Environ Biol Fish
DOI 10.1007/s10641-012-9990-8

The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*)

Cyril J. Michel · Arnold J. Ammann · Eric D. Chapman · Philip T. Sandstrom · Heidi E. Fish · Michael J. Thomas · Gabriel P. Singer · Steven T. Lindley · A. Peter Klimley · R. Bruce MacFarlane

Received: 1 March 2011 / Accepted: 9 March 2012

Abstract Understanding smolt migration dynamics is a critical step in the preservation and conservation of imperiled salmonids in California's Sacramento River system. Late-fall run Chinook salmon yearling smolts were acoustically tagged and tracked during their out-migration through California's Sacramento River and San Francisco Estuary during 2007–2009. Migration rates were 14.3 km·day^{-1} (± 1.3 S.E.) to 23.5 km day^{-1} (± 3.6 S.E.), similar to rates published for other West Coast yearling Chinook salmon smolt emigrations. Region-specific movement rates were fastest through the upper river regions, and slowest in the Sacramento/San Joaquin River Delta. River travel times were recorded for smolts travelling through a series of ten monitor-delimited reaches. Using these, a smolt travel time model determined by two parameters (movement rate and rate of population spreading) was then used to determine the influence of different factors on the model's fit, using model selection with Akaike's Information Criterion. The model that allowed for both year and reach to be expressed additively for both travel time and population spreading rate estimates, while accounting for a "release" effect, was the best supported model. Finally, several models incorporated environmental data as a linear predictor of movement rates. The addition of the environmental variables, in order of importance, river width to depth ratio, river flow, water turbidity, river flow to mean river flow ratio, and water velocity all resulted in improved model fit. Water temperature did not improve model fit. These environmental associations are discussed and potential improvements on the travel time model are suggested.

Keywords Environmental factors · Migration · Acoustic telemetry · Smolt · Chinook salmon · Sacramento River · Biotelemetry

C. J. Michel (✉) · A. J. Ammann · H. E. Fish · S. T. Lindley · R. B. MacFarlane
Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA National Marine Fisheries Service, 110 Shaffer Rd, Santa Cruz, CA 95060, USA
e-mail: cyril.michel@noaa.gov

E. D. Chapman · P. T. Sandstrom · M. J. Thomas · G. P. Singer · A. P. Klimley
Biotelemetry Lab, Department of Wildlife, Fish, & Conservation Biology, University of California Davis, 1334 Academic Surge Building, Davis, CA 95616, USA

Introduction

The migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha)* from their riverine origin to the food-rich ocean is considered one of the most

Published online: 15 April 2012

vulnerable periods in a Chinook salmon's life (Healey 1991). During this life stage, juvenile salmon undergo many morphological, physiological, and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River's Chinook salmon populations, this freshwater journey may be as long as 600 km, transiting many different habitats, all with varying natural conditions. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed and have contributed to the decline of these populations, to the point of their listing on the Endangered Species Act (ESA). It is therefore essential to the effective management of these stocks to understand the movement patterns and environmental relationships of this outmigration.

Studies have been investigating the timing and patterns of juvenile salmonid migrations on a large-scale focus for decades. Thorpe and Morgan (1978) tracked juvenile Atlantic salmon (*Salmo salar*) fry periodicity during outmigration in Scottish Rivers. Raymond (1968) calculated migration rates by marking and recapturing yearling Chinook salmon smolts traveling through the Snake and Columbia Rivers and their reservoirs. However, to best comprehend the challenges and intricacies of the migration, one must gain knowledge at a finer spatial-temporal scale. Advances in biotelemetry have allowed such resolution (Cooke et al. 2004); specifically the miniaturization of fish tracking tags has allowed the exploration of small-scale movement during smolt migration. These technologies have already yielded migration data on steelhead (*Oncorhynchus mykiss*) smolts in the Cheakamus River in British Columbia, Canada (Melnychuk et al. 2007) and on sockeye salmon (*Oncorhynchus nerka*) smolts in the Fraser River in British Columbia, Canada (Welch et al. 2009) at spatial resolutions that were previously unavailable. More relevantly, Perry et al. (2010) tagged and tracked outmigrating Central Valley late-fall run Chinook salmon smolts through the Sacramento-San Joaquin River Delta (a complex system of sloughs and channels) to determine movement rates and survival depending on the pathway chosen. Once small-scale movement information is available, our knowledge of salmon migrations can begin to delve into what might be governing variability in movement patterns.

A few studies have taken the next logical step and explored how environmental conditions might be influencing these migration dynamics. This step may be the crux of juvenile salmon management and conservation since the majority of the salmon rivers throughout the world have been faced with major anthropogenic influences, which can alter many environmental factors in a river. While these relationships have been studied in several rivers, one could argue that no river has been studied in this aspect as much as the heavily impounded Columbia River watershed. In this system, where environmental variables can be controlled to some extent (and have therefore been studied more), one study concluded that neither of the environmental predictor variables assessed (river discharge volume and water temperature) were found to correlate with migration rates (Giorgi et al. 1997), while another found a strong and consistent relationship between river flow and travel time (Smith et al. 2002), while yet another found strong evidence for a relationship between travel time and river flow on a seasonal basis (Zabel et al. 1998), in all cases with yearling outmigrating Chinook salmon smolts. However, these studies and others have assessed the influence of the environment on migration at large spatial and temporal scales, typically only using river flow and temperature as factors. These relationships are therefore usually limited to inter-annual and inter-population comparisons, thereby only uncovering the strongest and most persistent of patterns. Variations in movement are initiated at short intervals, and environmental factors there may exert significant influences, which may have higher order population consequences.

The study presented here aims to capitalize on one of the largest networks of acoustic receivers in the world, developed by the California Fish Tracking Consortium, and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to provide the first in-depth analysis of the spatial and temporal variation of Chinook salmon movement and migration in the Sacramento River and San Francisco Estuary. Using this information, we first determine total movement rate through the entire watershed during the outmigration. We then use a model of smolt travel time described in Zabel and Anderson (1997) to assess how the incorporation of year, release site, reach, and different environmental variables improve the models fit. Finally, we will discuss how migration and movement dynamics might be influencing smolt survival during this life stage.

