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Projected 21st century shifts in fish growth potential in the California Current Ecosystem

Kelly Vasbinder[1*], **Jerome Fiechter**[1], **Jarrod A. Santora**[2], **Nate Mantua**[2], **Steven T. Lindley**[2,3], **David D. Huff**[4], **Brian K. Wells**[2,4,5]

1 Department of Ocean Sciences, University of California Santa Cruz, Santa Cruz, California, United States of America, **2** Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, California, United States of America, **3** Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California, United States of America, **4** Fish Ecology Division, Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Newport, Oregon, United States of America, **5** College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, United States of America

* kvasbind@ucsc.edu

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Abstract

We present a modeling framework that quantifies 21st Century climate change impacts on early-marine fish growth potential along the central U.S. west coast using juvenile Chinook salmon as a case-study species. A bioenergetic model responding to future scenarios for krill concentrations and temperatures was used to calculate future growth potential for two ocean entry locations along the U.S. west coast from 2000-2100. Our results indicate that climate change impacts will vary by latitude and entry time, with increased future growth potential in the north regardless of entry time and reduced growth potential in the south for late entry fish. In addition, northern ocean locations will likely experience an increase in anomalously positive growth years over the course of the 21st century. Overall, our scenario reflects a warming ocean that causes spatiotemporal shifts in growth potentialfor juvenile salmon along the U.S. west coast and highlights the benefits of using such modeling frameworks to explore climate change impacts on early growth of marine fishes.

Introduction

Investigations of fish survival and fisheries recruitment have long been tied to the idea of a critical period during early life in which young fish must acquire enough nourishment to sustain bioenergetic processes and grow out of the life stages most vulnerable to predation [1,2]. These critical periods can encompass processes such as post-larval stage growth, density-dependence during early life, and the match/mismatch of this critical period to the availability of potential food sources, all with the central tenet that trophodynamics during early life are a key component of survival and recruitment variability [1–6]. For juvenile salmon (*Oncorhynchus spp.*), one of these critical periods is the period from the moment of ocean entry to the end of their

via the following DOI: https://doi.org/10.5061/dryad.63xsj3vf3 FORTRAN 90 formatted source code for the basic biogeochemical model has been published in the supplementary material of [97] Fiechter et al. 2018: https://doi.org/10.1002/2017GL076839. Bioenergetic starting parameters for the bioenergetic juvenile Chinook salmon model can be found in the supplementary material of Fiechter et al. 2015: https://doi.org/10.1002/2015GL063046.

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first summer in the marine environment. In some populations this critical period of expected high and variable mortality rates also occurs later during the first winter at sea [7,8]. Importantly, growth-dependent survival rate variations during the critical period are influenced by environmental variations that alter prey and temperature fields, which impacts fish bioenergetics and in turn their ability to escape size-selective pressures such as predation through rapid growth [9,10].

Here, we propose a framework for the general use of regionally downscaled global climate change projections in the investigation of environmentally mediated ecological variables. We implement this framework by projecting growth potential for juvenile Chinook salmon (*O. tshawytscha*) in the central California Current Ecosystem (CCE) for which we have extensive empirical knowledge of early growth and survival dynamics (Fig 1). Besides the wealth of empirical knowledge available on the species, Chinook salmon is also a valuable target species for study due to its strong ties to regional socioeconomic and cultural landscapes [11]. We frame our ecological predictions through a bioenergetics perspective because the elements required to investigate variability in growth are available at multiple spatio-temporal scales, allowing estimation of uncertainty through an ensemble approach using the ensemble spread between three earth system model projections (Fig 1). We focus our investigation of climate change impacts on two drivers important for fish growth: temperature and food availability. The effects of climate change, and temperature specifically, on marine species has been demonstrated for mobile fishes with the capacity to change their distribution to best mitigate habitat alteration (e.g., [12–15]) with some consideration of how both trophic relationships [16,17]and fisheries will respond to distribution shifts [18,19] and temperature-related physiological changes [20–22]. For many marine taxa, their ability to react to changes in environmental conditions is more complex than a simple habitat suitability indicator that is likely driven by temperature. Taxa with less motility like bottom fishes, structure-affiliated taxa, and emigrating anadromous fishes are challenged by the environment they are faced with [23]. Future warming conditions have the potential to affect physiology and bioenergetic dynamics, ultimately resulting in changes to growth potential ([24]) and associated vulnerability to size-selective predation [25].

In addition to temperature, we also explore the sensitivity of early marine growth potential to climate change impacts on prey availability. Environmentally mediated growth during the first few months at sea is a key period for juvenile Chinook salmon, especially in regards to growth and size mediated mortality [7,10,26,27]. Fish along the U.S. west coast rely on the productivity and features of the California Current upwelling system to achieve rapid growth at early life stages in order to reduce their size-dependent mortality risks [28–32]. Both prey quality and accessibility are important for juvenile Chinook salmon entering the CCE. Prey accessibility is dependent on ocean conditions, with early-season upwelling leading to higher and more persistent krill concentrations which are better matched to juvenile salmon emigration timing [26,33]. Prey quality is related to the availability of favorable, lipid-rich prey, and is correlated with improved body condition and stomach fullness for individual salmon [32,34]. Prey quality is typically regulated by processes associated with changes in

