life stage $LS-1$, and Q is a transition rate that can depend on multiple factors including, but not limited to, the quality of fish, the quantity of habitat available, and the quality of habitat available.

This modeling approach can be incorporated into appropriate life stages within the life cycle of the CV fall-run Chinook salmon (Figure 2; Table 2). Since the model, when applied to survival transitions, is a model of proportions, it is readily fit as a linear model in the logit scale (Warton and Hui 2011), with Q calculated as a function of one or more covariates thought to influence survival through a stage. We use the logit transformation rather than treating data as counts analyzed with a binomial distribution since the abundance estimates are not raw counts, but rather the result of complicated expansions (to

account for partial sampling, incomplete detection, etc.) that we do not treat in detail in this paper. For fecundity-related transitions, we used standard regression techniques for continuous response variables and allowed non-zero intercepts since we might expect, for example, that some minimum number of redds was needed before any fry would be observed. We checked that all estimated intercepts were reasonable—i.e., we might expect zero fry produced from a small number of redds, but would not expect non-zero fry production from zero redds. By using standard regression techniques we assumed the dependent variables were measured without error; more rigorous analyses of particular transitions should relax this assumption.

To test this conceptual model, we used information from a variety of data sets from the American, Mokelumne and Stanislaus rivers of the CV (Figure 1; Table 2). The primary environmental parameter used in these analyses was river discharge ($\text{m}^3 \text{sec}^{-1}$) and we relied on data from the California Data Exchange Center (CDEC: <http://cdec.water.ca.gov/>). For brevity, important life stages not considered in this study were: emigration (juveniles through the Delta and estuary to ocean), ocean existence (including ocean harvest) and immigration (upstream migration of adults including in-river harvest).

SPAWNING — ASSESSMENT OF POPULATION DEMOGRAPHICS AND AVAILABLE HABITAT

Demographics

We first hypothesized that adult escapement to a spawning stream significantly affects the number of redds constructed within a given stream. We tested this hypothesis using linear regression to analyze redd production as a function of total escapement. To test the hypothesis that redd production was a saturating function of spawner number (i.e., density dependence) we also fit models where spawner number was first log-transformed. We used adult escapement and redd data available from the Mokelumne (1990 to 2006) and American (1991 to 1995 and 2004 to 2009) rivers (Table 2).

Since only the female salmon constructs the redd, we also used the estimated female component of escapement as a predictor of redd production. We compared model fits using the total escapement for the Mokelumne and American rivers, and female escapement only from the Mokelumne River, because it was the only river with adequate sex composition data.

Spawning Habitat

We hypothesized that the number of successful redds is related to the amount of available spawning habitat. Therefore, we expected an inverse relationship between the amount of available habitat and the proportion of redds superimposed. Our model of redd superimposition incorporates both flow and spawner number, allowing us to disentangle the effects of increased numbers of competitors from the effects of extrinsic habitat quality. In this example, we hypothesize that as flows increase, the area of gravel available to spawning females should increase, reducing redd superimposition (assuming channel is not overly-incised and gravel surface area is not limited). At the same time, we expected more redd superimposition at a given level of habitat availability if there are more spawners competing for redd sites.

To test these hypotheses, we regressed mean flow during the spawning season against the estimated redd superimposition in the lower American River (Table 2). American River redd superimposition data were available from 1991 through 1995, and from 2004 through 2009 (Table 1). Because superimposition is recorded as a percent of total redds observed, we logit-transformed these data and then fit linear models assuming constant superimposition (null model), linear effect of redd count only, and linear effect of flow only; these were the parameters for which data were available. We also assessed additive effect of flow and redd count and interactive effect of flow and redd count. We used Akaike Information Criterion (AIC) to compare among model formulations, effectively accounting for the trade-off between increased fit allowed by extra parameters with the increased risk of overfitting (Burnham and Anderson 2002). Finally, for this component we calculated the AIC weight for each redd model. The weight was

interpreted as the probability that a particular model is the best model out of those considered.