Methods

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river to be fully contained within the state of California and is the third largest river that flows in to the Pacific Ocean in the contiguous United States. The headwaters are located south of Mount Shasta in the lower Cascade Range, and the river enters the ocean through the San Francisco Estuary at the Golden Gate Bridge (Fig. 1). The total catchment area spans approximately 70 000 km^2, and the annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 $m^3 s^{-1}$ (California Department of Water Resources DAYFLOW database).

The study area included approximately 92 % of the current outmigration corridor of late-fall run Chinook salmon, from release to ocean entry. Specifically, the study area's furthest upstream release site at Battle Creek (534 km upstream from the Golden Gate) is only 47 km downstream from Keswick Dam (the first impassable barrier to anadromy) at its confluence with the Sacramento River (Table 1).

Central Valley late-fall run Chinook salmon

The late-fall run is one of the four Chinook salmon runs found in the Sacramento River drainage and is the only run that migrates to sea predominately as yearlings (Moyle 2002). Coupled with the fall run, the pair form an evolutionary significant unit (ESU) deemed a "species of concern" by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which the smolts enter the ocean at 90 to 170 mm fork length (Fisher 1994; Snider and Titus 2000a, b). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

Acoustic telemetry

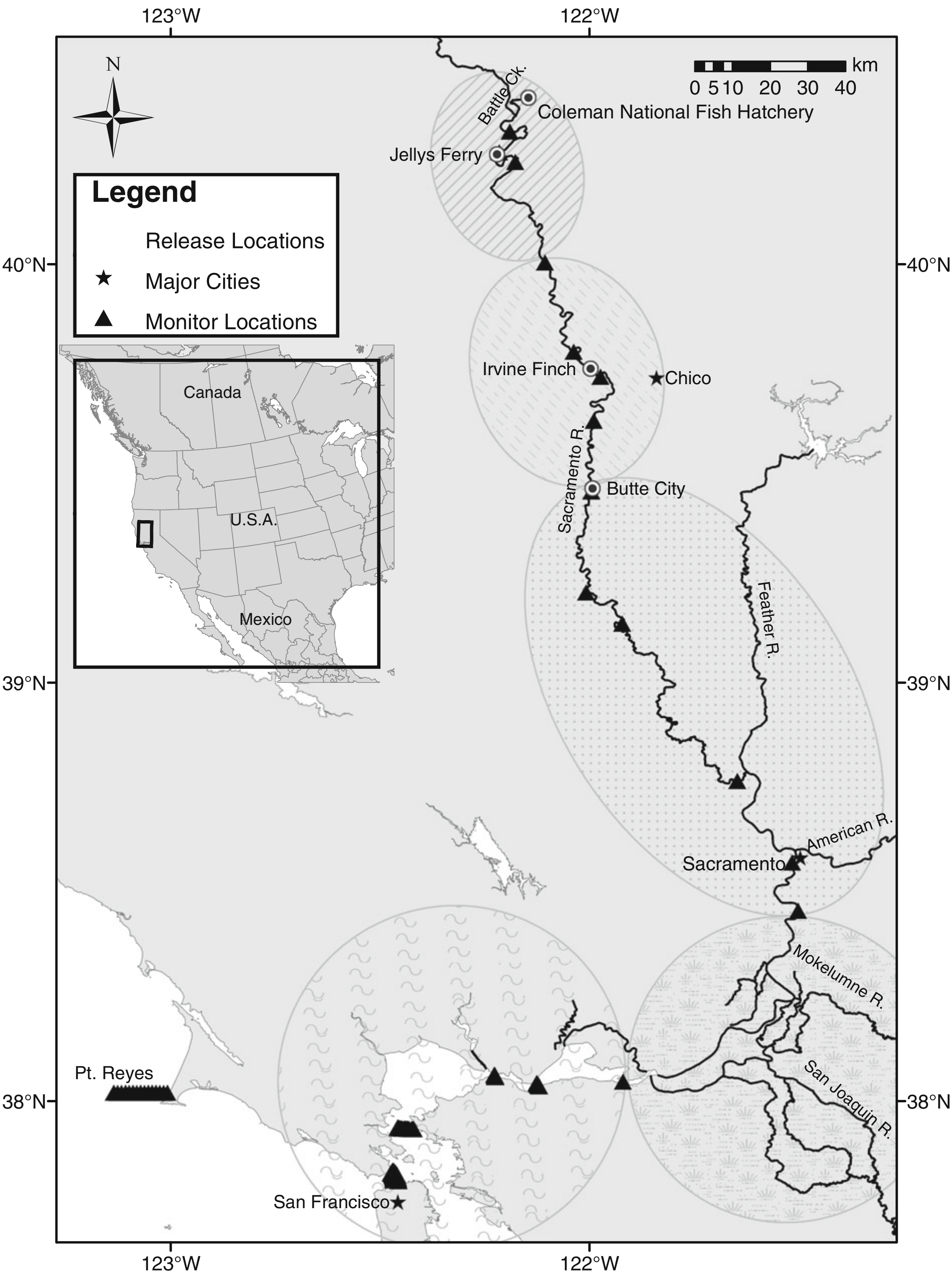
We used Vemco V7-2 L acoustic tags (1.58 g±0.03 S.D.; Amirix Systems, Inc. Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible receivers to track tagged fish. The receiver array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate) (Fig. 1; Table 1). This array of approximately 300 receivers at 210 receiver locations was maintained by the California Fish Tracking Consortium (a group of academic, federal and state institutions, and private consulting firms; http://californiafishtracking.ucdavis.edu/).

The acoustic receivers automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subjected to standardized quality control procedures to minimize the number of false detections. Specifically, we considered for removal detections flagged by an automated script that searched the detection records of each individual smolt to determine if they fulfilled any one of the three following independent conditions: (1) The detection occurred before release date-time of that tag. (2) A single detection that occurred at a location was not between valid upstream and downstream detections (a valid detection is defined as less than 10 d or 50 rkm to prior or next detection). (3) Multiple consecutive detections of a tag at one location were greater than 216 min apart (10 % less than the minimum observed time between consecutive known false detections of the same tag).

Tagging and releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 304 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged smolts (Table 2) was consistent with the observed size distribution for this Chinook salmon run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery origin yearling late-fall run Chinook salmon smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized smolts as described by Ammann et al. (2011, this issue). To minimize potential effects on survival, growth, and behavior, smolts were size selected resulting in an average tag weight to total body weight ratio of 3.6 %, and individual ratios rarely exceeded 5 %.


