

# Contrasting patterns in growth and survival of Central Valley fall run Chinook salmon related to hatchery and ocean conditions

Megan C. Sabal · David D. Huff · Mark J. Henderson ·  
Jerome Fiechter · Jeffrey A. Harding · Sean A. Hayes

Received: 5 February 2016 / Accepted: 14 October 2016  
© Springer Science+Business Media Dordrecht 2016

**Abstract** The objective of this study was to determine important ocean and hatchery covariates influencing early growth and survival of Central Valley fall run Chinook salmon. We used a dataset of recaptured coded wire tagged hatchery Chinook salmon to estimate early growth and cohort survival. Ocean conditions during the period of early ocean entry were based on output from a coupled physical-biogeochemical model configured for the broader California Current region. We built generalized additive and generalized linear models to describe growth and survival and used Akaike Information Criterion (AICc) model selection to determine which hatchery and ocean covariates related best to response variables. With regards to hatchery covariates, growth was best explained by release location, while survival

was best explained by release weight and hatchery of origin. The ocean conditions included in the best models for both growth and survival included diatoms, predatory zooplankton, temperature, and currents. We observed the highest rates of salmon survival when in situ physical ocean conditions were indicative of relaxation events. For all four ocean covariates, the response curves illustrated opposite patterns between growth and survival models. This result implies that during periods of low survival, juvenile salmon were either 1) growing at a faster rate, or 2) growth appeared to increase because smaller fish had a higher mortality rate than larger fish. The first explanation would imply density-dependence, whereas the second explanation would imply size-selective mortality. These alternatives have

---

**Electronic supplementary material** The online version of this article (doi:10.1007/s10641-016-0536-3) contains supplementary material, which is available to authorized users.

---

M. C. Sabal · M. J. Henderson  
Santa Cruz, Cooperative Institute for Marine Ecosystems and  
Climate (CIMEC), University of California, Santa Cruz, USA

M. C. Sabal (✉) · M. J. Henderson · J. A. Harding  
Southwest Fisheries Science Center, National Marine Fisheries  
Service, National Oceanic and Atmospheric Administration, 110  
Shaffer Road, Santa Cruz, CA 95060, USA  
e-mail: msabal@ucsc.edu

D. D. Huff  
Point Adams Research Station, Northwest Fisheries Science  
Center, National Oceanic and Atmospheric Administration, PO  
Box 155, Hammond, OR 97121, USA

J. Fiechter  
Institute of Marine Sciences, University of California, Santa Cruz,  
Santa Cruz, CA 95064, USA

S. A. Hayes  
Northeast Fisheries Science Center, National Oceanic and  
Atmospheric Administration, 166 Water Street, Woods Hole, MA  
02543, USA

M. J. Henderson  
United States Geological Survey, California Cooperative Fish and  
Wildlife Research Unit, Department of Fisheries Biology,  
Humboldt State University, 1 Harpst Street, Arcata, CA 95521,  
USA

implications on hatchery practices including salmon size at release and number of salmon in release groups.

**Keywords** Growth · Survival · Chinook salmon · California · Size-selective mortality · Density-dependence

## Introduction

Migratory species encounter a diversity of environments across space and time, making it difficult to determine which factors influence overall survival. Because enhancing and predicting survival is often a primary goal of fishery and wildlife managers, environmental complexity presents an enormous challenge for managing migratory species (Martin et al. 2007). Successful conservation must recognize the spatial connections across life histories to understand how factors that affect one life stage can subsequently impact future life stages (Heppell 1998; Klaassen et al. 2014). Furthermore, a mechanistic understanding of how individuals interact with their environment can contribute to individual-based models that typically incorporate more realistic environmental conditions and population dynamics than statistical models (McLane et al. 2011). Therefore, it is important to examine effects of various factors across life stages on individual-based biological responses.

Pacific salmon (*Oncorhynchus* spp.) are born in freshwater, migrate through streams and rivers to the ocean, and spend 1–4 years dispersing in coastal waters before returning to spawn in their natal rivers. They experience diverse environments and stressors over their lifetime which cumulatively impact adult survival. Previous studies have examined the influence of a variety of hatchery, river, and ocean conditions on salmon survival such as trucking of smolts (Holsman et al. 2012), water temperature (Mueter et al. 2002), climate (Martins et al. 2012; Sharma et al. 2013), predators (Holsman et al. 2012), prey (Wells et al. 2012; Losee et al. 2014), and migration timing (Scheuerell et al. 2009; Satterthwaite et al. 2014). However, the relative importance of these and other factors is highly variable and depends on the nature of the population under study (Martins et al. 2012), the location of the study (Quiñones et al. 2014), and the temporal and spatial scale over which variables are measured (Sharma et al. 2013). For example, warm ocean temperatures during a cohort's first year at sea have been associated with

increased survival of Alaskan salmon populations, while cool ocean temperatures have been associated with increased survival in more southern populations (Mueter et al. 2002).

One consistently important factor influencing adult survival is early ocean growth (Holtby et al. 1990; Friedland et al. 2000; Beamish and Mahnken 2001; Duffy and Beauchamp 2011). The first few months after juvenile salmon enter the ocean is a time of high mortality when salmon must avoid starvation and predation. Hence, salmon must enter the ocean when prey is plentiful to persist and grow to larger sizes and escape predation by gape-limited predators (Satterthwaite et al. 2014; Fiechter et al. 2015). In California, strong early season (Jan-Mar) upwelling is important to precondition areas with nutrients that support nekton production in the summer, which relates to positive marine growth of juvenile salmon (Wells et al. 2008; Schroeder et al. 2013; Fiechter et al. 2015; Wells et al. 2016). Likewise, warm or cool ocean temperatures, depending on the location and scale over which they are measured, have also been related to salmon growth (Friedland et al. 2000; Martins et al. 2012; Agler et al. 2013). Similarly, in the Pacific Northwest winter preconditioning and early season upwelling have shown to influence salmon survival, although relationships with spring upwelling are variable (Nickelson 1986; Ryding and Skalski 1999; Logerwell et al. 2003).

Our study examines early growth and cohort survival of Central Valley fall run Chinook salmon (*O. tshawytscha*). Due to California's arid and variable Mediterranean climate, freshwater stages of this population are periodically exposed to elevated river temperatures and reduced river flows relative to Chinook salmon populations north of California. These potentially more stressful freshwater migration conditions may alter the relative importance of hatchery and ocean conditions on survival. In addition, California coastal waters undergo intense upwelling and relaxation events, but are not influenced by large river plumes (De Robertis et al. 2005; Morgan et al. 2005; Burla et al. 2010) or productive downwelling regions (Mueter et al. 2002) which are important features in northern areas. In the Pacific Northwest, large river outflows have been shown to influence both nutrient inputs into the coastal ecosystem (Davis et al. 2014) and retention of zooplankton on the shelf (Banas et al. 2009). Therefore, we may expect to see different dynamics influencing juvenile salmon growth and survival relative to other regions.

Many Pacific salmon populations are heavily supplemented by hatchery operations, some of which use coded wire tags (CWTs) to monitor harvest and adult survival. CWTs are small pieces of wire inscribed with unique codes which are injected into the snouts of juvenile salmon. It is common to use CWT recoveries from adult salmon to estimate cohort survival. This study uses CWT recoveries from juvenile salmon during their first ocean year, providing information about the specific growth and ocean conditions salmon experienced during the critical period of early ocean entry. These fine-scale data were used to explore relationships with early growth and survival to age 3. This information is particularly valuable because local oceanographic conditions are important in driving salmon biological responses such as growth and survival (Mueter et al. 2002; Sharma et al. 2013), and because it may generate more mechanistic hypotheses than broader scale correlations.

Our objective was to determine important factors influencing early growth and survival to age 3 of Central Valley fall run Chinook salmon. Specifically, we fit a series of statistical models that included various combinations of potential explanatory variables through Akaike Information Criterion (AICc) model selection. We further examined model response curves to identify patterns that may signify mechanisms. Finally, we qualitatively compared covariates and model response curves from our early growth model with our survival model. Since previous studies suggest that early ocean growth is important for overall salmon survival, we expected similar covariates to be included in both models with similar response curves. However, differences among covariates or response curves may provide insights into other processes such as size-selective mortality or density-dependence.

## Methods

### Study system

The Sacramento-San Joaquin Rivers support the largest salmon populations in California, and Central Valley fall run Chinook salmon are the most numerous contributing race. Five hatcheries supplement fall run Chinook salmon populations producing over 32 million smolts per year; differences in rearing practices among hatcheries produce smolts that differ in release size, timing, and location within the watershed (Huber and Carlson 2015).

