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Marine biophysical conditions influence the vertical and horizontal distribution of sub-adult Chinook salmon in nearshore marine waters

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ABSTRACT: The present study quantified the vertical and horizontal distribution of sub-adult Chinook salmon *Oncorhynchus tshawytscha* in nearshore marine environments. Depth-specific hook and line sampling was conducted along the Pacific Ocean coast of Washington, USA. Our analysis, based on 187 Chinook salmon from 1299 sampling deployments and 6616 hooks, revealed a wide distribution of salmon in nearshore marine waters, with distinct patterns associated with fish size and age. Chinook salmon that spent one winter in marine waters were more likely to be caught at greater depths than those in their first year at sea, and larger fish were found at greater depths than smaller fish. The probability of Chinook salmon capture varied with depth, showing a higher likelihood of capture at midwater (>15 m from the surface and >5 m from the bottom) and near (<5 m) the bottom compared to near (<15 m) the surface. Additionally, environmental variables such as sea surface temperature, sea surface chlorophyll *a*, minutes to low tide, and boat speed unimodally influenced capture probability. Our study contributes valuable insights into the spatio-temporal ecology of Chinook salmon, offering a more mechanistic perspective for their management and conservation. The identified relationships between environmental covariates and Chinook salmon distribution can be used to inform life cycle models used to manage and protect this at-risk species and the ecosystem processes that depend on them, particularly in the context of changing oceanic conditions and their role as both predator and prey in marine ecosystems.

KEY WORDS: Chinook salmon · *Oncorhynchus tshawytscha* · Vertical distribution · Marine distribution · Depth-specific sampling

1. INTRODUCTION

Protection of threatened and endangered species depends on understanding their distribution and abundance over time and space, and those of their key prey, predators, and human activities within their ecosystem. Understanding ecological distributions provides information for the assessment of population

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dynamics, life cycle models, management of exploitation rates, and habitat conservation. The Northern California Current Ecosystem is critical habitat for several at-risk species, including multiple Endangered Species Act (ESA) listed stocks of Chinook salmon *Oncorhynchus tshawytscha*. After 2 decades of relatively stable population sizes, rapid declines in abundance in many Pacific salmon (*Oncorhynchus* spp.) followed recent marine heatwaves (Ford 2022). Understanding how the ocean's physical properties influence salmon distribution would improve our ability to project future responses and identify the most useful management options such as fisheries closures or harvest rates (Beamish 2022).

Sub-adult (sexually immature) Chinook salmon distribution along the coast of Washington State, USA, has primarily been investigated using fisheries-dependent data (e.g. coded wire tag recoveries; Weitkamp 2010, 2011). These studies show that the stocks present along the Washington coast originate from British Columbia (Canada) to California (USA) (Weitkamp 2010, Shelton et al. 2019). Chinook salmon have a more variable life cycle compared to other Pacific salmon. They can either migrate to the ocean in the same year as hatching (i.e. sub-yearling) or stay in the river for a winter and migrate the following year (i.e. yearling). Once in the ocean, they may remain close to their natal river or migrate long distances, and occupy inland marine waters, coastal waters, or the open ocean. Marine residence can vary from 1 to 5 yr, and spawning migrations can occur throughout the year (Quinn 2018, Riddell et al. 2018). For example, Salish Sea origin Chinook salmon may stay within those inland marine waters or migrate to the coastal ocean (Quinn & Losee 2022), whereas Snake River spring-run Chinook salmon tend to migrate north quickly after entering the ocean (Teel et al. 2015) and occupy offshore waters until they begin maturing (Sharma & Quinn 2012). Adding non-fisheries-dependent sampling in marine waters can provide samples in more habitats and across different spatiotemporal scales that can help us better understand the marine distribution of individual stocks of Chinook salmon.

In addition to patterns of horizontal movement along the coast and into offshore waters, the vertical distributions of Pacific salmon species are integral to their marine ecology as both predators and prey. The vertical distribution of Chinook salmon in marine waters varies by fish size and age; Orsi & Wertheimer (1995) reported that larger older fish tended to occupy deeper water. Additionally, Chinook salmon may change their vertical distribution seasonally, shifting to deeper water in fall and winter (Orsi & Wertheimer 1995, Hinke et al. 2005, Smith et al. 2015, Courtney et al. 2019). Such changes could reflect a shift in diet to prey that are deeper in the winter (Hinke et al. 2005, Courtney et al. 2019), the need to optimize ambient thermal regime (Hinke et al. 2005), or balance thermal regime and feeding opportunities, as is the case with salmonids in lakes (e.g. Thomas et al. 2023). Currently, our understanding of the vertical and horizontal distribution of Chinook salmon in the Northern California Current is incomplete, and there is a similar lack of detailed knowledge about the environmental variables influencing this distribution.

Understanding the horizontal and vertical distribution of Chinook salmon is particularly important because they are the preferred prey of southern resident killer whales (SRKW) *Orcinus orca*, listed as endangered under the US ESA (Ford et al. 1998, Ford & Ellis 2006). Prey limitation is a primary factor hindering SRKW recovery (NOAA 2022), and the vertical distribution of Chinook salmon may influence their availability to SRKW. Therefore, understanding the horizontal and vertical distribution of Chinook salmon, including habitat preferences, is important for developing effective conservation strategies for SRKW.

We combined depth-specific sampling with analysis of multiple environmental variables to understand the spatiotemporal distribution of Chinook salmon in the coastal waters of Washington. Our objectives were to: (1) determine the horizontal and vertical distribution of sub-adult Chinook salmon in nearshore marine waters along the Washington coast and (2) characterize the environmental conditions influencing their distribution. Specifically, we assessed the possible effects of both depth from the surface and distance from the bottom, ambient temperature, dissolved oxygen, tidal stage, and other variables known or hypothesized to affect Pacific salmon at sea.

2. MATERIALS AND METHODS

2.1. Study site, data collection, and sample processing

Our study area included nearshore marine waters of the Washington coast, USA, from Neah Bay to the mouth of the Columbia River (Fig. 1). We sampled between 5 and 27 km (mean = 10.3 km) from shore over bottom depths from 17 to 262 m (mean = 45.3 m). We captured fish using a modification of the microtrolling technique developed by Duguid & Juanes (2017). We used downriggers weighted with ~6.8 kg (15 lb) lead downrigger balls to deploy 'leaders' of terminal gear