Incubation and Emergence

Juvenile Chinook salmon production is a result of the number of redds produced and the number of embryos within each redd. We hypothesized that estimated fecundity would affect the number of embryos per redd. We regressed the estimated number of juveniles produced annually (RST estimates) against the estimated number of redds produced in the previous season for the Mokelumne River (1995 to 2006). We then estimated total embryo production by multiplying average annual estimated female fecundity by the number of redds observed each season on the Mokelumne River to see if this would improve our model of juvenile estimation. We estimated fecundity of females using the regression equation for FL and number of ova per Mokelumne River female, developed by Kaufman et al. (2009):

$$Y = 11.14X - 3066 \quad (2)$$

where Y = estimated number of ova and X = fish fork length (mm).

We used mean female FL estimated from video monitoring (Table 2) to provide an average fecundity value for each escapement year and multiplied this by the estimated number for redds observed to estimate number of fry available. We then regressed the estimated number of juveniles produced from RST data against the estimated number of fry available from combined fecundity and redd count estimates. This was compared against the regression of estimated numbers of juveniles produced from RST data against the estimated redd counts from the previous season. This allowed testing whether fecundity estimates improved estimates of fry production over predictions based on adult escapement or redd count alone.

Rearing and Emigration

We assumed the number of fry produced from the previous season's redds would be the major predictor of how many juveniles were available to emigrate from the natal stream. We also assumed environmen-

tal factors would affect the proportion of emergent fry that survived the river rearing period to produce emigrants from the natal stream. Potentially important environmental factors included water temperature, habitat quality, food, predators, and flow; but for this analysis we examined only flow because it was the only variable with readily available data. We used RST data from upper and lower portions of the Stanislaus River at Oakdale and Caswell State Park, respectively, to estimate spawning reach fry production and survival through the rearing reach (juvenile production). We divided the estimated annual juvenile production that emigrate from the lower portion of the river by the estimated fry production in the upper portion of the river to produce an annual index of juvenile rearing habitat survival for Stanislaus juvenile Chinook salmon. We then logit-transformed the survival index and regressed this against mean daily flow for the rearing period (January 1 through June 30).

During emigration, we assumed that higher flow during the rearing life stage would increase the proportion of individuals observed emigrating as fry. To test this hypothesis, we regressed the logit-transformed percent emigration as fry from the lowest trap operated on the Mokelumne and Stanislaus rivers against estimated mean annual flow of each river during emigration (January 1 through June 30) for each year available.

RESULTS

Regression between adult escapement and redd production confirmed that escapement estimates strongly predict how much spawning activity occurs on the Mokelumne and American rivers (Figure 4). A hyperbolic (saturating) relationship (or at least diminishing returns at higher escapement) was demonstrated and this was significant for both rivers (Mokelumne: $F = 223.1156$; $df = 2, 15$; $p < 0.0001$; American: $F = 41.9218$; $df = 1, 10$; $p < 0.0001$), with the hyperbolic relationship a better fit than linear (e.g. $R^2 = 0.72$ vs. 0.50 for the American River). It is important to note that when spawners are abundant it becomes difficult to see new redds, which

Table 3 Calculated Akaike Information Criterion (AIC) for each model used to predict redd superimposition on the lower American River, California (1991–1995). Weight can be interpreted as the probability that a particular model is the best model out of those considered.

Model	AIC	delta AIC	AIC weight
Additive	12.506	0	0.64512264
Interactive	14.466	1.96	0.24212169
Flow	16.088	3.582	0.10760213
Redd count	22.704	10.198	0.00393708
Constant survival	25.053	12.547	0.00121645

