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Influence of estuary conditions on the recovery rate of coded-wire-tagged Chinook salmon (*Oncorhynchus tshawytscha*) in an ocean fishery

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Abstract – Chinook salmon (*Oncorhynchus tschawytscha*) populations within the highly modified San Francisco Estuary, California, have seen precipitous declines in recent years. To better understand this decline, a decade of coded-wire tag release and recovery data for juvenile salmon was combined with physicochemical data to construct models that represented alternative hypotheses of estuarine conditions that influence tag recovery rate in the ocean. An information theoretic approach was used to evaluate the weight of evidence for each hypothesis and model averaging was performed to determine the level of support for variables that represented individual hypotheses. A single best model was identified for salmon released into the Sacramento River side of the estuary, whereas two competitive models were selected for salmon released into the San Joaquin River side of the estuary. Model averaging found that recovery rates were greatest for San Joaquin River releases when estuary water temperatures were lower, and salmon were released at larger sizes. Recovery rate of Sacramento releases was greatest during years with better water quality. There was little evidence that large-scale water exports or inflows influenced recovery rates in the ocean during this time period. These results suggest that conceptual models of salmon ecology in estuaries should be quantitatively evaluated prior to implementation of recovery actions to maximise the effectiveness of management and facilitate the recovery of depressed Chinook populations.

Key words: coded wire tags; mixed models; Sacramento River; San Joaquin River

Introduction

Pacific salmon (*Oncorhynchus* spp.) are well known for their long migrations between ocean feeding grounds and freshwater spawning and juvenile rearing habitats. Although estuaries are only utilised during a relatively short portion of salmon life cycles, they can provide critical habitats for juveniles by providing quality-rearing habitat (Gray et al. 2002; Bottom et al. 2005a; Greene et al. 2005) and supporting life-history diversity within populations (Bottom et al. 2005b). Additionally, estuaries are where juveniles make the critical physiological transitions that facilitate ocean residency (Jobling 1995). As the importance of estuaries to salmon is better understood, they are more frequently targeted for restoration and conservation actions to support recovery of threatened salmon populations (Simenstad & Cordell 2000). Understanding how improvements in estuarine conditions influence salmon populations is complicated both by the myriad of factors that influence salmon survival and by the large geographical area salmon require to complete their life cycle (Bradford 1997). However, this understanding is essential for effective recovery of salmon populations.

Estuaries throughout the range of Pacific salmon have been degraded by freshwater diversion, wetland loss, pollution, diking, dredging and invasion by non-native species (Simenstad & Cordell 2000; Borde et al. 2003). The San Francisco Estuary in California ranks as the largest estuary on the Pacific Coast of North America and serves as a migration route for the southernmost spawning populations of Chinook salmon (*Oncorhynchus tschawytscha*). Once supporting spawning runs of an estimated 1–6 million adults (Yoshiyama et al. 2001), the estuary has been subject

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to many of the alterations listed earlier beginning in the mid-19th century during California's Gold Rush. Presently, Chinook salmon stocks that utilise the San Francisco Estuary are in a depressed state, including populations listed as threatened or endangered (Williams 2006). As a result of declining adult salmon returns to upstream tributaries, considerable resources have been committed to improve conditions for juvenile salmon in the freshwater tidal reaches of the estuary; hereafter, referred to as the 'Delta' (CALFED 2007). This effort has largely focused on the manipulation of freshwater inflows from upstream and also through restriction of freshwater exports from two massive diversions within the Delta (NMFS 2009). However, the benefit of these actions for salmon at the population level remains equivocal (Brown et al. 2009).

Hydrologic dynamics of the Delta have been significantly altered relative to historic conditions. However, there have been concomitant changes in habitat quality, water quality, species assemblage structure and adult harvest (Williams 2006). Additionally, because salmon inhabit a wide range of habitats throughout their life, it is difficult to detect whether incremental improvements in survival at a single life stage translate into enhanced population-level performance. An essential step in the recovery of salmon populations is to understand how conditions in the estuary influence survival of migrating salmon which can provide guidance for future restoration activities.

In this study, we use 10 years of release and recovery data for hatchery-origin, coded-wire-tagged (CWT) fall-run Chinook salmon combined with physicochemical data from long-term monitoring programs to evaluate the weight of evidence for alternative hypotheses of the Delta conditions that influence ocean recovery rates. Our results indicate that factors previously assumed to strongly influence salmon migrating through the Delta were not well supported by the data and suggest that quantitative evaluation of conceptual models of salmonid ecology in estuaries can help direct restoration and conservation actions.

Methods

Study site

The Delta, located in the California Central Valley, is a large tidal freshwater estuary that drains a catchment of approximately 150,000 km^2 (Fig. 1). The Delta receives water from two major tributaries; the Sacramento River that drains the northern portion of the Central Valley, and the San Joaquin River that drains most of the southern portion of the Central Valley. Water entering the Delta flows through a complex network of tidal channels before entering the upper reaches of San Francisco Bay. Flow into the Delta is strongly seasonal with peaks from late winter to early spring and low inflows during summer and fall (Fig. 2). Additionally, there is a large amount of interannual variation in the total flow entering the Delta (Fig. 2).

