



Early ocean distribution of juvenile Chinook salmon in an upwelling ecosystem

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ABSTRACT

Extreme variability in abundance of California salmon populations is often ascribed to ocean conditions, yet relatively little is known about their marine life history. To investigate which ocean conditions influence their distribution and abundance, we surveyed juvenile Chinook salmon (*Oncorhynchus tshawytscha*) within the California Current (central California [37°30'N] to Newport, Oregon [44°00'N]) for a 2-week period over three summers (2010–2012). At each station, we measured chlorophyll-*a* as an indicator of primary productivity, acoustic-based metrics of zooplankton density as an indicator of potential prey availability and physical characteristics such as bottom depth, temperature and salinity. We also measured fork lengths and collected genetic samples from each salmon that was caught. Genetic stock identification revealed that the majority of juvenile salmon were from the Central Valley and the Klamath Basin (91–98%). We constructed generalized logistic-linear negative binomial hurdle models and chose the best model(s) using

Akaike's Information Criterion (AIC) to determine which covariates influenced the salmon presence and, at locations where salmon were present, determined the variables that influenced their abundance. The probability of salmon presence was highest in shallower waters with a high chlorophyll-*a* concentration and close to an individual's natal river. Catch abundance was primarily influenced by year, mean fork length and proximity to natal rivers. At the scale of sampling stations, presence and abundance were not related to acoustic indices of zooplankton density. In the weeks to months after ocean entry, California's juvenile Chinook salmon population appears to be primarily constrained to coastal waters near natal river outlets.

Key words: California Current, Chinook salmon, juvenile, migration, Pacific Ocean, upwelling

INTRODUCTION

The commercial fishery for Chinook salmon (*Oncorhynchus tshawytscha*) in California was closed in 2008 and 2009 owing to a population collapse that may have resulted from poor ocean conditions in the months after ocean entry (Lindley *et al.*, 2009). Variation in marine survival is linked to differences in migration and distribution during early ocean residence (Trudel *et al.*, 2009; Weitkamp, 2010; Wells *et al.*, 2012), which is reinforced by stock-specific spatial distributions that tend to be relatively consistent across years (Tucker *et al.*, 2012; Satterthwaite *et al.*, 2013; Teel *et al.*, 2015). While this suggests some degree of genetic imprinting to large-scale geospatial cues (Bracis and Anderson, 2012; Putman *et al.*, 2014), salmon distribution and abundance also tends to fluctuate in response to environmental conditions (De Robertis *et al.*, 2003; Pool *et al.*, 2012). We conducted a 2-week trawl survey from central California to southern Oregon to determine what biological and physical factors in an upwelling-driven system most influence spatial distribution and abundance of Chinook salmon first entering the ocean.

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Studies that have investigated the early ocean distribution of juvenile Chinook salmon in the northern California Current Ecosystem (CCS) are based on observations influenced by Columbia River plume (CRP) dynamics (Bi *et al.*, 2008; Pool *et al.*, 2012; Yu *et al.*, 2012; Burke *et al.*, 2013). The CRP entrains particles up to 50 km north and south of the river mouth and within this latitudinal range, increases dispersion of particles across the continental shelf by 25% (Banas *et al.*, 2009). In central and northern California, dispersion is primarily driven by upwelling produced by Ekman Transport and wind-stress caused by cross-shelf pressure gradients between the North Pacific High and Continental Thermal Low-pressure systems (Huyer, 1983; Murphree *et al.*, 2003). Upwelling is typically most intense from April to June and varies along the coast at the scale of topographic features that influence coastal winds (García-Reyes and Largier, 2012). This system exhibits strong mesoscale variability, with both retentive and dispersive features, and can experience rapid changes in the distribution of upwelled water (and productivity) over time. Thus, upwelling areas are likely to present salmon with habitats defined in part by temporally variable, spatially structured pulses of productivity that are subsequently mixed and advected along the coast and offshore. This contrasts with regions dominated by large riverine plumes, where plume waters can lead to greater alongshore retention and a more consistent local distribution of productivity (Robertis *et al.*, 2005; Banas *et al.*, 2009). To date, there has been no spatial analysis of stock-specific distribution and associated habitat of migrating juvenile Chinook salmon from California's rivers.

California supports the southern-most Chinook salmon runs on the west coast, with the most numerous populations originating in the Klamath River and Central Valley (Moyle, 2002). The Klamath River has a consistently wetter hydrology that tends to support more robust Chinook spawning runs than other parts of the state. Central Valley stocks are more abundant owing to hatchery production; five hatcheries contribute more than 32 million fall-run Chinook smolts each year to the population, which makes Central Valley fall-run the most abundant of California's Chinook salmon races. Races (aka runs) are defined by unique life-history strategies that are correlated with marine distributions (Fisher *et al.*, 2014). There is considerable variation in timing of adult and juvenile migrations for each of these runs (Lindley *et al.*, 2009). Runs captured during our survey primarily exhibit an 'ocean-type' to 'mixed' life-history, meaning they migrate to the ocean as sub yearlings, with some variation in time spent rearing in-river. Central Valley

spring-run can occasionally exhibit a 'stream-type' life history strategy, rearing in the river and delta long enough to enter the ocean as yearlings (Moyle, 2002).

To understand what factors in an upwelling-driven system are correlated with early ocean distribution of juvenile salmon, we analyzed 3 years (2010 to 2012) of June/July trawl survey data collected in the CCS. We focused specifically on young-of-the-year Chinook salmon entering the ocean in the weeks to months preceding the survey. Using a model designed to analyze over-dispersed data with a large number of zero observations, we evaluated environmental conditions (chlorophyll-*a*, depth, temperature and salinity) and intrinsic features of salmon, such as fork length and distance from natal river mouth, in relation to catch abundance. Although our time-series was short, these data were sufficient to compare with studies from the CRP and generate hypotheses regarding how environmental conditions influence juvenile Chinook salmon migration patterns and early ocean distribution in the upwelling-driven portion of the CCS.