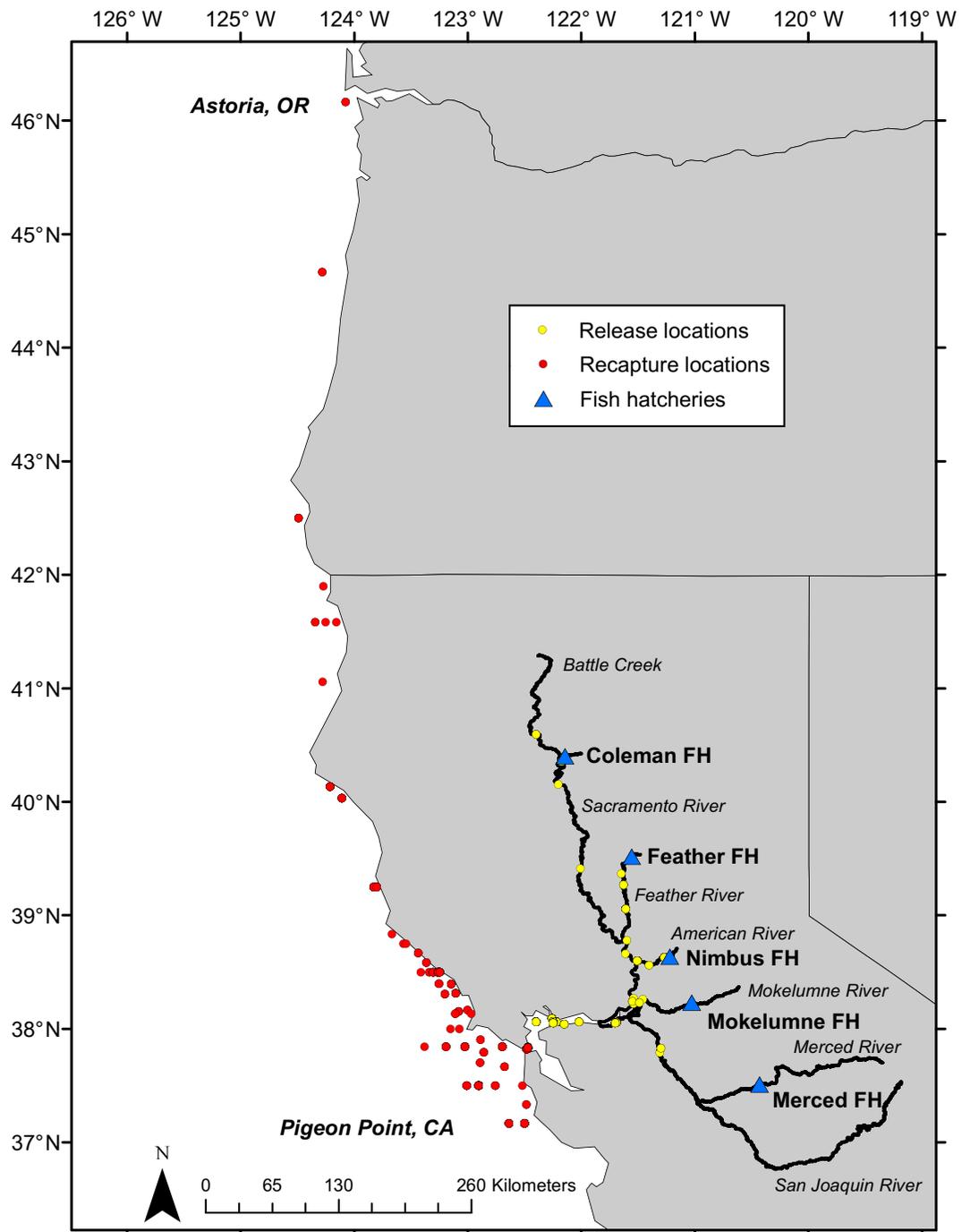
Approximately 25 % of hatchery released juvenile salmon are implanted with unique CWTs which identify salmon released in a given group and the characteristics of each release group. CWT release and recapture data are stored in the Regional Mark Identification System (RMIS, [www.mpc.org](http://www.mpc.org)) (Nandor et al. 2010). Fall run Chinook salmon juveniles enter the ocean at the Golden Gate Bridge from April–June and encounter ocean conditions driven by upwelling and relaxation events which have distinct physical ocean characteristics and dictate productivity and food availability (Pringle and Dever 2009). Chinook salmon disperse along the coastal ocean rim for 1–4 years, and return to rivers as adults to spawn in the fall. Adult salmon with CWTs are recovered from commercial and recreational fisheries, spawning ground surveys, and hatchery returns.

## Data collection

### Growth

To investigate salmon early growth, we utilized tag recoveries of CWT juvenile fall run Chinook salmon. Juvenile salmon during their first ocean year were sampled from NOAA Fisheries salmon ocean surveys from 1999 to 2012 (excluding 2006–2009), and were recovered from Pigeon Point, CA to Astoria, OR (Fig. 1). Cruise dates varied across years, but surveys were either conducted in the summer (mid-June to mid-August) or in the fall (mid-September to late-October) with three of the ten years completing both summer and fall cruises (Table 1). Salmon were captured using a surface trawl (264 Nordic Rope Trawl) that samples the upper 20 m of the water column for ~30 min tows (Harding et al. 2011). Biological data including weight, length, and a DNA sample were taken for all salmon, and these fish were brought back to the laboratory where salmon missing their adipose fins were electronically scanned for a CWT, and if present, the tag was extracted and read.

Of the coded wire tagged, age 1 Central Valley fall run Chinook salmon recovered in the juvenile salmon trawl surveys, 171 had sufficient data to estimate growth. We excluded fish that had less than 10 days between release and recapture because they would not have had sufficient time to exhibit differential growth due to exogenous conditions, and salmon from CWT groups that were released over a range of dates spanning greater than 5 days. Salmon age was determined by



**Fig. 1** Locations of juvenile salmon coded wire tag group releases (yellow circles), recoveries of salmon in their first ocean year on NOAA ocean surveys (red circles), and fish hatcheries (blue triangles)

subtracting the brood year, as provided from RMIS, from the recapture year. Early growth was calculated for each fish as the difference in recapture weight (g) from the ocean survey and mean release weight (g) from

the CWT release group. Because growth is estimated by subtracting a group mean from an individual measurement, there is the potential to over or under estimate growth if a salmon was released above or below the

**Table 1** Dates of NOAA salmon ocean surveys where juvenile Chinook salmon with CWTs were recovered

Cruise	Year	Dates
IW9901	1999	8/3–8/9
IW9902	1999	10/20–10/22
IW0001	2000	6/20–6/30
IW0101	2001	7/24–8/5
IW0201	2002	6/19–6/27
IW0202	2002	9/17–9/26
IW0301	2003	7/8–7/14
FR0401	2004	7/26–7/30
CA0501	2005	10/5–10/13
FR1001	2010	6/30–7/13
FR1101	2011	6/29–7/15
FR1102	2011	9/7–9/16
OS1201	2012	6/11–6/25

mean release weight. Our measure of early growth includes growth that occurred during river emigration, in the estuary, and in the coastal ocean.

Survival

Of juvenile salmon recovered with CWTs from the ocean surveys, 45 unique CWT release groups were represented between 1999 and 2010 from a dataset of 98 salmon. Again, we excluded salmon from CWT groups that were released over a range of dates spanning greater than 5 days. More recent years of recaptured juvenile salmon (2011–2012) did not have sufficient adult recaptures from subsequent years to estimate survival. We estimated survival to age 3 for each CWT release group using tag recoveries from multiple life stages from RMIS in a Virtual Population Cohort Analysis (VPA) (Magnusson and Hilborn 2003). For each CWT release group, we determined the total number of salmon released and the total number and dates of adult fish (age 1+) recovered from the RMIS database (Supplementary Table 1). The range of number of fish per release group was 15,770 to 396,000 (mean: 124,200). To estimate survival rates, we followed the methods of Magnusson and Hilborn (2003) and estimated the number of individuals from a release group that survived to age 3 ( $N_3$ ):

$$N_3 = C_2s_2 + C_3 + \frac{C_4}{s_3} + \frac{C_5}{s_3s_4} + \frac{C_6}{s_3s_4s_5}$$

Where  $C_a$  is the number of fish recovered at age  $a$  and  $s_a$  is the adult survival rate at age  $a$ . As with Magnusson and Hilborn, we assume that the adult survival rates were constant ( $s_2 = 0.6$ ,  $s_3 = 0.7$ ,  $s_4 = 0.8$ ,  $s_5 = 0.9$ ) and relatively minor components of the smolt-to-adult survival rate. The survival rate to age 3 for each release group was then estimated by dividing  $N_3$  by the number of individuals released.

It is important to note that survival was estimated for each release group based only on recoveries of adult tagged fish (age 1+), not those recaptured in the juvenile ocean survey (Supplementary Table 1). We then used the survival rate estimated for the release group as the response for the individual fish recovered in the juvenile survey (Table 2). As a result, if more than one fish from a single release group was recaptured in the juvenile survey they would have the same survival response.

Explanatory variables

We collected data on hatchery and ocean conditions that we hypothesized could affect salmon growth and survival (Table 2). Hatchery conditions were taken from the RMIS database for each CWT release group. We considered release date, release weight (g), release location, and hatchery of origin as potential important hatchery factors. The first two variables were treated as continuous and last two as categorical. Release location was described as the distance upstream (km) from the Golden Gate Bridge, and was calculated using linear referencing tools in ArcGIS 10.2. Locations that were less than 10 km apart were grouped together at a middle distance value, combining 17 release locations into 10 distance groups (35, 50, 70, 105, 126, 143, 167, 183, 215, 525 km). We treated release location as a categorical variable because locations may have multiple attributes that uniquely affect juvenile salmon; however, we were also able to visually assess trends related to distance upstream from the Golden Gate Bridge by defining the categories by distance.