Historically, the Delta contained vast areas of freshwater tidal wetlands, and inflow was driven by precipitation and spring snowmelt. During the late 19th and 20th centuries, the Delta experienced an intense period of alteration for agricultural and urban development (Yoshiyama et al. 2001). Major dams on upstream tributaries now exert considerable control over the timing and volume of flow into the Delta (Singer 2007). Water operations have reduced freshwater flows into the Delta during winter and spring when water is impounded in upstream reservoirs and increased flows during summer and fall when water is released for diversion in the Delta (Zeug et al. 2011). Two large pumping facilities in the South Delta divert water year round with up to 60% of total inflow diverted in some years (Fig 2). Wetland habitat has been extensively leveed and drained for farming, navigation and to protect the South Delta diversions from salt water intrusion during periods of low flows into the Delta.

Study population

Tributaries to the Delta support four distinct runs of Chinook salmon. However, fall run are currently the most abundant and widely distributed. The fall run supports a commercial ocean fishery as well as popular ocean and inland recreational fisheries. Central Valley fall run display an 'ocean type' life history. Adults enter freshwater and spawn during fall and early winter. Following incubation in spawning gravels, juveniles emerge and rear in lotic habitats for weeks to months before entering the Delta on their way to the Pacific Ocean. The majority of juvenile rearing and outmigration occurs between February and May that was historically a period of high inflow into the Delta. However, flows during this period have been truncated by dam operations upstream (Zeug et al. 2011).

Release-recovery data

Juvenile fall-run Chinook salmon are raised at five hatcheries located on tributaries of the Sacramento and San Joaquin rivers to mitigate for production lost through water development activities. A portion of these juveniles is marked with CWTs that are short (0.5–1.0 mm) lengths of steel wire containing a numerical code that is injected into the snout of each

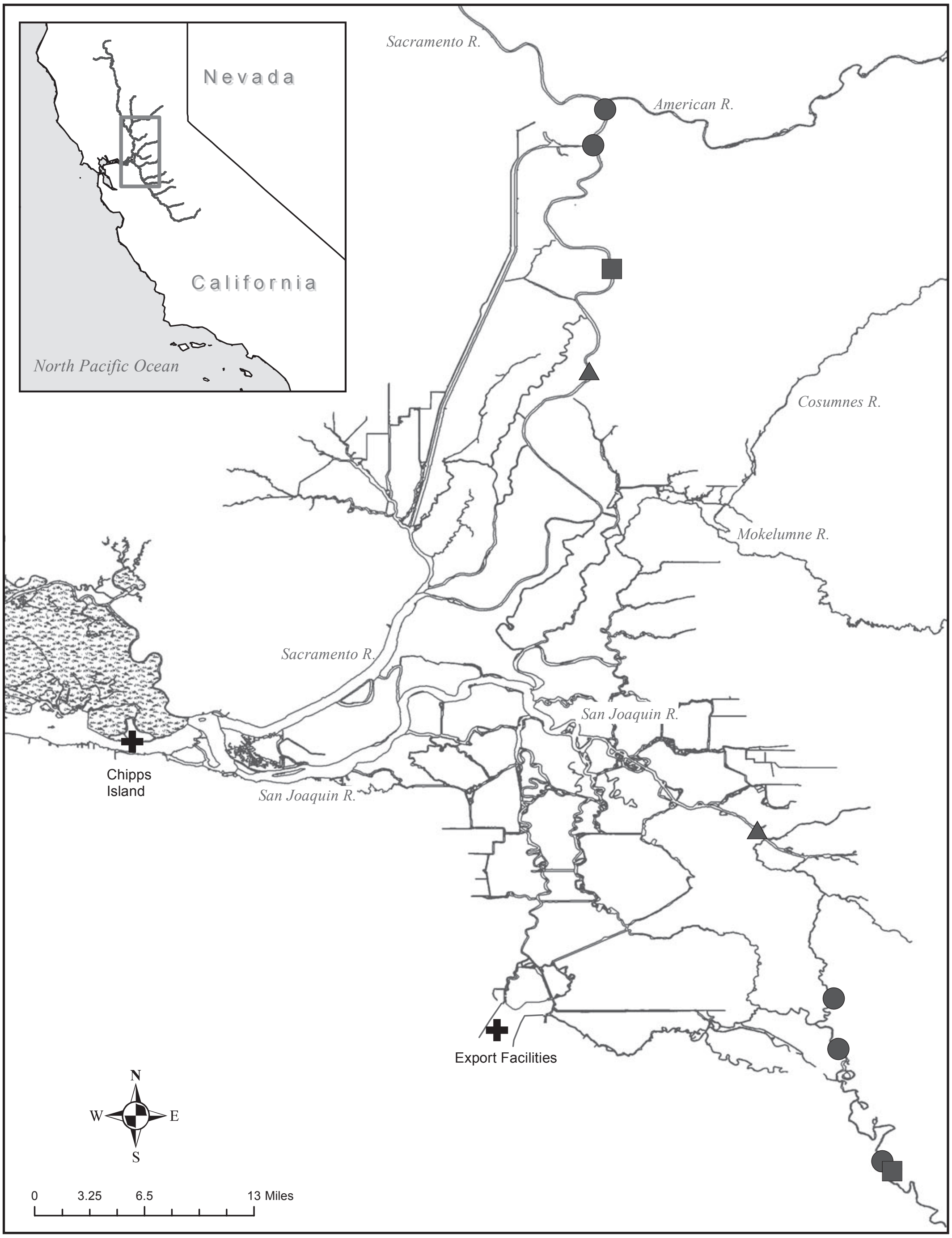

Fig. 1. Map depicting the location of coded-wire-tagged salmon releases in the Sacramento and San Joaquin Rivers (circles), recovery locations (crosses), locations of flow measurements (squares) and locations where water quality parameters were measured (triangles).