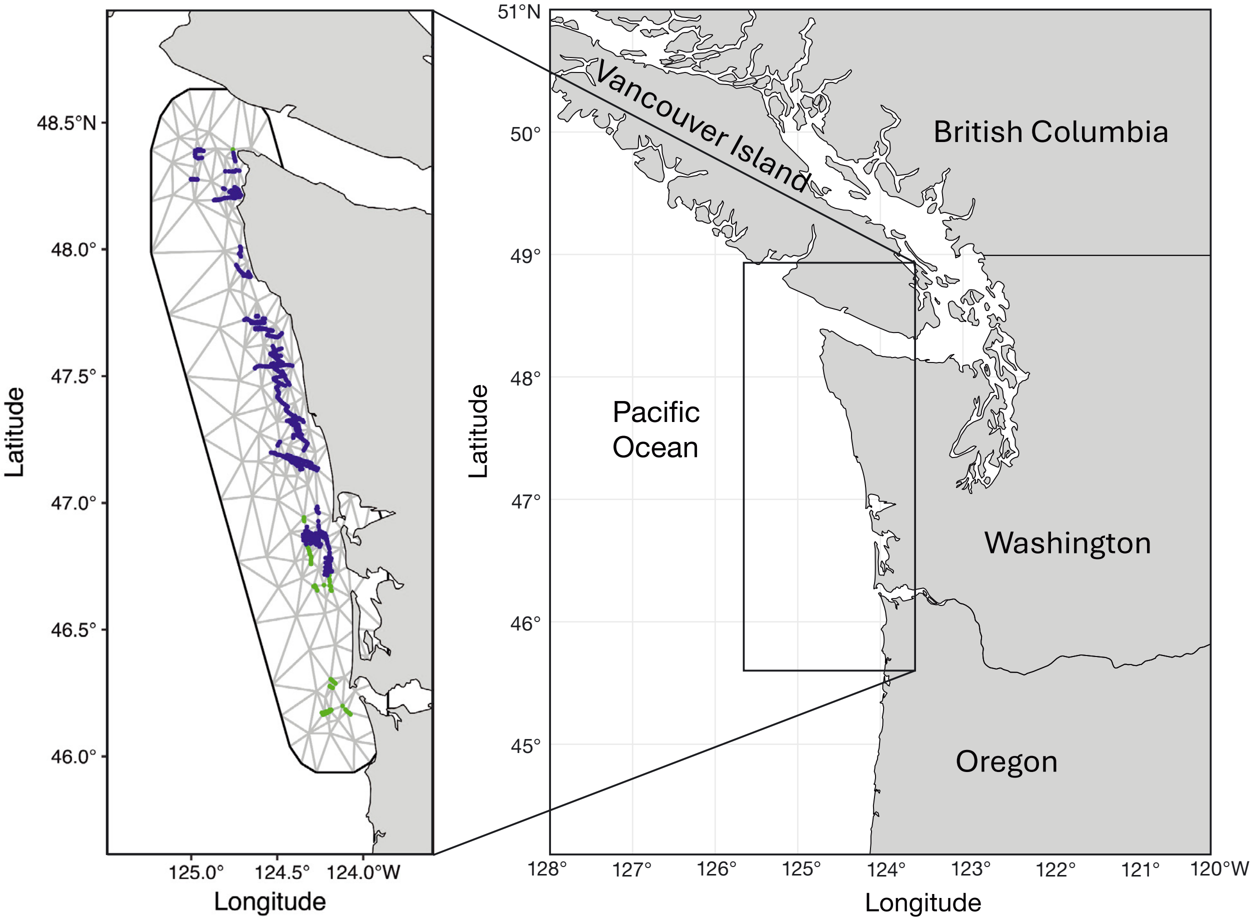

Fig. 1. Study location in Washington State, USA, showing the region of Chinook salmon sampling and zoomed-in sampling locations (green circles = 2018, blue circles = 2019) with spatial mesh map used for logistic regression analysis

at 5 m depth intervals (Fig. 2). Leaders consisted of a terminal clip, 1 m of 68 kg (150 lb) test monofilament line, a 14 cm (5.5 inches) Hot Spot microflasher, 0.5 m of 9.1 kg (20 lb) test monofilament, and a size-0 Dick Nite spoon with Gamakatsu #10 open-eye hooks. Each deployment consisted of a downrigger with up to 7 leaders fishing for 10 to 20 min. Depth loggers (Sensus Ultra by ReefNet) were attached to the downrigger line near the bottom hook and top hook to measure hook depth from the surface. Each downrigger deployment was assigned a unique identifier, and each hook of each deployment was assessed for fish capture. Hooks were fished from depths of 1 to 80 m from the surface. We recorded location tracks and boat speed (mean = 0.88 m s^{-1}, range = 0.21 to 2.0 m s^{-1}) for each deployment using a Garmin GPSMAP 64st during day sampling in June (n = 5 d), July (n = 1 d), and August (n = 3 d) 2018 and in May (n = 14 d), June (n = 7 d), July (n = 7 d), and August (n = 7 d) 2019.

We identified and collected data on each captured Chinook salmon, including fork length (mm), weight (g), and scale samples, for estimating life history strategy (sub-yearling or yearling migrants) and total age. European ages (MacLellan & Gillespie 2015) were determined by 2 scale readers counting the number of freshwater and marine annuli and designated using the decimal system; the numeral before the decimal point indicated the number of winters in fresh water and the numeral after the decimal point indicated the number of winters at sea. To determine the genetic origin, evolutionarily significant unit (ESU), and sex of each fish, we took fin clips from the dorsal or anal fin and stored them in 70% ethanol. An ESU is a population of organisms considered distinct for conservation purposes due to its genetic diversity, evolutionary history, and ecological role; under the ESA, an ESU can be listed as a threatened or endangered entity, allowing for specific conservation measures to protect it. After processing, the fish were released back into the

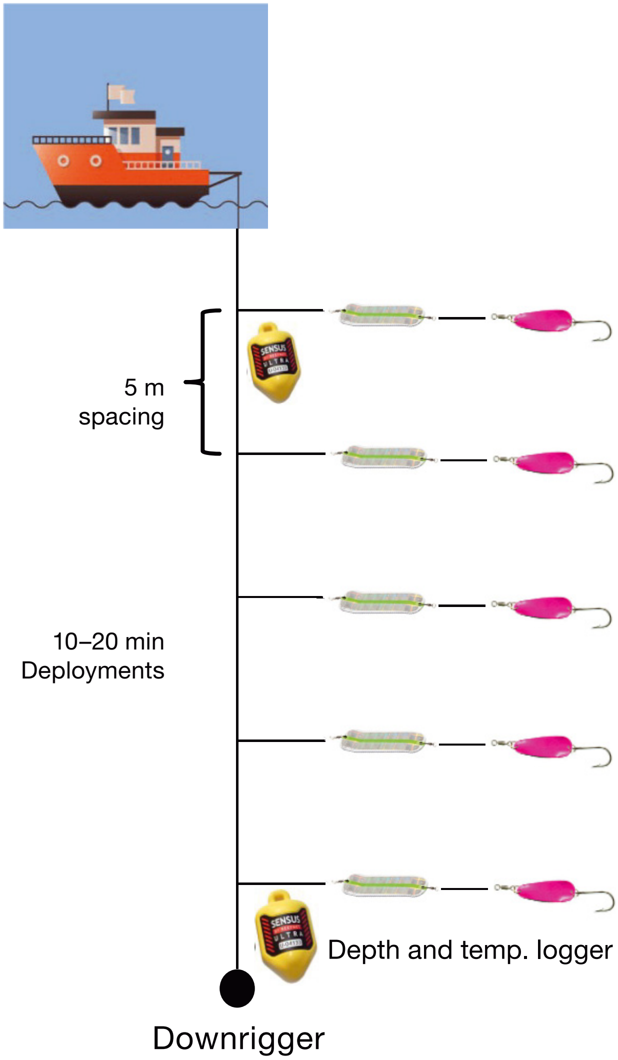

Fig. 2. Microtrolling setup for capturing Chinook salmon showing 5 m spacing between leaders with depth and temperature sensors. Each deployment lasted between 10 and 20 min