123°W
122°W
40°N
39°N
38°N
N
km
0 5 10 20 30 40
Legend
Release Locations
Major Cities
Monitor Locations
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
American R.
Sacramento
Mokelumne R.
San Joaquin R.
Pt. Reyes
San Francisco
Canada
U.S.A.
Mexico

◀ **Fig. 1** Map of the study area, including the Sacramento River, Sacramento—San Joaquin River Delta, San Francisco Estuary, and Pacific Ocean. Bull's-eye icons signify release locations, stars symbolizes major cities, and black dots symbolizes receiver locations. Shaded regions delimit (from north to south) the upper river, middle river, lower river, delta, and estuary

Lab experiments run concurrently with this study indicated that growth and survival were not significantly affected by the tag burden (Ammann et al. 2011, this issue).

Post-surgery, the smolts were held before release for 7 d in 2007 and 24 h in 2008 and 2009 to ensure proper recovery from surgery. In the 2007 season, a portion of the tagged smolts were released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

In the first year this study (2007), all 200 smolts were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter 2 years, 300 smolts a year were tagged and simultaneously released from three release sites in the upper 150 rkm of the mainstem Sacramento River (Table 1), allowing the lower release groups a greater likelihood of reaching the lower river and estuary in large numbers (to improve statistical confidence intervals).

Data analysis

Smolt outmigration

Detection probabilities for each receiver location were calculated using the Cormack-Jolly-Seber (CJS) model for live recaptures (Cormack 1964; Jolly 1965; Seber 1965) within Program MARK (created by Gary White, Colorado State University (White and Burnham 1999)). A subset of the receiver locations that had consistently high tag detection probabilities and that were strategically located were chosen to delimit the river reaches that were used in the spatial movement analysis. A total of 14 receiver locations were chosen, from just below the most upstream release site to the Golden Gate (Table 1).

Two metrics for smolt movement were utilized, the former describing total migration movement, and the latter describing small-scale movements during migration. Smolt movement rates from release site to the Golden Gate was calculated for each smolt that survived to the Golden Gate (3–13 % of all smolts, depending on release group and year (C. Michel unpubl. data)) and averaged by release group (by year and release site), representing the mean successful migration movement rate (MSMMR; Table 3). Migration time from release point to the entry of the Sacramento/San Joaquin Delta, as well as migration time from the entry of the Sacramento/San Joaquin Delta to

Table 1 Locations of acoustic receivers and tagged smolt release locations

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
Freeport	169	Monitor location, delta entry
Chipps Island	70	Monitor location, estuary entry
Golden Gate	2	Monitor location, ocean entry

Table 2 Means and standard errors for weight and fork length of acoustically-tagged smolts by year and for all years combined

Year	Weight±SE (g)	Fork length±SE (mm)	Sample size
ALL	46.0±0.4	161.5±0.5	804
2007	46.6±0.7[a]	164.6±0.8[a]	200
2008	52.6±0.8[b]	168.7±0.8[b]	304
2009	38.9±0.5[c]	152.1±0.5[c]	300

[a,b,c]Size distributions with different superscripts are significantly different ($P<0.05$)

the entry into the Pacific Ocean, were also calculated and averaged by release group.

Reach-specific movement

Smolt-specific movement rates were then calculated per major geographic region using the last detection time from the upstream receiver locations and the first detection time from the downstream receiver locations for that region. The regions selected consisted of the upper river (river km (rkm) 518 to 456), the middle river (rkm 456 to 363), the lower river (rkm 363 to 169), the Sacramento/San Joaquin Delta (rkm 169 to 70), and finally the San Francisco Estuary (rkm 70 to 2). Distances between receiver locations were calculated in kilometers using the geographic information system software program ArcGIS 9 (ESRI) and NHDPlus 1:100 K hydrography, giving a movement metric of km·day^{-1}. These movement rates were then represented graphically with boxplots for each region by year interaction (Fig. 2).

To explore the small-scale movements of the smolts tagged in this study, we used an *advection–diffusion* smolt travel time model, explained in detail with regard to the riverine movement of salmonids in Zabel and Anderson (1997) and subsequent publications by those authors (Zabel et al. 1998; Zabel 2002; Zabel et al. 2008). The advection–diffusion model allows a probability density function (p.d.f) for the distribution of travel times in a given reach. Specifically, the model incorporates an advection term (including the parameter r describing the mean rate of downstream movement), and a diffusion term (including the parameter σ describing the rate of population spreading). One key element of the model used is an absorbing boundary for movement rate r at the value of zero; this assumption is acceptable in the case of outmigrating Chinook salmon smolts because it is rare to see upstream movement once migration has commenced. The distribution of smolt travel times under these assumptions are described by the inverse Gaussian distribution, with the following probability density function:

$$g(t) = \frac{L}{\sqrt{2\pi\sigma^2 t^3}} \exp\left(\frac{-(L - rt)^2}{2\sigma^2 t}\right) \tag{1}$$

(Zabel and Anderson 1997). L represents the reach length (in kilometers) and t represents travel time. The inverse Gaussian p.d.f. is unimodal and right skewed which captures the occurrence of most smolts

Table 3 Mean travel time in days from release point to Sacramento—San Joaquin River Delta entry, mean travel time in days from Delta entry to Pacific Ocean entry, and mean successful migration movement rate (MSMMR) for all years and all release groups

Year	Release (rkm)[a]	# released	Release to Delta entry travel time (days)±SE	Delta entry to Ocean entry travel time (days)±SE	Total MSMMR (km·day^{-1})±SE
2007	534	200	13.7±1.6	8.5±2.4	23.5±3.6
2008	517	102	14.2±1.2	14.5±1.0	18.9±1.9
	413	101	10.8±1.2	16.7±3.1	18.1±3.3
	363	101	9.7±0.9	13.8±2.0	15.6±1.8
2009	517	100	14.6±0.5	12.1±4.0	22.7±3.1
	413	100	13.0±0.8	12.6±1.3	18.1±1.3
	363	100	11.0±0.6	14.1±1.9	14.3±1.3