To determine early ocean conditions likely encountered by individual salmon, we estimated where, and over which dates, salmon traveled in the coastal ocean. We estimated ocean entry dates following the methods from Fisher et al. (2014) with the exception that instead of using a constant mean value, we predicted river migration rate using a linear mixed-effects model and AICc model selection using CWT juvenile salmon recaptured between May 15th and June 16th from NOAA San Francisco Bay trawl surveys over 10 years

**Table 2** Description of covariates for growth (G) and survival (S) models of Central Valley juvenile Chinook salmon

Covariate	Level	Units	Source	Models
Recapture weight <sup>a</sup>	Individual	grams	NOAA cruise	G
Survival	CWT group	proportion of individuals surviving to age 3	RMIS	S
Pred zooplankton	Individual	mmol/m <sup>3</sup>	NEMURO	G, S
Diatoms	Individual	mmol/m <sup>3</sup>	NEMURO	G, S
Currents	Individual	m/s	ROMS	G, S
Temperature	Individual	°C	ROMS	G, S
Mean release weight <sup>a</sup>	CWT group	grams	RMIS	G, S
Hatchery of origin	CWT group	-	RMIS	S
Release location	CWT group	km upstream from Golden Gate Bridge	RMIS	G

<sup>a</sup>Recapture weight – mean release weight = growth

( $n = 121$ ). We considered four fixed variables (mean release weight (g), release date, distance released upstream, and May river flow), included release year and release location as random effects, and did not allow correlated variables ( $> 0.7$ ) to occur in the same model (Dormann et al. 2012). We excluded fish where the linear mixed-effects model estimated negative downstream migration rates (3 % of all growth data, 2 % of all survival data). These covariates come from the RMIS database, therefore ocean entry dates were estimated for each CWT release group.

To determine ocean travel routes for each salmon, we used ArcGIS cost distance and cost path tools to generate least-cost routes for juvenile salmon traveling from the Golden Gate Bridge to recapture locations. Based on previous research (Hassrick et al. 2016), we assumed salmon prefer depths less than 200 m in generating the least-cost routes. We extracted points along these routes every 10 km. For each salmon, we assigned a sequence of dates from ocean entry to recovery at each point along its travel route and assumed a constant rate of travel. From these specific locations and dates, we extracted oceanographic data from a coupled physical-biogeochemical model for the broader California Current region (Fiechter et al. 2014), including concurrent water temperature (°C), eastward and northward currents (m/s), predatory zooplankton (e.g., krill) (mmol/m<sup>3</sup>), and diatoms (mmol/m<sup>3</sup>). The physical model is an implementation of the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams 2005; Haidvogel et al. 2008) and the biogeochemical model is based on the NEMURO model (Kishi et al. 2007) with a spatial resolution of 10 km. We chose to use a physical-

biogeochemical model instead of empirical data because cloud cover along coastal waters was common generating many missing values in satellite datasets, we wanted values for zooplankton which are not available via satellite, and the ROMS and NEMURO models have been shown to correspond well with empirical oceanographic and biological data (Centurioni et al. 2008; Ivanov et al. 2009; Santora et al. 2013). Values from all points within a travel route were averaged for each fish.

## Data analysis

### Growth analysis

We used a generalized additive model (GAM) to determine how variables describing the oceanic and release conditions were related to the early growth of juvenile salmon. Although we considered using more traditional growth models (e.g., von Bertalanffy), we chose to use a GAM because it was a better fit to these short-term early life history growth patterns. The growth dataset consisted of 171 recovered juvenile salmon that represented 78 CWT releases from 1999 to 2012. Potential explanatory variables included in the GAM were: hatchery of origin, release location, mean release weight, release date, ocean temperature, predatory zooplankton, diatoms, and simultaneously smoothed eastward and northward currents (m/s). Prior to fitting the model, we examined the relationship between the different variables to reduce redundancy due to variables that were related or collinear. Hatchery and release location were related to each other because hatcheries had specific

locations where they released fish. Thus, during model selection we excluded any models that contained both hatchery and release location. Likewise, release date was collinear with release location because hatcheries farther upstream released fish earlier than downstream hatcheries. In this case, we only retained release location as a candidate variable because we were more interested in the potential connection of time spent in freshwater on growth. We did not include any interactions in the model because we had no a priori hypotheses regarding how different explanatory variables may interact.

Because our primary goal was to examine the effect of the environment on fish growth, we needed to control for the duration an individual was at large prior to recapture. To do this, we used a separate GAM to predict salmon growth given the number of days between release and recapture (days at large). We then included the predictions from this model as an offset in the full model containing the explanatory variables. In other words, we were testing the hypothesis that the ocean conditions and release variables could help explain if fish grew more or less than expected for a given duration at large. We used the predicted growth as an offset, rather than simply using days at large as an offset, because there was a non-linear relationship between days at large and growth.

We tested all possible combinations of the explanatory variables (96 possible models) and compared models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). We used the 'dredge' function in the 'MuMIn' package in R (Barton 2015), and averaged the models with  $\Delta\text{AICc}$  values  $<2$ . Model diagnostics, such as the QQ plot and residual plots, were used to assess normality and homogeneity of variance. To examine how well the model fit the data we used k-fold cross-validation, in which we split the data into equal-sized parts and then iteratively used part of the data to fit the model and a different part to test it (Hastie et al. 2009). K-fold cross-validation is a valuable tool to assess the predictive capabilities of a given model when challenged with a new dataset. This is an iterative process, thus, we repeated each k-fold cross validation process 500 times and examined the distribution of the  $r^2$  for the test data set based on the calibration model.

### Survival analysis

We examined variables influencing survival to age 3 with a dataset of 98 recovered juvenile salmon, which

represented 45 CWT release groups from 1999 to 2010. Cohort survival was estimated for each CWT group using recoveries from the RMIS database. We described the relationship of survival to age 3 to hatchery and ocean variables with a generalized linear model (GLM). We fit the models using a beta error distribution in the R package 'betareg' because our survival estimates were a proportional response (Ferrari and Cribari-Neto 2004). Prior to selecting the fixed effects, we used the fully parameterized model to select the most appropriate link function. The cauchit link with no bias reduction was overwhelmingly supported as the best link function based on AICc.

We considered the same suite of potential explanatory variables as the growth model, and tested all possible model combinations (360 possible models). The survival dataset had a smaller sample size ( $n = 98$ ) than the growth dataset ( $n = 171$ ) without years 2011 and 2012. As with the growth data set, each hatchery primarily released fish at one location; therefore, we restricted the model from including both variables at the same time. Release date was again excluded because it was collinear with release location. We built a full model, tested all possible model combinations, selected the top models with  $\Delta\text{AICc}$  value  $<2$ , and averaged those top models. We performed cross validation as described above.

## Results

### Growth analysis

In our dataset, growth ranged from 0.58 to 213 g from salmon who were at large from 31 to 169 days from release to recapture. Ocean sea surface temperatures ranged from 9.89 to 12.27 °C, eastward currents ranged from  $-0.02$  to  $0.04$  m/s, and northward currents ranged from  $-0.08$  to  $0.03$  m/s. Diatom densities ranged from  $0.25$  to  $1.27$  mmol/m<sup>3</sup> and predatory zooplankton ranged from  $0.14$  to  $0.36$  mmol/m<sup>3</sup> (Table 3). The juvenile salmon were released from CWT groups with mean release weights ranging from 3 to 19.2 g from locations that ranged from 35 to 528 km upstream from the Golden Gate Bridge. The top model for predicting downstream migration rate, which was then used to estimate ocean entry date and specific locations and dates to extract ROMS data for individual salmon, included mean release weight, release date, and random effects with a normal error distribution (conditional

**Table 3** Physical and biological covariate summary statistics for early growth dataset of Central Valley juvenile Chinook salmon from 1999–2012 (excluding 2006–2009)

Covariate	Mean	SD	Minimum	Median	Maximum
Temperature (°C)	11.08	0.70	9.89	11.38	12.27
Eastward current (m/s)	0.01	0.02	-0.02	0.01	0.04
Northward current (m/s)	-0.02	0.02	-0.08	-0.02	0.03
Diatoms (mmol/m <sup>3</sup> )	0.66	0.22	0.25	0.69	1.27
Pred zooplankton (mmol/m <sup>3</sup> )	0.25	0.06	0.14	0.22	0.36

$R^2 = 0.93$ ,  $k = 6$ ,  $df = 6$ ,  $AICc = 696.5$ , deviance = 683.8, weight of evidence = 0.86).

Model selection for the growth model resulted in two top models with  $\Delta AICc$  values less than two (Table 4). The averaged top model included the variables, predatory zooplankton, currents, temperature, release location, and diatoms, and had a median cross-validated adjusted  $R^2$  value of 0.81. Model response curves illustrate the shape of the nonlinear relationship between early growth and individual variables over the range of the selected covariate while keeping all other covariates constant at average values. We also plot the cross-validation model predictions to illustrate factor variance (Fig. 2). When all of the cross-validation lines (gray) fall close to the top model line (black) and exhibit the same pattern, this indicates more certainty in that covariates contribution to explaining patterns in growth or survival. We observed decreased juvenile salmon growth as the concentration of diatoms increased (Fig. 2a). However, some of the cross-validation lines show horizontal (no effect) or a U-shaped parabolic relationship, indicating considerable uncertainty in the relationship between diatom density and growth. The model response curve for predatory zooplankton indicated a parabolic relationship with lowest predicted growth values occurring at middle predatory zooplankton density with higher predicted values at high and low densities (Fig. 2b). Temperature was negatively related to growth (Fig. 2c). We display the relationship between growth and two directions of currents simultaneously.

Growth was highest with southwest flowing currents (Fig. 2d). Growth was greatest in fish released at locations nearest to the Golden Gate Bridge (Fig. 3).