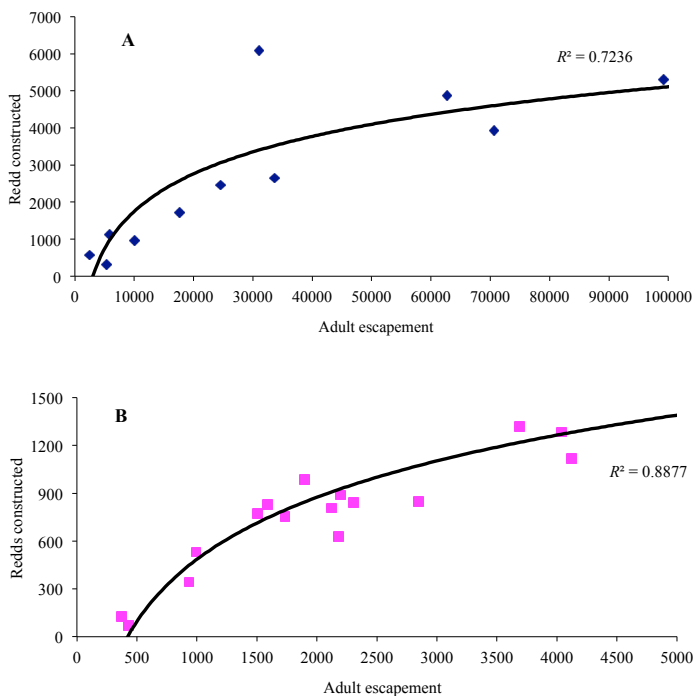


Figure 4 The relationship between estimated adult escapement and observed redds within the (A) American River (1991–1995; 2004–2009) and (B) Mokelumne River (1990–2006), California. Both rivers supplement populations with terminal hatcheries. Numbers on the adult escapement axis indicate estimated total escapement minus hatchery intake.

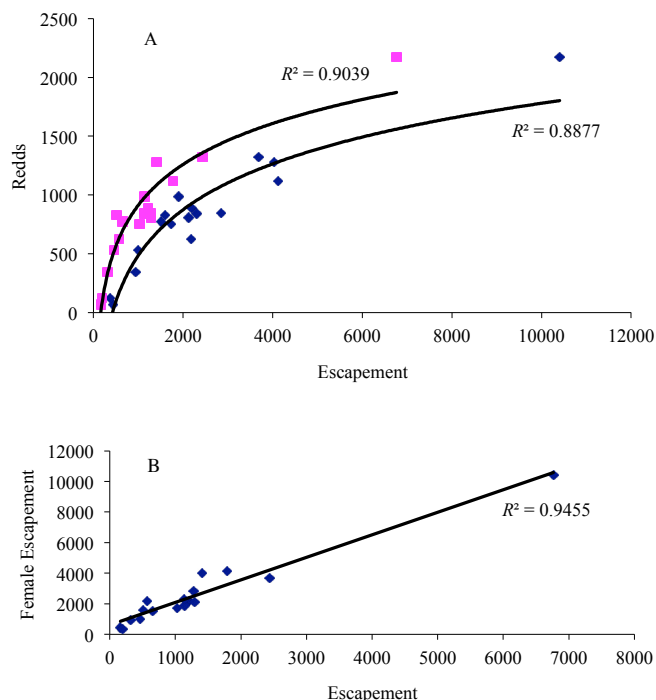


Figure 5 The relationship between (A) log estimated total escapement and estimated redds (diamond) and log total female escapement and estimated redds (square) and (B) total escapement and female escapement for the lower Mokelumne River, California (1990–2006)

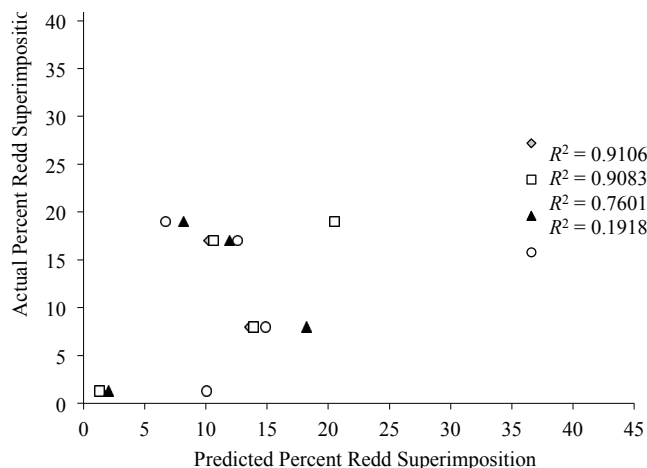


Figure 6 Regression between observed and predicted percent redd superimposition for 5 variable flow years (1991–1995) on the lower American River, California. Percent superimposition predictions were modeled using redd counts (white circles), flow (black triangles), interaction of redds and flow (white squares) and additive effects of redds and flow (gray diamonds).

could help account for the plateau in the relationship (Williams 2001).