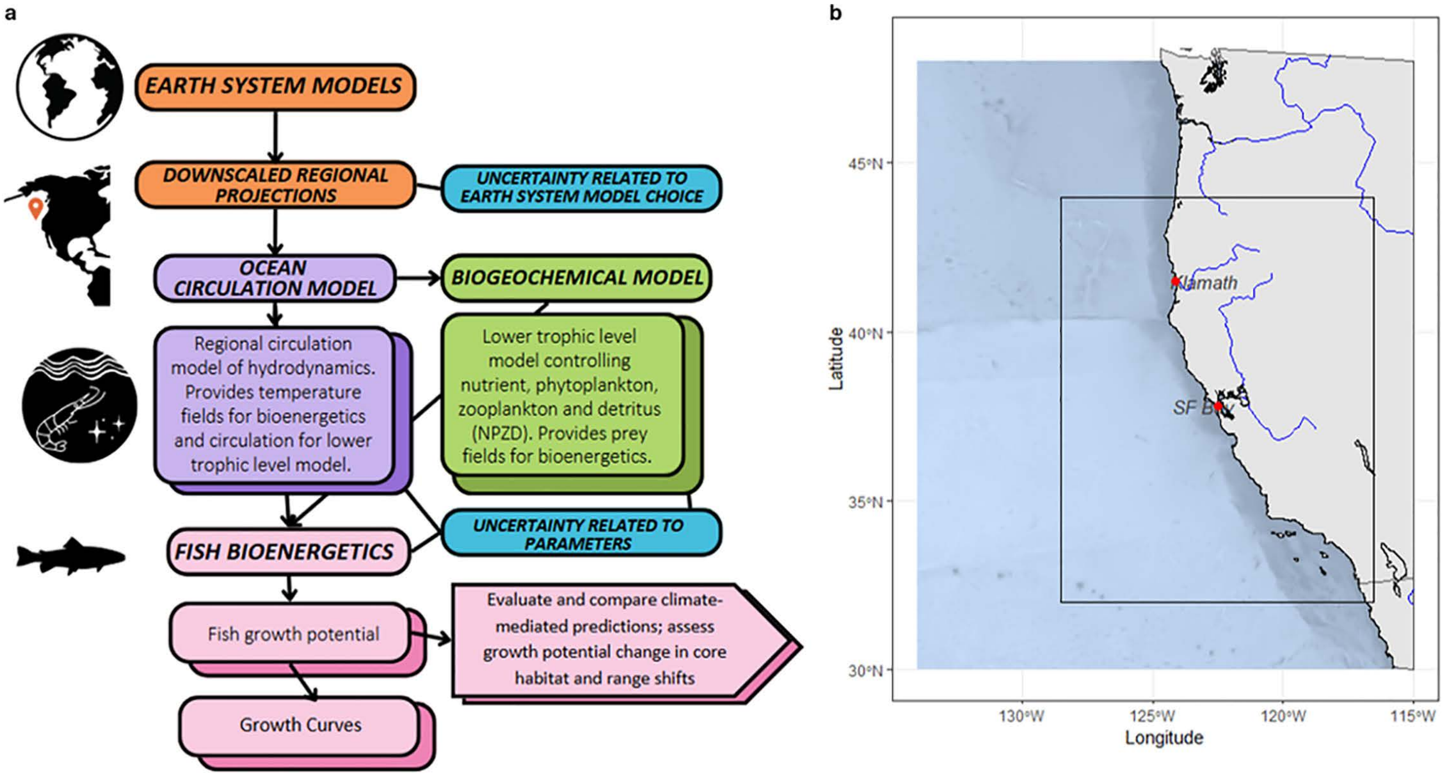

Fig 1. Modeling framework and geographical domain. (a) Model structure and methodology with related uncertainty sources. Each component incorporates ecological information ranging from physical observations to shipboard measurements of krill abundances and extensive salmon-specific field data. (b) Geographical region and model domain for high-resolution downscaled regional climate projections (black outline) used in this study. The red circles indicate ocean entry location for Central Valley and Klamath river salmon populations (corresponding river systems are in blue). Bathymetry is from ETOPO1 1 Arc-Minute Global Relief Model ([64] Amante and Eakins 2009); coastlines and rivers are from the *rnaturalearth* database ([65] Massicotte and South 2025).

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the regional- and basin-scale circulation, while prey accessibility tends to be controlled by local and mesoscale processes, necessitating the use of models that can represent processes at multiple scales [30,31,35]. In this study, we focus on the impacts of climate change on growth potential during this critical period in two ocean entry locations for Chinook salmon smolt along the U.S. west coast: the coastal marine areas connected to the Klamath river and San Francisco Bay, the latter being the exit point for Central Valley Chinook salmon. As climate change effects continue to progress, we expect changes in trends and variability in ocean conditions over a wide range of spatial scales (local to basin), and thus impacts on fish growth and survival rates throughout the CCE (e.g., [36–38].

Quantifying the impacts of climate change on the growth of a temperature-dependent, site-dependent mesopredator, such as salmon, requires linking climate change to prey and temperature both spatially and temporally. Tools are needed to assess simultaneously how likely a species may shift their distributions in response to changing climate, but also how a species may experience changing climate bioenergetically [39]. In the case of California Chinook salmon, ocean entry occurs at a fixed set of locations, and while they can adjust temporal overlap with varying poor conditionsby entering the system earlier or later, juveniles are still forced to experience the environment at these entry locations regardless of the ability of environmental factors at these locations to meet metabolic needs [40,41]. Substantial observational and modeling work for Chinook salmon has been conducted for decades in an ecosystem oceanography perspective [26,33,42,43]. Historical observations from the CCE show that salmon production, as well as ocean prey and temperature, vary on multiple scales. Here, we use an ensemble of regionally-downscaled climate projections ([44]) coupled to a fish bioenergetics model [10,33] to resolve processes that drive regional and sub-regional variability in temperature, prey availability, and their interactive effect on growth potential of juvenile salmon in the CCE (Fig 1). The bioenergetic model follows the properties of minimal realistic modeling, such that the same methods can be broadly applied and scaled to other species. Hence, our framework could be implemented for any region and species for which climate projections and bioenergetic relationships exist. This modeling infrastructure can be used to produce predictions of organismal growth potential and scales of variability underlying potential phenological and spatial shifts in growth patterns that may inform future management strategies and decisions.

Methods

Our modeling framework uses an ensemble of three downscaled regional climate projections and a fish bioenergetic model to assess the impact of a future scenario for krill and temperatures on juvenile salmon growth potential in the CCE (Fig 1). While detailed descriptions of all model components are available elsewhere [33,44], a summary of their overall implementation and formulation is provided below.