MATERIALS AND METHODS

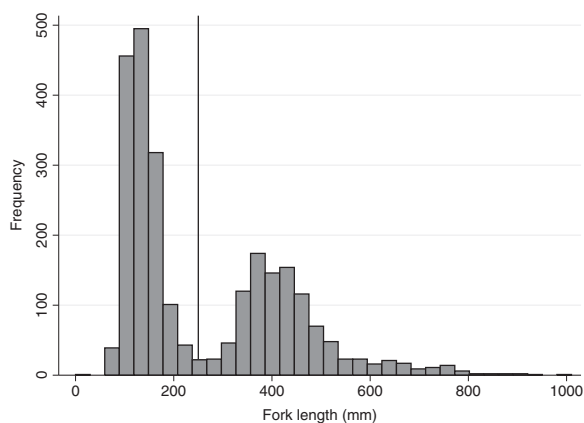
Study area and survey methods

Our study area was the coastal Pacific Ocean from shore to ~20 nautical miles offshore between Heceta Head, Oregon (44°00'N) and Pillar Point, California (37°30'N). The survey area extended from the southern extent of the CRP down to central California, ranging from 1219 to 1734 nautical miles. Each survey took place over approximately two weeks between the end of June and early July. We surveyed juvenile salmon and other epipelagic fish and invertebrates during daylight hours, using a trawl (264 Nordic Rope Trawl) with flotation added to the head-rope to sample the upper 18–24 m of the water column in ~30 min tows according to Harding *et al.* (2011). Because of the possibility of hang-ups on the sea floor, we generally did not sample in water <30 m deep. A large animal excluder was installed on the net beginning in 2012. It is suspected that catch efficiency may have been reduced as a result of this device because small fish were observed escaping through the excluder, and while relative catch efficiency across a survey is not affected by this change, the magnitude of the effect between years is unknown. Our study focused on juvenile Chinook salmon, defined as <250 mm fork length (MacFarlane and Norton, 2002). This length criterion was confirmed by consistent breaks in length-frequency histograms separating young-of-the-year fish from other age classes caught in the trawl (Fig. 1).

Genetic stock identification

We identified the genetic origin of each juvenile Chinook salmon caught in the trawl by taking a fin clip and extracting DNA using DNeasy 96 tissue kits on a BioRobot 3000 (Qiagen Inc., Venlo, Netherlands). Genotypes from 96 single nucleotide polymorphisms (SNPs) were then derived using either Taqman© (Applied Biosystems, Waltham, Massachusetts, USA) or SNPtype© (Fluidigm Corporation, South San Francisco, California, United States) SNP genotyping assays. The discovery of SNP genotyping and methods are described in Clemento *et al.* (2011). The SNP panel and associated genetic stock identification (GSI) baseline data are described in Clemento *et al.* (2014). This baseline contains SNP genotypes of known-origin fish from 38 reporting units, representing >99% of all Chinook salmon encountered in the study area, and has high power to discriminate among reporting units. Genotypes from all samples confirmed as Chinook salmon were analyzed with the program *gsi_sim* (Anderson *et al.*, 2008), which calculates the maximum likelihood assignment for each genotype to a specific population or reporting unit by comparison to allele frequencies in the baseline database. Collections from each sampling year were analyzed separately and fish with low-quality assignments (i.e., unusually small likelihood scores, extensive missing data or potential contamination) were excluded from analyses. The proportions of low-quality assignments excluded were 7%, 2% and 12% for 2010, 2011 and 2012, respectively.

Figure 1. Length-frequency distributions of Chinook salmon captured across all years (2010–2012). The vertical line designates a break at 250 mm that was taken as a threshold to distinguish between juvenile and older age classes.



Acoustics

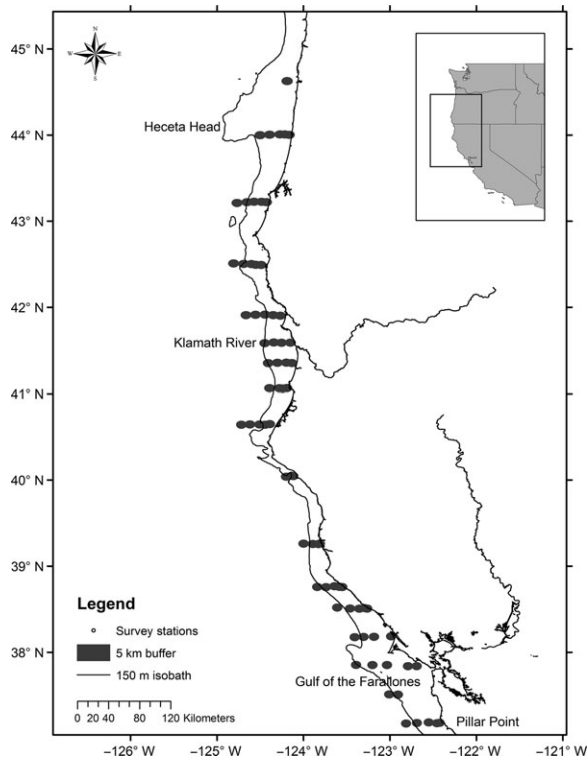
Prey distributions were mapped with acoustic survey techniques that have been used across a variety of marine ecosystems (MacLennan and Simmonds, 2005). Acoustically-derived measures of prey abundance were based on acoustic backscatter collected during a pre-dawn survey conducted east to west along transect lines. Pre-dawn measurements were taken to reduce the error in estimates of zooplankton density from diel vertical migrations. In our statistical analysis, we used all acoustic estimates within a 5 km radius around trawling stations to quantify prey available to salmon captured at a given station within the time lag between pre-dawn acoustic measurements and daytime trawling, with non-overlapping estimates of prey between adjacent stations (Fig. 2).

Aggregations of prey were quantified using acoustic volume backscattering data (S_v , dB) from a multi-frequency echosounder (SIMRAD EK60) configured with down-looking 38, 70, 120 and 200 kHz split-beam transducers mounted on the hull 3.3 m below the water line. A three-frequency ΔS_v method (Hewitt and Demer, 2000; Watkins and Brierley, 2002) was used to measure the strength of volume backscattering to estimate prey abundance. Volume backscattering signals were averaged and integrated over one nautical mile horizontal sections, and vertically from a depth of 250 m, or from the sea-floor in shallower regions, to the transducer. This acoustic estimate of relative prey abundance, called the Nautical Area Scattering Coefficient (NASC, $m^2 nmi^{-1}$), was derived from S_v using the program EchoView 4.9 (Myriax Pty Ltd, Hobart, Australia). We excluded a 1 m buffer from the transducers to minimize the effects of bubbles generated by the ships' hulls and we also excluded a 1 m buffer from the sea-floor to avoid confounding the bottom with organisms in the water column. We also visually examined the echograms and, if necessary, manually extended buffers in places where bottom or surface contamination affected integrated acoustic values. Sections of acoustic profiles with missing pings were masked and excluded from analysis.

