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1 **Early ocean distribution of juvenile Chinook salmon in an upwelling**
2 **ecosystem**

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1 ABSTRACT

2 Extreme variability in abundance of California salmon populations is often ascribed to ocean
3 conditions, yet relatively little is known about their marine life-history. To investigate which
4 ocean conditions influence their distribution and abundance, we surveyed juvenile Chinook
5 salmon (*Oncorhynchus tshawytscha*) within the California Current (central California (37° 30'
6 N) to Newport, Oregon (44° 00' N)) for a two-week period over three summers (2010-2012). At
7 each station, we measured chlorophyll *a* as an indicator of primary productivity, acoustic-based
8 metrics of zooplankton density as an indicator of potential prey availability, and physical
9 characteristics such as bottom depth, temperature, and salinity. We also measured fork lengths
10 and collected genetic samples from each salmon that was caught. Genetic stock identification
11 revealed that the majority of juvenile salmon were from the Central Valley and the Klamath
12 Basin (91-98%). We constructed generalized logistic-linear negative binomial hurdle models and
13 chose the best model(s) using AIC to determine which covariates influenced salmon presence
14 and, at locations where salmon were present, determined the variables that influenced their
15 abundance. The probability of salmon presence was highest in shallower waters with high
16 chlorophyll *a* concentration and close to an individual's natal river. Catch abundance was
17 primarily influenced by year, mean fork length, and proximity to natal rivers. At the scale of
18 sampling stations, presence and abundance was not related to acoustic indices of zooplankton
19 density. In the weeks to months following ocean entry, California's juvenile Chinook salmon
20 population appears to be primarily constrained to coastal waters near natal river outlets.

21 KEY WORDS

22 Juvenile, Chinook salmon, California Current, upwelling, migration, Pacific

23

1 **INTRODUCTION**

2 The commercial fishery for Chinook salmon (*Onchorhynchus tshawytscha*) in California was
3 closed due to a population collapse in 2008 and 2009, which may have resulted from poor ocean
4 conditions in the months following ocean entry (Lindley *et al.*, 2009). Variation in marine
5 survival is linked to differences in migration and distribution during early ocean residence (Wells
6 *et al.*, 2012; Weitkamp, 2010; Trudel *et al.*, 2009), which is reinforced by Stock-specific spatial
7 distributions that tend to be relatively consistent across years (Tucker *et al.*, 2012; Teel *et al.*,
8 2015; Satterthwaite *et al.*, 2013). While this suggests some degree of genetic imprinting to large-
9 scale geospatial cues (Bracis & Anderson, 2012; Putman *et al.*, 2014), salmon distribution and
10 abundance also tends to fluctuate in response to environmental conditions (De Robertis *et al.*,
11 2003; Pool *et al.*, 2012). We conducted a two-week trawl survey off the coast of central and
12 northern California to southern Oregon to determine what biological and physical factors in an
13 upwelling-driven system most influence spatial distribution and abundance of Chinook salmon
14 first entering the ocean.

15 Studies that have investigated early ocean distribution of juvenile Chinook salmon in the
16 northern California Current Ecosystem (CCS) are based on observations strongly influenced by
17 Columbia River plume (CRP) dynamics (Bi *et al.*, 2008; Burke *et al.*, 2013; Pool *et al.*, 2012; Yu
18 *et al.*, 2012). The CRP entrains particles up to 50 km north and south of the river mouth and
19 within this latitudinal range, increases dispersion of particles across the continental shelf by 25%
20 (Banas *et al.*, 2009). In central and northern California, dispersion is primarily driven by
21 upwelling produced by Ekman Transport and wind-stress caused by cross-shelf pressure
22 gradients between the North Pacific High and Continental Thermal Low pressure systems
23 (Huyer, 1983; Murphree *et al.*, 2003). Upwelling is typically most intense from April – June and

1 varies along the coast at the scale of topographic features that influence coastal winds (García-
2 Reyes & Largier, 2012). This system exhibits strong mesoscale variability, with both retentive
3 and dispersive features, and can experience rapid changes in the distribution of upwelled water
4 (and productivity) over time. Thus, upwelling areas are likely to present salmon with habitats
5 defined in part by temporally variable, spatially structured pulses of productivity that are
6 subsequently mixed and advected along the coast and offshore. This contrasts with regions
7 dominated by large riverine plumes, where plume waters can lead to greater alongshore retention
8 and possibly a more consistent local distribution of productivity (Robertis *et al.*, 2005, Banas et
9 al. 2009). To date there has been no spatial analysis of stock-specific distribution and associated
10 habitat of migrating juvenile Chinook salmon from California's rivers.

