

# Warm oceans exacerbate Chinook salmon bycatch in the Pacific hake fishery driven by thermal and diel depth-use behaviours

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## Abstract

Fisheries bycatch impacts marine species globally and understanding the underlying ecological and behavioural mechanisms could improve bycatch mitigation and forecasts in novel conditions. Oceans are rapidly warming causing shifts in marine species distributions with unknown, but likely, bycatch consequences. We examined whether thermal and diel depth-use behaviours influenced bycatch of a keystone species (Chinook salmon; *Oncorhynchus tshawytscha*, Salmonidae) in the largest fishery on the US West Coast (Pacific hake; *Merluccius productus*, Merlucciidae) with annual consequences in a warming ocean. We used Generalized Additive Models with 20 years of data including 54,509 hauls from the at-sea hake fishery spanning Oregon and Washington coasts including genetic information for five salmon populations. Our results demonstrate that Chinook salmon bycatch rates increased in warm ocean years explained by salmon depth-use behaviours. Chinook salmon typically occupy shallower water column depths compared to hake. However, salmon moved deeper when sea surface temperatures (SSTs) were warm and at night, which increased overlap with hake and exacerbated bycatch rates. We show that night fishing reductions (a voluntary bycatch mitigation strategy) are effective in reducing salmon bycatch in cool SSTs by limiting fishing effort when diel vertical movements bring salmon deeper but becomes less effective in warm SSTs as salmon seek deeper thermal refugia during the day. Thermal and diel behaviours were more pronounced in southern compared with northern salmon populations. We provide mechanistic support that climate change may intensify Chinook salmon bycatch in the hake fishery and demonstrate how an inferential approach can inform bycatch management in a changing world.

## KEYWORDS

bycatch, climate change, diel vertical migration, salmon, thermal refugia

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## 1 | INTRODUCTION

Fisheries bycatch is the incidental capture of non-target species and threatens sustainable harvest of marine species worldwide (Komoroske & Lewison, 2015). However, we often have limited insight about the ecological and behavioural mechanisms that drive bycatch dynamics, which can inhibit the ability to forecast and adapt management in novel conditions (Bühne et al., 2020; Scales et al., 2018; Urban et al., 2016). Marine environments are rapidly warming, and little is known about the potential impacts of climate change on fisheries bycatch or the associated mechanistic drivers (Johnson & Lyman, 2020). Increasing ocean temperatures are altering marine species distributions globally (Fredston et al., 2021; Hazen et al., 2013). Therefore, we can expect novel species interactions and spatial overlap, which may present a mechanism influencing fisheries bycatch (Santora et al., 2020). For example, during the Pacific marine heat wave humpback whales (*Megaptera novaeangliae*, Balaenopteridae) moved inshore to feed resulting in record numbers of whale entanglements with the Dungeness crab (*Metacarcinus magister*, Cancridae) fishery (Santora et al., 2020). Climate-driven horizontal shifts in marine species distributions have received more attention than associated vertical shifts in depth distributions, which also occur and may be of particular relevance to bycatch (Brown & Thatje, 2015; Shelton et al., 2021).

If target and bycatch species have distinct distributions in the water column, depth-use behaviours may impact bycatch because species moving shallower or deeper could increase spatial overlap. In addition to temperature-driven changes to vertical distributions, many marine species alter depth distributions across time of day (Behrenfeld et al., 2019; Brierley, 2014; Hays, 2003). Diel patterns in bycatch have also been observed and suggest that diel depth-use behaviours might be a causative link; however, this is rarely examined explicitly (Orbesen et al., 2017; Shirk et al., 2022). Understanding the behavioural, environmental and temporal mechanisms underlying spatial overlap in the water column could provide actionable information for bycatch mitigation, allowing fishermen to further avoid locations, depths, and times with higher bycatch rates (Holt et al., 2013; Humphries et al., 2016).

Thermal and diel depth-use behaviours may be important drivers of Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) bycatch in the Pacific hake (*Merluccius productus*, Merlucciidae) fishery (Holland & Martin, 2019). On average, hake occupy deeper water column depths (200–300 m) compared to Chinook salmon (<100 m) (Alverson & Larkins, 1969; Edwards et al., 2022; Erickson & Pikitch, 1994; Hinke, Foley et al., 2005). Therefore, ecological mechanisms that drive salmon deeper may exacerbate spatial overlap. Chinook salmon may change depth in search of thermal refugia by moving deeper in the water column when sea surface temperatures (SSTs) exceed their preferred ocean temperature (>12°C) (Hinke, Foley et al., 2005; Teahan, 2020). These presumed temperature-driven changes in depth took a tagged Chinook salmon from the upper 100 m of the water column to 250 m where hake are commonly located (Hinke, Foley et al., 2005). Diel vertical migration (DVM) behaviour in Chinook salmon may exist in the ocean but current evidence is variable. Prior studies on

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Chinook salmon have observed increased residence of shallow waters during the day, shallow waters at night, and no diel patterns (Arostegui et al., 2017; Courtney et al., 2019; Hinke, Watters et al., 2005; Pearcy et al., 1984; Smith et al., 2015). Therefore, we do not fully understand DVM in Chinook salmon or how it may interact with fisheries to affect bycatch.

Furthermore, the effects of depth-use behaviours on salmon bycatch may be population-specific. Chinook salmon populations are genetically distinct and can have different ocean distributions where SSTs vary, interactions with the hake fishery, and distributions in the water column (Bellinger et al., 2015; Moran et al., 2021; Otto et al., 2016; Rikardsen et al., 2021; Shelton et al., 2019; Weitkamp, 2010). Whether depth-use behaviours (e.g. thermal refugia, DVM) vary among populations is much less clear but could explain depth-use variation observed from Chinook salmon tagging studies across space (Arostegui et al., 2017; Courtney et al., 2019; Hinke, Foley et al., 2005). Chinook salmon populations are predicted to have different horizontal distributional responses to warming ocean temperatures, and so similar patterns may extend to the vertical dimension (Shelton et al., 2021).

Thermal and diel depth-use behaviours and variation among salmon populations could interact with current bycatch mitigation strategies with meaningful consequences. If there are predictable diel patterns when salmon move into the preferred depths of hake fisheries, bycatch could potentially be reduced by altering diel patterns in fishing effort. The hake fishery already voluntarily limits night fishing as one bycatch mitigation strategy. Hake fishers set more hauls during the day when bycatch of multiple species appears lower and process more hauls at night (Holland & Martin, 2019). Yet we lack a clear understanding of the effectiveness and mechanistic underpinnings of

this strategy related to Chinook salmon (Holland & Martin, 2019). If bycatch increases at depth due to warming oceans, this may be more challenging to mitigate as warm SSTs may be harder to avoid, which could result in climate change increasing Chinook salmon bycatch. If salmon populations exhibit variation in depth-use behaviours, mitigation strategies like night fishing reductions might only be effective for some populations, especially in a changing ocean.