Water sampling

A SEA-BIRD SBE19plus CTD, interfaced with a GPS and plumbed with flow-through water from a pump with a through-hull intake at ~3 m depth, recorded water temperature, salinity and fluorimeter volts twice a second. Chlorophyll-*a* concentration was determined from extracted chlorophyll-*a* analysis using a Turner 10AU fluorimeter according to calibration methods described in Harding *et al.* (2011). We also

Figure 2. Locations of trawling stations for the NOAA juvenile salmon surveys (2010–2012) shown with a 5-km buffer around each trawl station to estimate the mean Nautical Area Scattering Coefficient (NASC $\text{m}^2 \text{nmi}^{-1}$) for each station.



averaged sea surface temperature (SST) and chlorophyll-*a* from the Aqua-MODIS satellite (<http://coastwatch.pfeg.noaa.gov/erddap/>) over 14 days prior to the completion of each survey to gain a more comprehensive sample of water temperature and primary productivity throughout the survey area.

Statistical analysis

We modeled the relationship between stock-specific juvenile salmon catch abundance and multiple biotic and abiotic factors with a zero-altered negative binomial model, also known as a hurdle model. Hurdle models consist of two parts: (i) a logistic regression to model the probability that a zero value is observed (presence/absence) and (ii) a zero-truncated model that includes only the non-zero observations (Zuur *et al.*, 2009). Prior to model fitting, we tested whether any variable pairs were collinear based on their correlation coefficients and included only a single variable of any pair that had correlation coefficients greater than 0.7 (Dormann *et al.*, 2013). We did this during the model selection process by excluding models from consideration that included both collinear variables.

In each part of the hurdle model, we included covariates that describe environmental conditions and characteristics of the fish that were captured. Factors included in the logistic regression part of the model were the year, distance from the natal river, depth, water temperature, salinity, chlorophyll-*a* and acoustic estimates of prey abundance (NASC). Among these variables, water temperature and distance from the natal river were the only collinear factors, which reflect a general decrease in water temperatures from the south to north. Positive catches were modeled with a zero-truncated negative binomial model that included the same variables as those in the logistic regression as well as the mean fork length of juvenile Chinook salmon in the catch. Mean fork length could only be included in the negative binomial part of the model because it could not be estimated at stations where no salmon were captured. In both parts of the hurdle model, we standardized for the volume of water sampled during the trawl by including this value as an offset.

Akaike's Information Criterion for small sample sizes (AICc; Burnham and Anderson, 2002) was used to select the most parsimonious model with the best fit to the data. We used the 'MuMIn' package in R (Barton, 2015) to fit subsets of the hurdle model. As a result of a large number of variables included in the hurdle model analysis, we selected the least complex model with a ΔAICc (i.e., the difference in AICc values between a given model and the model with the lowest AICc) ≤ 2 . We used this procedure because AIC model selection has a tendency to select over-fitted models; thus, it is best to select the simplest model if it is nested within more complex models with nearly equivalent AIC values (Richards, 2008). Model residuals were used to validate the model fit and ensure that no model assumptions were violated. We used variograms of the hurdle model residuals to ensure that unexplained variation in catches of juvenile Chinook was not spatially auto-correlated. Finally, *k*-fold cross-validation ($k = 20$) was used to estimate the adjusted *r*-squared – an estimate of variation in the model response that was explained by the model.

RESULTS

Salmon stock distribution

In each of the three years over the study period, surveys took place over approximately 2 weeks between mid-June and mid-July. In 2010 and 2011, surveys were initiated on 30 June and extended through to 14 July (2010) and 16 July (2011). Owing to logistics, the survey period was earlier in 2012, extending from 11

June through to 26 June. Juvenile Chinook salmon were caught on eight out of 17 transect lines in 2010 and 2012 and on 12 out of 17 transect lines in 2011 (Fig. 3). The largest catches in 2011 occurred in the southern extent of the survey at stations near San Francisco Bay and, in 2010, they occurred further north near the mouth of the Klamath River. GSI revealed that most stocks were clustered near their respective points of ocean entry, with notable exceptions for individuals from Central Valley stocks caught in the northernmost transects in 2010 and 2011. Overall, the majority of juvenile Chinook salmon in the south originated in the Central Valley (Table 1). Fish that were captured in the northern part of the survey primarily originated in the Klamath River, with a small proportion of catch from rivers in southern Oregon.

Ocean conditions

Satellite and acoustic data indicated that ocean conditions in the survey area varied inter-annually (Fig. 4). SSTs were generally cooler throughout the survey area in 2010, whereas cooler waters were concentrated between Cape Mendocino and Point Arena in 2011 and 2012. Standing stocks of phytoplankton, a proxy for primary productivity that is measured as chlorophyll-*a*, were concentrated near the coast. The largest amounts of primary productivity were observed in 2011 and 2012. Similarly, acoustic indices of prey abundance were low in 2010, high in 2011 and concentrated in the northern portion of the survey in 2012.

Predictors of juvenile Chinook salmon presence/absence and abundance

Juvenile salmon were captured in 49 of 181 trawls during the 3 years of the study and the majority (53%) of these trawls contained five or fewer fish. The mean catch was 6.9 fish (SD = 32.5), but this estimate was skewed by two outlier trawls that contained 161 and 371 fish. These outliers occurred in 2010 and 2011, respectively, and were dominated (93% and 100%) by Central Valley fish. Because of the potentially extreme influence of these two outliers, they were excluded from statistical analysis. Results were the same regardless of whether or not these two outliers were included, but the fit of the model was reduced and the model residuals exhibited non-constant variance when they were included.