11 California supports the southern-most Chinook salmon runs on the west coast, with the
12 most numerous populations originating in the Klamath River and the Central Valley (Moyle,
13 2002). The large contribution of ocean stocks from the Klamath River may result from a
14 consistently wetter hydrology that tends to support more robust Chinook spawning runs. Central
15 Valley stocks are more abundant due to hatchery production; five hatcheries contribute more
16 than 32 million fall-run Chinook smolts each year to the population, which makes Central Valley
17 fall-run the most abundant of California's Chinook salmon races. Races (aka runs) are defined by
18 unique life-history strategies that are correlated with marine distributions (Fisher *et al.*, 2014).
19 There is considerable variation in the timing of adult and juvenile migrations for each of these
20 races (Lindley *et al.*, 2009). Runs captured during our survey primarily exhibit an 'ocean-type' to
21 'mixed' life-history, meaning they migrate to the ocean as sub yearlings, with some variation in
22 time spent rearing in-river. Central Valley spring-run can occasionally exhibit a 'stream-type'

1 life history strategy, rearing in the river and delta long enough to enter the ocean as yearlings
2 (Moyle, 2002).

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

14 **MATERIALS AND METHODS**

15 *Study area and survey methods*

16 Our study area was the coastal Pacific Ocean from shore to ~20 nautical miles offshore between
17 Heceta Head, Oregon (44° 00' N) and Pillar Point, California (37° 30' N; Fig. 1). The survey area
18 extended from the southern extent of the CRP down to central California, ranging between 1219
19 and 1734 nautical miles. Each survey took place over approximately 2 weeks between the end of
20 June and early July. We surveyed juvenile salmon and other epipelagic fish and invertebrates
21 during daylight hours, using a trawl (264 Nordic Rope Trawl) with flotation added to the head-
22 rope to sample the upper 18-24 m of the water column in ~30 min tows following Harding *et al.*
23 (2011). Because of the possibility of hang-ups on the sea floor, we generally did not sample in

1 water < 30 m deep. A large animal excluder was installed on the net beginning in 2012. It is
2 suspected that catch efficiency may have been reduced as a result of this device because small
3 fish were observed escaping through the excluder, and while the relative catch efficiency across
4 a survey is not affected by this change, the magnitude of the effect between years is unknown.
5 Our study focused on juvenile Chinook salmon, defined as < 250 mm fork length (MacFarlane &
6 Norton, 2002). This length criteria was confirmed by consistent breaks in length-frequency
7 histograms separating young-of-the-year fish from other age classes caught in the trawl (Fig. 1).

8 *Genetic stock identification*

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

1 of low-quality assignments excluded were 7%, 2% and 12% for 2010, 2011 and 2012,
2 respectively.

3 *Acoustics*

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

13 Aggregations of prey were quantified using acoustic volume backscattering data (S_v , dB)
14 from a multi-frequency echosounder (SIMRAD EK60) configured with down-looking 38, 70,
15 120, and 200 kHz split beam transducers mounted on the hull 3.3 m below the water line. A
16 three-frequency ΔS_v method (Watkins & Brierley, 2002; Hewitt & Demer, 2000) was used to
17 measure the strength of volume backscattering to estimate prey abundance. Volume
18 backscattering signals were averaged and integrated over one nautical mile horizontal sections,
19 and vertically from a depth of 250 m, or from the sea-floor in shallower regions, to the
20 transducer. This acoustic estimate of relative prey abundance, called the Nautical Area Scattering
21 Coefficient (NASC, $m^2 nmi^{-1}$) was derived from S_v using the program EchoView 4.9 (Myriax
22 Pty Ltd, Hobart, AUS). We excluded a 1 m buffer from the transducers to minimize effects of
23 bubbles generated by the ships' hulls and we also excluded a 1 m buffer from the sea-floor to

1 avoid confounding the bottom with organisms in the water column. We also visually examined
2 the echograms and, if necessary, manually extended buffers in places where bottom or surface
3 contamination affected integrated acoustic values. Sections of acoustic profiles with missing
4 pings were masked and excluded from analysis.