Chinook salmon and Pacific hake are both extremely valuable species and, therefore, salmon bycatch has social, cultural, ecological and economic consequences. Pacific hake is the largest fishery by tonnage on the US West Coast and contributed US\$311 million in total economic impact (revenue and jobs) in 2019 (Edwards et al., 2022). Chinook salmon 2021 US commercial landings were valued at US\$43.8 million and the Columbia River fall-run Chinook salmon recreational fisheries alone were valued at US\$25 million/year ([www.fisheries.noaa.gov](http://www.fisheries.noaa.gov)). Salmon are keystone species connecting disparate marine, riverine and terrestrial ecosystems, which provides benefits to humans and wildlife (Cederholm et al., 1999; Oke et al., 2020). Climate change effects, including warmer oceans, are contributing to widespread declines in salmon populations with multiple populations listed as endangered or threatened under the Endangered Species Act (Crozier et al., 2021; Daly et al., 2017). Therefore, efforts to minimize bycatch will benefit salmon populations, especially those which are threatened, while also benefiting the hake fishery by helping them avoid fishery closures or restrictions, which occur if bycatch caps are met (Holland & Martin, 2019).

We used Generalized Additive Models (GAMs) with 20 years of data (2002–2021) from over 54,000 hauls from the Pacific hake fishery to determine if thermal and diel depth-use behaviours influenced Chinook salmon bycatch with annual consequences in a warming ocean. We further used genetic identification from a subset of 8 years (2008–2015) to assess whether these patterns differed among five salmon populations distributed along a latitudinal gradient (south to north: Klamath – Trinity, S. Oregon – N. California, Oregon Coast, Puget Sound and S. British Columbia). We tested the thermal refugia hypothesis by assessing whether Chinook salmon bycatch rates increased deeper in the water column when SSTs exceeded physiologically preferred temperatures ( $>12^{\circ}\text{C}$ ). We tested the DVM hypothesis by assessing whether Chinook salmon bycatch rates were higher at deeper depths during the day or night compared to the other time period (day or night). Finally, we explored whether these behaviours influenced effectiveness of a common bycatch mitigation strategy, night fishing reductions, and whether years with increased SSTs were associated with overall increased bycatch rates.

## 2 | MATERIALS AND METHODS

### 2.1 | Fishery observer data

The data for this study came from the At-Sea Hake Observer Program (A-SHOP) of NOAA Fisheries. The US West Coast Pacific hake fishery uses mid-water trawl gear and runs from mid-May

through December along the Oregon and Washington coasts. The fishery consists of at-sea and shore-based sectors, and we focused solely on the at-sea fishery because the catch is sorted at sea and bycatch can be attributed to a particular haul. Fishery observers sub-sample approximately 50% of the hake fishery bycatch, record information about species and numbers caught extrapolated to haul-level bycatch, and document haul characteristics (e.g. fishing depth, location, haul duration). There has been greater than 99% observer coverage in the at-sea hake fishery since 1991 (Edwards et al., 2022). Our data set included 54,509 hauls from 2002 to 2021. Observers also collected biological data from Chinook salmon including length, weight, sex, adipose fin status, coded-wire tag scan and tissue sample (fin clip from pectoral fin) (NWFSC, 2022). Most Chinook salmon captured were adults: 97% were above 40 cm in length. For genetic analysis, a random sample of 4304 tissue samples were taken between 2008 and 2015. Genotyping and genetic mixture analysis was conducted previously at the Northwest Fisheries Science Center (NWFSC) (Moran et al., 2021). See Supporting Information for details on cleaning of these datasets (Data S1). This fishery-dependent data included sampling effort that was not systematic or randomized but instead driven by fisher behaviour including goals of avoiding bycatch and maximizing hake catch, which could bias results. An example is fishers limiting night fishing as a bycatch mitigation strategy, which is why we focus on bycatch rates to evaluate evidence for behavioural mechanisms instead of total bycatch patterns. Additionally, other studies have shown that ecological inference of bycatch species was similar between fishery-independent and dependent data sources, and, in fact, observer data were better at identifying relationships with environmental covariates (Pennino et al., 2016; Ward et al., 2015).

### 2.2 | Modelling Chinook salmon bycatch

We used GAMs to model Chinook salmon bycatch rates because they support flexibility for nonlinear interactions, which were central to evaluating our depth-use behaviour hypotheses (Wood, 2022). We included the number of Chinook salmon caught per haul as the response variable and haul duration (min) as an offset to account for variation in haul duration, which ranged from 10 to 1410 min. Many hauls had zero Chinook salmon caught and because our covariates help explain the occurrence of zeros, which relate to our hypotheses, we included hauls with zero salmon caught in our model response variable (Wood, 2022). We used a quasi-Poisson distribution with a log-link function to allow for flexibility in the mean–variance relationship associated with expected overdispersion given the patchy nature of bycatch. The quasi-Poisson and negative binomial have similar functionality, but we favoured the quasi-Poisson because it allows for non-integer count values (necessary for population-specific models) and gives higher weights to larger values (hauls with high bycatch), which is preferable as we were particularly interested in understanding instances of high bycatch (Hoef & Boveng, 2007). We assessed

whether our inference results were strongly impacted by these methodological choices by comparing key results across various model formulations (Table S2). Our inference takeaways were not affected if we included zero catches in our model response variable, removed the uncertainty in observers sampling 50% and extrapolating to total haul bycatch or used the negative binomial distribution (Table S2).

We built separate GAMs for the full Chinook salmon data set (2002–2021, no population differentiation) and for each of five focal salmon populations (2008–2015) following the same basic structure:

$$\log(\mu_i) = \alpha + f_1(\text{Lon}_i, \text{Lat}_i) + f_2(\text{Bottom depth}_i) + f_3(\text{Day of year}_i) + \text{Year}_i + f_4(\text{Fishing depth}_i, \text{SST}_i) + f_5(\text{Fishing depth}_i, \text{Time of day}_i)$$

Where  $\mu_i$  is the expected Chinook salmon catch per haul  $i$ ,  $\alpha$  is the intercept, and  $f_n$  are smooth functions where  $f_1$ ,  $f_4$  and  $f_5$  are multiple covariate tensor smooths and  $f_2$  and  $f_3$  are single covariate smooths all using thin plate regression splines. We included covariates  $f_1(\text{Lon}_i, \text{Lat}_i)$  and  $f_2(\text{Bottom depth}_i)$  to capture underlying spatial patterns and both terms were recorded onboard the fishing vessel (Barnes et al., 2018; Becerril-García et al., 2020). These spatial covariates exhibited high concavity but were more fully captured by including both terms, which GAMs can handle with large data sets (Santora et al., 2018; Wood, 2008). Temporal covariates included were  $f_3(\text{Day of year}_i)$  and  $\text{Year}_i$  as a factor to capture seasonal and interannual variability, respectively.