Downscaled climate projections

Three earth system models (IPSL-CM5A-MR, HadGEM2-ES and GFDL-ESM2M) from the Coupled Model Intercomparison Project 5 (CMIP5) were dynamically downscaled to produce regional climate and lower trophic-level (ending at the large zooplankter krill) projections at 10 km resolution for the broader CCE region under the Representative Concentration Pathway 8.5 (RCP8.5) high emissions scenario [44]. The earth system models supply the ROMS-NEMUCSC framework with boundary conditions using a one-way downscaling method with a time-varying delta bias correction [44]. Since the two main variables impacting bioenergetics in our fish model are temperature and krill, the three downscaled projections provide a range of future changes in upper ocean temperature and secondary productivity. ROMS-GFDL is a downscaled projection of the earth system model GFDL-ESM2M, ROMS-HAD is downscaled from HadGEM2ES, and ROMS-IPSL is downscaled from IPSL-CM5A-MR [44]. While all three projections used the same RCP8.5 emissions scenario, they differ in the location and intensity of warming and regional productivity patterns in the CCE [44].

The 10 km downscaled solutions were further nested into a gridded 3 km resolution ROMS-NEMUCSC domain for the central CCE to produce a more detailed representation of nearshore processes impacting juvenile salmon growth potential in coastal waters [46]. We use an ensemble approach to present the trend, mean, and spread of these three high-resolution, downscaled and nested projections for 2000–2100, and hereafter refer to them as ROMS-IPSL, ROMS-GFDL, and ROMS-Hadley. We estimate uncertainty related to earth system model choice with the ensemble spread. While the RCP8.5 scenario may be seen as an “extreme” pathway, we considered it useful for two reasons: (1) it allows exploring ecosystem properties under extreme warming (e.g., identify thresholds), and (2) the earth system model with the lowest rate of warming (GFDL) in RCP8.5 is representative of the high end of the more moderate RCP4.5 scenario.

Bioenergetic model

Fish growth potential under future climate conditions was calculated using bioenergetic equations that quantify the impacts of temperature and prey (i.e., krill) availability on metabolism and somatic assimilation. These bioenergetic equations are parameterized for juvenile Chinook salmon and can be found in the supplementary material for Fiechter et al. (2015) [33]. Our bioenergetic model reflects the simplicity of the dynamic energy-budget approach used by the DEBkiss framework [47]. In the model, krill primarily feed on diatoms, and thus are sensitive to simulated changes in primary production [45]. Changes in primary productivity are driven by spatially-varying differences in water column properties, such as upwelling source water chemistry, stratification, and subsurface nutrient concentrations [44,48]. Krill concentrations and sea surface temperatures are extracted from the downscaled projections and used to calculate juvenile Chinook salmon growth potential according to equation 1, in which the change in body weight (W) over time is equal to a conversion efficiency γ_{WA} times the sum of $J_{A,}$ the biomass assimilated, minus J_M, the biomass expended on maintenance, and $J_{S,}$ the biomass expended on swimming.

$$dW/dt = \gamma_{WA} \cdot (J_A - J_M - J_S) \qquad \text{Eq 1}$$

Growth potential therefore balances the assimilation of body material and loss of body mass through metabolic and activity costs. J_S is not dependent on environmental conditions, so the relationship between J_A and J_M is the mechanism through which body growth changes under differing environmental conditions.

$$J_A = \gamma_{XA} \cdot \mathbf{f} \cdot \mathbf{j}_{Xm} \cdot \mathbf{e}^{dt} \cdot \mathbf{W}^{2/3} \qquad \text{Eq 2}$$

$$\mathbf{f} = va \cdot Us \cdot X/(e^{dt} \cdot j_{Xm} + va \cdot Us \cdot X) \qquad \text{Eq 3}$$

The biomass assimilation is calculated according to equation 2 in which W is the fish body mass, and j_{Xm} is the maximum surface-area specific feeding rate and is exponentially dependent on temperature (T) and its associated coefficient for biomass assimilation (d), which is an empirically derived parameter. Resource biomass (X) consumed is converted to assimilated energy (A) with an efficiency of γ_{XA} according to equation 3, the functional response to feeding, using a tuning parameter (va) and swimming speed (Us).

$$J_M = j_m \cdot e^{dt} \cdot W \qquad \text{Eq 4}$$

The metabolic costs of maintenance are calculated in equation 4, where j_m is the mass specific maintenance cost. Parameter sensitivity analysis using the *lhs* package in R indicated that a +/-10% shift in key bioenergetic parameters does not exceed the range of the ensemble spread, so we proceeded with the ensemble approach [49].

We use a value of 7.4 g for W (87 mm) for juvenile Chinook salmon at ocean entry in accordance with macfarlane (2010) [50], and examine growth potential during entry periods of April/May for San Francisco Bay and June/July for Klamath River. We use this smolt ocean entry size for representative purposes, as field observations and model simulations show that smolts enter the ocean at a range of sizes and days that are sensitive to stream conditions [51]).

Analysis method

We used the R packages *ncdf4, rts, raster, terra* and *stats* [52–55] to calculate and visualize 21st century ensemble mean and trend of surface temperatures, krill concentrations, and juvenile Chinook salmon growth potentials for the coastal region of the CCS between 34 and 44N (S1 Fig). We only considered model locations inshore of the 400-meter isobath to correspond with coastal areas where juvenile salmon are typically found [34,50]. To further assess alongshore changes in growth potential, we zonally averaged the data over 1 degree latitude bins.

Here, we analyzed projected change in growth potential through its ensemble mean and spread, where ensemble spread was calculated as the standard deviation across all ensemble members relative to the ensemble mean:

$$\mathit{Ensemble\ Spread} = \sqrt{\left[\frac{((gfdl - mean)^2 + (ipsl - mean)^2 + (hadley - mean)^2)}{3}\right]} \qquad \text{Eq 5}$$

Phenology of Growth

We examined the impact of temperature change on early marine growth potential for juvenile Chinook salmon at ocean entry near the Klamath River (41° to 42°N) and theSan Francisco Bay (37° to 38°N). For each year and entry location, we calculated daily growth potentials for April to October using shelf-averaged values for the first (2000–2029) and last (2071–2100) thirty years of the 21st century. We compared the climatology of growth potential to the prescribed ocean entry dates (derived from observations and models) to identify potential phenology shifts in ocean entry conditions in the future [56]. Klamath River outmigration times are from model simulations of stream and juvenile salmon ocean entry [57,58]. We use a dataset of Chinook salmon out-migration days from Chipp's Island surveys (located within San Francisco Bay near the location of ocean entry) as a proxy for outmigration times [50]. We identified a peak ocean entry date as the annual mean day of the maximum number of smolts observed in Chipp's Island catches and modeled for the Klamath River. We calculated cumulative growth curves for fish entering the ocean during the month preceding and following the peak ocean-entry date using spatially averaged growth potential values near the entry location. To examine the phenology of ocean conditions that juveniles experience soon after ocean entry, we simulated fish size at age from the date of ocean entry for an 87mm smolt through their first 90 days at sea. Additionally, we evaluated projected climate change impacts on growth potential and size at age f for an 87mm smolt at ocean entry for different ocean entry dates over the course of the 21st century, including for fish entering earlier or later than the historical peak ocean-entry day.