water near the capture location. Genetic samples were processed, and the genetic stock identification was determined by the Northwest Fisheries Science Center, Division of Conservation Biology, Genetics and Evolution Program following the methods of Teel et al. (2015). We used a genetic assignment criterion of >80% probability for assigning individual Chinook salmon to specific genetic stock groups.

2.2. Data summaries

To compare capture depths between males and females, we used a Welch 2-sample *t*-test, which allows for unequal variances among groups. All analyses were performed with Program R version 4.4.0 (R Core Team 2024). To examine the depth distribution of captured Chinook salmon by age group, we plotted the proportion of hooked Chinook salmon by 5 m depth bins (e.g. 5 m depth bin = 0 to 5 m capture depth). We calculated the 95% confidence interval with the 'BinomCI' function using the 'Wilson' method from the 'DescTools' package using Program R (Signorell 2023). Chinook salmon enter the ocean in their first or second year of life, and these fish (termed sub-yearling and yearling) differ in size and timing, so they were distinguished in the analysis. In addition, fish in their first year and second year at sea were sampled, giving 4 combinations of freshwater and marine ages. These are designated 0.0 and 0.1 (sub-yearling, in their first or second year at sea), and 1.0 and 1.1 (yearling, in their first or second year at sea) following conventional designation in which the numeral corresponds to the number of full years (i.e. winters) spent in the specified habitat (Quinn 2018).

An ANCOVA was used to determine if there was an interaction effect of fish length and ESU on capture depth (the dependent variable) using the 'aov' function in R. For this analysis, only the 3 ESUs with >5 individuals were included: Lower Columbia River (n = 101), Upper Columbia Summer Fall (n = 52), and California Central Valley (n = 12). Statistical assumptions of linearity, homogeneity of variances, and normality of residuals were assessed visually using scatter plots, residual plots, box plots, and Q-Q plots. All assumptions were met.

2.3. Spatial modeling

We used a spatial generalized linear mixed effects model (GLMM) to estimate the relationship between environmental variables and the probability of catching Chinook salmon on a given hook. We used the 'sdmTMB' package in R, which was designed specifically for species distribution modeling (Anderson et al. preprint doi:10.1101/2022.03.24.485545). In this modeling framework, there was both a fixed effect component, which estimated the effects of our independent variables on the probability of capture using a logistic transformation, and a random effects component, which approximates the spatial variability in observations.

To understand how biophysical conditions may influence the probability of capturing Chinook salmon, we collated data from multiple sources. We extracted depth-specific environmental data from LiveOcean, a regional ocean modeling system, at the median latitude and longitude of each deployment (https://faculty.washington.edu/pmacc/LO/LiveOcean.html). LiveOcean has been extensively validated through comparison of key model outputs, e.g. temperature, salinity, nitrogen, sea surface height, velocity components, and chlorophyll, to a wide array of observational data (Davis et al. 2014, Giddings et al. 2014, Siedlecki et al. 2015). The observational data that LiveOcean uses to validate the model output include acoustic Doppler current profiles and conductivity, temperature, and depth (CTD) data from moorings, sea surface heights from NOAA tide gauges, chlorophyll *a* (chl *a*) observations from CTD casts taken during survey cruises (for validation of the phytoplankton model), cross sections of density and geostrophic velocity from glider transects, and monthly mean sea surface temperatures (SSTs) from satellite data. The model exhibits high skill overall, particularly for outputs driven primarily by physical processes (e.g. temperature and salinity), with generally higher discrepancies for fields strongly influenced by biological processes (e.g. nitrogen and chlorophyll), as is typical of ocean biogeochemical models. LiveOcean provided a range of variables at each specific hook depth, including temperature, oxygen, ocean bottom depth, east—west water velocity (*u*-momentum), north—south water velocity (*v*-momentum), vertical water velocity (*w*-momentum), and phytoplankton biomass. Two independent variables, namely SST and sea surface chl *a*, were obtained from satellite data (https://coastwatch.pfeg.noaa.gov/erddap/index.html) on 28 July 2022. For SST, we used NOAA's Daily Optimum Interpolation at 0.25°C resolution (variable name ncdcOisst21Agg_LonPM180). For chl *a*, we used a combination of 2 data sources to minimize missing data: NOAA VIIRS 750 m resolution 8 d composite (erdVHNchla8day) and Aqua MODIS 0.0125°C 14 d composite (erdMWchla14day_LonPM180).

Other independent variables included boat speed (m s^{-1}), time of day (h), day of the year, relative depth (proportion of water depth from the surface), minutes to low tide (min; positive values = after low, negative values = before low), minutes to high tide (min; positive values = after high, negative values = before high), minutes to slack tide (min; absolute value of minutes to the closest high or low slack tide), and flood or ebb tide as a factor. Additionally, we used a GIS file of bottom substrate (https://www.pacificfishhabitat.org/data/nearshore-cmecs-substrate-habitat/) to determine if the sample occurred on hard substrate as a factor variable, and the distance to hard substrate in km. We also used a digital elevation model to determine the percent slope of the ocean bottom at each sample location. We used linear interpolation to estimate the depth of each hook between the bottom and top hooks where depth loggers were deployed. These data were used to examine whether environmental variables affected the probability of capturing Chinook salmon.

Although each of these variables is plausibly related to the probability of capturing a Chinook salmon (e.g. Yu et al. 2012, Hassrick et al. 2016), many variables, such as those related to the tides, are correlated. To simplify the analysis, we refined this list by looking at the relationship between each variable and catch of Chinook salmon in single-variable logistic regression models. Using Akaike's information criterion (AIC), we chose the 12 most informative variables to evaluate in a multivariate model framework (Fig. 3).