fish. Fish receiving a CWT have their adipose fin clipped so they can be visually identified during subsequent sampling. Codes identify batches of salmon released at particular locations rather than individual salmon. Tagged fish are released at different Delta locations to estimate ocean harvest rates and as part of various studies conducted by state and federal resource agencies. Specific release locations vary among years; however, releases have consistently been made near the limit of tidal influence at two locations on the main stem Sacramento and three locations on the San Joaquin in April and May of each year (Fig. 1). Releases from these locations made in April and May of each year were used to estimate the effect of Delta conditions on ocean recovery rates.

There are four primary locations where tagged salmon can be recovered. First, the United States Fish

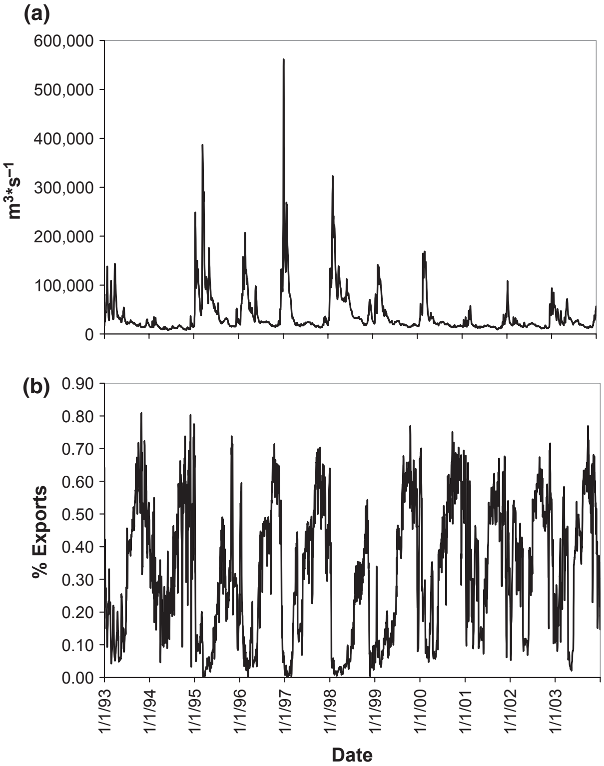

Fig. 2. Mean daily flow into the Delta (panel a) and the daily percentage of total inflow exported (panel b) during the study period (1993–2003).

and Wildlife Service (USFWS) operates a mid-water trawl at the exit of the Delta (Chipps Island; Fig. 1). The trawl is usually operated for 4–6 weeks during the salmon outmigration period; however, effort has varied within and among years and capture probability is very low (Newman 2008). Second, the water export facilities in the South Delta conduct salvage operations for fish entrained into the facilities. Fish taken into the facilities are collected live, subsampled and an expansion factor is applied to estimate the total number of fish that entered the facility. Then all fish (except the subsample) are trucked to the West Delta and released. Third, tagged fish are recovered in the commercial and recreational ocean fishery 2–5 years after release. A fraction of fish brought into ports along the coast by commercial and recreational fisherman is subsampled, and an expansion factor is applied to estimate the total catch for each age class in the release group. Fourth, tagged fish are recovered on the spawning grounds during escapement surveys by state and federal resource agencies.

Recovery information from the export facilities was not used in models because after subsampling to estimate total numbers, the fish are trucked to the Western Delta and released. Thus, fish accounted for at the salvage facility could potentially be recaptured in the ocean fishery or on the spawning grounds and 'double counted'. Investigation of the methods used during spawning surveys indicated that the probability of detecting CWT fish on the spawning grounds (or collecting a CWT detection) was considerably different among rivers and years, making the data unreliable. Thus, inland recoveries were not included in the analysis. The Chipps Island recovery data have often been used to estimate survival through the Delta; however, these data have several issues that restrict their usefulness (Newman 2008). The trawl is operated only during daylight hours and recent data suggest that most passage occurs at night (Perry 2010). Additionally, the number of recoveries at this location is low and the probability of capturing a fish passing Chipps Island is low and variable among sample dates and years (Newman 2008). Recoveries in the ocean fishery are high relative to Chipps Island, and data are available to estimate the probability of a fish being captured and the probability of being sampled given that it was captured. Thus, we used the ocean recoveries to model the effect of Delta conditions. Use of the ocean recovery data has the advantage of providing inferences about the influence of Delta conditions at the population level rather than only during the smolt migration period.

Tag recovery information for the commercial and recreational ocean fishery was obtained from the Regional Mark Information System database (www.rmpc.org) that is maintained by the Pacific States Marine Fisheries Commission. Rather than using the expansion calculated by the Regional Mark Processing Center, we used an alternative expansion that accounted for variation in harvest among years and sampling fractions for each age group. Recoveries for each release were estimated as:

$$\hat{R} = \sum_{i=2}^{n} \frac{R_{o,i}}{(S_i \times I_t)}$$

where $\hat{R}$ is the estimated number of recoveries for a release group, $R_{o,i}$ is the observed number of recoveries for age i, S_i is the fraction of the commercial and recreational catch sampled for ith age class, and I_t is the Sacramento Index (SI) value for combined recreational and commercial harvest in year t when each age was harvested. The SI provides an estimate of Central Valley fall-run Chinook harvest by combining the best estimates of recreational and commercial harvest in the ocean, in river harvest, and escapement to spawning tributaries (O'Farrell et al. 2008).