To examine thermal refugia, we included  $f_4(\text{Fishing depth}_i, \text{SST}_i)$ . Fishing depth (m) indicated the depth in the water column where the net was in fishing configuration. During net deployment and retrieval, fishing is inefficient, so it is possible Chinook salmon were captured shallower than the recorded fishing depth but is likely minimal. Fishing depths cannot extend below bottom depths and, therefore, these covariates may be confounded; however, only 6.4% of hauls occurred where bottom depths were less than 200 m (0.6% less than 100 m). Hence, the vast majority of hauls in our data set allowed Chinook salmon space to move vertically in the water column. Mean SSTs were extracted from the NOAA high-resolution 0.25° daily Optimum Interpolation SST V2 dataset (Huang et al., 2021). To evaluate diel vertical migration, we included  $f_5(\text{Fishing depth}_i, \text{Time of day}_i)$ . Time of day was recorded onboard the fishing vessel and converted to seconds since midnight and modelled as a cyclic cubic regression spline so the ends (0 [00:00:00], 86,340 [23:59:59] seconds) matched. In summary, our models evaluated whether there was evidence for either depth-use behaviour after accounting for background spatial and temporal influences on bycatch. This approach is conservative because the cubic splines fit with GAMs are very flexible such that a non-linear model including latitude, longitude, bottom depth, year and day of year can incorporate substantial variance driven by other mechanistic variables that themselves vary spatially (e.g. SST). To limit extrapolation, all predictions were constrained within the range of covariates used to fit the model. The upper limit of our predictions for SST (18°C) had the fewest observed data (186 hauls between 17.5°C and 19.2°C) but is still within range, and we

particularly wanted to examine dynamics in these warmest conditions as they may portend future conditions.

## 2.3 | Genetic population identification

Chinook salmon tissue samples that were taken onboard the hake fishing vessel were immediately folded in Whatman 3MM chromatography paper, dried and stored in barcoded coin envelopes. DNA was amplified and genotyped for 13 standardized microsatellite loci and conditional maximum likelihood mixture modelling (CMLMM) was used to estimate individual assignments to population of origin with bias correction (Anderson et al., 2008; Moran et al., 2021; Rannala & Mountain, 1997). CMLMM used a baseline data set of known-origin reference samples assumed to represent all potentially contributing populations (Moran et al., 2006). These population-level assignments were aggregated to Evolutionary Significant Unit (ESU) reporting group (or population). We considered an individual salmon to have originated from the ESU for which it had the highest probability of assignment. We followed a widely used and cautious assignment threshold and ignored 943 fish with individual assignment probabilities less than 0.8 (Moran et al., 2014, 2021; Satterthwaite et al., 2014). Southern or northern salmon populations were more likely to share genetic assignment probabilities among populations of the same region, so our regionally comparative conclusions are likely robust to potential genetic mischaracterizations (Moran et al., 2014). Sample sizes of genetic populations after passing the 0.8 filter included: Klamath – Trinity (1052 genotyped from 564 hauls), S. Oregon – N. California (722 genotyped from 488 hauls), Oregon Coast (223 genotyped from 206 hauls), Puget Sound (273 genotyped from 184 hauls) and S. British Columbia (459 genotyped from 334 hauls).

We scaled the composition of salmon that were genotyped to the haul-level to estimate population-specific catches. Consider the example where seven salmon were caught in a haul, three were genotyped with one assigning to Klamath – Trinity, one to S. OR – N. CA and one to Lower Columbia River. We would estimate population-specific catch for that haul to be 2.3 Klamath – Trinity, 2.3 S. OR – N. CA, 2.3 Lower Columbia River and 0 for all other populations. The quasi-Poisson distribution used in our models can accept non-integer count response variables. Hauls were excluded from the focal population analyses where Chinook salmon were caught but none were genotyped. Many hauls had small numbers of genotyped salmon (range: 1–28) introducing uncertainty in scaling to haul-level catch. However, these uncertainties did not affect our main results as focal population probability of occurrence models (with no extrapolation) supported our key inference patterns (Figures S6 and S7). Our focal population models have more steps introducing uncertainty and span fewer years than the full model that included all Chinook salmon with no population differentiation, and should, therefore, be interpreted with relatively more caution. The most robust support for our observed depth-use patterns come from the full model with population-specific models adding further nuance.

### 3 | RESULTS

#### 3.1 | Fishery and bycatch summary

From 2002 to 2021, the at-sea hake fishery captured 67,165 Chinook salmon with an average of  $3358 \pm 2030$  (SD) per year. When bycatch occurred in 8534 out of 54,509 hauls, it was patchy; 86% of hauls captured fewer than 10 salmon per hour yet six hauls had bycatch rates greater than 200 salmon per hour. However, most hake fishery hauls caught zero Chinook salmon, which suggests that these two species occupy overlapping yet distinct marine distributions. Fishing effort is a likely proxy for hake distribution because fishers target locations and depths where acoustic signatures suggest hake are present (Edwards et al., 2022). Therefore, hake have a spatial distribution centred along the continental shelf-break, whereas salmon bycatch occurs more often inshore, despite a wide spatial extent of fishing effort and bycatch (Figure 1a,b). See Shirk et al. (2022) for a similar map of hake catches per unit effort. Along depth in the water column, the highest observed Chinook salmon bycatch rates occurred in the shallowest fishing depths (0–100m), which was five times greater than bycatch rates at depths where hake were most commonly targeted (200–300m; Figure 1d,e). This implies that depth-use behaviours where salmon move deeper may result in increased spatial overlap with hake and exacerbate bycatch.

Using a subset of genetic data from a prior analysis, we focused on five Chinook salmon populations that spanned a latitudinal gradient (Figure 1c; Moran et al., 2021). Klamath – Trinity and S. Oregon – N. California populations had similar southerly distributions concentrated south of 45°N (Figure 1c). The OR Coast population had the widest latitudinal distribution, while Puget Sound and S. British Columbia populations were most often caught north of 47°N near the Strait of Juan de Fuca (Figure 1c). Bycatch rates were generally higher in shallow fishing depths (<200m) across populations, except for the Klamath–Trinity population, which had relatively higher bycatch rates at deeper depths (200–300m; Figure S1).

Fishing effort varied relative to parameters of interest for our depth-use behaviour hypotheses (thermal refugia, DVM). Fishery hauls spanned SSTs between 6.6°C and 19.2°C (mean  $\pm$  SD:  $12.8 \pm 1.6^\circ\text{C}$ ). However, the incidence of very warm SSTs above 17°C only occurred south of 46°N (Figure S2). For time of day, 75% (40,962) of hauls occurred during the day (between local sunrise and sunset) and the remaining 25% (13,547) occurred at night (Figure 1f). Fishing depth distributions were slightly deeper at night and in warm SSTs, but variation was minimal (Figure S3).

#### 3.2 | Thermal refugia

We found evidence for Chinook salmon moving deeper when SSTs were very warm ( $F=23.49$ ,  $p<.001$ ; Figure 2 and Table S1). When SSTs were near 18°C, predicted bycatch rates were almost zero in surface waters (0.05 Chinook salmon per hour at 50m) and highest

between 200 and 300m fishing depths (0.63 Chinook salmon per hour at 250m; Figure 2a). Predictions over relatively cooler SSTs between 10°C and 16°C indicated that bycatch rates were highest in surface waters and declined with depth (Figure 2a). These patterns support the mechanism of thermal refugia if salmon were moving deeper to remain in cool water where SSTs were warmest.