The weighted mean distance (\pm SD) away from their natal river where juvenile salmon were caught was 69 ± 38 km for Central Valley fish, 40 ± 47 km for Klamath fish and 120 ± 74 km for fish from other

stocks. Fish from other stocks (i.e., Chetco, Columbia, Rogue, Russian, or Umpqua rivers) were rare, and 83% of catches from these stocks contained fewer than five fish. As a result of this rarity, we fitted hurdle models only for the Central Valley and Klamath stocks. We fitted separate models for these stocks because we hypothesized that different environmental conditions experienced by these stocks after early ocean entry may lead to different distributions relative to the covariates.

The most appropriate hurdle models for the Central Valley and the Klamath stocks turned out to be similar. For both stocks, the logistic component of the hurdle model included chlorophyll-*a* concentration and distance from natal river (Table 2). The logistic model for the Central Valley also included depth. The negative binomial component of both models included fork length (Table 3), but the Central Valley model also included year and distance from natal river. For the hurdle models, a *k*-fold estimated *r*-squared was 0.61 for the Central Valley model and 0.50 for the Klamath model. Semi-variograms of model residuals did not indicate any spatial autocorrelation.

The statistical form of the logistic regression part of the Central Valley model was

$$\text{Logit}(P_i) = \mu + \beta_1 \cdot \text{depth}_i + \beta_2 \cdot \text{chl}_i + \beta_3 \cdot \text{dist}_i + \text{offset}(\log \text{vol}_i) + \varepsilon_i \quad (1)$$

where logit is the link function used to model the binomial response of juvenile salmon presence in each trawl (*i*), μ was overall mean logit (i.e., log of the odds), β s were the parameter estimates for fixed effects, depth was water depth, chl was concentration of chlorophyll-*a*, dist was the distance between the trawl location and the mouth of the natal river, offset (log-vol) was an offset included to standardize the catch for the volume of water sampled in each trawl and ε was unexplained variation. This was the least complex of two models with a $\Delta\text{AICc} \leq 2$ (Table 2, Table S1). Based on this model, Central Valley juveniles were more likely to be present in waters that were shallow (<200 m), close to their natal river and with higher concentrations of chlorophyll-*a* (Fig. 5).

The logistic regression model for the Klamath stock included chlorophyll-*a* and distance but did not include depth, although depth was included in four out five models with a $\Delta\text{AICc} \leq 2$ (Table 2, Table S1). The shapes of the responses for the Klamath stock were nearly identical to those from the Central Valley (Fig. S1).

The most appropriate negative binomial model for positive catches of the Central Valley stock was:

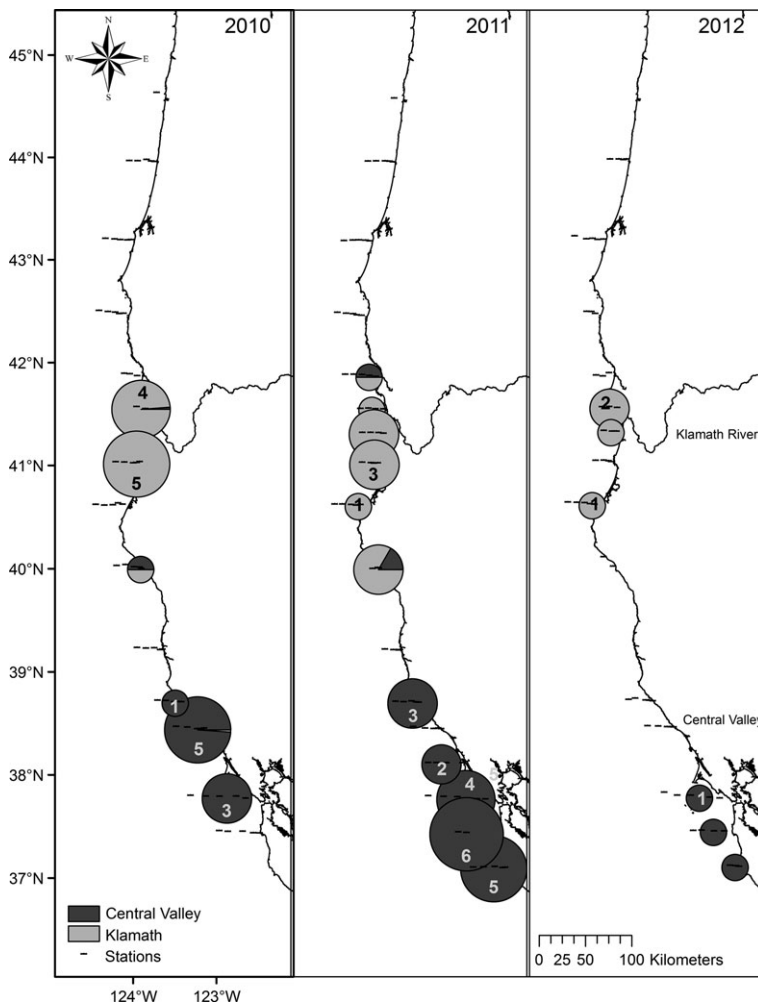


Figure 3. Results of genetic stock identification of juvenile Chinook salmon caught on the survey (left: 2010, middle: 2011, right: 2012). The majority of salmon originated from Central Valley stocks (dark shade) and Klamath River stocks (light shade), two major sources of hatchery production in California. Standardized salmon catch (catch * tow distance⁻¹) are presented as rings that increase in diameter with total catch per transect on a log scale (round numbers).

Table 1. Summary of juvenile Chinook salmon catch for the Central Valley and Klamath stocks in the NOAA Southwest Fisheries Science Center's juvenile salmon survey from 2010 to 2012. Hauls are the number of tows per survey, Catch is positive catches, which are the number of hauls with juvenile Chinook salmon, Proportion is the proportion of positive catches relative to the total number of hauls, Mean Catch is the average catch for each year, and Dist. is the maximum transit distance observed in each year.