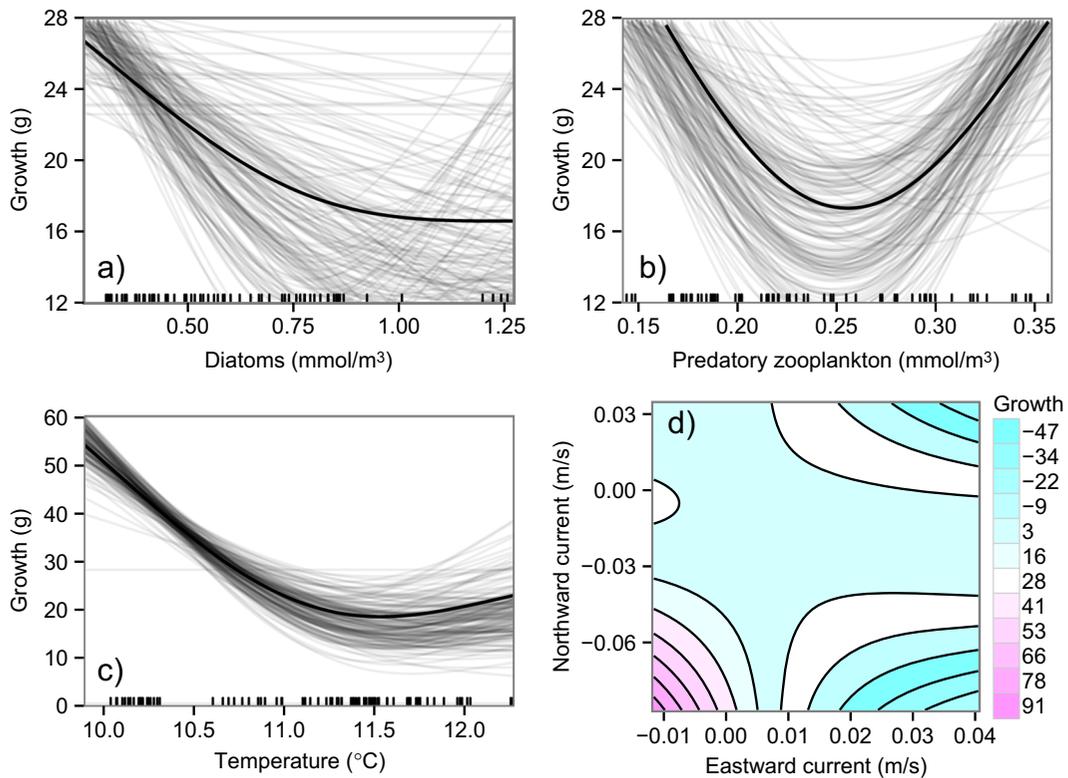
### Survival analysis

In our dataset, survival to age 3 ranged from 0.0058 to 0.0563. Ocean sea surface temperatures ranged from 9.89 to 12.25 °C, eastward currents ranged from -0.01 to 0.04 m/s, and northward currents ranged from -0.08 to 0.03 m/s. Diatom densities ranged from 0.25 to 1.27 mmol/m<sup>3</sup> and predatory zooplankton ranged from 0.14 to 0.34 mmol/m<sup>3</sup> (Table 5). The juvenile salmon were released from CWT groups with mean release weights ranging from 4.3 to 19.2 g from locations that ranged from 35 to 528 km upstream from the Golden Gate Bridge.

$AICc$  model selection resulted in three top models with  $\Delta AICc$  values less than two (Table 6). The averaged top model included the variables, predatory zooplankton, diatoms, currents, temperature, hatchery of origin, and mean release weight, and had a median cross-validated adjusted  $R^2$  value of 0.75. Model response curves indicated opposite relationships between survival and growth models. Diatom biomass was positively related to survival (Fig. 4a). For predatory zooplankton, survival peaked at middle zooplankton density with much lower survival estimated at high and low densities (Fig. 4b). Temperature showed a positive association with survival although there is a wide margin

**Table 4** Top models for early growth from  $AICc$  model selection of Central Valley juvenile Chinook salmon from 1999–2012 (excluding 2006–2009)

Top growth models	$AICc$	weight	$\Delta AICc$	LogLik	df	Deviance explained
Pred zooplankton + Currents + Temperature + Release location + Diatoms	1418	0.52	0	-684	21	47.1 %
Pred zooplankton + Currents + Temperature + Release location	1419	0.29	1.19	-688	19	44.6 %

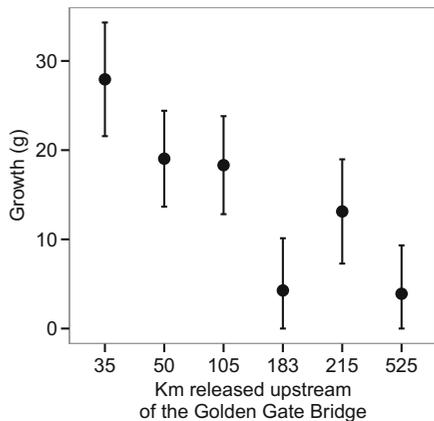


**Fig. 2** Growth across the range of **a** diatoms ( $\text{mmol}/\text{m}^3$ ), **b** predatory zooplankton ( $\text{mmol}/\text{m}^3$ ), **c** temperature ( $^{\circ}\text{C}$ ), and **d** currents (m/s) while keeping all other model covariates constant at average values. Solid *black* lines represent the mean and

individual k-fold runs were also plotted (*light gray lines*) to illustrate variability. Rug plots along the horizontal axis of plots **a-c** indicate the distribution of data points. **d** Currents, *blue* colors represent the highest modeled growth and *dark pink* the lowest

of uncertainty and some cross-validation lines indicated a horizontal (no effect) or negative relationship (Fig. 4c). The currents contour plot illustrated that survival was greatest with primarily northward flowing currents

which were slightly westward (Fig. 4d). As for hatchery effects, mean release weight showed a strong positive relationship with survival, and Feather and Coleman hatcheries produced the greatest survival, followed by Nimbus, Mokelumne, and Merced hatcheries respectively (Fig. 5).



**Fig. 3** Growth values from the top model across release location categories while keeping all other model covariates constant at average values. Release location categories with sample sizes less than five are not plotted

### Discussion

Our results indicate that both release conditions at the hatchery and early ocean conditions influence growth and cohort survival of Central Valley fall run Chinook salmon. We built two separate models for growth and survival with the expectation that similar covariates would be important because of the strong evidence that early growth is a critical component of adult survival (Holtby et al. 1990; Friedland et al. 2000; Beamish and Mahnken 2001; Duffy and Beauchamp 2011). Hatchery effects varied between survival and growth models, with release location included in the growth model, and

**Table 5** Physical and biological covariate summary statistics for cohort survival dataset of Central Valley juvenile Chinook salmon from 1999–2010 (excluding 2006–2009)

Covariate	Mean	SD	Minimum	Median	Maximum
Temperature (°C)	11.08	0.70	9.89	11.38	12.27
Eastward current (m/s)	0.01	0.02	-0.02	0.01	0.04
Northward current (m/s)	-0.02	0.02	-0.08	-0.02	0.03
Diatoms (mmol/m <sup>3</sup> )	0.66	0.22	0.25	0.69	1.27
Pred zooplankton (mmol/m <sup>3</sup> )	0.25	0.06	0.14	0.22	0.36

release weight and hatchery of origin included in the survival model. The same four ocean variables (currents, temperature, diatoms, and predatory zooplankton) were included in both models; however, covariate relationships were opposed in the growth and survival models.

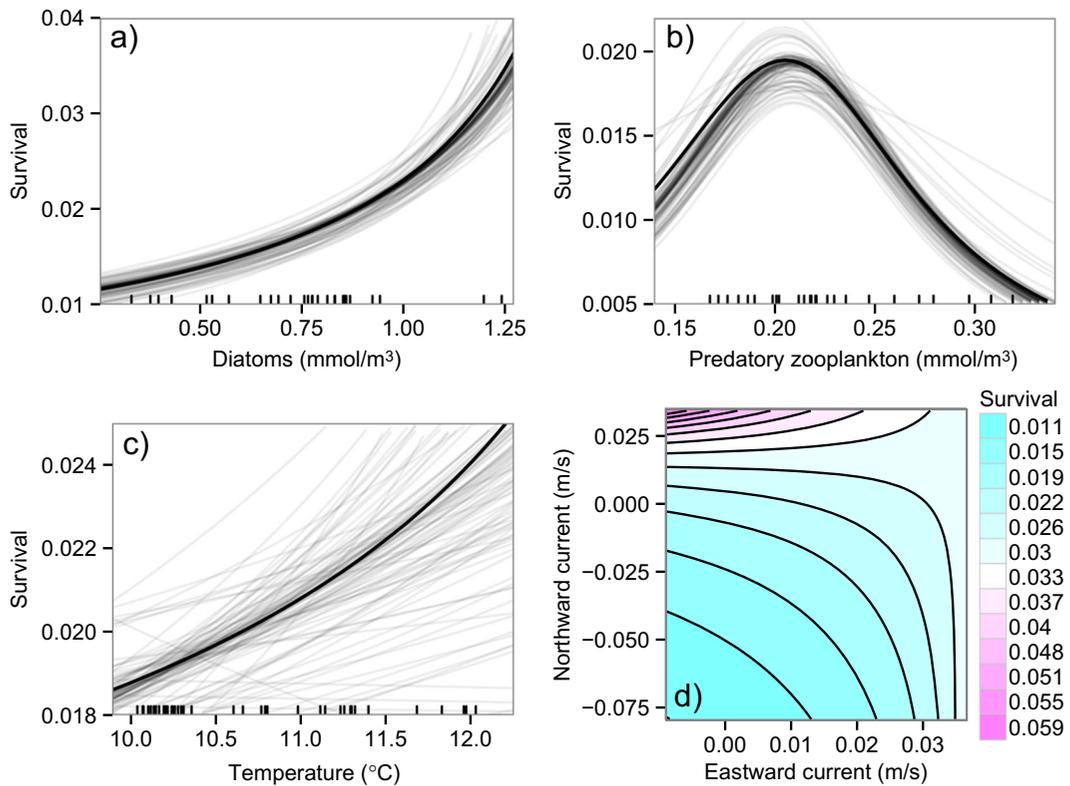
Two non-mutually exclusive hypotheses that may explain the opposing patterns between growth and survival model responses are size-selective mortality and density-dependence mechanisms (Miller et al. 2013). Under conditions in which survival is low, smaller fish may die at a greater rate than larger fish. Thus apparent high growth conditions could result from demographic shifts in size rather than actual growth differences. Evidence for size-selective mortality has been observed during early ocean entry for juvenile salmon in California (Woodson et al. 2013), the Pacific Northwest (Claiborne et al. 2011), and Alaska (Moss et al. 2005). Likely predators include piscivorous birds in the estuary and ocean (Anderson et al. 2004; Adrean et al. 2012; Tucker et al. 2016), predatory fish (Emmett et al. 2006; Emmett and Krutzikowsky 2008), and marine mammals (Yurk and Trites 2000; Kvitrud et al. 2005). Predation pressure can also vary with respect to oceanographic conditions (Emmett et al. 2006) making an assessment of the overall extent of predation impacts on juvenile salmon populations difficult.