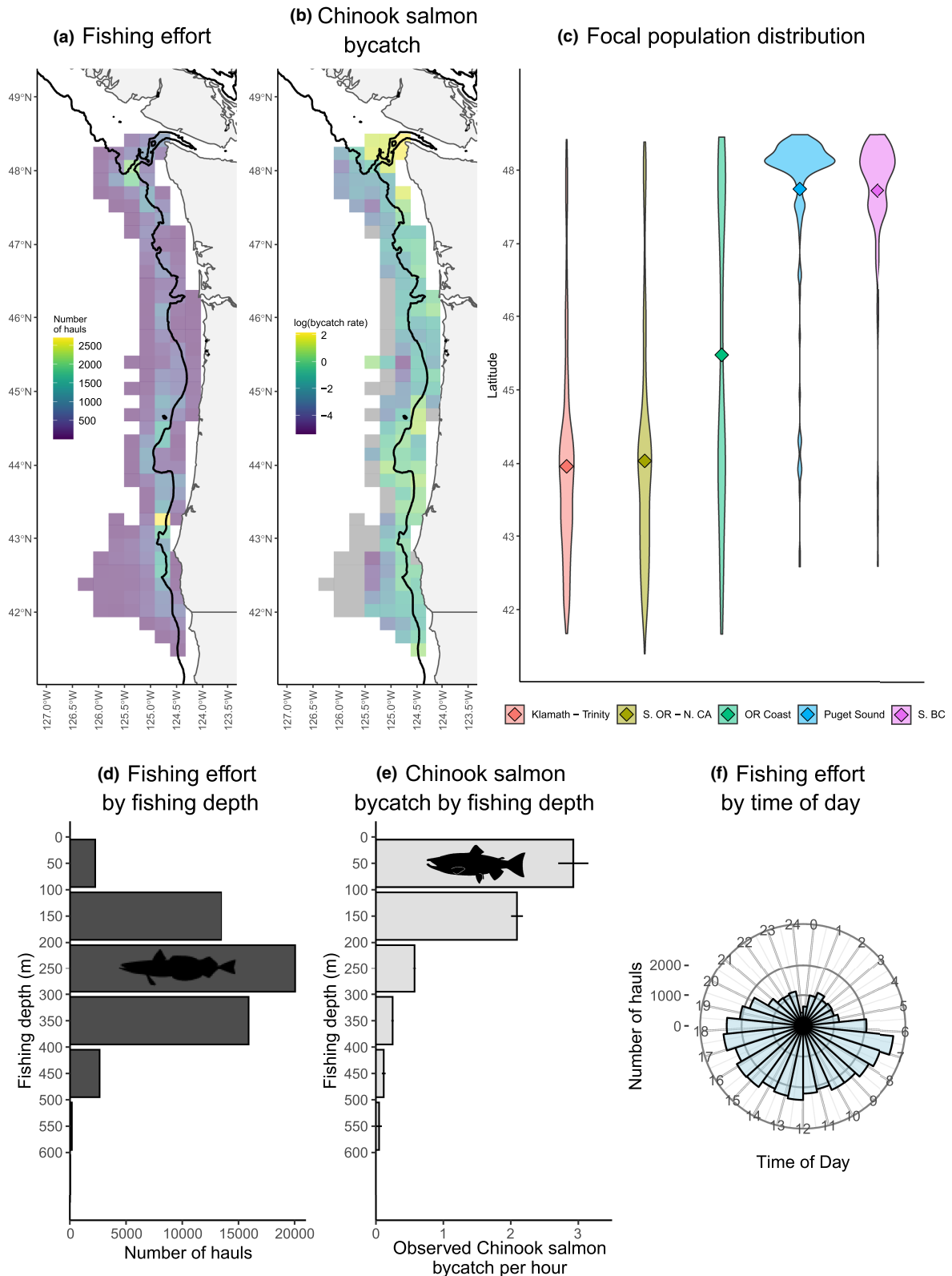
Patterns supporting thermal refugia were especially apparent in southern and absent in northern populations (Figure 2b–f). In southern population models, the decline in predicted bycatch rates in shallow waters occurred in all SSTs above 12°C and peaked at progressively deeper depths (Klamath – Trinity:  $F=21.81$ ,  $p<.001$ ; S. OR – N. CA:  $F=17.89$ ,  $p<.001$ , OR Coast:  $F=4.05$ ,  $p<.001$ ; Figure 2b–d and Table S1). For example, bycatch rates peaked near 100m at 14°C, 200m at 16°C, and 250m at 18°C, which fits expectations if salmon need to move deeper to find suitable temperatures as SSTs increase (Figure 2b–d). In contrast, northern populations did not appear to seek thermal refugia. For the Puget Sound population, bycatch rates increased at 16°C in shallow fishing depths and lacked a clear trend for other SSTs ( $F=3.44$ ,  $p<.001$ ; Figure 2e and Table S1). For the S. BC population, bycatch rates peaked between 100 and 200m fishing depths, but this pattern was consistent among SSTs and included overlapping uncertainty and so does not provide strong support for salmon seeking refugia ( $F=2.02$ ,  $p=.005$ ; Figure 2f and Table S1). We did not predict bycatch rates at 18°C for northern populations because SSTs above 17°C never occurred north of 47°N where Puget Sound and S. BC salmon were primarily caught (Figure 1c and Figure S2).