The 'sdmTMB' model was fit by maximizing the marginal likelihood at nodes of a generated mesh. For this application, we generated a mesh with 211 nodes (Fig. 1). Random effects were estimated using Gaussian Markov random fields, conditional on the estimated fixed effects, and were integrated via the La-

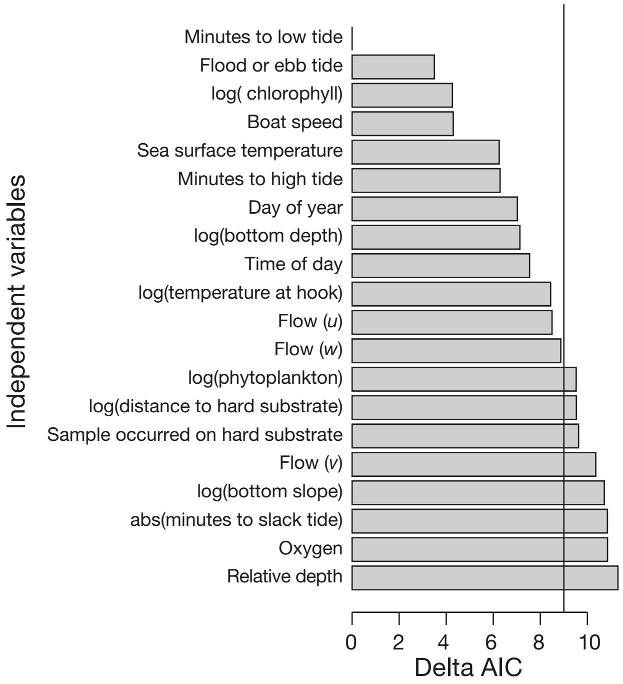

Fig. 3. To determine which independent variables should be considered for multi-model selection, we determined delta values of Akaike's information criterion (AIC) (*x*-axis) from single independent variable (*y*-axis) models. All variables within 9 delta AIC units were included as potential independent variables for multi-model selection to examine the relationship between Chinook salmon presence and multiple environmental variables (left of vertical line). *u*: east—west water velocity; *w*: vertical water velocity; *v*: north—south water velocity; abs: absolute value

place approximation (Anderson et al. preprint doi:10.1101/2022.03.24.485545). We included 3 relative depth bins: surface (<15 m to the surface, depths where the upper water layer is usually mixed), midwater (not near the surface or bottom), and bottom (<5 m from the ocean floor). Although each depth bin had a full spatial random field, they were constrained such that the transition at each node from the surface, to the midwater, to the bottom followed an autoregressive (AR1) process accounting for correlation among hooks among depth bins.

For model comparisons, we only considered combinations of up to 4 non-correlated independent variables to avoid overfitting or including correlated variables in the same model. We decided *a priori* to prevent any 2 variables with a correlation coefficient >0.7 (Dormann et al. 2013) from being in the same model; however, after reducing our variable set in the single-variable models, no 2 remaining variables were correlated. Each variable was also assessed to determine if a polynomial relationship with capture probability should be considered by visual examination of the relationship. In total, 794 separate models were assessed and compared using AIC. For the top model (lowest AIC), we plotted the response plots for each included variable with all other variables held at the mean. To determine how well the model fit our data, we calculated the area under the curve (AUC; Hosmer et al. 2013). We examined the partial residuals plots for evidence of any bias in the results and found none.

3. RESULTS

Our 1299 sampling events, deploying 6616 hooks, caught 187 Chinook salmon, ranging from 111 to 590 mm fork length (mean = 324 mm) at depths from 5 to 65 m (mean = 26.6 m, SD = 10.1 m, Fig. 4). All hooks with bycatch (i.e. other species) were removed from any analysis. The genetic samples that were identified represented 11 different ESUs of Chinook salmon, but Lower Columbia River and Upper Columbia River summer and fall ESUs predominated (Fig. 5). There was no significant difference in capture depth between sexes (male mean = 26.0 m, female mean = 27.0 m, $t = 0.55$, df = 102.99, $p = 0.580$), so they were combined for all subsequent analyses. The sex ratio of captured Chinook salmon was 51% male and 49% females. The ANCOVA detected no significant interaction between

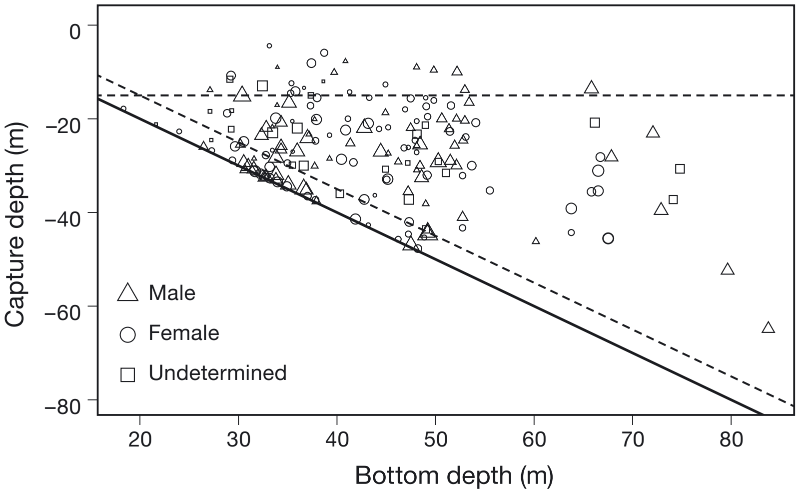

Fig. 4. Capture depth vs. bottom depth for each Chinook salmon captured along the coast of Washington State. Size of the symbol is proportional to the fork length of the fish (range = 111–590 mm). Solid black line indicates the sea floor depth. Values above the horizontal dashed line at 15 m capture depth were classified as 'surface'. Values below the diagonal dashed line (5 m from the bottom) were classified as 'bottom', and values between the 2 dashed lines were classified as 'midwater'

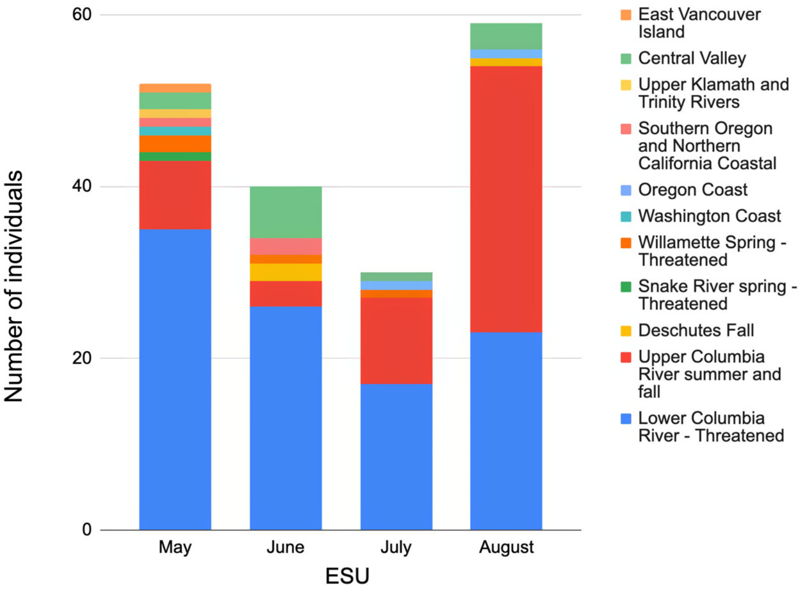

Fig. 5. Number of Chinook salmon individuals caught per month (2018 and 2019 combined) grouped by the evolutionarily significant unit (ESU) determined from genetic stock identification. ESUs listed as threatened under the Endangered Species Act are labeled in the key

fish length and ESU on capture depth ($p = 0.663$). After removing the interaction and examining each independent variable individually, only fish length was significantly related to capture depth; longer fish were caught in deeper water than smaller fish ($p < 0.0001$, $r^2 = 0.099$, slope = −0.031, Fig. 6).