5 *Water sampling*

6 A SEA-BIRD SBE19plus CTD, interfaced with a GPS and plumbed with flow-through water
7 from a pump with a through-hull intake at ~3 m depth, recorded water temperature, salinity, and
8 fluorimeter volts twice a second. Chlorophyll *a* concentration was determined from extracted
9 chlorophyll *a* analysis using a Turner 10AU fluorimeter following calibration methods described
10 in Harding *et al.*, (2011). We also averaged the sea surface temperature and chlorophyll *a* from
11 the Aqua-MODIS satellite (<http://coastwatch.pfeg.noaa.gov/erddap/>) over 14-days prior to the
12 completion of each survey to gain a more comprehensive sample of water temperature and
13 primary productivity throughout the survey area.

14 *Data Analysis*

15 We modeled the relationship between stock-specific juvenile salmon catch abundance and
16 multiple biotic and abiotic factors with a zero-altered negative binomial model, also known as a
17 hurdle model. Hurdle models consist of two parts: (1) a logistic regression to model the
18 probability that a zero value is observed (presence/absence), and (2) a zero-truncated model that
19 includes only the non-zero observations (Zuur *et al.*, 2009). Prior to model fitting, we tested
20 whether any variable pairs were collinear based on their correlation coefficients and included
21 only a single variable of any pair that had correlation coefficients greater than 0.7 (Dormann *et*
22 *al.*, 2013). We did this during the model selection process by excluding models from
23 consideration that included both collinear variables.

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

13 Akaike's Information Criterion for small sample sizes (AICc; Burnham & Anderson
14 2002) was used to select the most parsimonious model with the best fit to the data. We used the
15 'MuMIn' package in R (Barton, 2015) to fit subsets of the hurdle model. Due to a large number
16 of variables included in the hurdle model analysis, we selected the least complex model with a
17 ΔAICc (i.e., the difference in AICc values between a given model and the model with the lowest
18 AICc) less than or equal to 2. We used this procedure because AIC model selection has a
19 tendency to select over-fitted models; thus, it is best to select the simplest model if it is nested
20 within more complex models with nearly equivalent AIC values (Richards, 2008). Model
21 residuals were used to validate the model fit and ensure that no model assumptions were
22 violated. We used variograms of the hurdle model residuals to ensure that catches of juvenile
23 Chinook were not spatially auto-correlated. Finally, k-fold cross-validation (k=20) was used to

1 estimate the adjusted r-squared - an estimate of variation in the model response that was
2 explained by the model.

3 **RESULTS**

4 *Salmon stock distribution*

5 In each of the three years over the study period, surveys took place over approximately two
6 weeks between mid-June and mid-July. In 2010 and 2011, surveys were initiated on June 30th
7 and extended through July 14th (2010) and July 16th (2011). Due to logistics, the survey period
8 was earlier in 2012, extending from June 11th through June 26th. Juvenile Chinook salmon were
9 caught on eight out of 17 transect lines in 2010 and 2012 and on 12 out of 17 transect lines in
10 2011 (Fig. 3). The largest catches in 2011 occurred in the southern extent of the survey at
11 stations near San Francisco Bay and, in 2010, they occurred further north near the mouth of the
12 Klamath River. GSI revealed that most stocks were clustered near their respective points of
13 ocean entry, with notable exceptions for individuals from Central Valley stocks caught in the
14 northernmost transects in 2010 and 2011. Overall, the majority of juvenile Chinook salmon in
15 the south originated in the Central Valley (Table 1). Fish that were captured in the northern part
16 of the survey primarily originated in the Klamath River, with a small proportion of catch from
17 rivers in southern Oregon.

18 *Ocean conditions*

19 Satellite and acoustic data indicated that ocean conditions in the survey area varied inter-
20 annually (Fig. 4). Sea surface temperatures were generally cooler throughout the survey area in
21 2010, whereas the cooler waters were concentrated between Cape Mendocino and Point Arena in
22 2011 and 2012. Standing stocks of phytoplankton, a proxy for primary productivity that is
23 measured as chlorophyll *a*, were concentrated near the coast. The largest amounts of primary

1 productivity were observed in 2011 and 2012. Similarly, acoustic indices of prey abundance
2 were low in 2010, high in 2011, and concentrated in the northern portion of the survey in 2012.
3 *Predictors of juvenile Chinook salmon presence/absence and abundance*
4 Juvenile salmon were captured in 49 of 181 trawls during the three years of the study and the
5 majority (53%) of these trawls contained five or fewer fish. Mean catch was 6.9 fish (SD = 32.5),
6 but this estimate was skewed by two outlier trawls that contained 161 and 371 fish. These
7 outliers occurred in 2010 and 2011, respectively, and were dominated (93% and 100%) by
8 Central Valley fish. Because of the potentially extreme influence of these two outliers, they were
9 excluded from statistical analysis. Results were the same regardless of whether or not these two
10 outliers were included, but the fit of the model was reduced and the model residuals exhibited
11 non-constant variance when they were included.