Anomalous growth years and latitudinal shifts in growth

To quantify changes in growth potential by decade for the two ocean entry regions, we calculated the ensemble mean trend in growth potential for an 87 mm fish (average juvenile Central Valley Chinook salmon size at ocean entry) [33,50]. The trends were calculated for fish entering the ocean during the months preceding and following peak ocean entry time. Early/late ocean entry for Central Valley salmon corresponds to April/May, while early/late entry for the Klamath River corresponds to June/July. We used packages *dplyr, HH, matrixStats,* and *ggplot2* to calculate and visualize anomalies [59–63].

To examine growth potential anomalies by latitude, we evaluated an average sized fish after its first 45 days at sea (assuming it has reached 100mm FL). A present-day baseline was established as the ensemble mean of 2000–2030, similarly to the phenology analysis. Anomalous years are considered to be years that are more than 1 standard deviation away from the baseline, and extreme years are defined as years that are more than 2 standard deviations away from the baseline. Anomalous and extreme years were calculated per decade and latitude. We split the domain into a northern and southern subregion, each encompassing one of the two regions of ocean entry.

Our results follow the ensuing structure: We first present growth potential at ocean entry for the whole coast, using an 87mm fish, as this is the size of a fish at ocean entry (Fig 2). Next, we ask what would happen to the fish as it grows under new climatic conditions in the time period just after ocean entry, for which we use a latitude range directly surrounding the two ocean entry points (41–42 deg N and 37–38 deg N). Finally, we ask what anomalous conditions this grown fish would experience as it leaves its ocean entry point and spends its first month at sea, either near the Klamath 39.5-43.5 deg N, or the Central Valley and 35.5-39.5 deg N (Fig 4, 5). For these last two analyses, we use a larger fish of 100mm, the size of a fish after it has been at sea for 45 days, halfway through the "early ocean" period which is the first 90 days after entry.

Results

Growth conditions at time of ocean entry

Ensemble mean trends indicate that during the 21st century, all nearshore areas of the CCE will experience warming, while some subregions will experience an increase in krill availability due to increases in krill concentrations (krill biomass per area) and others a decrease (S1 Fig). Warming reduces growth potential by increasing metabolic costs if krill