Age was determined for 120 Chinook salmon from scale samples; the others had regenerated scales and age could not be determined (age = 0.0, n = 9; age = 0.1, n = 68; age = 1.0, n = 37; age = 1.1, n = 6; Fig. 7). The proportion of hooks that captured Chinook salmon by age group differed by depth bin. The effort was low in deep water and there were no successfully aged fish below 50 m depth, so we only included depth bins to 50 m. Age 0.0 fish (in their first year at sea) were the only age group caught within the <5 m depth bin, and all 0.0 fish were caught at depths less than 30 m (Fig. 7). Age 1.0 fish (also in their first year at sea, but after a full year in the river) were caught within all bins except <5 m (Fig. 7). Similarly, age 0.1 (second summer at sea) were caught within all bins except <5 m (Fig. 7). Age 1.1 fish were caught only below 20 m with the highest proportion in the 45−50 m bin (Fig. 7). Thus, overall, older (larger) individuals, in terms of both freshwater and marine age, were caught in deeper water than younger (smaller) individuals.

The top model from the spatial GLMM included log-transformed chl *a*, minutes to low tide, SST, and boat speed (Fig. 8). Each of these variables had a unimodal relationship with the probability of capture (explained more below). The likelihood of capture varied among depth bins. The vertical distribution of Chinook salmon was concentrated, according to the probability of capture, in the midwater and bottom depth bins (darkest shaded areas, Fig. 9). The surface depth bin had little spatial variability in probability of capture, and catch rate was generally low throughout the sampling area (Fig. 9). The horizontal (i.e. latitude and longitude) distribution of Chinook salmon for both the midwater and bottom depth bins was concentrated near the middle of the sampling area (off Grays Harbor, Washington) with the midwater depth having highest probability of capture farther south compared to the bottom depth bin (Fig. 9).

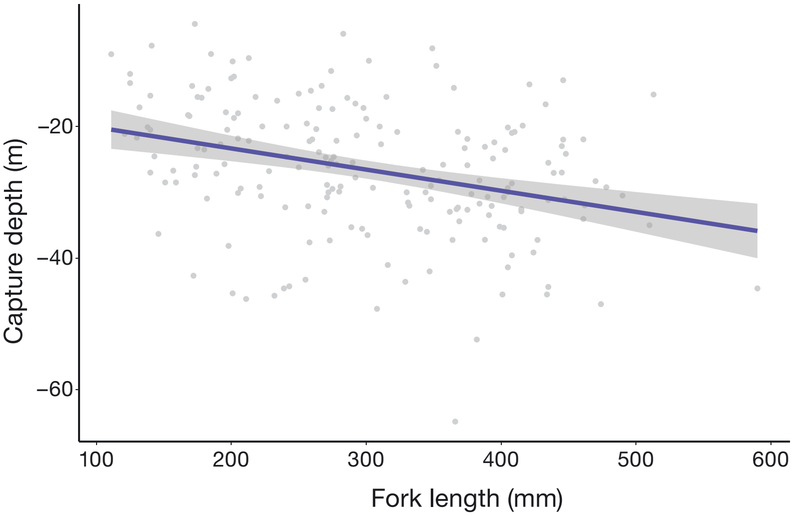

Fig. 6. Predicted relationship of capture depth and individual Chinook salmon fork length from linear regression. The 95% confidence interval is indicated in gray

When we examined the response of independent variables from the best model, all variables showed unimodal responses (i.e. dome-shaped rather than linear; Fig. 10). Specifically, probability of capture peaked (with other variables held constant at their mean) at log(chl *a*) values just below 2 (around 7 mg m^{-3}), shortly before low tide, with SSTs around 15°C, and boat speeds around 1.3 m s^{-1} (Fig. 10). This top model had an AUC value of 0.80, indicating a good fit (Hosmer et al. 2013).

4. DISCUSSION

Our data clearly showed variation in the horizontal and vertical distribution of Chinook salmon off Washington's coast. To our knowledge, our study is the first to quantify depth-specific probability of capturing Chinook salmon along the coast of Washington in the Northern California Current using trolling methods. These findings provide a better understanding of where and when sub-adult Chinook salmon are present along the coast of Washington. We also showed that these distributions are influenced by biophysical variables. Below we provide more detailed discussion on these findings and end with some management and conservation implications.

We found that sub-adult Chinook salmon tended to be captured more often in midwater (>15 m from the surface) and bottom habitats (<5 m from the bottom), particularly when sea floor depths were between 30 and 50 m (Figs. 4 & 9), and that older and longer individuals tended to be captured at deeper depths than younger and shorter fish (Fig. 7). Capture depths reported in our study were similar to capture depths of Chinook salmon reported by Candy & Quinn (1999) in Johnstone Strait