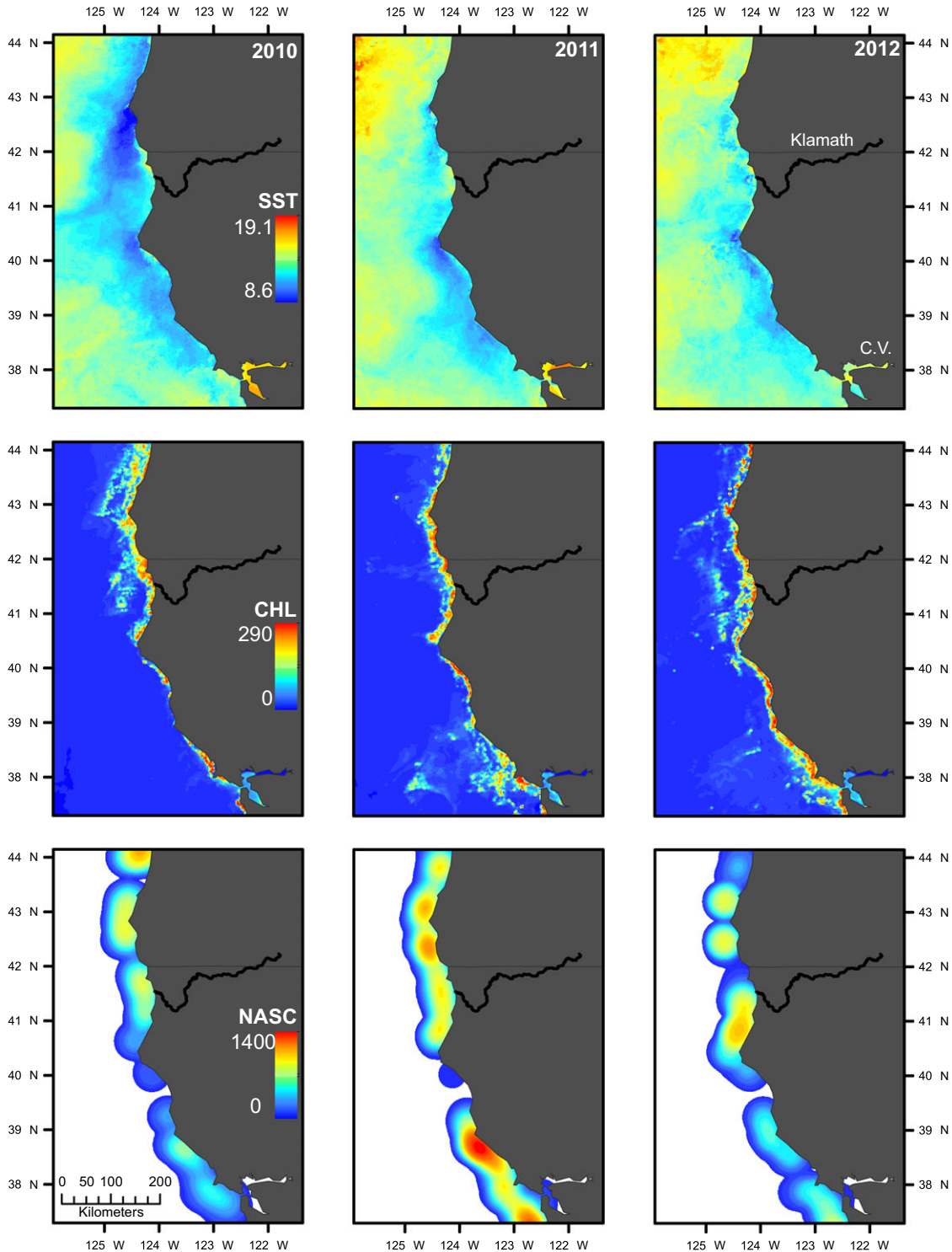
River	Year	Hauls	Catch	Proportion	Mean Catch	Dist.
Central Valley	2010	61	8	0.13	3.28	447
Central Valley	2011	68	12	0.18	9.51	482
Central Valley	2012	52	4	0.08	0.63	71
Klamath	2010	61	6	0.10	3.05	346
Klamath	2011	68	11	0.16	0.74	167
Klamath	2012	52	3	0.06	1.37	106

$$\text{Catch}_{ij} = \mu + \beta_1 \cdot \text{year}_j + \beta_2 \cdot \text{FL}_i + \beta_3 \cdot \text{dist}_i + \text{offset}(\log\text{vol})_i + \varepsilon_{ijk} \quad (2)$$

where catch was the abundance of juvenile Chinook salmon in each trawl (i) for each year (j), μ was the

overall mean, β s were the parameter estimates for the fixed effects, year was survey year ($j = 2010, 2011, 2012$), FL was mean fork length of juvenile Chinook salmon caught in the trawl, dist was distance between the trawl location and the mouth of the natal river, offset (logvol) was an offset included to standardize the catch for the volume of water sampled in each

Figure 4. Profiles of sea surface temperature (SST; top row) and chlorophyll-a (middle row) from NASA’s Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) for western U.S., daytime (14 Day Composite). Satellite data were downloaded from NOAA’s ERDDAP server: <http://coastwatch.pfeg.noaa.gov/erddap/index.html>. The bottom row shows smoothed Nautical Area Scattering Coefficient (NASC, $m^2 nmi^{-1}$) measures of meso-zooplankton (mean NASC of 25 km^2 grid cells) integrated to 250 m depth or the sea floor. This kernel density analysis was reclassified into 10 equal intervals, with warmer colors representing higher NASC values.



trawl, and ε was the random error. This was the least complex of five models with a $\Delta\text{AICc} \leq 2$ (Table 3, Table S2). Based on this model, the largest catches contained the smallest juvenile salmon (Fig. 6a–c). The small size of these fish indicates they had recently entered the ocean, which is most likely why they were captured in large abundance in close proximity to their natal river (Fig. 6d–f).

The least complex negative binomial model for the Klamath stock included only mean fork length, but there were nine models with a $\Delta\text{AICc} \leq 2$ (Table 3, Table S2). This suggests there was considerable uncertainty in which factors were related to the abundance of Klamath fish. Again, the shapes of the responses for the Klamath stock were nearly identical to those from the Central Valley (Fig. S1).

Standardized coefficient values from the logistic regression and the negative binomial indicate the relative importance of each covariate (Fig. 7). In the logistic regression, the order of the absolute coefficient values was depth (3.93), distance (2.46) and chlorophyll-*a* concentration (1.47). The order of the absolute coefficient values in the negative binomial was distance (−3.12), the year 2012 (−3.00), fork length (−1.73) and the year 2011 (0.53). Year coefficients were estimated relative to 2010, thus the coefficient estimate for 2010 was zero.