[a] distance (river km (rkm)) from Golden Gate

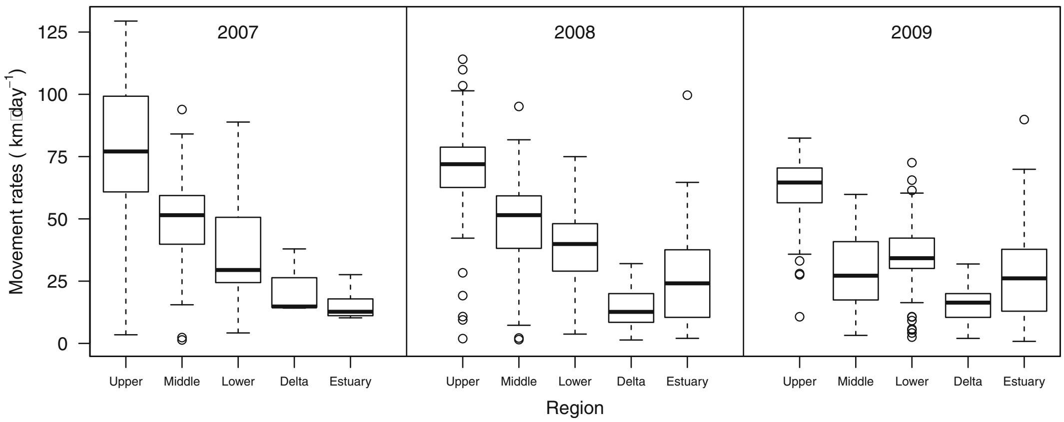


Fig. 2 Yearling late-fall run Chinook salmon migration movement rate distributions by region and year. The bold horizontal lines that dissect the boxes represents the median values, while the upper and lower edges of the boxes represent the 75th and 25th percentiles of the movement data, respectively. The upper and lower ends of the vertical lines represent the maximum and minimum values of the movement data, unless outliers are present. Outliers are data points that are above the 75th percentile or below the 25th percentile by more than 1.5 times the inter-quartile range (the range from the 25th to 75th percentile) of each specific boxplot

travelling at a very similar rate, with a small minority of individuals taking longer to complete the passage of the reach.

We then optimized function (1) using the Nelder-Mead algorithm, given the observed travel times t, to find the most likely estimation for r and σ (i.e. maximum likelihood estimation, MLE). By substituting in more complex parameter structures for r and σ, we explored potentially more accurate models, *e.g.* allowing for reach-specific variability or influence of environmental factors such as flow in estimates. Several models were therefore constructed based on *a priori* understanding of the target population, in an attempt to determine the different sources of variability in the data (Table 4). We used Akaike's Information Criterion to evaluate the strength of evidence for these different models.

The observed travel time data that was used to estimate r and σ included the ten river reaches that are upstream of the influence of tidal fluctuations. The first model we constructed was one that only allowed one movement and spreading rate parameter (r and σ), thereby essentially reducing the entire system to one reach. This model will be referred to hereafter as the *null* model. We also constructed a model allowing movement rate to vary per reach (10 parameters estimated) while spreading rate was again held constant (1 parameter). A third model was constructed in which both movement and spreading rates were allowed to vary per reach (20 parameters total). A fourth and fifth model were built to allow and test for a "release" effect, in other words, allowing smolts that were released from the two downstream sites (Irvine Finch and Butte City) to have a different r estimates (and in the fifth model, σ estimates as well) from the smolts passing through from a more upstream origin, for the one reach downstream of the release site (models referred to as "reach+release"). A sixth model allowed for reach-specific r and σ estimates to also vary by year, while still accounting for a release effect ("reach +release+year"). Finally a series of six more models were constructed to allow six different environmental variables to act as linear predictors for r and σ, as seen in Zabel et al. (1998). These models therefore included an environmental parameter beta coefficient (β), allowing determination of the direction and slope of the relationship. Additionally, by standardizing the environmental variables (subtracting the mean value from each raw data point, then dividing by the standard deviation, essentially giving all standardized variable datasets a mean of zero and a standard deviation of one), standardized beta coefficients were calculated, allowing for the comparison of the strengths of beta coefficients for different models. For a change in one standard deviation unit of the environmental variable, travel time will change by the amount specified by that

Table 4 Model statistics for all smolt travel time models run, with parameter listed first (either movement rate r or spreading rate σ), followed by resolution allowed by parameter structure in parentheses (a "1" represents no spatial or temporal variability). AICc represents Akaike's Information Criterion (corrected for small sample sizes). Models have been sorted from best (at top) to worse fit, in order of increasing AIC values

Model	Parameters	AICc	Standardized β Coefficient
r(reach+release+year) σ(reach+release+year)	28	2,193.4	
r(reach+WDR+flow) σ(reach)	22	2,297.7	−0.1; 0.1
r(reach+release) σ(reach)	22	2,310.4	
r(reach+release) σ(reach+release)	24	2,314.0	
r(reach) σ(reach)	20	2,322.4	
r(reach) σ(1)	11	2,398.4	
r(WDR) σ(1)	3	2,643.0	−3.2
r(flow) σ(1)	3	2,652.0	2.2
r(turbidity) σ(1)	3	2,658.9	1.7
r(FMFR) σ(1)	3	2,659.6	2.5
r(velocity) σ(1)	3	2,666.5	−1.5
r(1) σ(1) *Null model*	2	2,674.3	
r(temperature) σ(1)	3	2,675.8	−0.4

model's standardized beta coefficient. Once the environmental models were ranked based on their AIC, a final model was constructed using a combination of two or more of the best ranked environmental variables. The purpose of this final model is to attempt to construct the best possible model using environmental variables alone. In total we therefore used thirteen different models, and using model selection methods, we should not only be able to determine the best model, but also test for the effect of certain factors.

Once the best model was determined, the parametric estimates of movement rates ($\widehat{r}$; km·day^{-1}) and population spreading rates ($\widehat{\sigma}$; km·day$^{-½}$) were reported at the resolution offered by the model (Table 5).

Influence of the environment

Spatial-temporal environmental data were collected for this study for the majority of the river reaches, from the release points to the upper limit of tidal influence on the river (rkm 189; Table 6). All variables were chosen a priori based on salmon migration literature and data availability for the watershed.