Several factors that could not be quantified have the potential to influence estimates of recovery rate, including changes in Chinook salmon maturity schedules over the study period, spatial or temporal differences in gear susceptibility, duration of exposure to the fishery, and others. However, there is little information available to quantify or test for these differences among individual release groups. Thus, we assume that these characteristics of the fishery and Chinook population were similar among years and did not influence the recovery rate of CWT fish during the study. Pyper et al. (2012) found that harvest estimates for Sacramento River fall-run Chinook were robust to simulated variation in several similar population characteristics over 19 years, suggesting our assumption is reasonable for the time period examined.

Although recovery information is available for releases going back to the 1970s, we chose to analyse releases starting in 1993. Major changes in Delta water management began in the mid-1990s following the California State Water Resources Control Board ruling D-1641 known as the Bay-Delta Accord. These changes primarily involved restriction of exports during the juvenile salmon outmigration period that reduced the number of salmon encountering the export facilities. The last year of releases analysed was 2003. We chose this year because the ocean fishery was closed in 2008 in response to the collapse of the Central Valley fall-run stock that prevented collection of 4-year-old salmon released in 2004.

Environmental data

All flow data used in the analyses were averaged for 7 days following each release event to capture the conditions salmon experienced as they migrated through the Delta. The period of 7 days was chosen based on the mean migration rate of acoustically tagged juvenile Chinook salmon through the Delta (6.4 days; Michel 2010). Flow into the Delta from the Sacramento River was obtained from the California Data Exchange Center (CDEC) gauge at Freeport. The CDEC gauge at Vernalis was used for inflow from the San Joaquin River, and export flows were obtained from the online data archive, DAYFLOW http://www.water.ca.gov/dayflow/ (Fig. 1). The proportion of fish in each release group salvaged at the export facilities was obtained from the USFWS Chipps Island Survival Table (http://www.fws.gov/stockton/jfmp/Docs/Data%20Management/Chipps%20Island%20Survival%20Table%201993%20-%202008,%20Updated%20Dec.2008.pdf). Water temperature was measured by hatchery staff at the location where fish were released. Water quality data were obtained from the Interagency Ecological Program's Environmental Monitoring Program (http://www.water.ca.gov/iep/activities/emp.cfm). This program is a consortium of state and federal agencies that coordinate data collection in the San Francisco Estuary. Unlike flow for which daily data are available, water quality parameters were measured at monthly intervals; thus, these parameters could not be calculated as 7-day averages. Water quality parameters included Secchi depth (cm), NH_4^+ concentration ($mg \cdot l^{-1}$), and the ratio of dissolved inorganic nitrogen to dissolved inorganic phosphorus (DIN/DIP; Fig. 3). Secchi depth was chosen to represent the effect of water clarity on visually oriented salmon predators such as striped bass (*Morone saxatilis*). Predation on juvenile salmon would be expected to decrease as Secchi depth decreases and visually oriented predators become less efficient (Rodriguez & Lewis 1997). Ammonium ion concentration and DIN/DIP are indicators of changes in water quality as a result of wastewater discharge and have been predicted to influence Delta food webs over time (Glibert 2010). On the Sacramento River, water quality parameters were measured at Hood and, on the San Joaquin River, they were measured at Buckley Cove (Fig. 1). These sites were chosen because they were the most consistently sampled during the study period. Wells' index was used to represent ocean productivity (Fig. 3). This index is a composite of ocean conditions that has been significantly related to growth and maturity of California Chinook salmon in the Pacific Ocean (Wells et al. 2007). Wells' index in the year of ocean entry and the year following ocean entry were both included in the 'ocean productivity' hypothesis.

Data analysis

A correlation analysis was performed on all continuous predictor variables to identify potential sources of multicollinearity. When the absolute value of a correlation coefficient between two variables was ≥ 0.70, one of the predictors was arbitrarily excluded in the subsequent modelling exercise. Separate correlation analyses were performed for Sacramento and San Joaquin river releases.

A series of generalised linear mixed models (GLMM) were constructed *a priori* to represent hypotheses regarding the factors that affect juvenile salmon during migration through the Delta based on previous research. These hypotheses included: H_{A1} – conditions at the time of release have a strong influence on recovery rate of salmon; hereafter, referred to as 'release-specific factors' (Newman & Rice 2002). This hypothesis predicts that suboptimal temperature at the release site or small fish size result in higher mortality of the release group. Additionally, some release sites may have greater mortality (e.g., they are near predator holding areas). H_{A2} – flow conditions in the Delta during migration have a strong influence on recovery rate, hereafter referred to as 'hydrologic factors' (Kjelson & Brandes 1989; Newman & Rice 2002; Newman & Brandes 2010). This hypothesis predicts that recovery rate will be greatest when inflows are high, exports are low and