#### 3.3 | DVM

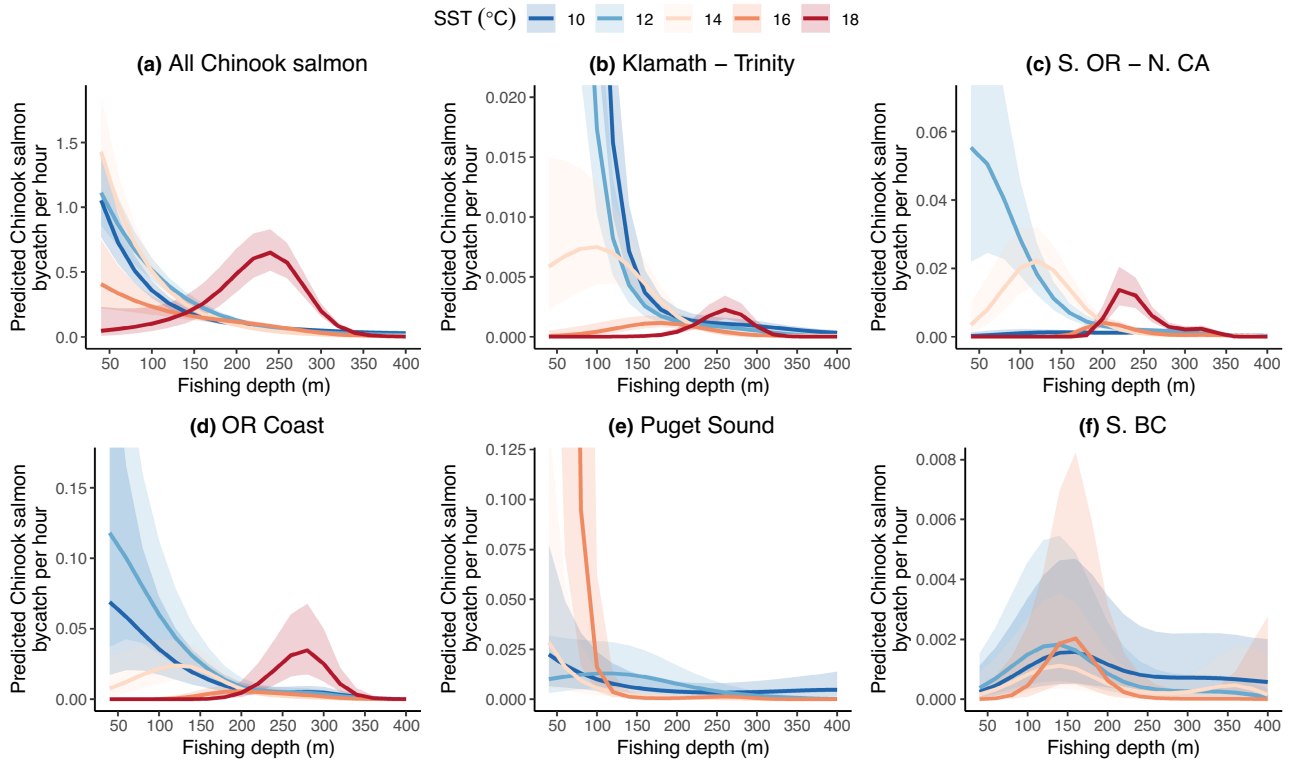
We found patterns in bycatch consistent with DVM. Chinook salmon moved between shallow fishing depths during the day and deeper fishing depths (200m) at night ( $F=41.54$ ,  $p<.001$ ; Figure 3 and Table S1). The highest mean predicted bycatch rate, while holding other covariates at median values, was 1.3 Chinook salmon per hour, which peaked in the shallowest water (50m) during the day (Figure 3a). This was approximately 10 times greater than concurrent bycatch at 200m (Figure 3a). At night, bycatch rates at 200m tripled becoming the depth of highest bycatch (1 Chinook salmon per hour), which was near three times higher than bycatch rates at 50m (Figure 3a). Differences in bycatch rates among fishing depths were smaller at night compared with daytime, which may suggest Chinook salmon were more concentrated in shallow water during the day and more dispersed at night (Figure 3a).

Southern populations also exhibited increased bycatch rates in shallow fishing depths during the day and the opposite pattern of around 200m at night (Klamath – Trinity:  $F=53.96$ ,  $p<.001$ ; S. OR – N. CA:  $F=49.25$ ,  $p<.001$ , OR Coast:  $F=12.43$ ,  $p<.001$ ; Figure 3b–d and Table S1). However, the diel patterns in northern populations had higher uncertainty and were less pronounced (Puget Sound:  $F=1.33$ ,  $p=.01$ , S. BC:  $F=0.93$ ,  $p=.15$ ; Figure 3e,f and Table S1).

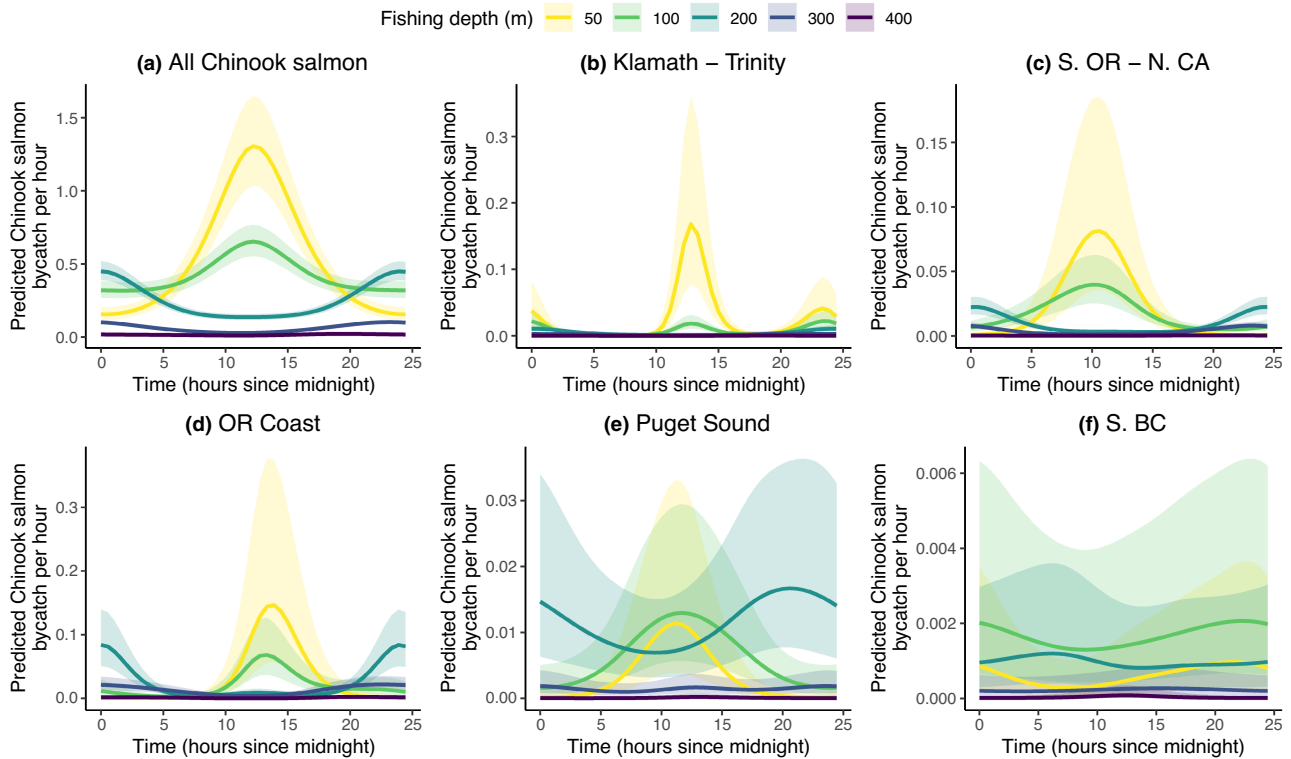




**FIGURE 1** (a) Total number of hauls and (b) observed Chinook salmon bycatch rates (log base 10) across all years by latitude and longitude bins. In (a, b) locations are only shown with at least three vessels; in (b) grey cells indicate zero Chinook salmon caught. (c) Violin plots depicting the density of positive detections of focal populations by latitude with the diamond indicating the median latitude. Summaries of (d) total number of hauls, (e) Chinook salmon bycatch per hour by fishing depths and (f) number of hauls by time of day.