12 The weighted mean distance (\pm SD) away from their natal river where juvenile salmon
13 were caught was 69 ± 38 km for Central Valley fish, 40 ± 47 km for Klamath fish, and 120 ± 74
14 km for fish from other stocks. Fish from other stocks (i.e., Chetco, Columbia, Rogue, Russian, or
15 Umpqua rivers) were rare, and 83% of catches from these stocks contained fewer than five fish.
16 Due to this rarity, we fit hurdle models only for the Central Valley and Klamath stocks and we fit
17 separate models for these stocks because we hypothesized that different environmental
18 conditions experienced by these stocks after early ocean entry may lead to different distributions
19 relative to the covariates.

20 The most appropriate hurdle models for the Central Valley and the Klamath stocks turned
21 out to be similar. For both stocks, the logistic component of the hurdle model included
22 chlorophyll *a* concentration and distance from natal river (Table 2). The logistic model for the
23 Central Valley also included depth. The negative binomial component of both models included

1 fork length (Table 3), but the Central Valley model also included year and distance from natal
2 river. For the hurdle models, a k-fold estimated r-squared was 0.61 for the Central Valley model
3 and 0.50 for the Klamath model. Semi-variograms of model residuals did not indicate any spatial
4 autocorrelation.

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

$$6 \quad \text{Logit}(P_i) = \mu + \beta_1 \cdot \text{depth}_i + \beta_2 \cdot \text{chl}_i + \beta_3 \cdot \text{dist}_i + \text{offset}(\log \text{vol}_i) + \varepsilon_i \quad (\text{Eq. 1})$$

7 where logit is the link function used to model the binomial response of juvenile salmon presence
8 in each trawl (i), μ was overall mean logit (i.e., log of the odds), β s were the parameter estimates
9 for fixed effects, depth was water depth, chl was concentration of chlorophyll *a*, dist was
10 distance between the trawl location and the mouth of the natal river, offset (logvol) was an offset
11 included to standardize the catch for the volume of water sampled in each trawl, and ε was the
12 unexplained variation. This was the least complex of the two models with a ΔAICc of less than
13 or equal to 2 (Table 2). Based on this model, Central Valley juveniles were more likely to be
14 present in waters that were shallow (<200 m), close to their natal river, and with higher
15 concentrations of chlorophyll *a* (Fig. 5).

16 The logistic regression model for the Klamath stock included chlorophyll *a* and distance
17 but did not include depth, although depth was included in four out five models with a ΔAICc less
18 than or equal to two (Table 2). Results for the Klamath stock are not shown because the shapes
19 of the responses were nearly identical to those from the Central Valley.

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

$$22 \quad \text{Catch}_{ij} = \mu + \beta_1 \cdot \text{year}_j + \beta_2 \cdot \text{FL}_i + \beta_3 \cdot \text{dist}_i + \text{offset}(\log \text{vol}_i) + \varepsilon_{ijk} \quad (\text{Eq. 2})$$

1 where catch was the abundance of juvenile Chinook salmon in each trawl (i) for each year (j), μ
2 was the overall mean, β s were the parameter estimates for the fixed effects, year was survey year
3 (j=2010, 2011, 2012), FL was mean fork length of juvenile Chinook salmon caught in the trawl,
4 dist was distance between the trawl location and the mouth of the natal river, offset (logvol) was
5 an offset included to standardize the catch for the volume of water sampled in each trawl, and ε
6 was the random error. This was the least complex of 5 models with a Δ AICc of less than or equal
7 to 2 (Table 3). Based on this model, the largest catches contained the smallest juvenile salmon
8 (Fig. 6 a-c). The small size of these fish indicate they had recently entered the ocean, which is
9 most likely why they were captured in larger abundances in close proximity to their natal river
10 (Fig. 6 d-f).

11 The least complex negative binomial model for the Klamath stock included only mean
12 fork length, but there were nine models with a Δ AICc of less than or equal to 2 (Table 3). This
13 suggests there was considerable uncertainty in which factors were related to the abundance of
14 Klamath fish. Again, results for the Klamath stock are not shown because the shape of the
15 response was nearly identical to that of the Central Valley.