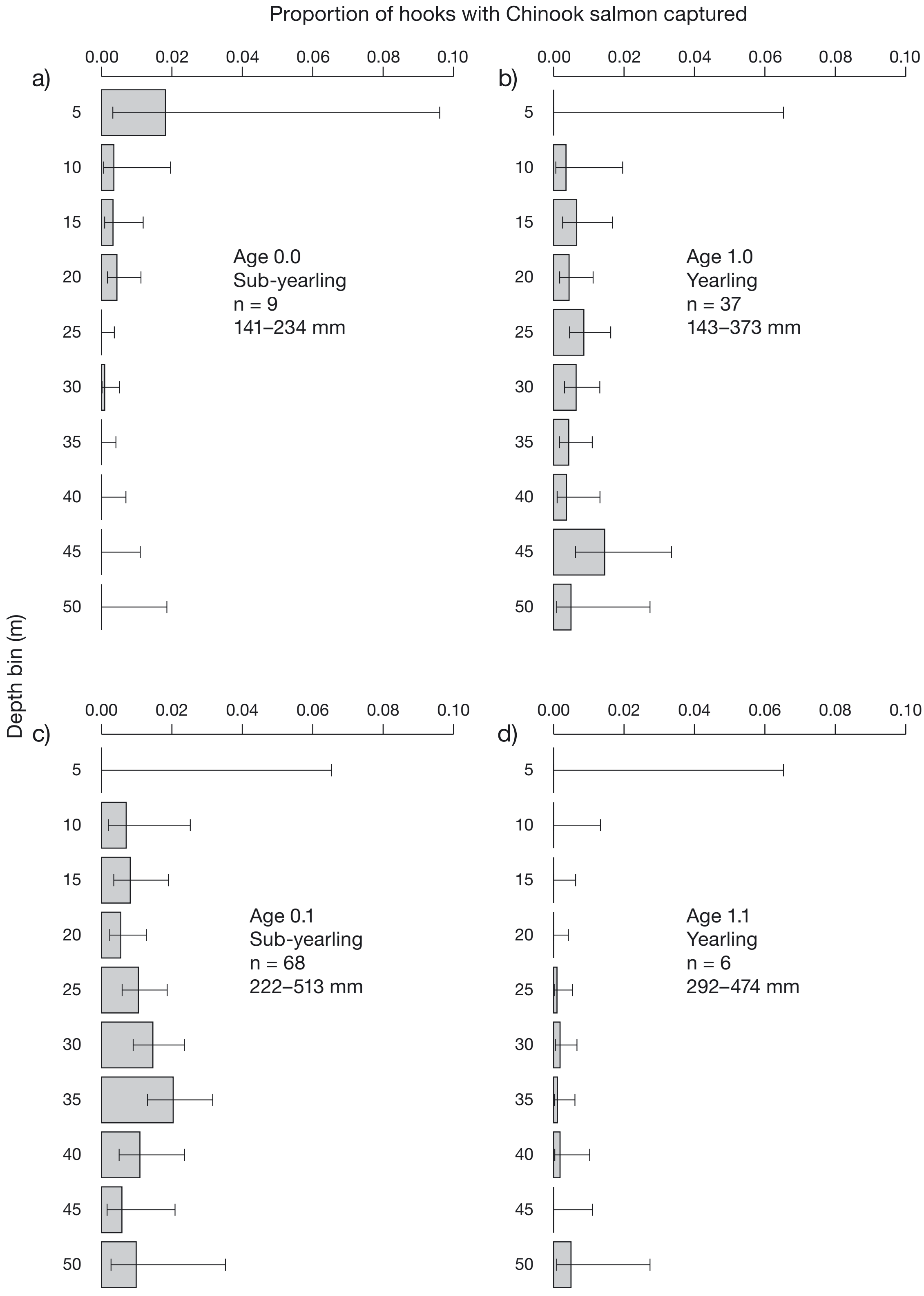

Fig. 7. Proportion of hooks with Chinook salmon captured for each depth bin for each age group: (a) age 0.0, (b) age 1.0, (c) age 0.1, and (d) age 1.1. Error bars represent the 95% confidence intervals for binomial proportions. Each quadrant represents a different age group and includes labels for age, life history type (sub-yearling or yearling), number of Chinook of that age group captured, and the range of fork lengths in mm. See Section 2.2 for explanation of decimal ages

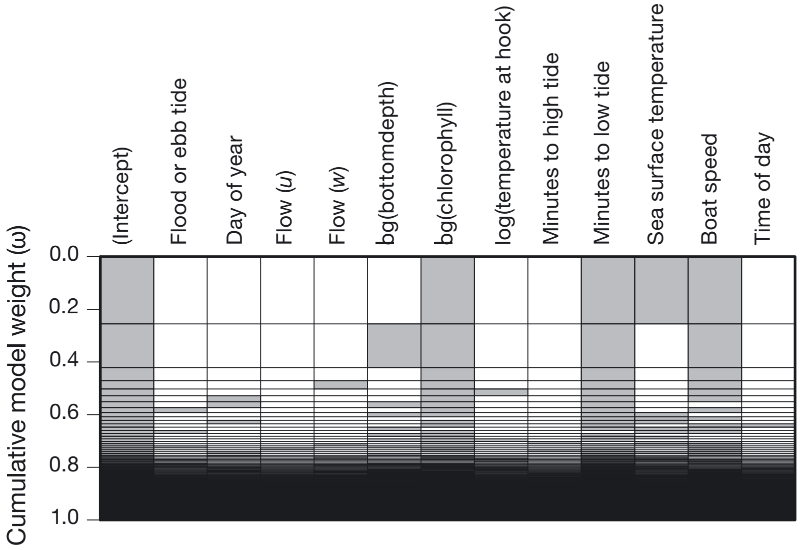

Fig. 8. Model selection table, indicating the cumulative model weight for each of the models (rows) considered to examine the relationship between Chinook salmon presence and environmental variables. For each row, if a cell is gray it was included in a model. The top model (i.e. top row) had the most cumulative model weight and included log-transformed chlorophyll *a*, minutes to low tide, sea surface temperature, and boat speed. See Fig. 3 for definitions of flow

(between Vancouver Island and mainland British Columbia [BC]), which ranged from 25 to 64 m during the day measured with acoustic telemetry, although the fish in that study were larger (80–90 cm) and in an area with deeper bottom depths (300–400 m). Studies in and near Cowichan Bay, BC, that targeted smaller fish (116–236 mm) had higher capture rates in shallow habitats at 9–19 m (Duguid & Juanes 2017) and 15–25 m (Duguid et al. 2021), but these studies were limited by shallow bottom depths. Additionally, Smith et al. (2015) used acoustic telemetry and reported a mean depth for sub-adult Chinook salmon (254–505 mm) of 22 m during the summer in Puget Sound, Washington, which has a mean bottom depth of 140 m. Furthermore, Wright et al. (2017) reported a mean depth of 43.4 m for Chinook salmon that was determined from a meta-analysis of 12 telemetry studies. Overall, our findings add to the growing body of evidence that reinforces specific depth preferences among Chinook salmon across different environmental contexts and timeframes.

We found that longer and older fish were more likely to be captured at greater depths than shorter and younger individuals, consistent with previous studies (Orsi & Wertheimer 1995, Emmett et al. 2004). Fewer yearling Chinook salmon were captured compared to sub-yearlings. This may result