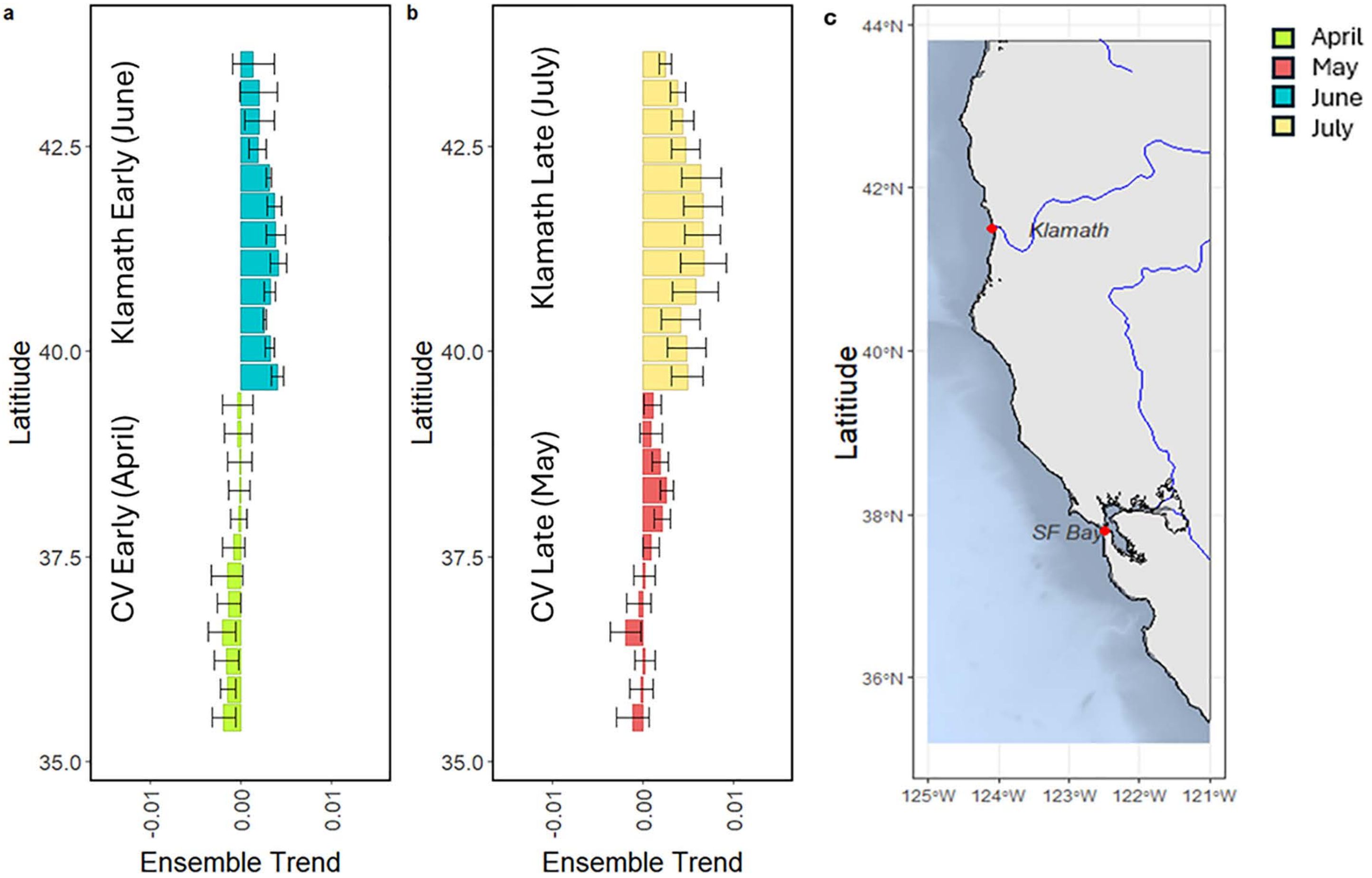

Fig 2. Projected change in growth potential (ensemble mean trend) as a function of latitude for (a) early and (b) late entry juvenile salmon originating from the Klamath River (KR: blue and yellow bars) and San Francisco Bay (CV: Central Valley) (green and red bars) (see red circles in panel (c) for entry locations). Growth potential was calculated based on an 87 mm fish. Trend in climate represents a linear rate of change in a variable over the period considered, in this case the century from 2000-2100. Here, we present trend as change in growth potential (g) per decade and the error bars represent the ensemble spread for the trend. Bathymetry is from ETOPO1 1 Arc-Minute Global Relief Model ([64] Amante and Eakins 2009), coastlines and rivers are from the *rnaturalearth* database ([65] Massicotte and South 2025).

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concentrations are constant (Equations 1, 4). Similarly, increasing krill with no change in temperature increases growth potential (assuming consumption rates also increase) (Equations 1, 2). Hence, spatial differences in the ensemble mean trend for growth potential reflect increasing metabolic demand interacting with spatially varying changes in krill availability.

Growth potential at the time of ocean entry is projected to increase for the ocean entry point at the Klamath, but stay the same or decrease for the ocean entry point at San Francisco Bay (Fig 2). For coastal regions surrounding the Klamath River (KR) entry location, daily growth potential increases in the future compared to present from Julian day 150–220 (Fig 3a). Mean cumulative size of fish entering in either June or July (Julian day 151–210) increases by ~15% and ~8% for June and July entry, respectively (Fig 3b-c). For CV salmon entering the ocean from San Francisco Bay (37–38°N), daily growth potential between current and future is similar for days 90–120, then increases in the future for days 121–175, before falling much lower than present day growth potentials (Fig 3d). CV salmon size at age is unaffected for April entry dates, but declines by the end of the first 90 days at sea for May entry dates (Fig 3e-f). Box and whisker plots of estimated fish size at the end of the first 90 days at sea show that KR fish diverge in size with future fish