Table 5 Parametric estimates for movement rate $\widehat{r}$ (km·day^{-1}) and population spreading rate (km·day$^{-½}$) for all ten non-tidally influenced river reaches, from the "r(reach+release+year) σ(reach+release+year)" model. For reaches six and eight, estimates for both "run-of-river" (ROR) and downstream released (REL) smolts have been included for 2008 and 2009 (only one release site in 2007)

Reach	Rkm from Golden Gate	Total N	$\widehat{r}$ 2007	$\widehat{\sigma}$2007	$\widehat{r}$2008	$\widehat{\sigma}$2008	$\widehat{r}$2009	$\widehat{\sigma}$2009
1	518–504	293	33.0	25.7	36.8	21.5	34.4	15.1
2	504–492	278	61.3	23.6	65.1	19.4	62.7	13.0
3	492–456	194	27.2	26.3	31.0	22.1	28.6	15.7
4	456–421	147	13.9	31.1	17.7	27.0	15.3	20.5
5	421–412	145	13.0	27.3	16.8	23.2	14.4	16.8
6 ROR	412–389	105	10.6	25.5	14.4	21.3	12.0	14.9
6 REL	412–389	161	–	–	21.3	21.9	18.9	15.5
7	389–363	212	11.1	32.3	15.0	28.1	12.5	21.7
8 ROR	363–325	97	22.2	29.3	26.0	25.1	23.6	18.7
8 REL	363–325	88	–	–	24.1	23.8	21.7	17.4
9	325–309	135	25.6	31.0	29.4	26.8	27.0	20.4
10	309–226	163	25.4	43.0	29.2	38.9	26.8	32.5

The variables included water temperature (°C), river flow ($m^3 \cdot s^{-1}$), water turbidity (ntu), channel water velocity ($m \cdot s^{-1}$), a ratio of river surface width (m) to maximum river depth (m) (WDR), and a ratio of daily river flow to mean river flow over the migration season of the year in question (FMFR). The WDR will increase as the river becomes shallower and wider. If the FMFR value is above one, this means the daily flow was above average for that particular migration season, and if the value is below one, the daily flow was below average for that particular migration season. Variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 6). Measurements such as water velocity and WDR were simulated using actual flow recordings, high-resolution bathymetric cross-sections, and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers). All reach-specific environmental variables were then averaged by reach and by day. All reach-specific spatial-temporal environmental variables were then associated with their respective reach-specific movement rates in a relational database (Microsoft SQL Server 2005, Microsoft Corporation).

Results

Smolt outmigration

The mean successful migration movement rate (MSMMR) per release group varied by release site and by year (Table 3). Mean total movement rates decreased the further downstream the release group was released. Movement rates varied from 14.3 $km \cdot day^{-1}$ (S.E. =± 1.3 $km \cdot day^{-1}$) for the 2009 Butte City release group (rkm 363) to 23.5 $km \cdot day^{-1}$ (± 3.6 S.E.) for the 2007 Battle Creek release group (rkm 534). An ad hoc analysis of variance confirmed this pattern: release location had a significant effect on MSMMR ($P < 0.05$), while year did not ($P = 0.2$).

Reach-specific movement

Movement rates decreased as smolts moved from upstream regions downstream toward ocean entry, with the fastest movement rates found in the upper river region, followed by a decreasing trend up until the slowest region: the Sacramento-San Joaquin River Delta (Fig. 2). The interaction between region and year suggested a similar trend in all years of generally decreasing movement rates the further downstream the region, but in 2009 movement rates were generally slower and more uniform among regions.

The different smolt travel time models were constructed, and ordered in terms of their AICc value (Table 4). The "r(reach) σ(1)" was found to be much better supported (AICc difference larger than seven) than the null model, suggesting that there is heterogeneity in reach specific movement rates. Additionally, the "r(reach) σ(reach)" model was also much better supported than the "r(reach) σ(1)" model, suggesting that the population spreading rate is also heterogeneous on a reach-specific basis.

Table 6 Sources of environmental data for this study

Environmental variables	Data source[a]	Data Location
Water temperature (°C)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow ($m^3 \cdot sec^{-1}$)	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel water velocity ($m \cdot sec^{-1}$)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]
Maximum river depth (m)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]
River surface width (m)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]

[a] Agency Acronyms: *UCD* University of California—Davis, *BOR* United States Bureau of Reclamation, *DWR* California Department of Water Resources, *USGS* United States Geological Survey, *USFWS* United States Fish and Wildlife Service, *USACE* United States Army Corps of Engineers

[b] Ricky Doung (rdoung@water.ca.gov); Todd Hillaire (hillaire@water.ca.gov)

Parameters allowing for newly released smolts to have a different movement rate from the "run-of-river" smolts (ROR; smolts that are migrating through the reach in question, i.e. smolts that were not recently released) were incorporated into the "r(reach+release) σ(reach)" model, and this substantially improved the models support over the "r(reach) σ(reach)" model (which served as the framework for the new model). Additionally, this model was marginally better supported than the "r(reach+release) σ(reach+release)" model, suggesting that spreading rates were not substantially different between newly released smolts and ROR smolts. The maximum likelihood estimate (MLE) for movement rate for the Irvine Finch group (middle release site) in the first reach after release was 22.3 km·day^{-1} versus 13.4 km·day^{-1} for the ROR smolts in that reach. As for the Butte City release group (furthest downstream release site), their MLEs for movement rate in the first reach after release was 22.3 km·day^{-1} versus 24.0 km·day^{-1} for the ROR smolts.

Parameters allowing for an additive effect of year of release were also incorporated into the smolt travel time model. Given that a release effect had been found, and that 2007 did not have any downstream released fish, the year model had to account for the release effect. Therefore the model "r(reach+release+year) σ(reach+release+year)" was constructed, and was found to have substantially better support than the "r(reach+release) σ(reach+release)" base model. This implies that year had an influence of reach-specific movement and spreading rates in an additive way. The movement rate β coefficients for the 2008 and 2009 years (2007 was the intercept) are both positive, with 2008 having the larger value. This indicates that in general, 2008 had the fastest movement rates, followed by 2009, then 2007. The spreading β coefficients for 2008 and 2009 were both negative, with 2008 having the larger value. This means that 2007 had the largest spreading rates, followed by 2008, and finally 2009 had the smallest spreading rates. This year model was the best supported model of all the models run, and therefore the MLEs for each parameter are shown in Table 5.