**FIGURE 2** Salmon seek thermal refugia: predicted Chinook salmon bycatch per hour across the range of fishing depths and five SSTs while holding other covariates at median values. Predicted bycatch rates for (a) the full model with no population differentiation and focal population models (b-f). For focal population models, we used the median latitude of positive catch unique to that population. Solid lines represent the mean and shaded areas represent standard errors.



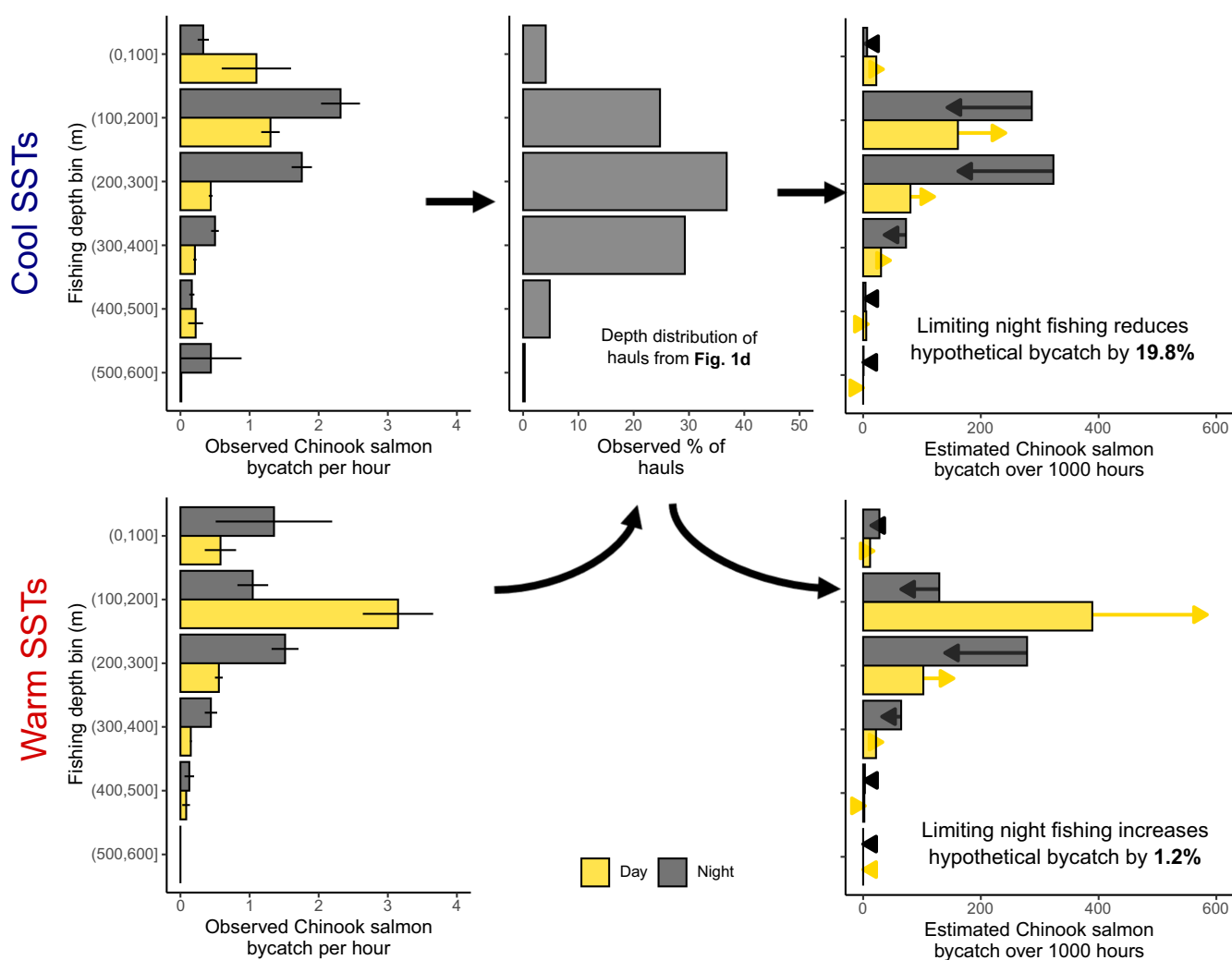
**FIGURE 3** Chinook salmon move deeper at night: predicted Chinook salmon bycatch per hour across the range of time of day and five fishing depths while holding other covariates at median values. Predicted bycatch rates for (a) the full model with no population differentiation and focal population models (b-f). For (b-f), we used the median latitude of positive catch for each population. Solid lines represent the mean and shaded areas represent standard errors.

### 3.4 | Depth-use behaviours and night fishing reductions

We conducted simple scenarios to determine whether thermal and diel depth-use behaviours may influence the effectiveness of a voluntary bycatch mitigation strategy: reducing night fishing. We only conducted scenarios using data from southern latitudes (below the zoogeographical boundary at 45.77°N) because that was where our model results suggested both depth-use behaviours were present. First, we summarized observed Chinook salmon bycatch rates among categories of fishing depth, day vs. night, and cool and warm SSTs (above or below 14°C) (Figure 4). Signals of both depth-use behaviours were apparent in these snapshots of the observed data. In warm SSTs, there were greater bycatch rates at mid-depths (100–200m) compared with cool

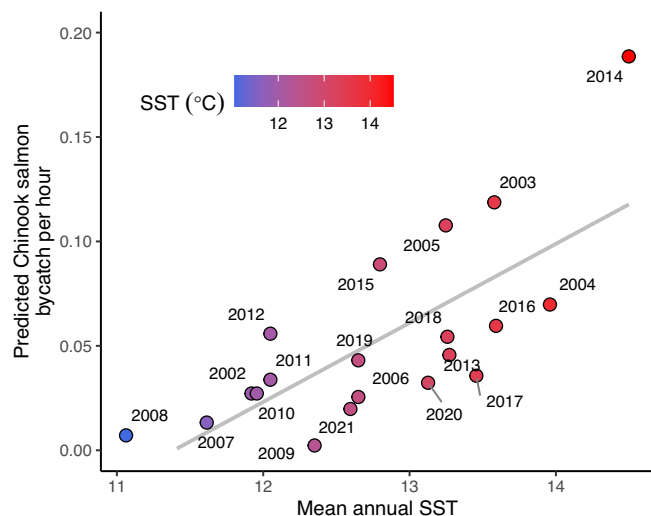
SSTs (Figure 4), and there were increased night bycatch rates at depths greater than 200m in both SSTs (Figure 4).

Next, we scaled these patterns of bycatch per effort across an arbitrary and standard 1000hours of towing distributed by observed fishing depths (Figure 4). We further split effort between day and night either with even effort (50% night, 50% day) or night fishing reductions (25% night, 75% day). Limiting night fishing reduced hypothetical bycatch by 19.8% when SSTs were cool because fishing predominately occurred during the day when vertical spatial separation between salmon and hake was highest. However, this benefit disappeared (1.2% increase in bycatch) in warm SSTs as salmon were deeper during the day and suggests that night fishing reductions are relatively less effective in warm SSTs. Our projections rely on simple snapshots of the observed data and, therefore, should not be interpreted as precise quantitative measures of effectiveness.