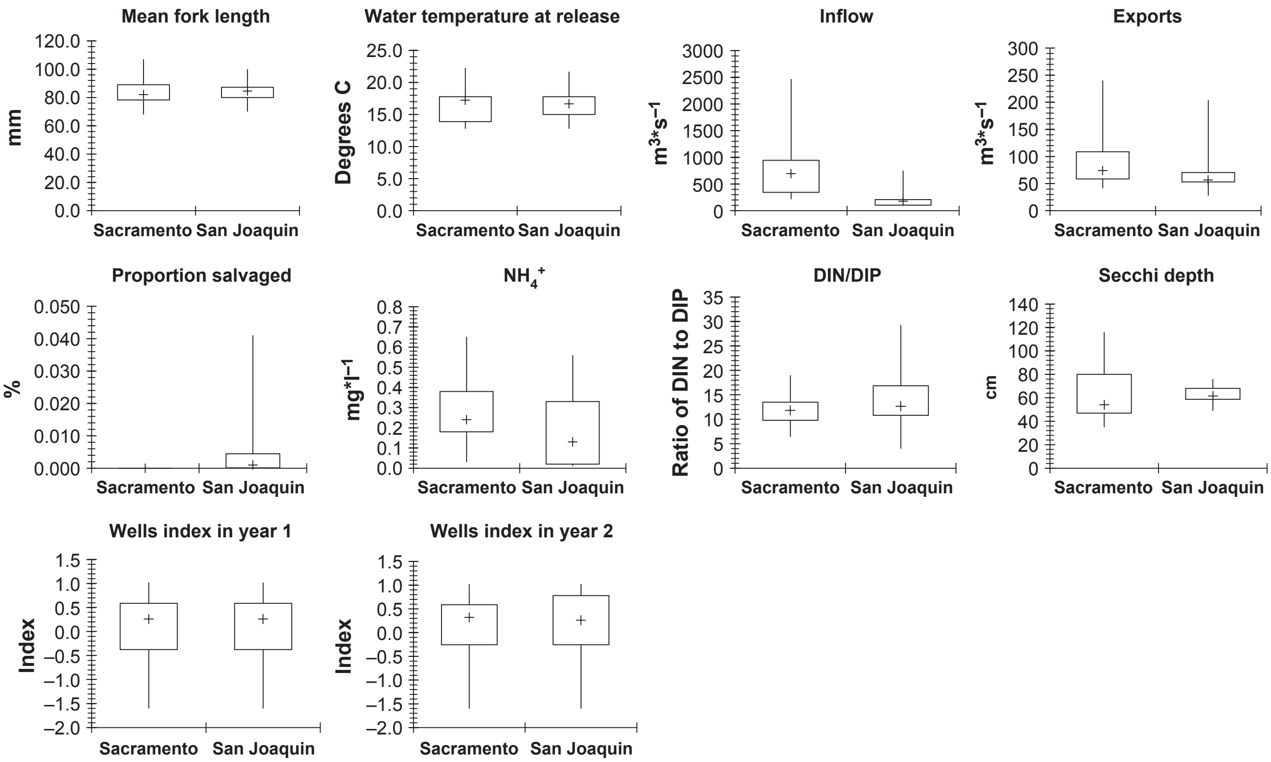

Fig. 3. Box and whisker plots of continuous fixed effects used to model survival of juvenile salmon. Crosses are median values, boxes represent 25th and 75th percentile values, and lines are minimum and maximum values.

the proportion of the release group encountering the export facilities is low. H_{A3} – changes in Delta water quality over time have increased mortality of migrating salmon, hereafter referred to as 'water quality' (Glibert 2010). This hypothesis predicts that changes in the Delta food web driven by changes in water quality as described by Glibert (2010) have reduced the capacity of the Delta to support juvenile salmon resulting in greater mortality through time. H_{A4} – ocean conditions during ocean residency exert a strong influence on recovery rate, hereafter referred to as 'ocean productivity' (Mantua et al. 1997; Wells et al. 2007; Lindley et al. 2009). This hypothesis predicts that conditions experienced by salmon in the Pacific Ocean off the California Coast will be the strongest influence on recovery rate.

The specific variables used to represent each alternative hypothesis are listed in Table 1. Each GLMM utilised a binomial error structure for the response variable (expanded number of fish recovered and number of fish released) with a logit link function. We chose to model release-recovery data as a binomial distribution (with extra-binomial variation modelled as a random effect) rather than transformed proportions for several reasons. First, by calculating a simple proportion, information is lost about the size of each individual release group and ignores variability in the sampling process that generates the response variable. Second, Warton & Hui (2011) found that the analysis of transformed proportions was less powerful and less interpretable for binomial data. Third, GLMMs are effective for modelling longitudinal fisheries data where repeated measurements are taken over time because correlations among observations can be addressed by attributing a random effect to temporal units (Venables & Dichmont 2004). In our models, year was included as a random variable, and an observation-level random variable was included to account for over dispersion in the recovery data. All continuous predictor variables were transformed into *z*-scores so results could be interpreted in units of standard deviation. A total of 15 models were constructed that represented each potential combination of hypotheses. Additionally, a model with only an intercept and the random effects was calculated to evaluate how well the fixed effects fit the data. Releases from the Sacramento and San Joaquin rivers were modelled separately. All models were constructed in the statistical program R with the package 'lme4' (R Development Core Team 2012).