Female escapement further provided a clear indication of spawning activity for the lower Mokelumne River. However, the female proportion of adult escapement did not vary substantially from year to year and female enumeration did not add significantly to Mokelumne River redd production estimates (Figure 5).

Spawning Habitat

Our results demonstrated little support for models that depict lower American River redd superimposition as constant from year to year, or models that describe flow as unimportant (Table 3). The models with both flow and redd count fit the data best and received considerably more support than the model with flow alone (Figure 6).

Using the summed weights of different models that all included a particular parameter, there was a 99.5% chance that out of all the models considered, the best model included flow, and an 89.1% chance that the best model included redd count. There is essentially no support (0.01% probability) for a model saying that neither redd count nor flow is important in predicting redd superimposition in the lower American River.

Predicting Fry Production from Female Fecundity

Mokelumne River data from 1998 and 1999 were excluded because hatchery juveniles escaped into the river in both years. For the 1995–1997 and 2000–2006 data, both models based on redds alone and models based on redds and fecundity performed well. The number of Mokelumne River redds explained over 82% of annual variability in juvenile emigrants and this was significant ($F = 38.5278$; $df = 8,1$; $p = 0.0003$; Figure 7A). Similarly, estimated fecundity multiplied by the estimated number of redds explained over 83% of variation in juvenile emigrants and this was significant ($F = 34.4061$; $df = 8,1$; $p = 0.0004$; Figure 7B).

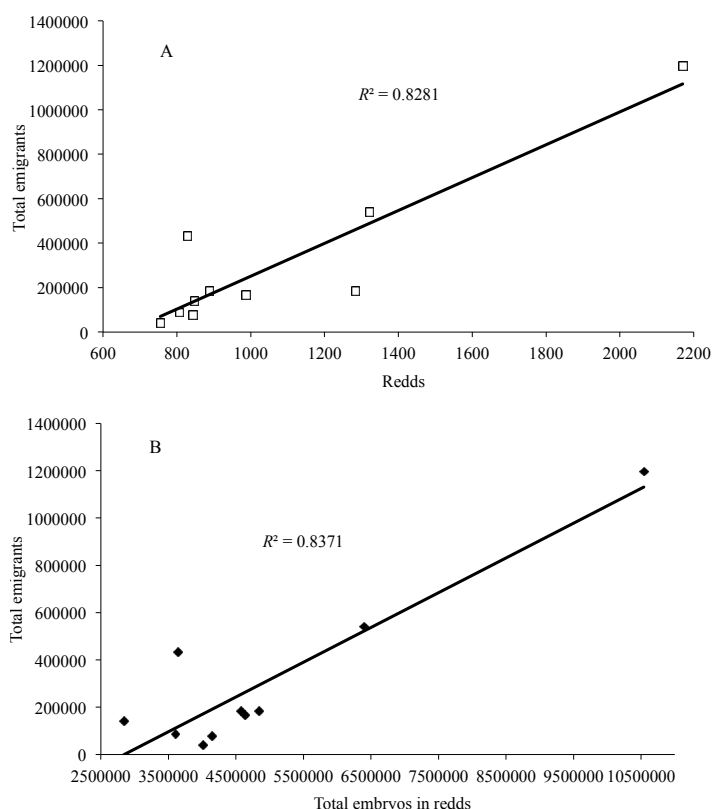


Figure 7 Regression between estimated juvenile emigrants and (A) estimated number of redds; and (B) estimated average adult female fecundity multiplied by estimated number of redds for the lower Mokelumne River (1995–1997 and 2000–2006)

Emigration

For the Stanislaus River, the estimated survival of juveniles passing between the Caswell State Park trap and the Oakdale trap at the bottom of the spawning reach increased significantly with flow (Figure 8, regression of logit-transformed proportions, $p = 0.011$). For both the Mokelumne and Stanislaus rivers, the proportion of emigrants that left as fry increased with flow (Figure 9; $p = 0.017$ for Mokelumne; $p = 0.007$ for Stanislaus). However, the proportion of juveniles leaving as fry was not linear to flow and there was considerable unexplained variability in the relationship for both systems.