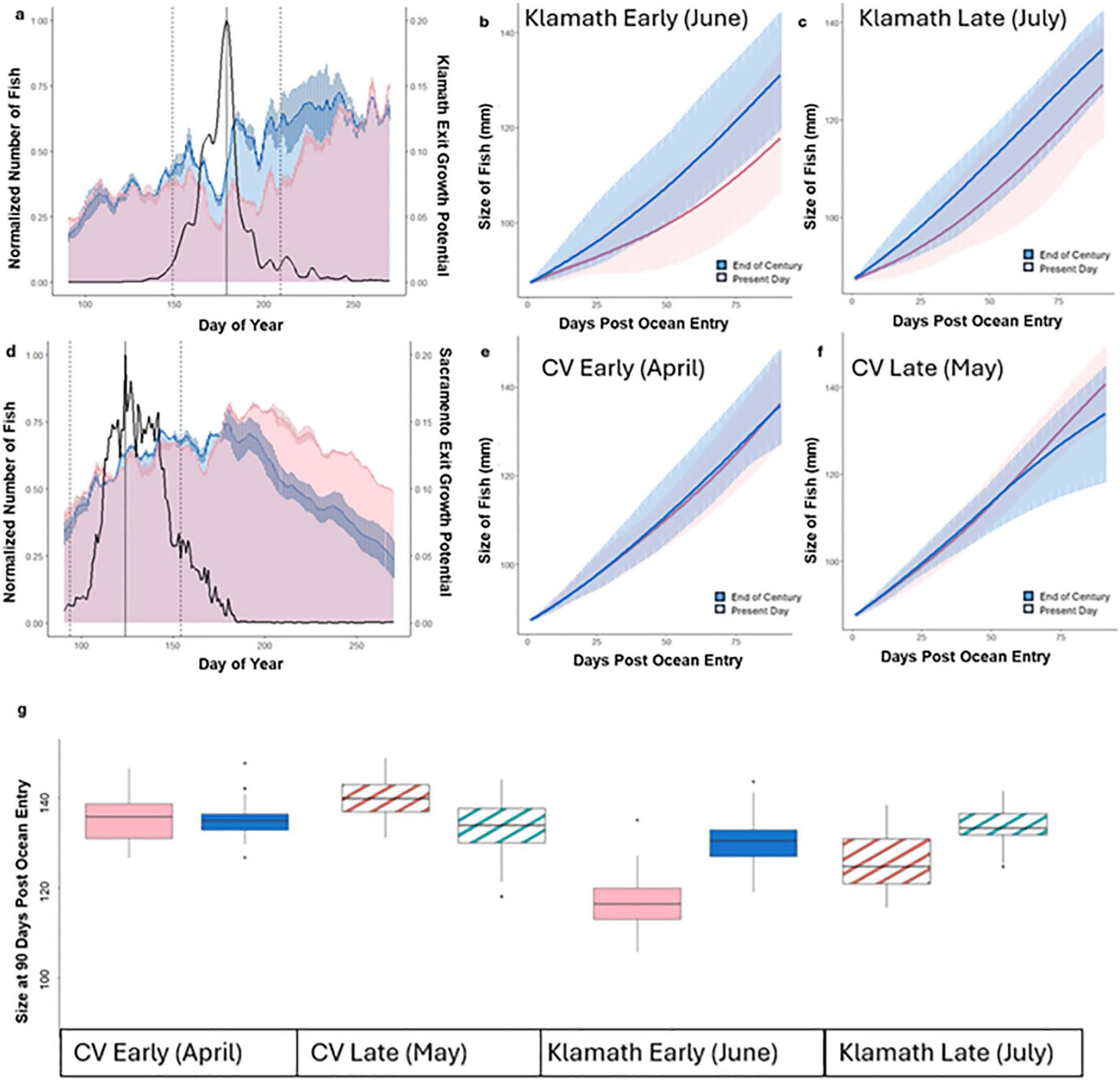

Fig 3. Projected daily climatological growth potential (ensemble mean) for the (a) KR and (d) CV ocean entry locations for present day (2000–2029; pink) and end of the century (2071–2100; blue) conditions, with error bars denoting the ensemble spread. The black lines in (a) and (d) represent the normalized historical daily number of fish entering the coastal ocean at each location. Vertical lines indicate the date of entry with the maximum number of smolts (solid) and the entry window we chose based on that date (dashed - one month before and one month after). Panels (b-c and e-f) represent simulated cumulative growth curves for (b-c) KR fish and (e-f) CV fish entering of the ocean during the month (b, e) preceding and (c, f) following peak entry time (April-May for CV and June-July for KR. Box and whisker plots (g) for all time/place combinations (April – early CV, May – late CV, June – early KR, July – late KR) show projected smolt size at 90 days post ocean entry. Solid boxes represent early ocean entry fish, and hatched boxes represent late ocean entry fish. Except for CVearly entry, the differences between present-day and end-of-the-century cumulative growth distributions are significant ($p < 0.001$).

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being larger, while CV salmon are projected to remain similarly sized to present for early entry and become smaller for late entry (Fig 3g). This indicates that the loss in growth occurs later in the summer after entry, once the growth potential per day in present time falls below those for the end of the century (Fig 3d,g). Based on the ensemble spread (S1 Fig c), the projected changes are relatively robust across all ensemble members in regions of marked increases or decreases in growth potential.

Growth conditions during first 90 days

While changes in growth potential at the time of ocean entry are relatively easy to interpret based on projected temperature and krill abundance, cumulative daily growth conditions during the early marine phase (i.e., first 90 days at sea) are shown in Fig 3 to compare size at age trajectories among years and between ocean entry points. Increasing growth potential is projected for the Klamath region for a 2–3 month period starting around the time of peak entry, which allows for higher sustained cumulative growth (and larger size at age) over the first 90 days at sea regardless of entry times (i.e., month preceding or following entry peak) (Fig 3a-c). Here, the temporal match between future changes in growth potential and entry time leads to a situation in which changes in conditions at ocean entry are reliable predictors of cumulative early growth. In contrast, large declines in growth potential for the CV population (San Francisco Bay ocean entry location) are predicted to occur 2–3 months later than peak entry time (Fig 3d). As a result, cumulative growth and size at age during the first 90 days are predicted to be mostly unaffected for fish entering the ocean in April (early, *i.e.,* they will not experience the period of largest change), but substantially decreased for May (late) ocean entry fish. Here, the temporal mismatch between future changes in growth potential and ocean entry times results in a situation where growth potential changes at ocean entry provide poor (and even erroneous) information about cumulative growth during the first few months at sea.

Anomalous and extreme growth conditions

In addition to long-term changes, annually-varying anomalous and extreme growth potential variations provide another view of climate change impacts on salmon populations along the U.S. west coast. In the north, both early and late entry fish will experience an increase in anomalously and extremely good growth potential years relative to present. In addition, Klamath Basin fish will also be exposed to less frequent anomalously poor growth years by the end of the century (Fig 4a,b). By 2080 late entry Klamath Basin fish are projected to experience 5 years per decade with anomalously or extremely good growth conditions. In contrast, both early and late entry CV fish are predicted to experience an increasing frequency of anomalously poor years each decade as the century progresses, with a higher fraction of those years being extremely poor compared to the ensemble mean baseline (Fig 4c,d). Early entry CV fish will also progressively experience a reduced frequency of anomalously good growth years. By 2080, all CV fish are projected to experience 3–4 anomalously or extremely poor years per decade.

Patterns of the long-term change in anomalous and extreme growth conditions are also projected to vary spatially around the latitudes of each entry location. For the KR region, anomalously and extremely good years at the end of the century are projected to occur more frequently south (39–40°N) of the entry location for fish out-migrating earlier and in the direct vicinity (41–42°N) of the entry location for fish out-migrating later (Fig 5a,b). For the San Francisco Bay region, anomalously and extremely poor growth conditions are projected to occur more frequently south of the entry location, regardless of entry time (Fig 5c,d). Central Valley fish moving north following ocean entry are projected to experience little change in the frequency of anomalously/extremely poor and good growth conditions.

Discussion

Our case study for Chinook salmon demonstrates how multi-model frameworks can be used to address questions of both regional and coast-wide climate impacts on juvenile fish. First, we identified overall spatial patterns and trends in growth