Influence of the environment

The influence of different environmental variables was also assessed using the smolt travel time model. Each of these models can be compared to the null model for an indication of fit; the environmental models are based off the null model, and therefore, any improvement in fit is purely due to movement rate variability explained by variability in the environmental factor in question. The environmental model to perform the best was the river width-to-depth ratio model (WDR) (Table 4). WDR had a negative relationship with movement rates, indicating that the deeper and narrower reaches (low WDR) will have faster movement rates. The WDR model also had the strongest standardized β coefficient. The next best supported smolt travel time model was the river flow model, with a positive relationship between flow rates and movement rates. The turbidity and FMFR models were the next best supported models, again with positive relationships with smolt movement rates. The velocity model was also well supported, albeit much less than some of the previously mentioned models, and with one of the weakest standardized β coefficients. The relationship between velocity and smolt movement was negative. Finally, the temperature model was the only environmental model that was not found to be better supported than the null model.

Using the two environmental variables that had the best fitting models, WDR and river flow, we then constructed a new model incorporating both into the "r(reach) σ(reach)" model. This model far outperformed all other environmental models, and was second only to the "r(reach+release+year) σ(reach+release+year)" model.

Discussion

Migration rates from the Battle Creek release site to the ocean in 2007 (23.5 km·day^{-1}), were similar to a mean migration rate of late-fall run Chinook salmon smolts released at the same site and recaptured at the beginning of the San Francisco Estuary using a mid-water trawl (30.25 km·day^{-1}, USFWS Stockton FWO data 1994–2010, [http://www.fws.gov/stockton/jfmp/datamanagement.asp]). The mean migration rate for yearling Chinook salmon smolts on the Columbia River, another large West Coast river, was 21.5 km·day^{-1} (Giorgi et al. 1997). Although migration rates of yearling Chinook salmon on the

Fraser River (a large undammed West Coast river that runs through British Columbia) are not available in the literature, similarly sized sockeye salmon (Oncorhynchus nerka) smolts navigated the watershed at a rate of 15 to 30 km·day^{-1} (Welch et al. 2009). The results for late-fall Chinook salmon smolts presented here in combination with those of yearlings from other studies strongly suggest that like-sized smolts exhibit very similar migration rates regardless of the large river system.

Smolt movement rates varied substantially throughout the watershed. The fastest movement rates were seen in the river regions, with the Upper Sacramento River having the fastest rates of the three, potentially due to the faster water velocities seen there, allowing for faster passive transport of an actively migrating smolt. The slowest movement rates were seen in the Sacramento-San Joaquin River Delta, a highly modified and complex system of sloughs and channels. Water diversions in the southern delta remove nearly 40 % of the historic flows through the delta, resulting in substantial modifications in flow dynamics and directions (Nichols et al. 1986). This creates a region in which smolts have a high susceptibility of entering the interior delta, predisposing them to longer routes, higher predation, and the risk of entrainment into water pumps, inevitably leading to higher mortality rates (Perry et al. 2010).

The use of the smolt travel time model was an effective tool for exploring movement in this system, as well as determining longitudinal patterns of activity interacting with different environmental variables. As we uncover characteristics specific to movement dynamics in this system, we will be able to further improve the conceptual model to explain more of the variability in the observed data. As such, the careful discussion of model fit and parameter estimates should provide insight into more complex models worth exploring.

Movement and population spreading rates were seen to vary on a reach basis, as suggested by different smolt movement model comparisons. This heterogeneity in movement rates was expected, especially when considering the changing river habitats throughout the reaches. This variability demonstrates the need for delving into what environmental variables may be governing these reach specific differences. The changing population spreading rate appears to be in large part due to varying reach length, with the longest reaches having the largest spreading rates. This could be due to the fact that one of the models underlying assumptions is a lack of any diel migratory behavior. In the case of this study, smolts would mostly travel at night (Chapman et al. 2012, this issue), and in the case of the largest reaches (since they could not be traversed in one single night) the smolts would have had to experience diurnal time periods within that reach, thereby slowing the migration for some and effectively increasing the population spreading. We suggest that an improved smolt travel time model be created that allows for diel migration behavior as this is a staple in many smolt populations.

The smolt travel time model that allowed for reach and year variability, while accounting for a “release” effect, was the best supported model of the models tested. This suggests that movement rates varied by year, with 2008 having the fastest movement rates, followed by 2009 then 2007. The rate of population spreading did not follow the same pattern, with a general decrease from 2007 through to 2009. However, all 3 years of the study were all similarly dry years resulting in low river flows (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices, [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). This could indicate that movement and population spreading rates may be more similar in these years than when compared to “wet” years. In addition, it is important to note that movement rates and environmental associations found in this study may only be indicative of dry year dynamics.

Given that several release sites were used in this study, there was a need to test for potential release effects on movement rates. The reach-specific smolt travel time model that allowed for a release effect on movement rates was indeed better supported than the similar model without a release effect. Specifically, movement rates for smolts released at Irvine Finch (the middle release site) were substantially faster than movement rates of “run-of-river” (ROR) smolts in the first reach after Irvine Finch, while the relationship between the further downstream Butte City released smolts and their ROR counterparts was both weaker and the opposite. One potential reason for this was that smolts from Irvine Finch were released at dusk, while ROR smolts entered reaches at all times of the day. Given the predisposition for nocturnal migration in this population, there is a strong possibility newly-released smolts moved faster since they all experienced night conditions immediately after release, as opposed to the ROR smolts that did not all experience such an advantage. As for the Butte City smolts, a potential explanation for the lack of a similarly strong pattern could be due to the attenuation of the nocturnal migration behavior in this further downstream reach (Chapman et al. 2012, this issue). Interestingly, although Irvine Finch smolts appear to move faster than ROR smolts immediately after release, the smolts released furthest upstream have the fastest mean successful migration movement rate (MSMMR). This inconsistency brings to light an important distinction to make: travel times used in this modeling exercise are from all smolts in the study, while migration rates provided above are only for the small fraction of the study individuals that successfully outmigrated to the ocean. We determine that there is an appreciable release effect on movement rates in this system, meriting consideration of this occurrence into the construction of smolt travel time models when using several release sites.