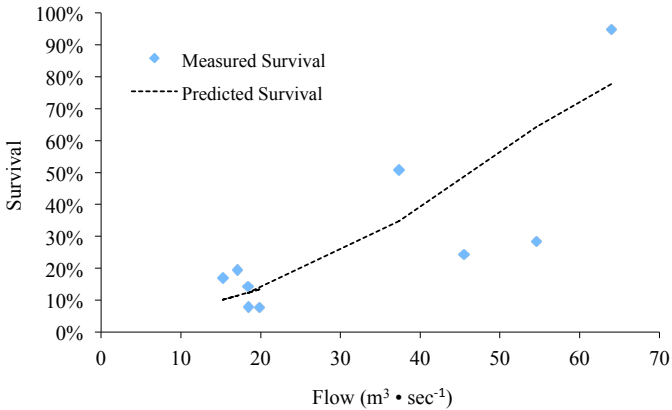


Figure 8 Modeled relationship between flow and estimated juvenile survival between Caswell and Oakdale traps on the Stanislaus River (1996, and 1998–2006)

DISCUSSION

Reliable population abundance estimates at key life stages—such as adult escapement, redd counts, fry abundance, and emigrant production—are essential to effectively manage salmonids and to identify actions that will afford the best possibility of recovering stocks. To provide a method for evaluating management actions within the freshwater component of anadromous salmon life histories, we developed a generalized approach for applying linear models to production within stage classes and used the CV fall-run Chinook salmon to investigate the general premise. We then tested the model using available data from short- and long-term monitoring programs on several freshwater life stages. The model showed that estimates of previous stage class production correlated well with the estimated number of individuals produced in the next class, but in many cases predictions could be improved by including covariates that measured factors plausibly hypothesized to affect life stage survival or productivity. This same approach could be applied, along with model comparison techniques as used here, to evaluate alternate or additional covariates. Such analyses could provide increased understanding of environmental factors that affect productivity at a given life stage, or help evaluate the effects of specific restoration actions. By compar-