The density-dependence hypothesis would argue that under conditions in which survival is high, salmon may occur at higher densities, and intraspecific competition

may lead to reductions in growth. Density-dependence may be important for salmon during freshwater life stages (Jonsson et al. 1998), but has been difficult to document in the ocean. In Alaska, density-dependence in the ocean has been observed to impact salmon growth and survival in multiple species (Ruggerone et al. 2003; Beamish et al. 2008; Martinson et al. 2008; Agler et al. 2013), although signals were much weaker for Chinook salmon in the Puget Sound, WA (Greene and Beechie 2004). Furthermore, juvenile salmon catches in Alaska are 10–100 times higher than standardized catches in central California, potentially making conspecific density-dependence more likely in northern areas (Fisher et al. 2007). In the California Current, there has been little work evaluating density dependence, although the potential exists as resource limitation has been documented for juvenile salmon in the ocean (Daly et al. 2009). Miller et al. (2013) found Columbia River juvenile Chinook salmon growth to be negatively related to juvenile salmon abundance; however, they did not find further support for density-dependence. There is potential for density-dependence to impact salmon in the ocean especially when populations are robust or habitat is restricted (Greene and Beechie 2004). Furthermore, it is important to emphasize that size-selective mortality and density-dependence hypotheses are not mutually exclusive, and may interact if larger salmon out-compete smaller individuals at high densities (Reinhardt et al. 2001).

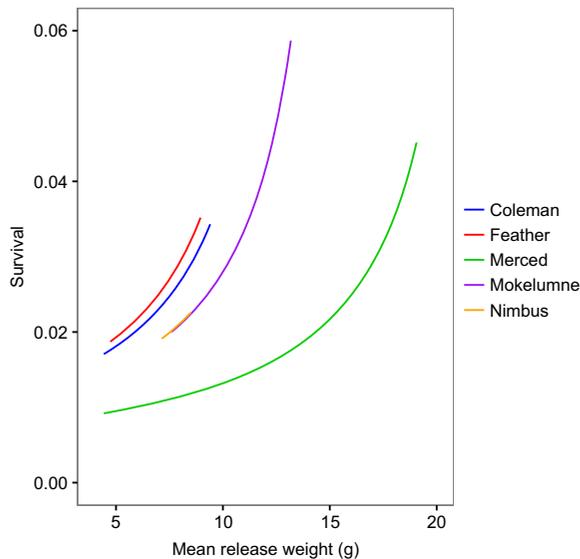
**Table 6** Top models for cohort survival from AICc model selection of Central Valley juvenile Chinook salmon from 1999–2010 (excluding 2006–2009)

Top survival models	AICc	weight	ΔAICc	LogLik	df	Pseudo R <sup>2</sup>
Pred zooplankton + Diatoms + Release weight + Hatchery + Currents	-679	0.375	0	354	13	0.36
Pred zooplankton + Diatoms + Release weight + Hatchery + Temperature	-678	0.269	0.66	353	12	0.35
Pred zooplankton + Diatoms + Release weight + Hatchery + Currents + Temperature	-677	0.154	1.79	355	14	0.36



**Fig. 4** Modeled survival values across the range of **a** diatoms (mmol/m<sup>3</sup>), **b** predatory zooplankton (mmol/m<sup>3</sup>), **c** temperature (°C), and **d** currents (m/s) while keeping all other model covariates constant at average values. Individual k-fold runs were also plotted

(light gray lines) to illustrate variability. Rug plots along the horizontal axis of plots a-c indicate the distribution of data points. **d** Currents, blue colors represent the highest modeled survival and dark pink the lowest



**Fig. 5** Modeled survival values across the range of release weight values while keeping all other covariates constant for each hatchery category. The plotted range for mean release weight for each line represents the observed release weights in our survival dataset

### Productivity and food

The diatoms and predatory zooplankton covariates were chosen to represent productivity and food at two different trophic levels. Diatoms are food for predatory zooplankton such as krill which may be an important component of juvenile salmon diets. We expected increasing productivity, represented by diatoms, and increasing food resources, represented by predatory zooplankton, to be positively related to increased juvenile salmon growth and survival.

Our model results indicated survival increased with diatoms, as hypothesized, but the relationship with zooplankton was more complex. Our model indicated a parabolic relationship between survival and predatory zooplankton in which the highest survival occurred at moderate zooplankton concentration. Previous studies have shown that measures of productivity and food correlate with increased salmon survival, and discuss mechanisms falling into two categories: (1) via an increase in growth which allows salmon to avoid

starvation and escape gape-limited predators, and (2) via indirect interactions between forage, salmon, and predators that mediate juvenile salmon losses due to predation (Willette et al. 2001; Emmett and Sampson 2007; Wells et al. 2012; Daly et al. 2013). Therefore, there is the potential for complex bottom-up and top-down mechanisms to explain relationships between productivity and salmon survival. The relationship we observed between survival and diatoms was consistent with previous studies. However, the parabolic pattern observed between predatory zooplankton and survival deviates, and may be explained by either foraging efficiency relative to prey density or predator aggregations. Many species of zooplankton use schooling behavior as an anti-predator tactic, and foraging on high densities may be less efficient for visual feeders like salmon, while at low densities salmon may have reduced encounter probabilities (Hamner and Hamner 2000; Goldbogen et al. 2011; Crook and Davoren 2014). In this case, foraging behavior may impact survival via growth. Also, predators and competitors may aggregate to areas with abundant food (Ainley et al. 2009; Santora et al. 2011; Santora et al. 2012), which may increase the risk for salmon predation or create a competitive disadvantage that reduces salmon feeding and growth (DeCesare et al. 2009). For example, common murres (*Uria aalge*) may aggregate at frontal features where there is abundant forage where they may compete with juvenile salmon for zooplankton and/or directly prey on salmon, both which may negatively affect salmon growth and survival (Ainley et al. 2009). Alternatively, although not consistent with our results, abundant forage may serve as alternative prey and dampen juvenile salmon losses due to predation (Cooney et al. 2001; Willette et al. 2001; Emmett and Sampson 2007). At low forage abundances, juvenile salmon may be forced to venture further to feed into habitats where they are more likely to be predated upon (Cooney et al. 2001; Willette et al. 2001).

Contrary to our original hypothesis, we observed that the relationships between growth and productivity were the opposite of those observed for survival. Generally, growth declined as diatom density increased, however some cross-validation lines showed no effect or a u-shaped parabolic relationship. The sizeable variability in cross-validation lines indicates uncertainty in diatoms explaining patterns in growth. This is also evident in that diatoms were not included in the second best model (Table 4). The important, consistent pattern is the model

always predicts high growth at low diatom densities. We observed the highest growth at low and high densities of zooplankton. In the current literature, we failed to find an ecological mechanism that explains this u-shaped relationship between growth and zooplankton abundance, and negative relationship between growth and diatom density. It is possible that our modeled outputs of productivity could have missed zooplankton patchiness clouding patterns at low densities. However, as we previously discussed, our apparent estimate of growth may be affected by factors influencing survival of smaller fish, such as size-selective mortality or intraspecific competition through density-dependence.

Limitations in the ROMS-NEMURO model are worth noting. Because the ROMS solution was not formally constrained by observations (i.e., data assimilation) during the model run, spatial and temporal mismatches between actual and simulated physical fields (e.g., ocean currents and temperatures) are bound to occur, which will translate to similar discrepancies in the biological fields (e.g., diatom and krill concentrations). However, Santora et al. (2013) found reasonable spatial and temporal agreement between observed krill abundances (from acoustic and trawl surveys) and simulated large zooplankton concentrations from a coupled physical-biological model similar to the one used here. Because the predatory zooplankton component of NEMURO was parameterized to represent krill in a broad sense, the model captures more accurately the spatial distribution and temporal variability associated with *Euphausia pacifica*, the most abundant species off of Central California. Hence, simulated krill concentrations may miss some of the characteristics associated with the less numerous, nearshore species, *Thyanoessa spinifera*, which could in turn impact predicted salmon growth during periods when *T. spinifera* is an important prey item. Both krill species occur in salmon diets, and Wells et al. (2012) have shown *T. spinifera* to correlate with increased salmon body condition (Wells et al. 2012). While it is difficult to assess the exact impact of these potential discrepancies on the model results, earlier studies have demonstrated that the coupled ROMS-NEMURO model is capable of reproducing the temperature, diatom and krill conditions that modulate juvenile salmon growth off of central California (Fiechter et al. 2015). Hence, the relationships identified here for growth and survival are generally expected to hold over the same spatial (> 10 km) and temporal (> days) scales. However, these relationships

may differ (or at least not hold as strongly) under conditions when salmon growth is significantly influenced by coastal dynamics and biological responses occurring at spatiotemporal scales not adequately represented by the model (e.g., krill diel vertical migration or patchiness associated with sub-mesoscale frontal dynamics).