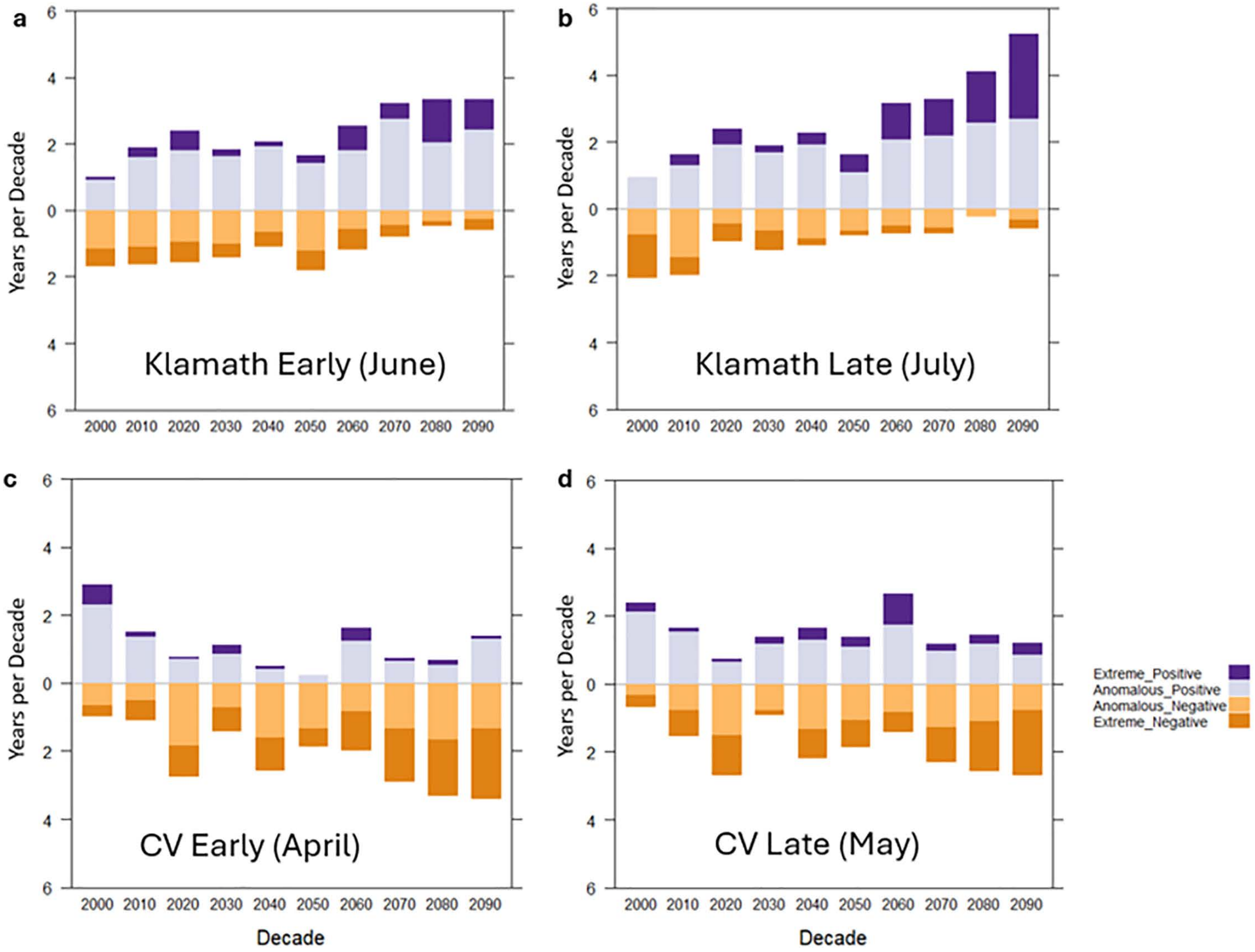

Fig 4. Projected number of anomalous and extreme growth potential years (ensemble mean) per decade for the (top) Klamath and (bottom) Central Valley juvenile salmon ocean entry locations. "Anomalous" and "extreme" are defined as 1 and 2 standard deviations above or below the 2000–2030 baseline mean, respectively. Light/dark purple shading indicates anomalous/extreme high growth potential and orange/red shading indicates anomalous/extreme low growth potential.

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potential anomalies at the regional scale. Second, we examined the climatology of two ocean entry locations to predict future match/mismatch between the timing of outmigration and favorable growth conditions. Next, we predicted size at age over the first few months at sea for these two regions to identify sensitivity to earlier or later ocean entry times. Finally, we predicted the likelihood of anomalous and extreme years compared to present-day conditions and explore uncertainty related to increased variability.

Our model framework suggests spatiotemporal variability in growth potential for both long-term change (i.e., ensemble trend) and changing frequencies for anomalous and extreme years. This analysis indicates that projected climate impacts on juvenile salmon growth along California will exhibit alongshore (north-south) differences, with a transition occurring at latitudes around 38–40°N. This separation corresponds with distinct biogeographic regions characterized by differences