DISCUSSION

Our study describes environmental conditions that shape the early marine distribution of two dominant stocks of Chinook salmon in California. We had expected that salmon might distribute differently between regions in response to habitat differences arising from a narrowing shelf south of the CRP and different mechanisms that cause cross-shelf dispersion of nutrients between upwelling and plume-driven systems. However, California's juvenile Chinook salmon were consistently concentrated near shore over the

shelf in shallow, coastal water within the 200-m isobath, exhibiting a similar inshore distribution to ocean-type juvenile Chinook from the CRP (Schabetsberger *et al.*, 2003; Daly *et al.*, 2009) and stocks from Oregon and Washington (Trudel *et al.*, 2009; Tucker *et al.*, 2011). One exception to this pattern is stream-type Chinook salmon, which emerge from the Columbia River as yearlings and move offshore more quickly, suggesting an ontogenetic component to the coastal proximity of dispersing juveniles (Fisher *et al.*, 2014). While an abundance of smaller fish in close proximity to natal rivers suggest this survey could have occurred before juvenile salmon had a chance to fully disperse, Teel *et al.* (2015) observed that sub yearling Chinook salmon move close to shore in the autumn as well.

The highest levels of production in upwelling systems tend to occur along the coastal margin where deep, nutrient-rich bottom water is pulled into the euphotic zone near the coast and then carried offshore by Ekman transport (Huyer, 1983). Wells *et al.* (2012) and MacFarlane and Norton (2002) showed that krill is important for juvenile salmon condition and later survival. Our results indicated that the small-scale distribution of juvenile Chinook salmon was not correlated with acoustic estimates of krill abundance, suggesting that either foraging was not a primary factor driving their movements after entering the ocean or that juvenile salmon are able to satisfy their needs over a much smaller range of krill densities than observed in our data. Alternatively, the migration of these fish after early ocean entry may be based on geospatial cues, such as a magnetic compass (Putman *et al.*, 2013; Quinn and Brannon, 1982); however, it is difficult to separate fixed geospatial covariates from environmental covariates that influence distribution across all years (see Burke *et al.*, 2013). If the early ocean migration strategy of juvenile salmon is based on geospatial cues, their growth and survival during this period are likely to be more dependent on local foraging conditions.

Table 2. Logistic regression model selection with the least complex models with a ΔAICc less than or equal to two shown in bold for each stock.

River	Model	ΔAICc	Weight
Central Valley	presence ~ dist + chla + depth	0	33.4
	presence ~ dist + chla + depth + NASC	0.34	28.2
Klamath	presence ~ dist + chla + depth + sal	0	18.9
	presence ~ dist + chla + depth	0.1	17.8
	presence ~ dist + chla + depth + sal + NASC	1.8	7.6
	presence ~ dist + chla + depth + sal + year	1.9	7.4
	presence ~ dist + chla	2.0	7.1

Table 3. Zero-truncated negative binomial model selection with the least complex models with a ΔAICc less than or equal to two shown in bold for each stock.

River	Model	ΔAICc	Weight
Central Valley	catch ~ year + FL + dist + chla	0	14.8
	catch ~ year + FL + dist + chla + NASC	0.9	9.2
	catch ~ year + FL + dist + chla + sal	1.1	8.5
	catch ~ year + FL + dist + depth + sal	1.9	5.7
	catch ~ year + FL + dist	2.0	5.3
Klamath	catch ~ FL + dist	0	5.5
	catch ~ FL	0.3	4.7
	catch ~ year + FL + depth + temp	0.8	3.6
	catch ~ FL + dist + depth	1.2	3.1
	catch ~ FL + dist + sal	1.4	2.7
	catch ~ FL + depth	1.6	2.5
	catch ~ year + FL	1.8	2.3
	catch ~ FL + temp	1.9	2.1
	catch ~ FL + dist + NASC	2.0	2.1

Small size may be a critical factor in determining how far offshore juvenile Chinook will venture. Scaling constraints on the swimming capabilities of small fish may cause them to resort to prey in their immediate surroundings. Krill, which are a patchy resource, were encountered more frequently in the stomachs of captured subadults and adults, which can range over a greater area and take advantage of more dispersed and patchily distributed prey. Remaining closer to shore to

avoid high predation rates may be related in some way to increased turbidity associated with high concentrations of chlorophyll-*a*, which has been a good predictor of juvenile salmon presence in this and in other studies (Peterson *et al.*, 2010; Pool *et al.*, 2012; Yu *et al.*, 2012; Burke *et al.*, 2013). It is difficult to assess a foraging benefit of chlorophyll-*a* to salmon because time lags between primary production and the trophic level at which juvenile salmon feed are too large to

Figure 5. Response plots showing the probability of capturing Central Valley juvenile Chinook salmon relative to (a) depth, (b) chlorophyll-*a* and (c) distance to natal rivers. In these plots, only the variable of interest is changed and all other model variables are held constant at their median value. The black line is the output from the logistic regression portion of the hurdle model and the gray lines are the output from 100-k fold model runs to provide an indication of model error. The rugs along each x-axis show the range of the observed data.