An information theoretic approach was used to select best approximating models for releases in both rivers (Burnham & Anderson 2002). Akaike's information criterion corrected for small sample size (AIC_c) was calculated for each candidate model, and

Table 1. Definition of variables used to represent hypotheses proposed to explain recovery rate of juvenile salmon migrating through the Sacramento-San Joaquin Delta.

Hypothesis	Variable	Definition
Release-specific	Temperature	Water temperature of the river at the site where fish were released (°C)
	Fork length	Mean fork length of salmon in each release group (mm)
	Location	A dummy variable in Sacramento River models that indicates whether a release was at West Sacramento or Miller Park
	Mossdale	A dummy variable in San Joaquin models that indicates Mossdale was the release site
	Dos Reis	A dummy variable in San Joaquin models that indicates Dos Reis was the release site
	Durham Ferry	A dummy variable in San Joaquin models that indicates Durham Ferry was the release site
	Old River barrier	A dummy variable in San Joaquin models that indicates the presence of a temporary barrier to keep fish out of a route leading to the export facilities
Hydrologic	Flow	A 7-day average of flow into the Delta from the Sacramento or San Joaquin River ($m^3 \cdot s^{-1}$)
	Exports	A 7-day average of combined water exports from the Delta ($m^3 \cdot s^{-1}$)
	Proportion salvaged	The proportion of each release group that encountered the export facilities
Water quality	NH_4^+	Ammonium concentration in the month of each release ($mg \cdot l^{-1}$)
	DIN/DIP	Ratio of dissolved inorganic nitrogen to dissolved inorganic phosphorous in the month of each release
	Secchi depth	Secchi depth in the month of each release (cm)
Ocean Productivity	Wells' index	Index of ocean productivity in the year of ocean entry for each release
	Wells' index $t + 1$	Index of ocean productivity in the second year of ocean residence for each release

model weights (AIC_cw) were calculated using the difference in AIC_c between each candidate model and the best approximating model in the set (ΔAIC_c). Model weights are interpreted as the probability that a given model is the best relative to all candidate models. Models with a ΔAIC_c value of 0–3 were considered competitors to best explain the data. The AIC_c values of the intercept-only models were compared to the full model for each river as a measure of how well the fixed effect models fit the data.

To evaluate the level of support in data for each of the variables that composed the hypotheses identified in the model selection exercise, multi-model averaging was performed. This technique provides a way to use all the information contained in the candidate models to calculate model averaged coefficients and unconditional confidence intervals (Burnham & Anderson 2002). Predictor variables were considered to have good support in the data when unconditional confidence intervals did not include zero (Burnham & Anderson 2002).

Results

A total of 44 releases comprising >1.4 million juvenile Chinook salmon occurred in the Sacramento River and 76 releases comprising >2.2 million salmon occurred in the San Joaquin River over the study period. Release sizes in the Sacramento River ranged from 16,600 to 55,872 fish, with a mean and standard deviation of 31,651 ± 12,035. In the San Joaquin River, release size varied from a minimum of 15,796 to a maximum of 54,810, with a mean and standard deviation of 29,388 ± 9,647. All releases occurred in the months of April and May.

Delta conditions

A wide range of Delta conditions were experienced by emigrating juvenile salmon during the 10-year study period (Fig. 3). Flow during the releases ranged from 215–2466 $m^3 \cdot s^{-1}$ and 94–750 $m^3 \cdot s^{-1}$ in the Sacramento River and San Joaquin River, respectively (Fig. 2). Export volume during the CWT releases ranged from 28 to 240 $m^3 \cdot s^{-1}$. For releases in the Sacramento River, few fish were collected at the export facilities (116). A larger number of fish released in the San Joaquin River were collected at the export facilities (8620); however, these numbers were relatively small in relation to the numbers released (0.008% and 0.386% in the Sacramento and San Joaquin rivers, respectively). Median fork length of fish in each release group, temperature at release, and Wells' Index values were similar for releases in both rivers. Ammonium ion concentration was higher but less variable in the Sacramento River. A greater range of Secchi depths was observed in the Sacramento River, whereas DIN:DIP had similar median values although a greater range of values was observed in the San Joaquin (Fig. 3).

Model selection and averaging

Correlation analysis of predictor variables used to model San Joaquin releases revealed a strong correlation between Wells' Index in year 1 and flow ($r = -0.86$). Thus, Wells Index in year 1 was excluded from the survival models. Analysis of predictor variables used to model Sacramento releases did not produce any correlations $\geq |0.70|$, and the full set of variables was used.

Model selection indicated that the best model to explain recovery rate of salmon released in the Sacramento River represented the water quality hypotheses $AIC_c w = 0.725$ (Table 2). No other model had a $\Delta AIC_c < 4.025$. The difference in AIC_c values between the intercept-only model and the full model was 8.330 indicating that the model with covariates was a better fit to the data.

All predictor variables included in the water quality hypothesis for Sacramento River releases had good support in the data after model averaging (Table 3). There was a well-supported negative relationship between recovery rate and NH_4^+ concentration and recovery rate and Secchi depth. Additionally, DIN:DIP had a well-supported positive relationship with ocean recovery rate.

Selection of models describing recovery rate of San Joaquin salmon releases resulted in two competing models (Table 2). The most likely model ($AIC_c w$ = 0.498) included release-specific and water quality hypotheses. The next best model ($AIC_c w = 0.377$) included release-specific, water quality and ocean productivity hypotheses. The intercept-only model was a poor fit to the data relative to the full model $\Delta AIC = 17.306$.