### Physical Ocean conditions

Ocean currents are tied to ocean productivity via wind-driven, offshore Ekman transport that causes deep, cold, nutrient-rich water to be upwelled to the surface near the coast (Pringle and Dever 2009). In the summer, the California Current coastal waters typically alternate between phases of upwelling and relaxation. During relaxation events, winds weaken and currents shift to alongshore and northward while temperatures increase (Melton et al. 2009). Upwelling conditions are important to pre-condition areas for productivity (Vander Woude et al. 2006; Thompson et al. 2012); however, we expect a period with many relaxation events to benefit salmon growth and survival. Warmer in situ temperatures associated with relaxation events may increase growth (Beckman et al. 2004), and weaker, alongshore currents may promote retention of prey (Wing et al. 1998; Vander Woude et al. 2006; Wilson et al. 2008) and reduce the energetic cost for salmon to swim against advection offshore. Therefore, increased growth and survival of juvenile salmon should be more strongly correlated with frequent relaxation events, rather than periods of prolonged, active upwelling. Although coastal upwelling and relaxation events also occur in the Pacific Northwest, the Columbia River interacts with upwelling dynamics to increase retention of upwelled waters along the coast (Banas et al. 2009) and subsequent productivity and zooplankton (Peterson et al. 1979), which potentially explains why Pacific Northwest studies show positive trends of winter pre-conditioning with salmon survival (Logerwell et al. 2003), but relationships with in situ upwelling are variable (Nickelson 1986). Contrastingly, in California there is not the influence of a large river plume, and strong upwelling has been shown to increase advection of productivity off the shelf (Jacox et al. 2016). Since retention of productivity on the shelf where salmon reside is important for salmon growth and survival, the absence of a large river plume may explain why we observe distinct dynamics in coastal California compared to more northerly regions.

Physical environmental covariates that best explained growth and survival were water temperature and surface currents. Model response curves indicated greatest survival during northward currents and a positive relationship with temperature, which correspond with relaxation events when weakened winds allow for alongshore, northward transport of warm water. Although, temperature exhibited the most uncertainty in explaining survival patterns as evident in widely spread cross-validation lines (Fig. 4c) and that it was included only in the second and third top models (Table 6). These survival patterns with respect to physical ocean conditions are consistent with our expectation that relaxation events are important for juvenile salmon. Previous studies indicated increased salmon growth and survival in years with strong early season upwelling (Schroeder et al. 2013), and cool water temperatures (Mueter et al. 2002; Wells et al. 2008). These studies examined physical ocean conditions at broad spatial and temporal scales (averages over 100 s to 1000s of km and multiple months), whereas other studies that examined finer scales failed to find a strong influence of upwelling on salmon survival (Scheuerell et al. 2009; Holsman et al. 2012). Therefore, it is possible that years with strong early upwelling and cool temperatures pre-condition regions for high productivity, but on finer spatial and temporal scales, relaxation events are important.

Opposing our original hypothesis and our findings relative to survival, the growth model indicated greatest growth in active upwelling conditions. We saw greatest growth during southwest flowing currents and a negative relationship with temperature. There is an expected time lag of weeks to months between upwelling and bottom-up processes that produce food for salmon (Croll et al. 2005; Thompson et al. 2012). Therefore, we would not expect abundant prey to be available in active upwelled waters, unless they were transported from a different area or concentrated in eddies or upwelling shadows adjacent to upwelling centers (Santora et al. 2012). Furthermore, areas of persistent, strong upwelling are expected to have reduced productivity due to physical processes that advect nutrients offshore or below the euphotic zone (Jacox et al. 2016). Once again, our two models offered contradictory results: conditions related to high growth correspond to those with low survival, indicating that this pattern may be influenced by size-selective mortality or density-dependence.

## Hatchery release effects

The influence of hatchery of origin and release location differed between growth and survival models. For release location, fish released at locations lower in the river had more growth than fish released at locations higher in the river. Salmon released farther downstream likely spent less time in the river between release and recapture, and reached the ocean more quickly than salmon released farther upstream in the watershed. There is ample evidence for large growth potential in the ocean (Atcheson 2010; Duffy and Beauchamp 2011; Woodson et al. 2013), and due to the great reduction of floodplain habitat in the Sacramento and San Joaquin watersheds (Opperman 2012), there may be less growth opportunities for juvenile salmon in the freshwater environment than there was historically (Sommer et al. 2001). Also, salmon that reach the ocean more quickly might have more energy reserves to help them actively find prey in the marine environment. Alternatively, our measure of growth may still be confounded, which, following our previous logic, might suggest salmon released further downstream have experienced more size-selective mortality or density-dependence. However, since release location was not an important covariate in the survival model, we speculate this is a less compelling hypothesis.

Mean release weight was positively correlated with survival which is consistent with previous studies (Irvine et al. 2013; Zeug and Cavallo 2013; Satterthwaite et al. 2014). Larger salmon may be less susceptible to predation or starvation in both freshwater (Sogard 1997) and marine environments (Moss et al. 2005; Claiborne et al. 2011; Woodson et al. 2013). Our results also indicated that survival was greatest among fish produced at the Feather River Fish Hatchery. The hatchery primarily releases large smolts, which they transport and release close to San Francisco Bay, potentially avoiding high in-river mortality (Buchanan et al. 2013) (Table 7). Among

the remaining hatcheries, we saw a latitudinal gradient with more northerly hatcheries exhibiting greater survival. The Merced River Hatchery is the most southerly hatchery in our study, and salmon produced there must travel down the San Joaquin River to reach the sea. The San Joaquin River was designated one of the nation's most endangered rivers in 2014 due to degraded habitat (Saiki et al. 1992; Baker et al. 1995) and excessive water diversion (Newman and Brandes 2010) which may contribute to the low survival estimates.

## Conclusions

Our findings suggest that both oceanic and hatchery release conditions influence juvenile salmon early growth and survival. Interestingly, all four ocean covariates included in both growth and survival models showed opposite patterns. One possible mechanism to explain this result is size-selective mortality. Under conditions when survival is low, smaller fish may die at a greater rate than larger fish, and apparent high growth may actually result from demographic shifts in size. Size-selective mortality has previously been documented in Central Valley fall run Chinook salmon (Woodson et al. 2013). If juvenile salmon size influences survival, managers may be tempted to increase the size at which they release juvenile salmon. However, increased growth in hatcheries could have unintended consequences. Selection of large sizes and fast growth rates in hatcheries could result in domestication and alteration of other behaviors such as reduced predation defenses (Alvarez et al. 2003), increased metabolism, thus, greater fitness cost in the wild where food is less available (Metcalf et al. 2003), and increased aggression towards wild salmon (Weber and Fausch 2005). Additionally, growth in the hatchery can affect maturation rate, with too much growth resulting in an increase of precocious

**Table 7** Range of Central Valley juvenile Chinook salmon CWT group release attributes by hatchery from 1999–2010 (excluding 2006–2009)

Hatchery	Release dates	Release locations (km upstream)	Mean release weight (g)
Coleman FH	Apr 7 - May 24	48–528	3.0–10.0
Feather FH	Apr 25 - Jun 8	35–126	4.2–9.1
Merced FH	Apr 18 - May 25	105–167	4.3–19.2
Mokelumne FH	Apr 20 - Jun 7	104–143	7.1–13.3
Nimbus FH	May 4 - Jun 18	48–215	6.8–8.7

salmon returning years earlier than normal (Larsen et al. 2006), and in steelhead (*O. mykiss*) populations can increase the incidence of residualism with a host of ecological effects (Berejikian et al. 2012). Perhaps a promising conservation strategy would be to increase available floodplain or estuarine habitat within a heterogeneous landscape to increase growth potential of juvenile salmon of both origins before they enter the ocean (Magnusson and Hilborn 2003).

Another potential mechanism to explain the opposing patterns between growth and survival covariates is density-dependence. Under conditions when survival is high, salmon may occur at higher densities, and intra-specific competition may cause reduced growth. No studies have documented density-dependence in California salmon populations in the ocean, although this is a research area that deserves further examination. Density-dependence has been observed in northern salmon populations, creating concerns about the density of salmon and the time interval of hatchery releases (Beamish et al. 2008). Competition resulting from unnatural crowding and other artifacts of hatchery production may suppress growth and lower survival, and releasing many salmon at once may also amplify density-dependence effects. Hatchery and natural juvenile salmon exhibit spatial, temporal, and trophic overlap during early marine residency, setting the stage for potential competition (Daly et al. 2011).

Across geographic regions, unique local conditions are important to that stock's survival (Sharma et al. 2013). The effect of ocean conditions on juvenile salmon growth and survival appear to be sensitive to the scale at which measurements are taken. Unique to this study, we examined ocean conditions at spatial and temporal scales of 10 km resolution specific to individual fish migration routes and dates in the ocean. In our study, warmer ocean temperatures appeared to enhance salmon survival. This result contradicts other studies conducted at larger basin scales (Mueter et al. 2002; Wells et al. 2008; Schroeder et al. 2013), and deviate from regional patterns where the Pacific Northwest shows a negative relationship with SST (Mueter et al. 2002; Sharma et al. 2013). We also saw a signal of relaxation events being important for survival, while most previous studies fail to observe a consistent pattern with upwelling (Nickelson 1986; Scheuerell et al. 2009; Sharma et al. 2013). This may be because the influence of upwelling on biological productivity is reliant on intermittent relaxation events and it is difficult to select

an appropriate metric for analyses that captures this dynamic. It is possible that within broader climatic regimes, finer-scale relationships are important for understanding salmon population dynamics because they relate more closely to specific mechanisms affecting salmon responses. A mechanistic understanding of salmon ecology is important for building life cycle and individual-based models which can arguably perform better than statistical models to understand salmon population dynamics, predict changes under future conditions, and assess conservation strategies. This paper explores the importance and relationships of various oceanic and hatchery release conditions on salmon growth and survival. It also lays a foundation for many future hypothesis-driven studies to ultimately understand mechanisms that affect salmon responses at various life stages to incorporate into a holistic understanding of salmon population dynamics.