16 Standardized coefficient values from the logistic regression and the negative binomial
17 indicate the relative importance of each covariate (Fig. 7). In the logistic regression, the order of
18 the absolute coefficient values was depth (3.93), distance (2.46), and chlorophyll *a* concentration
19 (1.47). The order of the absolute coefficient values in the negative binomial was distance (-3.12),
20 year 2012 (-3.00), fork length (-1.73), and year 2011 (0.53). Year coefficients were estimated
21 relative to 2010, thus the coefficient estimate for 2010 was zero.

22 **DISCUSSION**

1 Our study describes environmental conditions that shape the early marine distribution of two
2 dominant stocks of Chinook salmon in California. We had expected that salmon might distribute
3 differently between regions in response to habitat differences arising from a narrowing shelf
4 south of the CRP and different mechanisms that cause cross-shelf dispersion of nutrients
5 between upwelling and plume-driven systems. However, California's juvenile Chinook salmon
6 were consistently concentrated near shore over the shelf in shallow, coastal water within the 200
7 m isobaths, exhibiting a similar inshore distribution to ocean-type juvenile Chinook from the
8 CRP (Daly *et al.*, 2009; Schabetsberger *et al.*, 2003) and stocks from Oregon and Washington
9 (Trudel *et al.*, 2009; Tucker *et al.*, 2011). One exception to this pattern is stream-type Chinook
10 salmon, which emerge from the Columbia River as yearlings and move offshore more quickly,
11 suggesting an ontogenetic component to coastal proximity of dispersing juveniles (Fisher *et al.*
12 2014). While an abundance of smaller fish in close proximity to natal rivers suggest this survey
13 could have occurred before juvenile salmon had a chance to fully disperse, Teel *et al.*, (2015)
14 observed that sub yearling Chinook salmon move close to shore in the autumn as well.

15 The highest levels of production in upwelling systems tends to occur along the coastal
16 margin where deep, nutrient-rich bottom water is pulled into the euphotic zone near the coast and
17 then carried offshore by Ekman transport (Huyer, 1983). Wells *et al.* (2012) and MacFarlane and
18 Norton (2002) showed that krill are important for juvenile salmon condition and later survival.
19 Our results indicated that the small-scale distribution of juvenile Chinook salmon was not
20 correlated with acoustic estimates of krill abundance, suggesting that either foraging was not a
21 primary factor driving their movements after entering the ocean or that the juvenile salmon are
22 able to satisfy their needs over a much smaller range of krill densities than observed in our data,
23 and thus responded to conditions we could not detect. Alternatively, the migration of these fish

1 after early ocean entry may be based on geospatial cues, such as a magnetic compass (Putman *et*
2 *al.*, 2013; Quinn & Brannon, 1982); however, it is difficult to separate fixed geospatial covariates
3 from environmental covariates that influence distribution across all years (see Burke *et al.*,
4 2013). If the early ocean migration strategy of juvenile salmon is based on geospatial cues, their
5 growth and survival during this period are likely to be more dependent on local foraging
6 conditions.

7 Small size may be a critical factor in determining how far offshore juvenile Chinook will
8 venture. Scaling constraints on the swimming capabilities of small fish may cause them to resort
9 to prey in their immediate surroundings. Krill, which are a patchy resource, were encountered
10 more frequently in the stomachs of captured subadults and adults, which can range over a greater
11 area and take advantage of more dispersed and patchily distributed prey. Remaining closer to
12 shore to avoid high predation rates may be related in some way to increased turbidity associated
13 with high concentrations of chlorophyll *a*, which has been a good predictor of juvenile salmon
14 presence in this and in other studies (Pool *et al.*, 2012; Peterson *et al.*, 2010; Yu *et al.*, 2012;
15 Burke *et al.*, 2013). It is difficult to assess a foraging benefit of chlorophyll *a* to salmon because
16 time lags between primary production and the trophic level at which juvenile salmon feed are too
17 large to infer trophic transfer (Miller *et al.*, 2010). It takes approximately 100 days after the
18 initiation of upwelling for the meso-zooplankton community to develop (Croll *et al.*, 2005). This
19 is one explanation for why juvenile Chinook salmon survival is higher for hatchery releases that
20 occur 70-115 d after the initiation of upwelling (Satterthwaite *et al.*, 2014).