River width-to-depth ratio (WDR) was found to have a strong negative relationship with movement rates, meaning that smolts moved slower through wider, shallower reaches. In that the upper river had the fastest smolt movement rates, and was intermittently wide and shallow, this relationship may seem counter-intuitive. However, the upper river region did not have the highest mean WDR, and was composed of deeper river sections interspersed with wider, shallow runs and riffles, suggesting that the movement rates in this region may be associated more with complex differential travel behavior incorporating a range of WDR habitats.

Flow has often been suggested to influence movement rates of yearling Chinook salmon (Zabel et al. 1998; Smith et al. 2002). In this study, flow was found to be positively related with movement rates. Flow generally increases in the downstream direction, in large part due to the progressive additions of water from the numerous tributaries in this system. However, the mean flows experienced by smolts in this study were very similar across regions. One possible interpretation of the relationship between flow and movement could be that it is the temporal (and not the spatial) variability in flow that drives this relationship. Salmonid smolts are known to initiate their downstream migration during storm events (McCormick et al. 1998), analogous with high flows. This was the motivation in creating the model using flow to mean flow ratio (FMFR) as a linear predictor. This relationship was also positive, further supporting our hypothesis. There was indeed some evidence of increased watershed-wide smolt movements during particularly strong storm events. We therefore conclude that the relationship between flow and movement rate may be strong past a certain flow threshold and a more complex model should be explored that may capture the occurrence.

The model using both aforementioned environmental variables was found to be the second best supported model tested. While the beta coefficients for both WDR and river flow were relatively small, they were in agreement with coefficients from their respective individual models. The purpose of taking the two best environmental variables and using them both in one model was an exercise to determine if we could find a well-supported model that resource managers could use in predicting future smolt migration travel times based on environmental variables alone, and in some instances, exercise their control over dam releases to meet salmon management goals. Building such a model is especially important in light of the fact that the best supported model incorporated both reach and year variability; while this does provide meaningful information, the year factor prevents us from making future predictions with it, and it is therefore less useful to resource managers.

Turbidity was seen to have a strong positive relationship with movement rates in this study. From associated work, we know that increases in turbidity correlate strongly with increases in survival (C. Michel, unpubl. data), perhaps because turbidity dramatically decreases predator efficiency (as seen with various predators on salmon smolts in the Fraser River (Gregory and Levings 1998) and with smallmouth bass (*Micropterus dolomieu*) in a laboratory setting (Sweka and Hartman 2003)). Survival rates were low in the upper reaches of the Sacramento River (C. Michel, unpubl. data), coinciding with the location of the primarily nocturnal migration, while higher survival in the lower river coincided with the more even migration through the day seen in the lower river reaches (Chapman et al. 2012, this issue). These results suggest that the relatively clear waters of the upper and middle river regions have much higher predation rates, which may have driven the evolution of a nocturnal migration strategy. However, the lower region has more turbid water and therefore may be more cryptic and beneficial for smolt survival. Perhaps this is what allowed the easement of the nocturnal strategy in the lower river, as also seen by Moore et al. (1998) and Ibbotson et al. (2006) with Atlantic salmon smolts. This then may have allowed migration at all hours which in turn provided smolts with the opportunity to travel larger distances per day, potentially explaining the positive relationship between movement rates and turbidity. Alternatively, or perhaps acting in concert, the relationship between turbidity and movement rates could spawn from the fact that turbidity tends to increase during high river flows during storm events, during which smolts usually initiate migration.

Water velocity was found to be the fifth strongest relationship, and somewhat counter intuitively, was found to be negatively correlated with movement rates. Water velocity can help a smolt move downstream at faster rates by increasing passive transport. This relationship was believed to be the most important environmental factor a priori, however, the direction of the correlation was the opposite of what was expected. One potential explanation is that only travel events during which the smolt was recorded at the upstream and downstream receiver station were used in this correlation analysis. This created a problem in that during high flow events (with fast water velocities), detection probability decreased due to increased noise, increased monitor tilt, and increased turbidity, and therefore fewer movement recordings were available during high flows. This potential shortcoming may have further reaching consequences in this analysis; it could be that other environmental variables tested did not have many associated travel events near their extremes during high flow events due to low detection probabilities.

Temperature was the only environmental variable to show no indication of influencing movement rates. Much work has been done on the effect of increases in temperature on smolt migration initiation, suggesting that temperature should indeed be tightly linked to movement rates. However, the negative results seen in this study are not the uncommon in the literature. Two other studies have found no significant relationship between temperature and migration rate in yearling Chinook salmon smolts (Giorgi et al. 1997; Smith et al. 2002). One potential reason for the lack of effect could be that the smolts were released all at once, during two releases each season, and therefore experience a narrow range of temperatures. This is in contrast with many studies that do find a relationship between temperature and migration rate; data used are frequently from random sampling of the outmigrating smolt population using continuous trapping methods over a long field season. This problem could be further exacerbated by the fact that the Upper Sacramento River displays relatively constant water temperatures because Shasta Dam releases cold water from the bottom of Lake Shasta year round (which offers the question of how well can smolts time their outmigration to enter the ocean at the optimal time for feeding and growth if a potentially critical temperature cue is subdued?). Finally, since the study occurred during three similarly dry years (low rainfall and snowpack) in northern California, there is good evidence that there may not have been enough variability in temperatures to obtain a measurable effect.

The patterns and rates elucidated in this paper can provide valuable insight into the migration dynamics of Chinook salmon smolts of other runs, sizes, and stages of development, but caution should be employed in this extrapolation. The smolts used in this study were relatively large yearling Chinook salmon, and were force released into the river system, and therefore could be expressing patterns different from natural and other hatchery populations.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for any hope of an eventual recovery, and this cannot be achieved without understanding the movement and migration dynamics and causal mechanisms of emigrating smolts, arguably the most vulnerable life stage. This study provides new insights on temporal and spatial movement dynamics through the entire watershed, and suggests some environmental factors that shape the emigration. We also present a conceptual model for smolt travel times than can be applied to the Sacramento River Chinook salmon populations. Future directions for this model should include the construction of more complex models to capture certain intricacies that we have presented. Furthermore, due to unavailability of sufficient environmental data, we applied the model to the river section only, but future work should attempt to include the delta and estuary sections of the watershed. A more accurate conceptual model for smolt travel time in the Sacramento River will allow resource managers to fully consider the consequences of anthropogenic activities that may have detrimental effects on salmon populations, and also to best predict migration dynamics of future cohorts facing environmental changes.