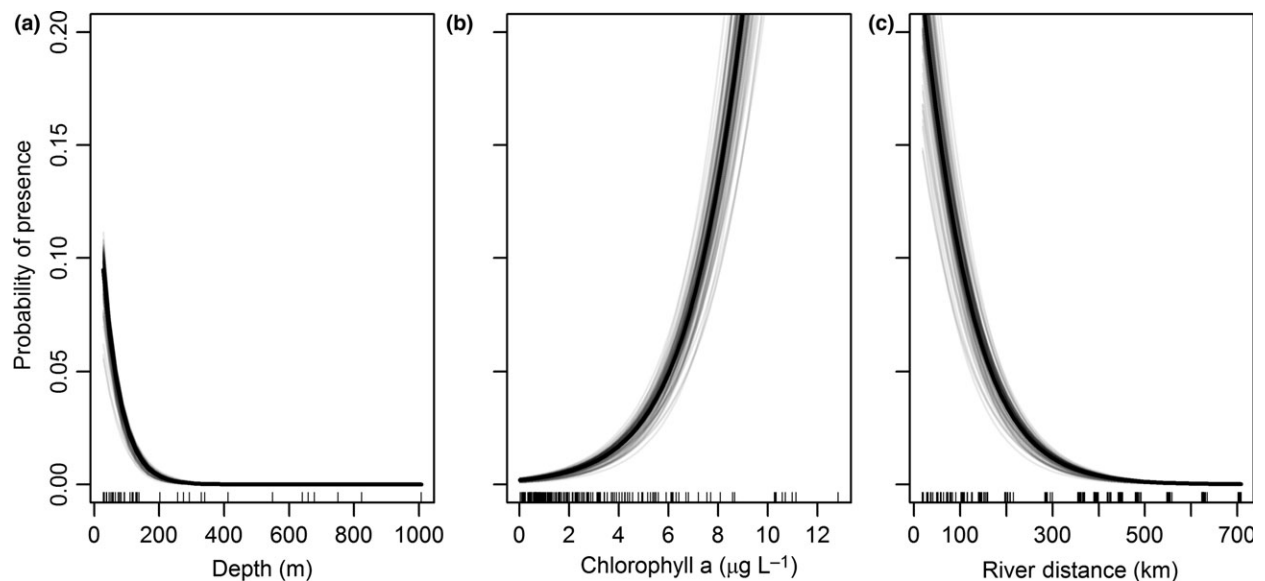
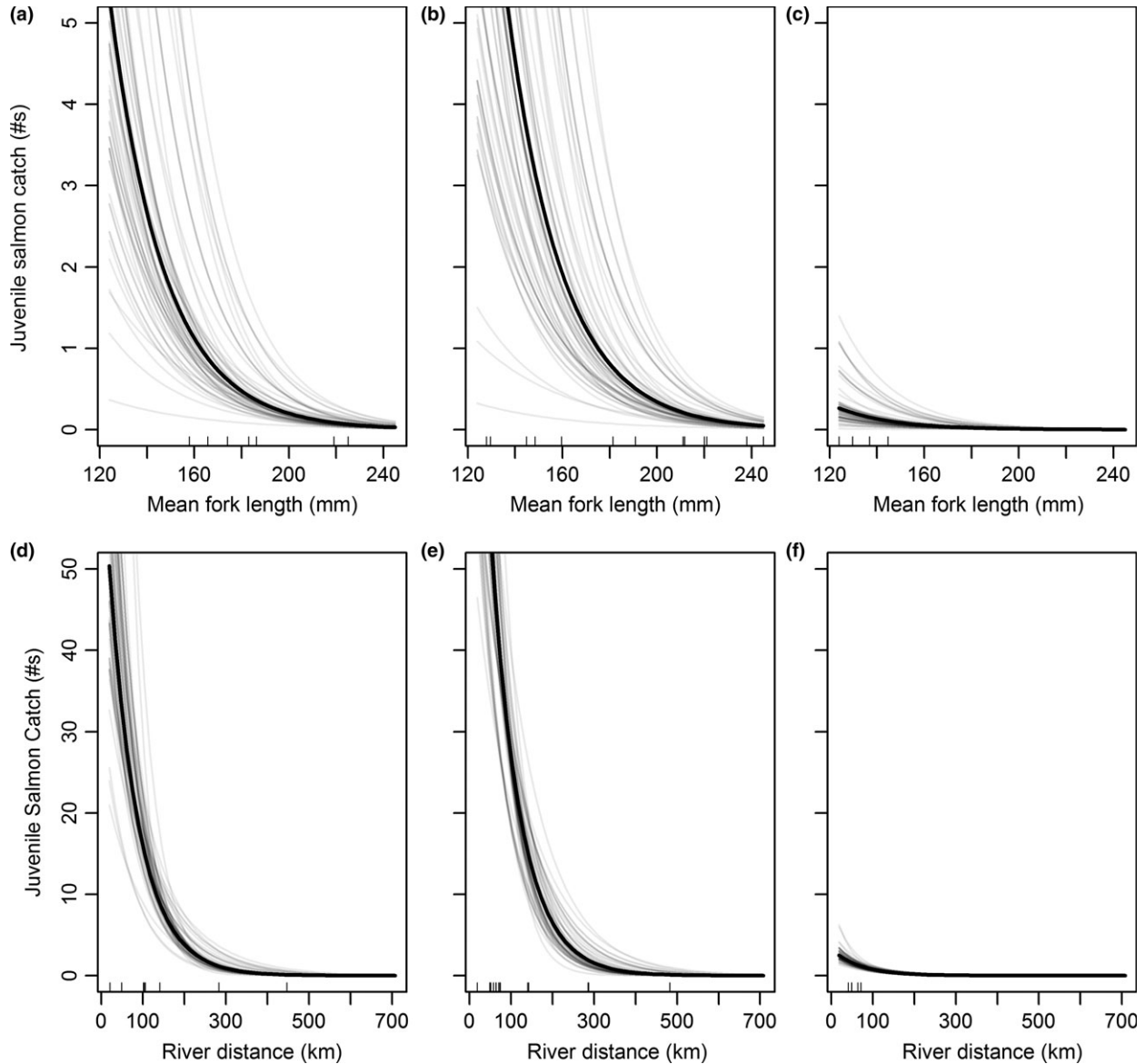


Figure 6. Predicted catch of juvenile Chinook salmon as a function of mean fork length (top) and distance to natal rivers (bottom) for fish from the Central Valley. The columns are for years 2010 (a, d), 2011 (b, e) and 2012 (c, f). The black line is the output from the negative binomial (abundance) portion of the hurdle model and the gray lines are the output from 100-k fold model runs to provide an indication of model error. The rugs along each x-axis show the range of the observed data.



infer trophic transfer (Miller *et al.*, 2010). It takes approximately 100 days after the initiation of upwelling for the mesozooplankton community to develop (Croll *et al.*, 2005). This is one explanation for why juvenile Chinook salmon survival is higher for hatchery releases that occur 70–115 days after the initiation of upwelling (Satterthwaite *et al.*, 2014).