**FIGURE 4** Night fishing reductions are less effective in warm SSTs. Left column: mean observed Chinook salmon bycatch per hour summarized by categories of fishing depth, day vs. night, and SSTs (above or below 14°C). Horizontal lines represent standard errors. Middle column: observed depth distribution by fishing depths (same data as Figure 1d). Right column: estimated total bycatch as calculated from mean bycatch rates (left column) projected over 1000hours of towing distributed over observed towing depth distributions (middle column). The number of tows were either split evenly between day and night (bar plot) or with night fishing reductions (25% night, 75% day). Yellow and black arrows indicate the change in bycatch estimates from even effort to those under night fishing reductions. Data included from southern latitudes only (<45.77°N).





**FIGURE 5** Higher Chinook salmon bycatch in warm ocean years. Predicted Chinook salmon bycatch per hour attributed to each year, while holding other covariates at median values, related to the mean SST values from all hauls from the respective year. The grey line indicates the linear fit between predicted bycatch rates and mean SST values.

### 3.5 | Annual bycatch rates by SST

We further examined the potential annual effect of these depth-use behaviours by relating annual estimates of predicted bycatch rates, while holding other covariates at median values, with the mean SSTs from haul locations from that year. Chinook salmon bycatch rates increased in years with warm SSTs ( $\beta=0.04$ ,  $t=4.5$ ,  $p<.001$ ,  $R^2=0.5$ ; Figure 5) and total annual bycatch indicated a similar pattern (Figure S4). Estimated bycatch over a typical fishing season (7170 h of towing) derived from the predicted annual bycatch rates, suggests a difference between 51 and 1352 Chinook salmon between the coolest (2008; mean  $\pm$  SD:  $11.1 \pm 1.1^\circ\text{C}$ ) and warmest (2014;  $14.5 \pm 2.2^\circ\text{C}$ ) years in our dataset. Although focal population models only included years from 2008 to 2015, southern population bycatch rates also increased with annual SSTs driven by high bycatch rates during marine heatwave years (2014, 2015; Figure S5). The Puget Sound population also had high bycatch rates in 2014, but not in other warm years, while the highest bycatch rates for the S. BC population were in cooler years (2010, 2011; Figure S5).

## 4 | DISCUSSION

Fisheries bycatch threatens sustainable fisheries management worldwide, yet we lack a mechanistic understanding of how warming oceans may affect bycatch, which is critical to inform adaptive management and forecasts in novel conditions (Komoroske & Lewison, 2015; Scales et al., 2018; Urban et al., 2016). Furthermore, salmon bycatch carries large cultural, economic and ecological consequences. The hake fishery must engage in costly bycatch avoidance

measures, many salmon populations are declining or threatened with extinction, and bycatch mitigation affects diverse user groups desiring informed and fair decisions (Holland & Martin, 2019; Moran et al., 2021). Our results demonstrate that Chinook salmon thermal and diel depth-use behaviours exacerbate bycatch in the deeper-dwelling Pacific hake fishery resulting in increased bycatch in warm ocean years. Bycatch rates increase in warm SSTs as salmon move deeper to seek thermal refugia. This thermal behaviour also lessens the effectiveness of a voluntary bycatch mitigation strategy (night fishing reductions), which, in cool SSTs, reduces salmon bycatch by limiting fishing when salmon move deeper at night. Thermal and diel depth-use behaviours were more pronounced in southern compared with northern salmon populations. Cumulatively, these behaviours contributed to a broad-scale temperature effect on annual bycatch dynamics, mechanistically suggesting that climate change and increased frequency of marine heat waves will intensify Chinook salmon bycatch in the Pacific hake fishery.

Our evidence suggests that salmon moving deeper to seek thermal refugia mechanistically exacerbated bycatch rates in warm ocean temperatures. We observed the strongest signal of thermal depth-use behaviour when SSTs were near  $18^\circ\text{C}$  as bycatch rates were minimal in shallow and peaked near 250 m water column depths (Figure 2). Because most hake fishing effort occurs at these depths (200–300 m), warm surface water likely has a disproportionate effect on total bycatch dynamics over the increased bycatch rates in cool SSTs in shallow waters. Adult salmon behaviourally avoid warm waters to minimize metabolic energy costs in the ocean and during upstream migration with  $18^\circ\text{C}$  representing a threshold of extreme thermal sensitivity in freshwater (von Biela et al., 2020; Brett & Glass, 1973; Goniea et al., 2006; Tanaka et al., 2000). A prior tagging study found that Chinook salmon moved deeper to avoid temperatures greater than  $12^\circ\text{C}$  in the ocean, and this threshold was also apparent in our observations (Hinke, Foley et al., 2005; Teahan, 2020). In southern salmon populations, bycatch rates peaked at progressively deeper fishing depths as SSTs increased above  $12^\circ\text{C}$ , which mechanistically supports salmon needing to move deeper to encounter cool water as the depth extent of warm SSTs increases (Figure 2). The contrasting warm SST patterns between northern and southern stocks might explain why we only saw a signal of thermal refugia at  $18^\circ\text{C}$  in the full model with all stocks combined. Warming ocean temperatures are predicted to shift marine species distributions, including different horizontal shifts among Chinook salmon populations (Santora et al., 2020; Shelton et al., 2021). We show how temperature-driven changes to salmon vertical distributions exacerbates overlap with hake and increases bycatch rates.

Diel patterns also influenced Chinook salmon depth-use behaviours with implications for bycatch and mitigation. Chinook salmon moved between shallow water column depths during the day and deeper depths at night (Figure 3), which represents the opposite diel pattern of many marine fishes (Brierley, 2014; Hays, 2003). Salmon may be using daylight in surface waters for foraging or navigation and/or retreating deeper at night to avoid nocturnal, surface-oriented marine predators (Byron & Burke, 2014;

Tanaka et al., 2000; Todd et al., 2022; Wilson et al., 2014). Two tagging studies also found that the deepest Chinook salmon dives occurred at night; however, other studies have observed opposite and variable patterns (Arostegui et al., 2017; Courtney et al., 2019; Hinke, Foley et al., 2005). We add broader spatial and temporal evidence for Chinook salmon diel depth-use behaviours of moving deeper at night, which increased overlap with deeper-dwelling hake at the most common fishing depths of the hake fishery. This provides a previously unknown behavioural explanation for why Chinook salmon bycatch rates in the hake fishery are greater at night and suggests that DVM could explain diel patterns in fisheries bycatch in other systems (Orbesen et al., 2017; Shirk et al., 2022). Hake fishers voluntarily limit night fishing as a strategy to avoid bycatch of multiple species with only 25% of the observed hauls occurring at night (Holland & Martin, 2019). Increased salmon bycatch rates at depth at night mechanistically supports this bycatch mitigation strategy to reduce fishing effort when spatial overlap between Chinook salmon and hake is temporally highest (Holland & Martin, 2019). However, further interactions with warm water suggest nuanced impacts.