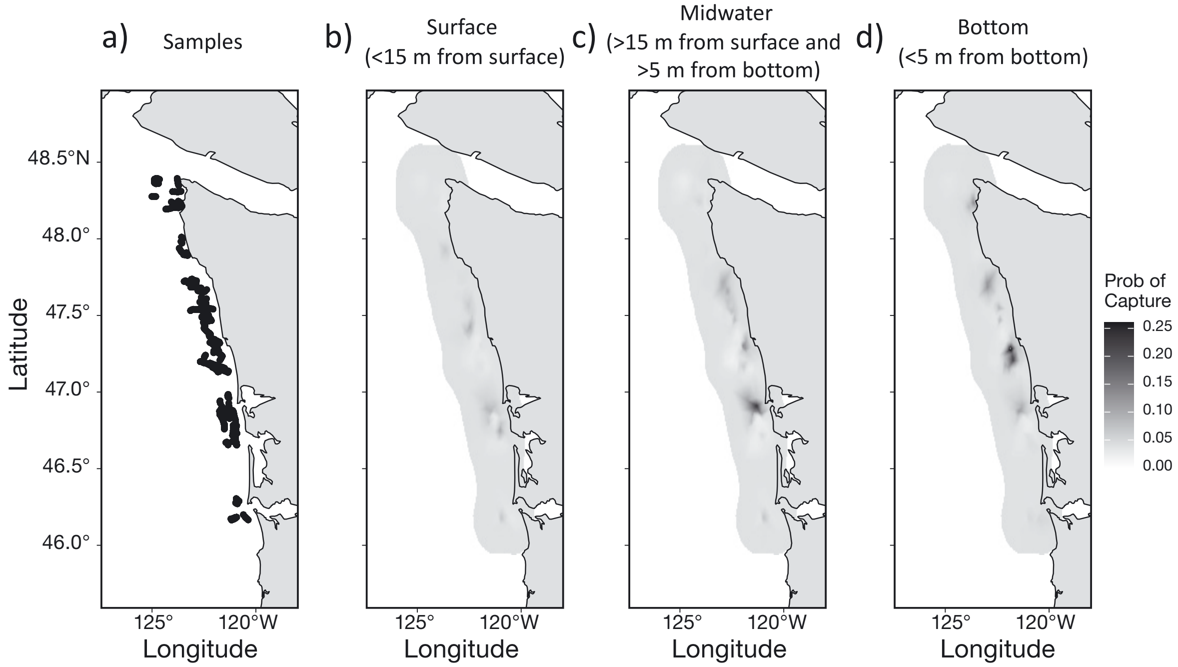

Fig. 9. (a) Sample locations and (b–d) the predicted values of the probability of capture of Chinook salmon within the study area (gray to black color area of water) from logistic regression by relative depth strata for (b) surface = <15 m depth, (c) midwater = between shallow and bottom, and (d) bottom = within 5 m of the bottom. Darker values indicate a higher probability of capturing a Chinook salmon

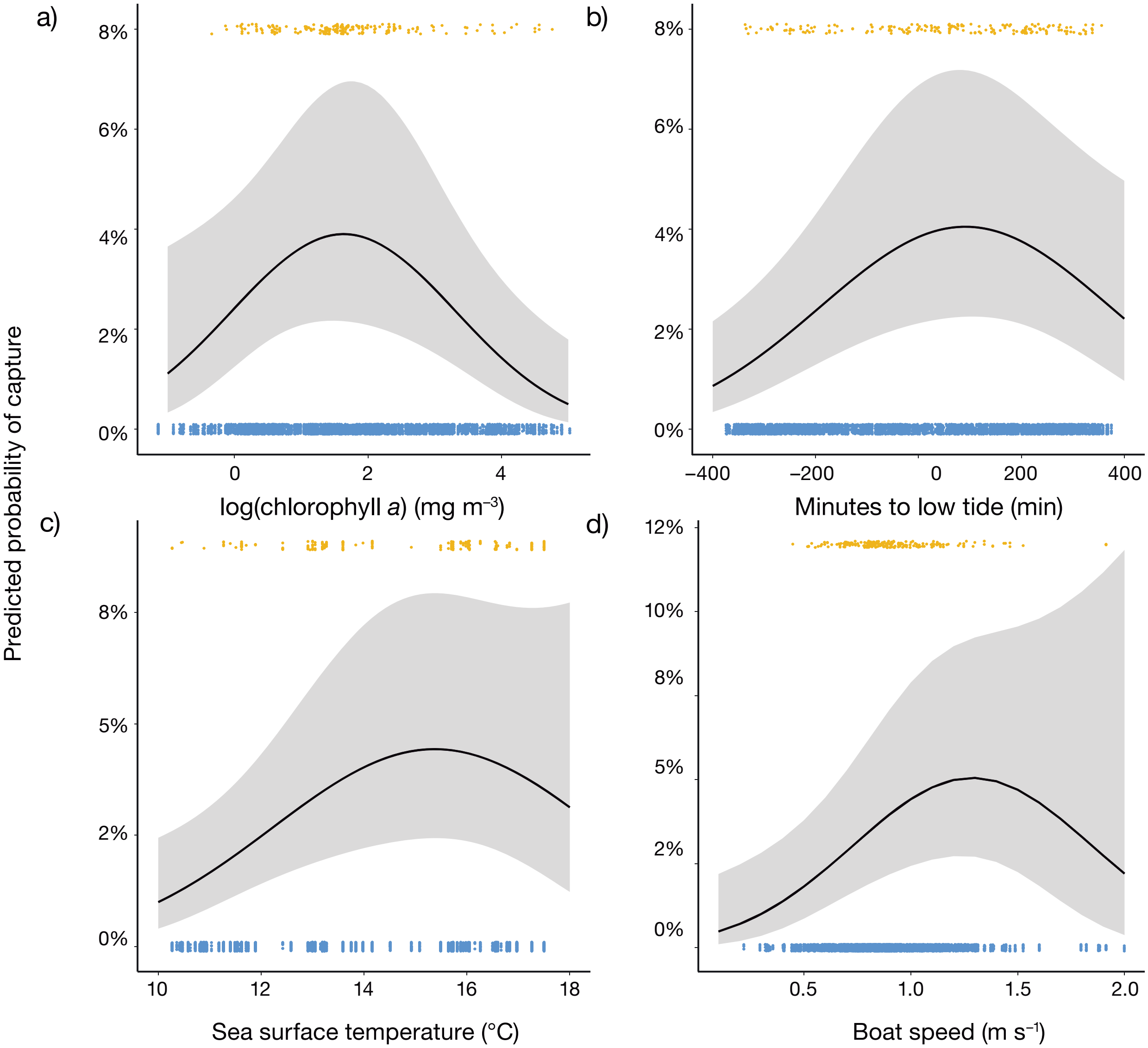

Fig. 10. Predicted probability of capture with 95% confidence intervals (gray) of Chinook salmon from the independent variables (a) log of chlorophyll *a*, (b) minutes to low tide, (c) sea surface temperature, and (d) boat speed, included in the top model according to AIC. Yellow circles near the top of each plot indicate presence of Chinook salmon for that value of the independent variable. Blue circles represent the values where sampling occurred, but no Chinook salmon were captured

from Pacific Northwest yearlings migrating quickly northward towards Alaska in spring or farther offshore, while sub-yearlings stay closer to their natal rivers and shore (Trudel et al. 2009, Sharma & Quinn 2012, Fisher et al. 2014, Riddell et al. 2018). We found no difference in capture depth between sexes, aligning with other research (Orsi & Wertheimer 1995). These findings highlight the need to consider age-specific migration patterns and depth preferences when developing targeted conservation or management strategies for Chinook salmon.