Three predictor variables were found to be well supported in the San Joaquin River release data following model averaging (Table 3). For the release-specific hypothesis, temperature had a negative relationship with ocean recovery rate and mean fork length had a positive relationship. Within the water quality hypothesis, NH_4^+ concentration had a positive relationship with ocean recovery rate. Wells' Index had poor support following model averaging.

Discussion

Model selection and averaging revealed that the conditions that most strongly influenced ocean recovery rate were dependent on the tributary where fish were released. Temperature and mean fork length were well supported for juvenile salmon released in the San Joaquin River. Survival of juvenile salmon in the Delta has been linked to temperature in several studies that incorporated earlier CWT releases, suggesting that this variable has a strong influence on migrating Chinook (Kjelson & Brandes 1989; Newman & Rice 2002; Newman 2008). The Delta is located at the southern limit of Chinook salmon distributions where temperatures can often approach the tolerance of the

Table 2. Results of model selection describing recovery rate of juvenile salmon released in the Sacramento and San Joaquin Rivers based on differences in AIC_c values between each candidate model and the best model. Models are listed in order from most to least likely.

	Release specific	Hydrologic	Water quality	Ocean productivity	AIC_c	ΔAIC_c	$AIC_c w$
Sacramento			X		308.270	0.000	0.725
	X		X		312.294	4.024	0.097
			X	X	312.714	4.444	0.079
		X	X		313.094	4.824	0.065
	X		X	X	317.350	9.080	0.008
	X				318.270	10.000	0.005
				X	319.479	11.209	0.003
		X	X	X	319.550	11.280	0.003
	X	X	X		319.865	11.594	0.002
		X			320.470	12.200	0.002
	X			X	322.714	14.444	0.001
	X	X			323.394	15.124	0.000
	X	X	X	X	324.383	16.112	0.000
		X		X	325.014	16.744	0.000
	X	X		X	328.550	20.280	0.000
San Joaquin	X		X		437.527	0.000	0.498
	X		X	X	438.085	0.557	0.377
	X				442.347	4.820	0.045
	X	X	X	X	443.071	5.544	0.031
	X	X	X		443.952	6.425	0.020
	X			X	444.149	6.622	0.018
		X	X		446.649	9.122	0.005
		X	X	X	448.427	10.900	0.002
	X	X			448.885	11.357	0.002
	X	X		X	450.925	13.398	0.001
		X			452.617	15.090	0.000
		X		X	454.947	17.420	0.000
				X	456.863	19.336	0.000
			X	X	457.317	19.790	0.000
			X		457.585	20.057	0.000

Table 3. Model averaged parameter estimates and unconditional confidence intervals for variables that represent hypotheses in competing models of recovery rates. Asterisks indicate parameters that had good support in data (interval does not include zero).

Hypothesis	Variable	Sacramento River	San Joaquin River
Release-specific	Temperature	N/A	−0.624* (−0.845 to −0.403)
	Fork length	N/A	0.642* (0.253 to 1.030)
	Location	N/A	N/A
	Mossdale	N/A	−0.510 (−1.160 to 0.139)
	Durham Ferry	N/A	−0.382 (−1.150 to 0.385)
	Old River barrier	N/A	−1.558 (−3.656 to 0.540)
Hydrologic	Flow	N/A	N/A
	Exports	N/A	N/A
	Proportion salvaged	N/A	N/A
Water quality	NH_4^+	−0.559* (−0.789 to −0.329)	2.414* (1.209 to 3.620)
	DIN:DIP	0.341* (0.102 to 0.579)	−0.618 (−1.284 to 0.047)
	Secchi depth	−0.278* (−0.505 to −0.050)	−0.266 (−0.738 to 0.206)
Ocean productivity	Well's index	N/A	N/A
	Well's index $t + 1$	N/A	−1.003 (−2.302 to 0.297)

species (Williams 2006). In the Sacramento River, releases were made just below the confluence of the American River which contributes cold water released from an upstream reservoir. Thus, measurements taken at the release site on the Sacramento may not be representative of the temperatures salmon experienced when migrating through the Delta. Populations located at geographical extremes are expected to be sensitive to even small changes in temperature (Gustafson et al. 2007), reinforcing the importance of this variable in salmon management.

For San Joaquin River releases, there also was good support for a positive effect of mean fork length on ocean recovery rate. Larger size at release may confer survival advantages such as greater swimming ability and escape from gape-limited predators (Wootton 1998). These advantages may be important for San Joaquin River origin salmon because they all must pass through the interior Delta on their way to the ocean. The interior Delta is a region of the estuary that has been identified as supporting high densities of non-native piscivores such as striped bass and black bass (*Micropterus* spp.) (Brown & Michniuk 2007; Nobriga & Feyrer 2007). Only a small proportion of Sacramento River origin fish migrate through this route (Perry et al. 2010) and fork length was not a well-supported variable for releases in this river.