California's ocean salmon fishery was closed completely in 2008 for the first time in history, with the presumed cause being the extremely poor survival of

juvenile salmon entering the ocean in 2005. Ocean entry for this cohort coincided with unusually low productivity associated with delayed upwelling (Barth *et al.*, 2007; Brodeur *et al.*, 2006; Mackas *et al.*, 2006). At the same time, the Columbia River experienced a booming fall run escapement that may have been as a result of plume-driven dynamics less susceptible to disruption by variability in wind patterns. Given that juvenile Chinook salmon tend to remain near shore and close to natal river mouths in both

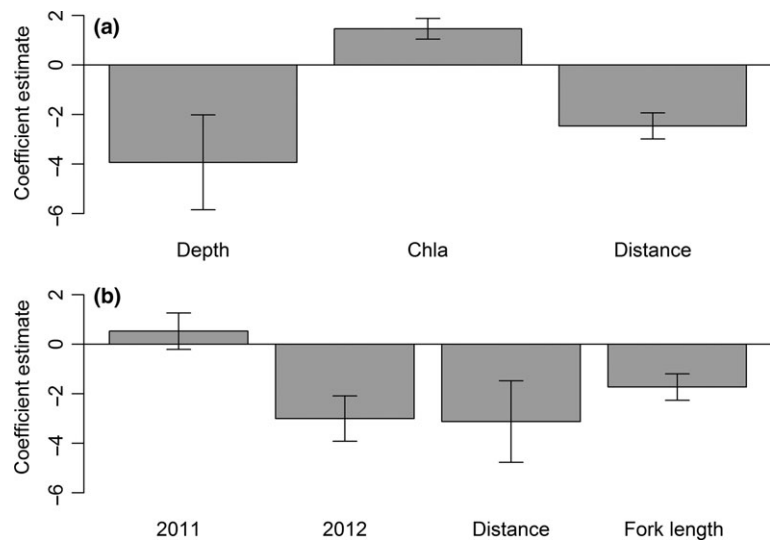


Figure 7. Hurdle model coefficient estimates for the (a) Logistic regression and (b) Zero-truncated negative binomial. With the exception of year, which was a factor, all variables were standardized so model coefficients are on the same relative scale. The coefficient estimates for 2011 and 2012 were estimated relative to 2010. Error bars are one standard error.

regions, such spatial differences in survival may be explained, in part, by different mechanisms driving production. In contrast to the greater dependence on upwelling-driven production off California, production in coastal waters off Oregon can be enhanced by retention of riverine nutrients in the Columbia River plume (Robertis *et al.*, 2005). Such unusually low production from delayed spring upwelling in 2005 and associated differences in escapement between the two regions for cohorts entering the ocean that year point to the potential for local dynamics in coastal waters to impact juvenile salmon survival on the west coast.

Pacific salmon have now been extirpated from 40% of their historical habitat and nearly half of the remaining populations are at risk of extinction (Levin and Schiewe, 2001). In the northern California Current, the majority of Chinook salmon in our survey originated from rivers with sizable hatchery production. Despite contributions from hatcheries, half of the runs of Chinook salmon in the Central Valley are listed as threatened or endangered under the US Endangered Species Act (Nehlsen *et al.*, 1991; Yoshiyama *et al.*, 1998, 2001). The predominance of fall-run Central Valley and Klamath basin stocks in our study highlight a continuing decline in stock diversity for California's Chinook salmon.

Our results indicate that California's Chinook salmon populations remain close to natal rivers for months after ocean emergence. If loss of life history diversity described above homogenizes timing of ocean entry, this may leave them more susceptible to fluctuations in local conditions. Along the west coast of the United States, Kilduff *et al.* (2015) observed that

variability in salmon survival in response to ocean variability from the North Pacific Gyre Oscillation (NPGO) has become increasingly more coherent since the 1980s, suggesting a general decline in life history diversity. This loss of biodiversity is occurring in the face of increasing climate variability (Bond *et al.*, 2015; Hartmann, 2015) and as these large-scale physical processes intensify through greenhouse forcing (Wang *et al.*, 2014), extreme events are likely to become more frequent.

Increasing climate variability (Intergovernmental Panel on Climate Change 2007) results in a greater frequency of warm water years (Sydeman *et al.*, 2013). North Pacific krill (*Euphausia pacifica*) populations can decline by 90 percent during El Niño events (Brinton and Townsend, 2003) and anomalous warming associated with 2005 lead to greater starvation of krill, and thus reduced the availability of krill to fish in the Gulf of the Farallones (Dorman *et al.*, 2011). Warm water and anomalously species-rich conditions have been associated with the 2009–2010 El Niño that altered prey composition during the period of ocean entry with relatively warm water and low productivity associated with dampened upwelling (Bjorkstedt *et al.*, 2010). Juvenile salmon entering the coastal ocean will be confronted with phenological shifts in marine prey responding to these changes (Edwards and Richardson, 2004; Anderson *et al.*, 2013). In our study, the largest catches of juvenile salmon occurred at stations near natal river mouths with relatively low estimates of zooplankton density, suggesting that concentrations of young salmon in those areas was likely a result of limited dispersal, rather than a response to concentrated prey, which

highlights the importance of local conditions for early marine survival.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Hurdle model response plots for the Klamath River stock. (a) Zero-truncated negative binomial estimated catch of juvenile salmon as a function of mean fork length. Logistic regression estimates of capture probability as a function of (b) chlorophyll-*a* and (c) distance to natal river. In these plots, only the variable of interest is changed and all other model

variables are held constant at their median value. The black line is the output from the hurdle model and the gray lines are the output from 100-k fold model runs to provide an indication of model error. The rugs along each *x*-axis show the range of the observed data.

Table S1. Logistic regression model selection table for all models with an AICc weight >1. Model response is the probability of fish presence in a haul. Model variables are the distance between a haul location and the natal river (dist), concentration of chlorophyll-*a* (chl_a), station depth (depth), acoustic estimate of prey abundance (NASC), salinity (sal), temperature (temp) and survey year (year).

Table S2. Zero-truncated negative binomial model selection table for all models with an AICc weight >1. Model response was the number of salmon caught in a haul. Model variables are the survey year (year), the mean fork length in each haul (FL), distance between a haul location and the natal river (dist), concentration of chlorophyll-*a* (chl_a), acoustic estimate of prey abundance (NASC), station depth (depth), salinity (sal) and temperature (temp).