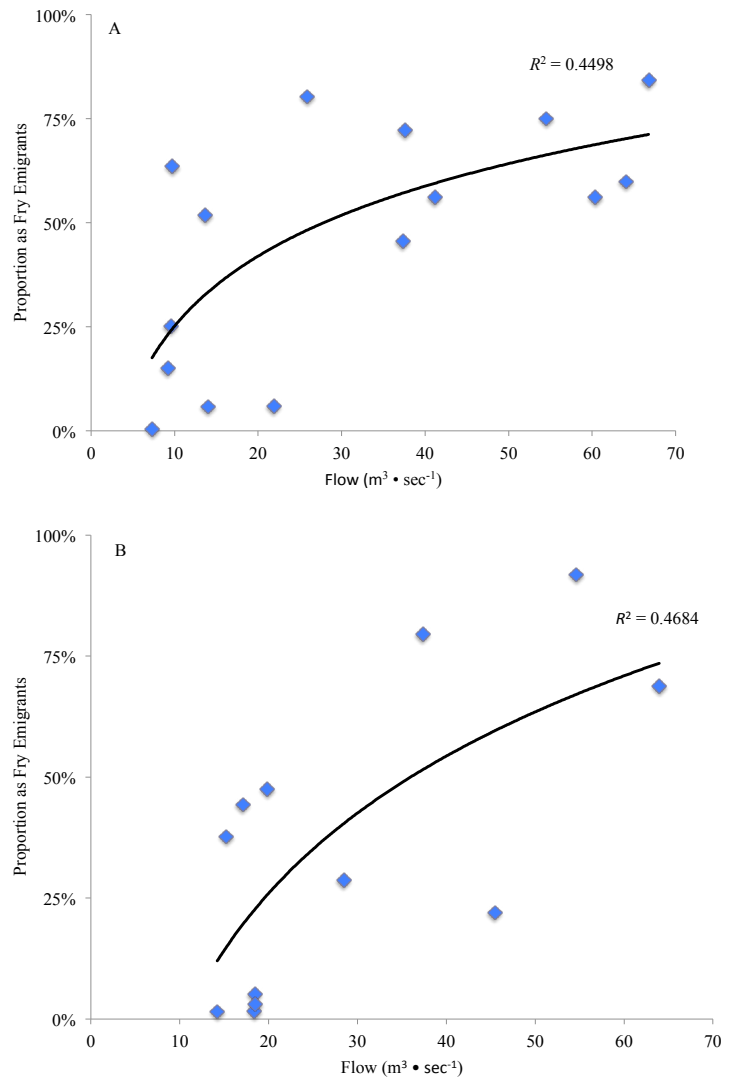


Figure 9 Fitted relationships between flow and proportion of juveniles leaving as fry each season for the (A) Mokelumne River (1993–2006) and (B) Stanislaus River (1996 and 1998–2006)

ing models fitted to data collected before and after the restoration action, a similar approach could be used to evaluate whether model coefficients change in response to particular restoration actions. Ideally, such comparisons would include simultaneous model applications to control and treatment areas, such that temporally concordant changes in vital rates for reasons unrelated to the restoration action could be ruled out.

MODEL STRENGTHS AND WEAKNESSES

All of the modeling examples we tested were useful. This suggests that monitoring data available at the time of this study are promising for identifying key stressors within and among CV watersheds, and also for tracking restoration effort success when viewed in the context of the life cycle. Our framework is advantageous in its simplicity and because much of the data needed to populate the framework are already being collected in key watersheds. However, this is not to say such a modeling effort will be easy or without significant cost. In 1997, the estimated total expenditure of conducting CV monitoring programs for adult and juvenile salmon was \$28.7 million (Montgomery Watson et al. 1997). When adjusting for inflation (2013), the costs to conduct the requisite monitoring today are much greater (\$41.5 million). Justifying such an effort will be difficult if biologists cannot clearly demonstrate how monitoring data are being used to inform effective management actions. The high costs but great opportunity provided by such monitoring programs emphasizes the need to implement a modeling framework such as described here so that valuable data already being collected can be put to work immediately.

Teasing apart co-varying dependent variables may also be challenging. For instance, flow was used in this exercise because it is easy to quantify and data are readily available. However, flow correlates with temperature, turbidity, dissolved oxygen, substrate quality, water quality, predation and even fish growth. High flow may offer benefits in one regard but potentially negative effects where habitat is degraded, including scoured channels, decoupled floodplains and sediment deficits (Kondolf 1997). Long-term datasets on physical habitat attributes, within and among watersheds monitored for salmon populations are needed to refine causative mechanisms for observed flow-abundance relationships.

Relatively accurate, unbiased and consistently collected data on life stage-specific abundance are essential for effective application of our modeling framework. For presentation simplicity, we did not explicitly model observation error, separate out observation from process error, or attempt to account

for sources of bias. When life stage counts are provided with estimates of error for each data point, a more sophisticated state-space or hierarchical model (LaDeau and Clark 2006; Clark 2007; Royle and Dorazio 2008) may be justified. It is also crucial that estimated counts be unbiased. Bergman et al. (2012) recently provided comprehensive suggestions for improved CV escapement monitoring and we advocate similar careful attention to estimation at all life stages. This is especially true for carcass mark-recapture surveys where there is significant potential for surveyor error or poor sampling design to bias resulting estimates (Bergman et al. 2012).