Acknowledgements Funding for the project was provided by a CALFED Bay Delta program grant, project U-05-SC-047 (A.P.K and R.B.M principle investigators). We are grateful for the help from many technicians and volunteers including (but not limited to): Ian Cole, Alison Collins, Nicholas Delaney, Alex Hearn, Andrew Jones, and Ian Ralston. Special thanks to Kevin Niemela, Kurtis Brown, and Scott Hamelburg of U.S. Fish and Wildlife Service (USFWS) and the helpful staff of the Coleman National Fish Hatchery for providing late-fall run Chinook salmon smolts and logistical support for this study. Bathymetrical river data was graciously provided by Ricky Doung and Todd Hillaire. Statistical help from Ole Shelton and Jonathan Moore was greatly appreciated. GIS assistance was provided by Ethan Mora and Holly Davis. The California Fish Tracking Consortium allowed the realization of this project through the collaboration and data sharing of several academic, federal, and state institutions. Mark Carr, Jonathan Moore, Sean Hayes, and anonymous reviewers provided valuable comments that improved the manuscript.

References

Ammann Aj, Michel CJ and MacFarlane RB (2011) The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. Environ Biol Fish. doi:10.1007/s10641-011-9941-9

Chapman ED, Hearn AR, Michel CJ, Sandstrom PT, Ammann AJ, Thomas MJ, Singer GP, Peterson ML, Lindley SL, MacFarlane RB (2012) Diel movements of outmigrating Chinook salmon (Oncorhynchus tshawytscha) and steelhead (O. mykiss) smolts in the Sacramento/San Joaquin watershed. Environ Biol Fish. doi:10.1007/s10641-012-0001-x

Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19(6):334–343. doi:10.1016/j.tree.2004.04.003

Cormack RM (1964) Estimates of survival from the sighting of marked animals. Biometrika 51(3/4):429–438

Fisher FW (1994) Past and present status of central valley Chinook salmon. Conserv Biol 8(3):870–873

Giorgi AE, Hillman T, Stevenson JS, Hays SG, Peven CM (1997) Factors that influence the downstream migration rates of juvenile salmon and steelhead through the hydroelectric system in the mid-Columbia River basin. N Am J Fish Manag 17(2):268–282

Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. Trans Am Fish Soc 127 (2):275–285

Healey MC (1991) In: Margolis CGaL (ed) Pacific salmon life histories. University of British Columbia Press, Vancouver, pp 312–230

Ibbotson AT, Beaumont WRC, Pinder A, Welton S, Ladle M (2006) Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. Ecol Freshw Fish 15(4):544–551. doi:10.1111/j.1600-0633.2006.00194.x

Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52(1/2):225–247

McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Natl Research Council Canada, pp 77–92

Melnychuk M, Welch D, Walters C, Christensen V (2007) Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. Hydrobiologia 582 (1):55–65. doi:10.1007/s10750-006-0541-1

Moore A, Ives M, Scott M, Bamber S (1998) The migratory behaviour of wild sea trout (Salmo trutta L.) smolts in the estuary of the River Conwy, North Wales. Aquaculture 168 (1–4):57–68

Moyle PB (2002) Inland fishes of California. University of California Press, Berkeley

Moyle PB, Yoshiyama RM, Wikramanayake ED, Williams JE (1995) Fish species of special concern, 2nd edn. California Department of Fish and Game, Sacramento

Nichols FH, Cloern JE, Luoma SN, Peterson DH (1986) The modification of an estuary. Science 231(4738):567–573

Perry RW, Skalski JR, Brandes PL, Sandstrom PT, Klimley AP, Ammann A, MacFarlane B (2010) Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin river delta. N Am J Fish Manag 30(1):142–156. doi:10.1577/M08-200.1

Raymond HL (1968) Migration rates of yearling Chinook salmon in relation to flows and Impoundments in the Columbia and snake rivers. Trans Am Fish Soc 97(4):356–359. doi:10.1577/1548-8659(1968)97[356:MROYCS]2.0.CO;2

Seber GAF (1965) A note on the multiple-recapture census. Biometrika 52(1/2):249–259

Smith SG, Muir WD, Williams JG, Skalski JR (2002) Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. N Am J Fish Manag 22(2):385–405

Snider B, Titus RG (2000a) Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1996-September 1997 (trans: Division HC). Stream Evaluation Program Technical Report. California Department of Fish and Game

Snider B, Titus RG (2000b) Timing, composition, and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1997-September 1998 (trans: Division HC). Stream Evaluation Program Technical Report. California Department of Fish and Game

Sweka JA, Hartman KJ (2003) Reduction of reactive distance and foraging success in Smallmouth bass, *Micropterus* *dolomieu*, exposed to elevated turbidity levels. Environ Biol Fishes 67(4):341–347. doi:10.1023/a:1025835031366

Thorpe JE, Morgan RIG (1978) Periodicity in Atlantic salmon *Salmo salar* L. smolt migration. J Fish Biol 12(6):541–548. doi:10.1111/j.1095-8649.1978.tb04200.x

Welch DW, Melnychuk MC, Rechisky ER, Porter AD, Jacobs MC, Ladouceur A, McKinley RS, Jackson GD (2009) Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Can J Fish Aquat Sci 66(5):736–750. doi:10.1139/f09-032

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46(1 supp 1):120–139

Zabel RW (2002) Using "Travel Time" data to characterize the behavior of migrating animals. Am Nat 159(4):372–387

Zabel RW, Anderson JJ (1997) A model of the travel time of migrating juvenile salmon, with an application to Snake River Spring Chinook salmon. N Am J Fish Manag 17(1):93–100

Zabel RW, Anderson JJ, Shaw PA (1998) A multiple-reach model describing the migratory behavior of Snake River yearling Chinook salmon (Oncorhynchus tshawytscha). Can J Fish Aquat Sci 55(3):658–667

Zabel R, Faulkner J, Smith S, Anderson J, Van Holmes C, Beer N, Iltis S, Krinke J, Fredricks G, Bellerud B, Sweet J, Giorgi A (2008) Comprehensive passage (COMPASS) model: a model of downstream migration and survival of juvenile salmonids through a hydropower system. Hydrobiologia 609(1):289–300. doi:10.1007/s10750-008-9407-z