Our study found a mix of Chinook salmon ESUs in each month of sampling. This suggests that some individuals from these ESUs do not migrate long distances from their river of origin, at least during the first 2 yr at sea. The most abundant group detected was the Lower Columbia River Chinook salmon ESU, which is listed as threatened under the ESA (https://www.fisheries.noaa.gov/west-coast/endangered-species-conservation/lower-columbia-river-chinook-salmon). The second most abundant group was the Upper Columbia Summer and Fall ESU (not listed under the ESA), which was the most represented ESU in August in both years. These 2 stock groups have been identified as priority prey stocks for SRKW (NOAA 2018), and SRKW have been documented to consume Chinook salmon within the age ranges included in this study (age 0.1 and 1.1) based on the aging of scales from SRKW diets (Hanson et al. 2021). The distribution of these ESUs along the coast of Washington is consistent with findings by Weitkamp (2010) based on coded wire tags. These ESUs may be particularly important for SRKW that feed on Chinook salmon along the coast of Washington, as they may provide a reliable source of prey when other stocks are in distant locations and not actively returning to rivers (Hanson et al. 2013). Overall, these findings highlight the importance of considering the distribution and abundance of different Chinook salmon ESUs to understand their potential impacts on SRKW and other species that rely on them for food.

Our analysis of probability of capture for Chinook salmon also showed non-linear responses of the independent variables sea surface chl *a*, SST, minutes to low tide, and boat speed. We found a unimodal relationship between chl *a* and probability of capture. Others have found a positive (Bi et al. 2007, Peterson et al. 2010, Hassrick et al. 2016) or non-linear (Yu et al. 2012, Burke et al. 2013) relationship between chl *a* and Chinook salmon presence. This may be because localized areas with higher SSTs and chl *a* concentrations are often more productive and may support higher concentrations of Chinook salmon prey. The decreased probability of capture with high chl *a* concentrations could reflect a time lag between increased chl *a* and increased salmon prey. Greater chl *a* concentrations can also increase the turbidity of the water, potentially limiting the ability of Chinook salmon to see prey and decrease capture probability. Additionally, some algal blooms can create conditions that have negative impacts on Chinook salmon such as damaging gills, increasing predators, or altering the availability of preferred food (Chittenden et al. 2018).

Temperature has been linked to the distribution of Chinook salmon at sea (Burke et al. 2013), and the unimodal response that we observed (peak ~15°C) is likely because the optimal rearing temperatures for juvenile Chinook salmon range from 12.2 to 14.8°C (Hicks 2002, Richter & Kolmes 2005) and negative impacts can start to occur at 17.5°C (Richter & Kolmes 2005). However, Hinke et al. (2005) showed that Chinook salmon persistently used a narrow range of thermal habitats between 8 and 12°C, so the association might not be with temperature directly, but with one or more local biological variables that were not evaluated, such as abundance of prey (Railsback 2022).

We found a higher probability of capture before low tide during maximum ebbing tides. Duguid & Juanes (2017) also found that time relative to low tide was important for Chinook salmon catch probability. A possible mechanism for this is that the change in tidal flow energy disrupts fish prey and makes them more susceptible to predation (Lea et al. 2020, Swieca et al. 2020), but the precise links between tides, salmon behavior in open water, and capture probability remain unclear.

Boat speed also affected the probability of capture of Chinook salmon. The optimal swimming speed for salmonids is about 1 body length (BL) s^{-1} (Ware 1978, Quinn 1988), but Chinook salmon can have burst swimming speeds of around 4 BL s^{-1} (Kraskura et al. 2024). The probability of capture peaked at around 1.25 m s^{-1} (Fig. 10), which is near 4 BL s^{-1} of the mean size of Chinook salmon that we captured (4 BL s^{-1} of mean size fish = 1.28 m s^{-1}). Speeds faster than 1.25 m s^{-1} had reduced probability of capture of Chinook salmon, which is approaching the maximum burst speed for the size of Chinook salmon caught in this study. Additionally, the boat speed likely affects the presentation of fishing gear in water. Speeds that are too slow or too fast will result in the flasher spinning differently in the water, likely changing how attractive the gear is to salmon as potential prey.

Our study on Chinook salmon distribution was conducted in a limited geographic area with a small sample size, restricted length and age groups, and a limited number of ESUs. This narrow scope may not represent the species as a whole. Chinook salmon exhibit complex and highly variable migratory behaviors, differing significantly even among individuals originating within the same river system. This variability necessitates caution when generalizing results from specific, localized studies. However, this study offers rare, depth-specific nearshore sampling of Chinook salmon in a region crucial for SRKW foraging and both recreational and commercial Chinook salmon fishing. Salmon predators, such as harbor seals *Phoca vitulina* and killer whales, have known diving capabilities and tendencies (Lesage et al. 1999, Heaslip et al. 2014, Tennessen et al. 2023). Therefore, findings from this study and other similar studies (Freshwater et al. 2024) could be used to model the vulnerability of Chinook salmon as a function of both size-selection and depth distribution. Our finding of larger and older fish at deeper depths could help reduce size-specific bycatch in fisheries (Erickson & Pikitch 1994, Sabal et al. 2023). Future studies on sub-adult Chinook salmon marine distributions can utilize our findings on the relationships between probability of capture and environmental variables to refine their research questions.

Recent research has indicated the need for quantifying biological mechanisms to better understand salmon population dynamics (Beamish 2022) and that salmon can have phenological shifts that result in mismatches with marine productivity (Wilson et al. 2023). This study provides support for the importance of biophysical variables influencing the distribution of Chinook salmon. Temperature and phytoplankton via chl *a* are linked to primary productivity. A phenological mismatch between salmon and primary productivity could become exacerbated due to climate change. This could result in a trophic cascade that lowers salmon abundance (e.g. Satterthwaite et al. 2014), reducing prey availability for SRKW that are dependent on Chinook salmon as a critical prey resource.

5. CONCLUSION

Our study of Chinook salmon off the coast of Washington provides valuable insights into their ecological patterns of vertical and horizonal distribution. We observed distinct variations in the horizontal and vertical distribution of Chinook salmon, influenced by size, age, and biophysical variables. Notably, Chinook salmon that spent one winter in marine waters were more likely to be caught at greater depths than those that had not. This is supported by a linear relationship between capture depth and fish size, with larger fish being found at greater depths. The presence of multiple ESUs of Chinook salmon throughout the summer months, especially the abundant Lower Columbia River and Upper Columbia Summer and Fall ESUs, underscores the importance of stock-specific migratory behaviors and the implications for local SRKW reliant on them as a food source. Our analysis also revealed the influence of biophysical factors such as sea surface chl *a*, SST, and tidal movements on the probability of Chinook salmon capture. This aspect is crucial for understanding the long-term sustainability of Chinook salmon populations and their predators, like the SRKW. In summary, our study contributes to a more comprehensive understanding of Chinook salmon ocean ecology, revealing the complex interplay of biological and physical factors that define their distribution. This information can be used in fisheries management to avoid Chinook salmon as fisheries bycatch (e.g. hake fishery) or by modeling Chinook salmon distribution as a critical prey resource for the conservation of SRKW. These insights are vital for effective management and conservation strategies, particularly in the context of changing oceanic conditions and their cascading effects on marine ecosystems.

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