Our model suggests that at least on the Mokelumne River, the added effort of quantifying adult female escapement does not substantially increase our ability to estimate redd production. This lack of demonstrative results is less a consequence of poor model function than the simple fact that adult escapement sex ratios do not vary substantially in the Mokelumne River annually, at least over the years in question (mean proportion of female escapement 48%; SD 12%). However, this may not be the case for other systems or species (Holtby and Healey 1990; Olsen et al. 2006).

Spawning Habitat

Since superimposition data did not span the full range of American River redd counts, we might not expect it to fully capture the importance of redd count data. Certainly, though, it shows that we can better predict superimposition if we take flow into account. Also, the lower American River has experienced channel scour since Nimbus Dam was constructed (James 1991), and this may affect redd superimposition if channelization decouples the relationship between flow and spawning gravels. Recent implementation of gravel augmentation within the active channel may offer a unique opportunity to study this relationship further.

Our model of redd superimposition incorporates both flow and spawner number, allowing us to disentangle the effects of increased competitor numbers from the effects of extrinsic habitat quality. A similar

approach, which allows us to account for the effects of externally driven factors (e.g., escapement, flow) could be used to further assess (i.e., with before–after comparisons) the success of restoration actions.

Incubation and Emergence

Only Mokelumne River data allowed us to assess the relationship between fecundity (embryos produced) and juvenile production. Though the relationship was positive, with a relatively high R^2 , this relationship was strongly influenced by one data point above 1.25 million juveniles, which may be driving the strong regression. Also, the observed positive relationship may have been counteracted to some degree by the known trade-off between fecundity and egg size (Hankin and McKelvey 1985). That is, females of a given size, but with greater fecundity, tend to produce smaller eggs. Smaller eggs may yield more fry at emergence, yet these fry will be smaller and may have poorer survival than fry produced females who produce large eggs (Fowler 1972).

Emigration

Flow significantly affected the number of juveniles that survived from the spawning reach to emigrate from the Stanislaus River, as well as the proportion of juveniles that left as fry from both the Stanislaus and Mokelumne rivers. However, flow often correlates with temperature, water quality, diversion, floodplain activation, predation and a myriad of other parameters that are also thought to affect successful survival and emigration (Jeffres et al. 2008; Cavallo et al. 2012). Therefore, these correlative results should be interpreted with caution.

APPLICATION TO CENTRAL VALLEY CHINOOK SALMON RECOVERY EFFORTS

Fresh water is a limited resource, especially in the Mediterranean climate of California. Water has been the biggest factor in CV salmon resource policy, far overshadowing attention to other factors such as physical habitat quality, predatory effects, and adverse effects from hatchery production, although this situation may be changing (NOAA Fisheries

2009, draft recovery plan). The perspective our analytical framework provides may allow a better understanding of the limiting factors for freshwater life stages of CV salmon and where the allocation of limited resources for management may provide the most likely benefits.

The potential applications of our model are numerous, but perhaps one of the most important uses demonstrated here is validating the utility of at least some existing sampling programs. Without having independent estimates generated by different methodologies within specific life stages, we believe that our alternative of comparing transitions between life stage classes provides the next best means for testing the validity of current monitoring programs (see Miyamoto and Hartwell 2001).

A clear limitation of these analyses is the use of fragmented monitoring data from different watersheds to make inferences about the progression of juvenile salmon abundance as they move from one life stage to the next. Under ideal conditions, complete monitoring data for different life stages within a single watershed would have been used to assess how fish abundance transfers from one life stage to the next during the freshwater phase; such an analysis could have been done separately in different streams to assess the magnitude of inter-watershed differences. Unfortunately, data availability from all watersheds is still limited and trap efficiencies for many monitoring programs have not been quantified. This lack of coordination results in the use of methods that may not provide statistically robust population estimates of the life history stage of interest. The disjointed monitoring efforts also make the resulting information, including metadata on methods, not readily available to scientists and managers (Brown 2005). Separate or non-existent reports and different analytical techniques employed in independent programs have made it difficult to understand how restoration activities influence salmon production (McDonald and Banach 2010). Even so, our goal was to demonstrate the potential of using our modeling framework to clarify the life stage-specific limiting factors of CV salmon, and not necessarily to develop a more coordinated monitoring program.