We observed an annual impact of warm ocean years coinciding with higher bycatch rates, which can be explained by the interaction of thermal and diel depth-use behaviours. More warm water likely increases the frequency of salmon seeking thermal refugia exacerbating spatial overlap in the water column with hake and subsequently increasing bycatch. Furthermore, we found that the bycatch mitigation strategy of limiting night fishing becomes less effective for avoiding Chinook salmon bycatch in warm oceans (it may still be effective for avoiding other bycatch species). When SSTs are warm, salmon remain deeper across day and night, and fishers lose their ability to temporally avoid bycatch at depth, which eliminates the bycatch savings from night fishing reductions (Figure 4). In cool SSTs, night fishing reductions cause fishing effort to predominantly occur during the day when depth separation in the water column is greatest between salmon and hake resulting in reduced Chinook salmon bycatch (Figure 4). Cumulatively, increased frequency of thermal depth-use behaviours combined with the drop in effectiveness of a common bycatch mitigation strategy likely drove the striking annual pattern of increased Chinook salmon bycatch rates in warm ocean years (Figure 5).

Our results suggest that climate change and marine heatwaves will intensify Chinook salmon bycatch in the Pacific hake fishery. The top 6 years (out of 20), representing the highest annual predicted bycatch rates, occurred during known warm ocean years during the 2014–2016 Pacific marine heat wave and 2003–2005 warm Pacific Decadal Oscillation phase (Figure 5). Climate change is expected to increase SSTs and the frequency of marine heat waves in the California Current potentially making these high bycatch years more common (Cheung & Frölicher, 2020; Xiu et al., 2018). Early warnings of warm SSTs and marine heatwaves could alert salmon managers to account for increased bycatch mortality or inform hake fishers to utilize more or different bycatch mitigation strategies, such as hotspot closures or move on rules (Holland &

Martin, 2019). However, simple avoidance of warm water may have limited effectiveness if salmon also redistribute to areas with cool SSTs (Shelton et al., 2021). Cool water habitat compression (vertically or horizontally) could heighten spatial overlap among species that prefer these limited future habitats, which represents a broad ecological mechanism that may affect climate trends in fisheries bycatch in other systems (Santora et al., 2020).

Both thermal and diel depth-use behaviours and their subsequent consequences were more prevalent in southern (Klamath – Trinity, S. OR – N. CA, OR Coast) compared with northern (Puget Sound, S. BC) salmon populations. Warm SSTs were more common in southern latitudes, suggesting that lack of sufficient exposure to warm water may have precluded us from observing thermal depth-use behaviour in northern populations. However, population-specific behavioural differences in response to warm water are also a possibility (Eliason et al., 2011; Martínez-Porchas et al., 2009). Mechanisms influencing latitudinal or population-specific DVM patterns in Chinook salmon are unclear, but could relate to latitudinal variation in forage, predators, predation risk or genetic differences (Chasco et al., 2017; Friedman et al., 2018; Williams et al., 2015). Evidence for DVM was observed in tagging studies in California, Oregon, and Washington, but was absent in Alaska much further north (Arostegui et al., 2017; Courtney et al., 2019; Hinke, Watters et al., 2005). Despite only having an 8-year time series for population-specific models, 2014 (the warmest ocean year in our time series occurring during a marine heat wave) had among the highest predicted bycatch rates for all salmon populations except for the S. BC population. The next warmest years (2013, 2015) had relatively higher bycatch rates in southern compared to northern populations. This suggests that our lack of observed thermal and diel depth-use behaviours in northern salmon populations may explain the subsequently weaker trend between annual SSTs and bycatch rates. Variability in depth-use behaviours could inform spatial or population-specific management. For example, threatened northern salmon populations may experience less benefits from night fishing reductions and require alternative bycatch mitigation strategies, while southern salmon population forecasts may need to account for increased bycatch rates under climate change.

Our inference approach provides valuable mechanistic insights into drivers of Chinook salmon bycatch in the hake fishery, which should be applied through future studies to address additional population and management concerns. (1) We focus on bycatch rates because they signal our hypothesized behavioural mechanisms; however, these rates could be expanded to total bycatch estimates in a more thorough framework than our simple scenario. For example, we show high bycatch rates at depth in warm SSTs, and this could be integrated with spatiotemporal dynamics of warm SSTs (seasonal, latitudinal, longitudinal, depth extent) to further examine total impacts. Previous assessments have not determined bycatch to be a primary threat to salmon populations (Ianneli & Stram, 2015; NMFS, 2017). Our results suggest that bycatch will increase with warming oceans although we do not quantify here the precise population-level effects, which

would require alternative analyses. (2) Evaluating environmentally driven behaviours in hake could provide more information about the extent and dynamics of Chinook salmon-hake spatial overlap. Hake exhibit temperature-driven horizontal shifts and diel vertical shifts in distribution (dispersing shallower at night) (Emmett & Krutzikowsky, 2008; Malick et al., 2020). Understanding these behaviours could facilitate or limit opportunities for avoiding Chinook salmon bycatch while catching hake. (3) The ultimate goal is to inform bycatch mitigation, which will require understanding the drivers of fisher behaviour, the effectiveness of various mitigation strategies, and the trade-offs between bycatch and hake catch. Shirk et al. (2022) examined this exact trade-off and found that removing only the top 1% of hauls with the highest predicted Chinook salmon bycatch reduced the bycatch-to-hake ratio by 20%. Thus, there is potential for thermal and diel depth-use behaviours to inform adaptive management with minimal costs to hake catches (Pons et al., 2022).

Mitigating climate impacts to fisheries bycatch and, hence, sustainable fisheries can benefit from understanding the behavioural and ecological mechanisms driving bycatch dynamics. Our approach highlights how thermal and diel depth-use behaviours interacted with current bycatch mitigation strategies to intensify Chinook salmon bycatch in the Pacific hake fishery in warm ocean years. These results have potential far-reaching implications to those relying on hake and salmon fisheries, sustainable seafood, and healthy ecosystems. A mechanistic perspective can, therefore, provide insights into species biology, inform adaptive bycatch mitigation, and warn of bycatch consequences in a changing world. With rapidly warming oceans and increased frequency of marine heat waves causing horizontal and vertical shifts in marine species distributions, it is essential to consider how climate-driven behaviours will reshape species interactions and subsequently patterns in and mitigation for fisheries bycatch.

#### AUTHOR CONTRIBUTIONS

MCS developed research questions, conducted analyses and wrote the first draft of the manuscript. MB and KR secured funding and VJT and KR facilitated observer data access. PM conducted genetic analyses. TL assisted with statistical advice. All authors contributed to development of ideas and writing edits.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

The fishery-dependent data from the hake fishery is confidential and cannot be shared under the Magnuson-Stevens Act at section 402(b), 16 U.S.C. 1881a(b).

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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