**Acknowledgments** The authors thank B. Wells for scientific insight, B. Lehman for extracting tags, the NW Fisheries Science Center and Fisheries and Ocean Canada for sharing data on tagged juvenile salmon, and Northwest Marine Technology for reading coded wire tags. This project would not have been possible without the efforts from current and past members of the salmon ecology team and crews of the vessels AR4 Jensen, Bell Shimada, Cassandra Anne, David Starr Jordan, Frosti, Irene's Way, Long Fin, Ocean Starr, Shana Rae, and Whitsel. Comments from four reviewers were valuable and greatly improved the quality of this manuscript. Funding was provided by the National Oceanic and Atmospheric Administration, and the collection procedures were conducted under IACUC guidelines.

## References

- Adrean LJ, Roby DD, Lyons DE, Collis K, Evans AF (2012) Potential effects of management on Caspian tern *Hydroprogne caspia* predation on juvenile salmonids at a colony in San Francisco Bay, California. *Trans Am Fish Soc* 141:1682–1696
- Agler BA, Ruggerone GT, Wilson LI, Mueter FJ (2013) Historical growth of Bristol Bay and Yukon River, Alaska chum salmon (*Oncorhynchus keta*) in relation to climate and inter- and intraspecific competition. *Deep Res Part II Top Stud Oceanogr* 94:165–177
- Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California current: competition, facilitation, and co-occurrence. *Mar Ecol Prog Ser* 389:271–294
- Alvarez D, Nicieza AG, Oviedo D (2003) Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *J Fish Biol* 63:1565–1577

- Anderson CD, Roby DD, Collis K (2004) Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. *Can J Zool* 82:541–554
- Acheson M (2010) Interannual variation in steelhead trout (*Oncorhynchus mykiss*) diet, growth and consumption in North Pacific marine ecosystems. University of Washington
- Baker PF, Speed TP, Ligon FK (1995) Estimating the influence of temperature on the survival of Chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento-San Joaquin River. *Can J Fish Aquat Sci* 52:855–863
- Banas NS, MacCready P, Hickey BM (2009) A model study of tide- and wind-induced mixing in the Columbia River estuary and plume. *Cont Shelf Res* 29:278–291
- Barton K (2015) Package MuMIn: Multi-Model Inference
- Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog Oceanogr* 49:423–437
- Beamish RJ, Sweeting RM, Lange KL, Neville CM (2008) Changes in the population ecology of hatchery and wild Coho salmon in the strait of Georgia. *Trans Am Fish Soc* 137:503–520
- Beckman BR, Shimizu M, Gadberry BA, Parkins PJ, Cooper KA (2004) The effect of temperature change on the relations among plasma IGF-I, 41-kDa IGFBP, and growth rate in postsmolt coho salmon. *Aquaculture* 241:601–619
- Berejikian BA, Larsen DA, Swanson P, Moore ME, Tatara CP, Gale WL, Pasley CR, Beckman BR (2012) Development of natural growth regimes for hatchery-reared steelhead to reduce residualism, fitness loss, and negative ecological interactions. *Environ Biol Fish* 94:29–44
- Buchanan RA, Skalski JR, Brandes PL, Fuller A (2013) Route use and survival of juvenile Chinook salmon through the San Joaquin River delta. *North Am J Fish Manag* 33:216–229
- Burla M, Baptista AM, Casillas E, Williams JG, Marsh DM (2010) The influence of the Columbia River plume on the survival of steelhead (*Oncorhynchus mykiss*) and Chinook salmon (*Oncorhynchus tshawytscha*): a numerical exploration. *Can J Fish Aquat Sci* 67:1671–1684
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, second. Springer, New York
- Centurioni LR, Ohlmann JC, Niiler PP (2008) Permanent meanders in the California current system. *J Phys Oceanogr* 38:1690–1710
- Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook salmon. *Trans Am Fish Soc* 140:1135–1144
- Cooney RT, Allen JR, Bishop MA, Eslinger DL, Kline T, Norcross BL, McRoy CP, Milton J, Olsen J, Patrick V, Paul AJ, Salmon D, Scheel D, Thomas GL, Vaughan SL, Willette TM (2001) Ecosystem control of pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasii*) populations in Prince William sound, Alaska. *Fish Oceanogr* 10:1–13
- Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. *Mar Ecol Prog Ser* 289:117–130
- Crook KA, Davoren GK (2014) Underwater behaviour of common murrens foraging on capelin: influences of prey density and antipredator behaviour. *Mar Ecol Prog Ser* 501:279–290
- Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult Coho and Chinook salmon in coastal marine waters: important for marine survival? *Trans Am Fish Soc* 138:1420–1438
- Daly EA, Brodeur RD, Fisher JP, Weitkamp LA, Teel DJ, Beckman BR (2011) Spatial and trophic overlap of marked and unmarked Columbia River basin spring Chinook salmon during early marine residence with implications for competition between hatchery and naturally produced fish. *Environ Biol Fish* 94:117–134
- Daly EA, Auth TD, Brodeur RD, Peterson WT (2013) Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California current. *Mar Ecol Prog Ser* 484:203–217
- Davis KA, Banas NS, Giddings SN, Siedlecki SA, MacCready P, Lessard EJ, Kudela RM, Hickey BM (2014) Estuary-enhanced upwelling of marine nutrients fuels coastal productivity in the U.S. Pacific northwest. *J Geophys Res Ocean* 119:8778–8799
- De Robertis A, Morgan CA, Schabetsberger RA, Zabel RW, Brodeur RD, Emmett RL, Knight CM, Krutzikowsky GK, Casillas E (2005) Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. *Mar Ecol Prog Ser* 299:33–44
- DeCesare NJ, Hebblewhite M, Robinson HS, Musiani M (2009) Endangered, apparently: the role of apparent competition in endangered species conservation. *Anim Conserv* 13:353–362
- Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. *J Biogeogr* 39:2119–2131
- Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget sound, Washington. *Can J Fish Aquat Sci* 68:232–240
- Emmett RL, Krutzikowsky GK (2008) Nocturnal feeding of Pacific hake and jack mackerel off the mouth of the Columbia River, 1998–2004: implications for juvenile salmon predation. *Trans Am Fish Soc* 137:657–676
- Emmett RL, Sampson DB (2007) The relationships between predatory fish, forage fishes, and juvenile salmonid marine survival off the Columbia river: a simple trophic model analysis. *Calif Coop Ocean Fish Investig Reports* 48:92–105
- Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Prog Oceanogr* 68:1–26
- Ferrari S, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. *J Appl Stat* 31:799–815
- Fiechter J, Curchitser EN, Edwards CA, Chai F, Goebel NL, Chavez FP (2014) Air-sea CO<sub>2</sub> fluxes in the California current: impacts of model resolution and coastal topography. *Glob Biogeochem Cycles* 28:371–385
- Fiechter J, Huff DD, Martin BT, Jackson DW, Edwards CA, Rose KA, Curchitser EN, Hedstrom KS, Lindley ST, Wells BK (2015) Environmental conditions impacting juvenile