MANAGEMENT IMPLICATIONS AND FUTURE DIRECTION

Despite the apparent need for site-specific restoration actions, it is difficult to assess their impact at the population level. First, salmon are influenced by a complex interplay of factors that range from flow levels and temperature in individual streams to long-term degradation of habitat associated with altered sediment budgets, highly altered migration routes through the Sacramento–San Joaquin Delta, and shifts in ocean conditions. Thus, understanding whether a change in abundance results from a single factor or a combination is exceedingly difficult. Second, the release of large numbers of hatchery fish hampers the ability to track population trends in naturally spawned salmon (Brown 2005). Third, ocean harvest rates are high and variable between years (Pyper et al. 2012) and thus can readily obscure changes caused by inland habitat conditions. By putting data in the context of life stage-specific survival and fish quality, we allow managers to look at stage-specific effects, which allow a more practical and informative evaluation of specific cause–effect relationships. While this does not necessarily remove all confounding issues (e.g., unknown or limited measurement of hatchery inputs to natural production) it does allow for quantifying relationships between specific life stage transitions and environmental parameters.

Recently, highly unusual coastal ocean conditions off California caused a severe reduction in all CV Chinook salmon populations that had already been depleted (Lindley et al. 2009). While ocean conditions and climatic variability have and will continue to have profound effects on the future health of California salmon, so too have the availability and quality of freshwater habitats. Because of this widespread degradation of freshwater habitats, the AFRP Restoration Plan identified 172 freshwater actions that would help achieve the anadromous fish doubling goal. These actions included habitat improvements for all life stages of anadromous fish through provisions of flows of suitable quality, quantity, and timing, as well as enhanced physical habitat conditions.

CV salmon are clearly influenced by a variety of natural and anthropogenic factors. However, their future also depends greatly upon the efficacy of restorative management actions for freshwater habitats (e.g., those mentioned above) so the potential benefits for salmon survival at each life stage must be quantified, based on the multifarious effects of flow management, habitat restoration, and population structure, and perhaps other unconsidered factors. Our model provides a potential framework to identify where management actions can create the greatest benefits within each freshwater life stage, and which of the measured physical parameters most influence salmon production, or, alternatively, whether the most influence can even be quantified with currently available information.

Although extensive efforts are being made to track adult and juvenile CV salmon abundance, the demonstration of direct relationships between restoration actions and population responses for different life stages has been elusive (Williams et al. 2007). This is particularly true for juvenile salmonids. Though adult escapement estimates provide tributary and stock-specific trends, they are less useful for identifying underlying mechanisms. Measures such as juveniles or smolts produced per spawning female could be developed to provide an additional level of resolution about the function of instream processes (Cummins et al. 2008). More specific and quantitative recovery goals could be developed for CV Chinook salmon to provide a clearer benchmark against which to measure progress. This would require more detailed conceptual and numerical modeling of the specific limiting factors in individual watersheds, population modeling, and additional monitoring and studies. Finally, agencies could carefully and systematically document and assess individual restoration actions intended to affect CV Chinook salmon. To document cause–and–effect relationships, performance assessments of these actions that result in quantitative estimates of change in key system parameters are ultimately necessary. The modeling exercise we have presented provides some suggestions for a stage class model approach to assess the extent of salmon population recovery at the life stage level. Though we provided examples for the California Central Valley, these concepts can be

implemented wherever migratory salmonid populations and associated environmental data are being adequately monitored.

ACKNOWLEDGEMENTS

We thank W. Satterthwaite for significant insight and guidance on this manuscript; N. Kogut, S. Vincenzi and S. Zeug for providing helpful reviews of an earlier draft; and J. Williams and R. Yoshiyama for providing further review. We greatly appreciate data collected by the California Department of Fish and Wildlife, Cramer Fish Sciences, East Bay Municipal Utility District, the U.S. Bureau of Reclamation, and various entities that provided data cited in Table 2 of this paper. Partial funding for this project was provided by the U.S. Fish and Wildlife Service. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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