21 California's ocean salmon fishery was closed completely in 2008 for the first time in
22 history, with the presumed cause being extremely poor survival of juvenile salmon entering the
23 ocean in 2005. Ocean entry for this cohort coincided with unusually low productivity associated

1 with delayed upwelling (Barth *et al.*, 2007; Brodeur *et al.*, 2006; Mackas *et al.*, 2006). At the
2 same time, the Columbia River experienced a booming fall run escapement that may have been
3 due to plume-driven dynamics less susceptible to disruption by variability in wind patterns.
4 Given that juvenile Chinook salmon tend to remain near shore and close to natal river mouths in
5 both regions, such spatial differences in survival may be explained, in part, by different
6 mechanisms driving production. In contrast to the greater dependence on upwelling-driven
7 production off California, production in coastal waters off Oregon can be enhanced by retention
8 of riverine nutrients in the Columbia River plume (Robertis *et al.*, 2005). Such unusually low
9 production from delayed spring upwelling in 2005 and associated differences in escapement
10 between the two regions for cohorts entering the ocean that year point to the potential for local
11 dynamics in coastal waters to impact juvenile salmon survival on the west coast.

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

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

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

7 Increasing climate variability (Solomon *et al.*, 2007) results in greater frequency of warm
8 water years (Sydeman *et al.*, 2013). North Pacific krill (*Euphausia pacifica*) populations can
9 decline by 90 percent during El Niño events (Brinton & Townsend, 2003) and anomalous
10 warming associated with 2005 lead to greater krill starvation and reduced availability to fish in
11 the Gulf of the Farallones (Dorman *et al.*, 2011). Warm water and anomalously species-rich
12 conditions have been associated with the 2009-2010 El Niño that altered prey composition
13 during the period of ocean entry with relatively warm water and low productivity associated with
14 dampened upwelling (Bjorkstedt *et al.*, 2010). Juvenile salmon entering the coastal ocean will be
15 confronted with phenological shifts in marine prey responding to these changes (Edwards &
16 Richardson, 2004; Anderson *et al.*, 2013). In our study, largest catches of juvenile salmon in
17 2010 occurred at stations near natal river mouths with low estimates of zooplankton, suggesting
18 that concentrations of young salmon in those areas was likely a result of limited dispersal, not
19 prey distribution, which highlights the importance of local conditions on early marine survival.

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1 **FIGURE LEGENDS**

2 **Figure 1.** Length-frequency distributions of Chinook salmon captured across all years (2010-
3 2012). The vertical line designates a break at 250 mm that was taken as a threshold to distinguish
4 between juvenile and older age classes.

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

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

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

22 **Figure 5.** Response plots showing the probability of capturing Central Valley juvenile Chinook
23 salmon relative to (a) depth, (b) chlorophyll *a*, and (c) distance to natal rivers. In these plots, only

1 the variable of interest is changed and all other model variables are held constant at their median
2 value. The black line is the output from the logistic regression portion of the hurdle model and
3 the gray lines are the output from 100 k-fold model runs to provide an indication of model error.
4 The rugs along each x-axis show the range of the observed data.

5 **Figure 6.** Predicted catch of juvenile Chinook salmon as a function of mean fork length (top)
6 and distance to natal rivers (bottom) for fish from the Central Valley. The columns are for years
7 2010 (a, d), 2011 (b, e), and 2012 (c, f). The black line is the output from the negative binomial
8 (abundance) portion of the hurdle model and the gray lines are the output from 100 k-fold model
9 runs to provide an indication of model error. The rugs along each x-axis show the range of the
10 observed data.

11 **Figure 7.** Hurdle model coefficient estimates for the (a) Logistic regression and (b) Zero-
12 truncated negative binomial. With the exception of year, which was a factor, all variables were
13 standardized so model coefficients are on the same relative scale. The coefficient estimates for
14 2011 and 2012 were estimated relative to 2010. Error bars are one standard error.

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 2010-2012.

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	4
Central Valley	2011	68	12	0.18	9.51	4
Central Valley	2012	52	4	0.08	0.63	7
Klamath	2010	61	6	0.10	3.05	3
Klamath	2011	68	11	0.16	0.74	1
Klamath	2012	52	3	0.06	1.37	1

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

Table 4. Generalized additive model selection results where the response is distance traveled from the natal river (Dist) and the predictor variables are sea surface temperature (SST), Chlorophyll a (Chl), and the acoustic estimate of prey abundance (NASC).

River	Model	$\Delta AICc$	Weight
Central Valley	Dist ~ SST + NASC	0	69
	Dist ~ SST	1.7	29
Klamath	Dist ~ Chl + NASC	0	4