- Chinook salmon growth off Central California: an ecosystem model analysis. *Geophys Res Lett* 42:2910–2917
- Fisher J, Trudel M, Ammann A, Orsi JA, Piccolo J, Bucher C, Casillas E, Harding JA, MacFarlane RB, Brodeur RD, Morris JFT, Welch DW (2007) Comparisons of the coastal distributions and abundances of juvenile Pacific salmon from Central California to the northern gulf of Alaska. *Ecol Juv Salmon Northeast Pacific Ocean Reg Comp* 57:31–80
- Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Orsi JA, Farley EV, Morris JFT, Thiess ME, Sweeting RM, Trudel M (2014) Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. *Trans Am Fish Soc* 143:252–272
- Friedland KD, Hansen LP, Dunkley DA, MacLean JC (2000) Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES J Mar Sci* 57:419–429
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214:131–146
- Greene CM, Beechie TJ (2004) Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci* 61:590–602
- Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E, Fennel K, Geyer WR, Hermann AJ, Lanerolle L, Levin J, McWilliams JC, Miller AJ, Moore AM, Powell TM, Shchepetkin AF, Sherwood CR, Signell RP, Warner JC, Wilkin J (2008) Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the Regional Ocean modeling system. *J Comput Phys* 227:3595–3624
- Hamner WM, Hamner PP (2000) Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Can J Fish Aquat Sci* 57:192–202
- Harding JA, Ammann AJ, MacFarlane RB (2011) Regional and seasonal patterns of epipelagic fish assemblages from the Central California current. *Fish Bull* 109:261–281
- Hassrick JL, Henderson MJ, Huff DH, Sydeman WJ, Sabal MC, Harding JA, Ammann AJ, Crandall ED, Bjorkstedt EP, Garza JC, Hayes SA (2016) Early ocean distribution of juvenile Chinook salmon in an upwelling ecosystem. *Fish Oceanogr*
- Hastie TJ, Tibshirani RJ, Friedman JH (2009) The elements of statistical learning: data mining, inference, and prediction. Springer
- Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation application of life-history theory and population model analysis to turtle conservation. *Copeia*:367–375. doi:10.2307/1447430
- Holsman KK, Scheuerell MD, Buhle E, Emmett R (2012) Interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Chinook salmon from the Columbia River, Washington, U.S.A. *Conserv Biol* 26:912–922
- Holtby LB, Andersen BC, Kadowaki RD (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can J Fish Aquat Sci* 47:2181–2194
- Huber ER, Carlson SM (2015) Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley. *San Fr Estuary Watershed Sci* 13:1–23
- Irvine JR, O'Neill M, Godbout L, Schnute J (2013) Effects of smolt release timing and size on the survival of hatchery-origin coho salmon in the strait of Georgia. *Prog Oceanogr* 115:111–118
- Ivanov LM, Collins CA, Marchesiello P, Margolina TM (2009) On model validation for meso/submesoscale currents: metrics and application to ROMS off Central California. *Ocean Model* 28:209–225
- Jacox MG, Hazen EL, Bograd SJ (2016) Optimal environmental conditions and anomalous ecosystem responses: constraining bottom-up controls of phytoplankton biomass in the California current system. *Sci Rep* 6:27612
- Jonsson N, Jonsson B, Hansen LP (1998) The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *J Anim Ecol* 67:751–762
- Kishi MJ, Kashiwai M, Ware DM, Megrey BA, Eslilinger DL, Werner FE, Noguchi-Aita M, Azumaya T, Fuji M, Hashimoto S, Huang D, Iizumi H, Ishida Y, Kang S, Kantakov GA, Kim H, Komatsu K, Navrotsky VV, Smith SL, Tadokoro K, Tsuda A, Yamamura O, Yamanka Y, Yokouchi K, Yoshie N, Zhang J, Zuenko YI, Zvalinsky VI (2007) NEMURO—a lower trophic level model for the North Pacific marine ecosystem. *Ecol Model* 202:12–25
- Klaassen RHG, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo KM, Bairlein F, Alerstam T (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J Anim Ecol* 83:176–184
- Kvitrud MA, Riemer SD, Brown RF, Bellinger MR, Banks MA (2005) Pacific harbor seals (*Phoca vitulina*) and salmon: genetics presents hard numbers for elucidating predator-prey dynamics. *Mar Biol* 147:1459–1466
- Larsen DA, Beckman BR, Strom CR, Parkins PJ, Cooper KA, Fast DE, Dickhoff WW (2006) Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: a comparison with wild. *Trans Am Fish Soc* 135:1017–1032
- Logerwell EA, Mantua N, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. *Fish Oceanogr* 12:554–568
- Losee JP, Miller JA, Peterson WT, Teel DJ, Jacobson KC (2014) Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook salmon. *Can J Fish Aquat Sci* 71:1747–1757
- Magnusson A, Hilborn R (2003) Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. *Estuaries* 26:1094–1103
- Martin TG, Chadès I, Arcese P, Marra PP, Possingham HP, Norris DR (2007) Optimal conservation of migratory species. *PLoS One* 2:3–7
- Martins EG, Hinch SG, Cooke SJ, Patterson DA (2012) Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorhynchus nerka*): a synthesis of the current state of knowledge and future research directions. *Rev Fish Biol Fish* 22:887–914
- Martinson EC, Helle JH, Scarnecchia DL, Stokes HH (2008) Density-dependent growth of Alaska sockeye salmon in

- relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Mar Ecol Prog Ser* 370:1–18
- McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ (2011) The role of agent-based models in wildlife ecology and management. *Ecol Model* 222:1544–1556
- Melton C, Washburn L, Gotschalk C (2009) Wind relaxations and poleward flow events in a coastal upwelling system on the Central California coast. *J Geophys Res* 114:1–18
- Metcalfe NB, Valdimarsson SK, Morgan IJ (2003) The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *J Appl Ecol* 40:535–544
- Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci* 70: 617–629
- Morgan CA, De Robertis A, Zabel RW (2005) Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. *Mar Ecol Prog Ser* 299:19–31. doi:10.3354/meps299019
- Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Trans Am Fish Soc* 134:1313–1322
- Mueter FJ, Peterman RM, Pypers BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can J Fish Aquat Sci* 59:456–463
- Nandor GF, Longwill JR, Webb DL (2010) Overview of the coded wire tag program in the greater Pacific region of North America. Portland, Oregon
- Newman KB, Brandes PL (2010) Hierarchical modeling of juvenile Chinook salmon survival as a function of Sacramento–San Joaquin delta water exports. *North Am J Fish Manag* 30:157–169
- Nickelson TE (1986) Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. *Can J Fish Aquat Sci* 43:527–535
- Opperman JJ (2012) A conceptual model for floodplains in the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science*, 10(3)
- Peterson WT, Miller CB, Hutchinson A (1979) Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep Sea Res Part A, Oceanogr Res Pap* 26:467–494
- Pringle JM, Dever EP (2009) Dynamics of wind-driven upwelling and relaxation between Monterey Bay and point arena: local-, regional-, and gyre-scale controls. *J Geophys Res* 114: C07003
- Quiñones RM, Holyoak M, Johnson ML, Moyle PB (2014) Potential factors affecting survival differ by run-timing and location: linear mixed-effects models of Pacific salmonids (*Oncorhynchus* spp.) in the Klamath River, California. *PLoS One* 9:e98392
- Reinhardt UG, Yamamoto T, Nakano S (2001) Effects of body size and predators on intracohort competition in wild and domesticated juvenile salmon in a stream. *Ecol Res* 16:327–334
- Ruggerone GT, Zimmermann M, Myers KW, Nielsen JL, Rogers DE (2003) Competition between Asian pink salmon (*Oncorhynchus gorbusha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish Oceanogr* 12: 209–219
- Ryding KE, Skalski JR (1999) Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Can J Fish Aquat Sci* 56:2374–2384
- Saiki MK, Jennings MR, Wiedmeyer RH (1992) Toxicity of agricultural subsurface drainwater from the San Joaquin Valley, California, to juvenile Chinook salmon and striped bass. *Trans Am Fish Soc* 121:78–93
- Santora JA, Ralston S, Sydeman WJ (2011) Spatial organization of krill and seabirds in the Central California current. *ICES J Mar Sci* 68:1391–1402
- Santora JA, Field JC, Schroeder ID, Sakuma KM, Wells BK, Sydeman WJ (2012) Spatial ecology of krill, micronekton and top predators in the Central California current: implications for defining ecologically important areas. *Prog Oceanogr* 106:154–174
- Santora JA, Sydeman WJ, Messié M, Chai F, Chao Y, Thompson SA, Wells BK, Chavez FP (2013) Triple check: observations verify structural realism of an ocean ecosystem model. *Geophys Res Lett* 40:1367–1372
- Satterthwaite WH, Carlson SM, Allen-Moran SD, Vincenzi S, Bograd SJ, Wells BK (2014) Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Mar Ecol Prog Ser* 511:237–248
- Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *J Appl Ecol* 46:983–990
- Schroeder ID, Black BA, Sydeman WJ, Bograd SJ, Hazen EL, Santora JA, Wells BK (2013) The North Pacific high and wintertime pre-conditioning of California current productivity. *Geophys Res Lett* 40:541–546
- Sharma R, Vélez-Espino LA, Wertheimer AC, Mantua N, Francis RC (2013) Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fish Oceanogr* 22:14–31
- Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model* 9:347–404
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129–1157
- Sommer TR, Nobriga ML, Harrell WC et al (2001) Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Can J Fish Aquat Sci* 58:325–333
- Thompson SA, Sydeman WJ, Santora JA, Black BA, Suryan RM, Calambokidis J, Peterson WT, Bograd SJ (2012) Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Prog Oceanogr* 101:106–120
- Tucker S, Hipfner JM, Trudel M (2016) Size- and condition-dependent predation: a seabird disproportionately targets sub-standard individual juvenile salmon. *Ecology* 97:461–471
- Vander Woude AJ, Largier JL, Kudela RM (2006) Nearshore retention of upwelled waters north and south of point Reyes (northern California)-patterns of surface temperature and

- chlorophyll observed in CoOP WEST. Deep Res Part II Top Stud Oceanogr 53:2985–2998
- Weber E, Fausch K (2005) Competition between hatchery-reared and wild juvenile Chinook Salmon in enclosures in the Sacramento River, California. Trans Am Fish Soc 134:44–58
- Wells BK, Grimes CB, Sneva JG, McPherson S, Waldvogel JB (2008) Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska, USA. Fish Oceanogr 17:101–125
- Wells BK, Santora JA, Field JC et al (2012) Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the Central California coastal region. Mar Ecol Prog Ser 457:125–137. doi:[10.3354/meps09727](https://doi.org/10.3354/meps09727)
- Wells B, Santora J, Schroeder I, Mantuna N, Sydeman WJ, Huff DD, Field JC (2016) Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar Ecol Prog Ser 552:271–284
- Willette TM, Cooney RT, Patrick V, Mason DM, Scheel D (2001) Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William sound, Alaska. Fish Oceanogr 10:14–41
- Wilson JR, Broitman BR, Caselle JE, Wendt DE (2008) Recruitment of coastal fishes and oceanographic variability in Central California. Estuar Coast Shelf Sci 79:483–490
- Wing SR, Botsford LW, Ralston SV, Largier JL (1998) Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol Oceanogr 43:1710–1721
- Woodson LE, Wells BK, Weber PK, MacFarlane RB, Whitman GE, Johnson RC (2013) Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar Ecol Prog Ser 487:163–175
- Yurk H, Trites AW (2000) Experimental attempts to reduce predation by harbor seals on out-migrating juvenile salmonids. Trans Am Fish Soc 129:1360–1366
- Zeug SC, Cavallo BJ (2013) Influence of estuary conditions on the recovery rate of coded-wire-tagged Chinook salmon (*Oncorhynchus tshawytscha*) in an ocean fishery. Ecol Freshw Fish 22:157–168