Sacramento River releases were strongly influenced by water quality parameters. Glibert (2010) reported negative relationships between the abundance of certain native Delta fishes, NH_4^+ concentration, and DIN:DIP and suggested these relationships were mediated by changes in food web structure. Changes in Delta food webs have been well documented, yet the effect of these changes on fishes has largely focused on non-salmonid species (Bennet et al. 1995; Feyrer et al. 2003; Nobriga and Feyrer 2008). Little is known about the diets of juvenile salmon in the Delta or how they may have changed over time. However, MacFarlane (2010) found that juvenile salmon migrating through the Delta and San Francisco Bay experienced little or no growth that may indicate poor food web support. Nobriga & Feyrer (2008) suggested that food web changes in the Delta may exceed the trophic adaptability of juvenile striped bass and the same may be true of juvenile Chinook. Additional studies of diet and growth of juveniles in the Delta would be needed to confirm the indirect pattern observed in this study.

The water quality hypothesis was included in a competing model for San Joaquin River releases, yet only one variable had good support (NH_4^+ concentration), and the relationship was opposite of expectations (positive). Glibert (2010) reported lower and less variable NH_4^+ concentrations in the San Joaquin that may have produced this result. Nutrient concentrations in the Sacramento River are strongly influenced by a municipal wastewater plant and flows from the Sacramento dominate Delta inflow.

The hydrologic hypothesis was not included in competing models for releases in either river. Other studies of juvenile salmon survival also have produced equivocal relationships with flow (Smith et al. 2002; Zabel et al. 2008; Michel 2010). A potential explanation for this result is the relative influence of tidal flux over river inflow during migration through the Delta. In a large portion of the Delta, daily tidal flux represents a greater movement of water than river inflow (Cavallo et al. 2012). Juvenile salmon may respond more strongly to flow near or upstream of release locations where flow is unidirectional but less so in downstream portions of the Delta dominated by tidal flux. Miller & Sadro (2003) found that the movement of juvenile coho salmon (*Oncorhynchus kisutch*) smolts followed tidal movements in an Oregon estuary. The use of ocean recovery data also may have influenced the lack of a detectable flow effect. Tagged fish recovered in the ocean have been exposed to both

Delta and ocean mortality prior to capture. Ocean recoveries provide a measure of population-level effects of Delta conditions and the effect of flow during Delta migration may be small relative to other mortality sources. Indeed, there is an increasing recognition that mortality during ocean residency can be a strong driver of salmon population trends (Mantua et al. 1997; Brodeur et al. 2000; Greene et al. 2005).

Previous salmon studies in the Delta found a significant effect of flow on survival (Kjelson & Brandes 1989; Brandes & McLain 2001). The data set used here includes the years after water operations in the Delta changed in response to legislation to protect native fishes, whereas previous analyses used data prior to these management actions to establish a relationship with flow. Thus, although releases were made over a wide range of flows in the current study, changes in operations may have reduced the previously observed effect. Michel (2010) did not find an effect of flow on survival of acoustically tagged salmon released in the Sacramento from 2007 to 2009. The information theoretic approach used here allowed us to compare the relative weight of evidence for different hypotheses rather than looking for statistical significance of bivariate relationships (Burnham & Anderson 2002). Thus, although flow may be important, it may be less important than the other variables examined.

Water exports from the Delta are actively managed to protect salmon migrating through the Delta. However, we did not find a well-supported effect of exports on ocean recovery rate for releases in either river. Other investigations of export effects on survival of Sacramento origin salmon also have failed to find strong evidence for the hypothesised negative relationship (Kjelson & Brandes 1989; Newman & Rice 2002; Newman & Brandes 2010). A multi-year study of San Joaquin River releases also did not yield a significant export effect (Newman 2008). Our analysis took a unique approach by evaluating export effects using both the number of juvenile salmon that actually encountered export facilities (the proportion of each release group salvaged), and by the more indirect measure (recovery rate in relation to exports) used in previous analyses but still failed to detect a well-supported effect.

Although model selection and averaging provided strong evidence for certain hypotheses, several factors should be considered when interpreting results. First, the information theoretic approach only evaluates the weight of evidence for the hypotheses presented. There could be other hypotheses not presented here that could explain the data better. For example, the Delta supports populations of non-native piscivores that could potentially impact salmon survival (Brown & Michniuk 2007; Nobriga & Feyrer 2007). Direct measures of a predation effect or even indicators of an effect could not be quantified here but future evaluations may reveal that predation is an important component of salmon survival. The advantage of information theoretic methods is that new hypotheses can be directly evaluated against those presented here if more data become available (Hobbs & Hilborn 2006).

The response variable in our analysis was a joint survival and capture probability (recovery rate). We assumed that capture probability is similar among releases to facilitate modelling; however, results could change if this assumption is incorrect. Technologies such as acoustic tags that allow direct estimation of capture probabilities are increasingly used in the Delta but survival estimates over long time periods are not yet available. Finally, all salmon released in this study were hatchery origin and it is unknown how well the behaviour of hatchery fish matches that of wild fish in the Sacramento and San Joaquin Rivers.

Estuaries are increasingly recognised as critical habitats for salmon as they transition from freshwater to marine habitats and restoration actions in these areas is likely to increase in the future. This study suggests that assumed relationships and conceptual models should be quantitatively evaluated before implementing management actions. Our evaluation of the relationship between estuarine conditions and ocean recovery rate revealed that there was no clear hypothesis that best explained patterns of recovery rates. However, we found that the factors previously hypothesised to be important (flow, exports) were less important than others (temperature, fish size, water quality) when models were pitted against each other. Many of the relationships described here are indicators of particular effects (food web changes, size-mediated survival) and direct evidence of causal relationships would help reduce uncertainty in future management of the Delta.

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