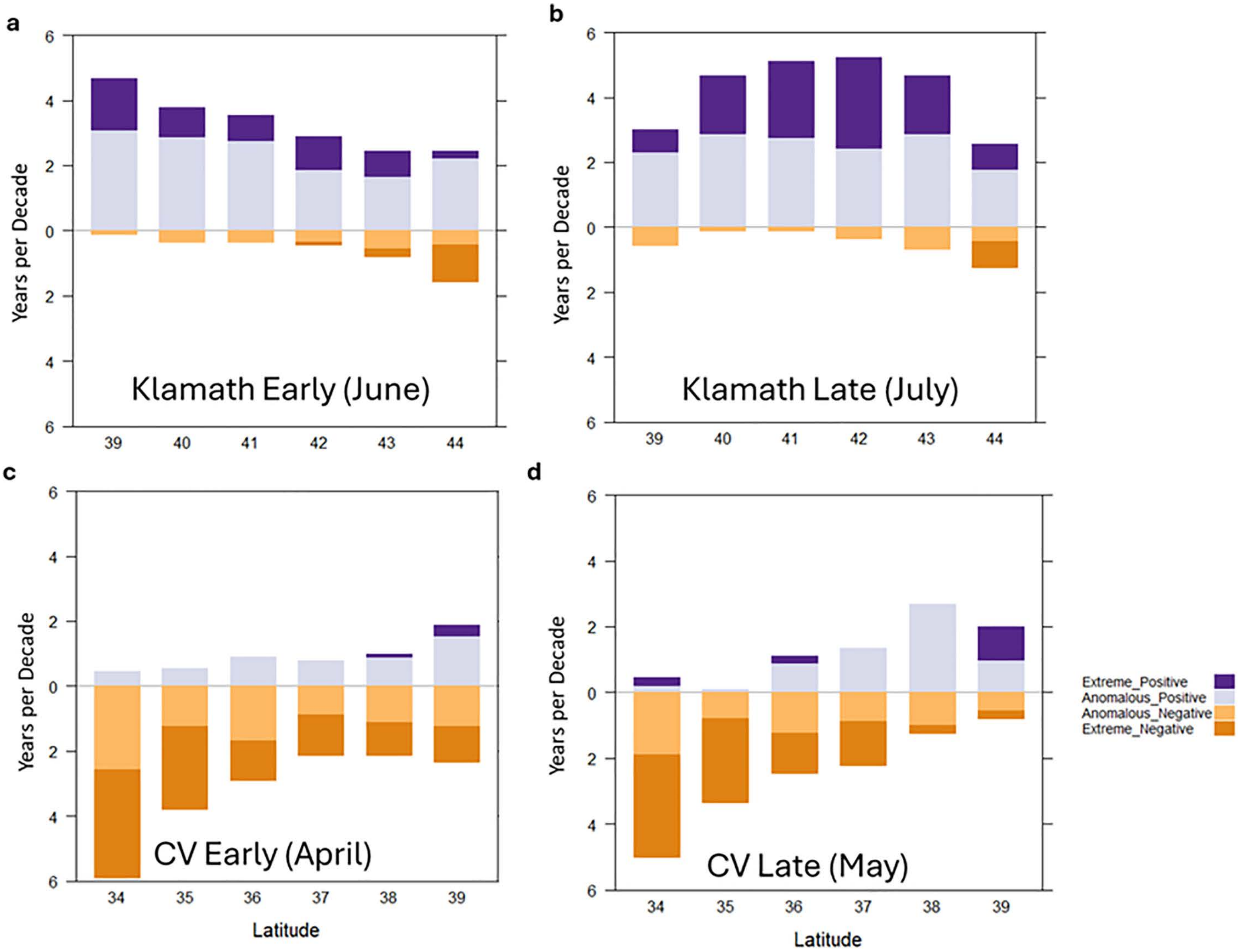

Fig 5. Projected frequency of occurrence of anomalous and extreme growth potential years (ensemble mean) per decade by 1° latitude bin at the end of the century (2070–2100 average) for the (top) KR and (bottom) Central Valley salmon ocean entry locations. "Anomalous" and "extreme" are defined as 1 and 2 standard deviations above or below the 2000–2030 baseline mean, respectively. Light/dark purple shading indicates anomalous/extreme high growth potential and orange/red shading indicates anomalous/extreme low growth potential.

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in spatiotemporal oceanographic conditions (e.g., upwelling dynamics), forage dynamics and communities, and overall productivity [31,66–68]. Under the scenario evaluated here, juvenile salmon growth potential and size at age are projected to decline in the southern subregion by the end compared to the beginning of this century. In contrast, growth potential and size at age in the northern subregion is projected to increase for juvenile salmon entering the ocean in late spring and early summer. Furthermore, the frequency of anomalously and extremely low growth potential years is expected to increase substantially at southern latitudes over the course of the 21st century (Fig 4,5).

While we use growth potential and size at age as the metrics to assess the impacts of a changing climate on juvenile Chinook salmon early marine success, our work should be framed in the context of growth as a driver for other factors impacting survival, such as predation mortality (e.g., [7,10,27]). Size-selective mortality during early marine life stages is an indicator of recruitment success for several Pacific salmon stocks, and a productive California Current Ecosystem better growth of early marine stages [69–71]. As juvenile Chinook salmon are spatially tied to areas of ocean entry, their ability to experience favorable growth conditions at these locations is necessary for increasing growth and reducing size-selective predation during their first few months at sea.

Prey availability as a mediator for temperature rise

Shift in harvestable production along a north-south gradient is a common metric by which to assess climate change impacts on fisheries. Under high emissions scenarios, north Atlantic fisheries are predicted to experience losses in current high catch areas while simultaneously experiencing increases in harvestable production in Arctic and sub-Arctic regions by 2090, and North Sea fishes have already begun to show range shifts due to changes in climate since the 1980s [72,73]. These shifts are expected to continue to be poleward for demersal species, deep sea species, and habitat building species or species tied to specific habitats [74,75]. Latitudinal differences in growth potential, such as those predicted by our model, may be indicative of whether habitat in a particular area has the potential to improve or degrade compared to present day, as well as whether specific fish complexes or stocks in that region will show losses or gains over the course of the century. The ability to resolve both temporal and spatial nuances in prey fields makes this model a good candidate for exploring the ways in which prey availability mediates temperature rises under climate change scenarios.

In the CCE, the growth of many marine fish species relies on the strength and productivity of coastal upwelling, which itself varies as a function of upper ocean temperatures, alongshore wind stress, and subsurface nutrient concentrations [28,33]. Estuarine and marine life stages of CV Chinook salmon are considered highly vulnerable to climate change, and increasing sea surface temperature has been identified as a specific marine attribute contributing to this vulnerability due to the high magnitude of change to which CV Chinook are exposed [37]. The future climate scenario used here includes situations where projected increases in krill abundance locally offset the increase in metabolic costs for juvenile salmon associated with rising temperatures. The latitudinal patterns in the trend and frequency of growth potential anomalies highlight the relative importance of the underlying factors that modulate growth. While a reduction in coastal upwelling is directly detrimental to krill concentrations and hot-spot persistence [[45,76]], associated warmer temperatures may also increase the bioenergetic costs for early life marine fishes. Hence, future growth potential of juvenile salmon along the U.S. west coast will be determined locally by a balance between the magnitude of changes in ocean productivity and upper ocean warming.

Implications for mitigating climate change impacts

Anadromous fish such as Chinook salmon will experience the effects of climate change in both freshwater and marine environments [37,77], so climate change mitigation strategies must address both phases of their life cycle. Freshwater-focused management tactics such as cold-water storage and timed cold-water releases may offer a way to maintain suitable freshwater thermal habitat for juvenile Chinook in the Sacramento River system [78–81]. This work, through its evaluation of carry-over effects ([82]), provides a framework to consider strategies that mitigate mortality in the marine realm. Determining whether climate change mitigation strategies in freshwater and during the first few months at sea are synergistic or antagonistic will help identify strategies that take into account both life phases.

Marine temperature affects growth and therefore size-selective processes such as predation, which in turn cause variation in recruitment [10,41,83]. In our case, juvenile Chinook salmon at the time of ocean entry are vulnerable to gape limited predators (e.g., seabirds) and the faster they are able to grow out of these gape ranges, the lower their risk of being preyed upon [7,10,27]. Spatial and temporal changes in growth potential therefore impact when and where juvenile salmon may be vulnerable to size-selective predation. For example, close proximity of high growth potential areas to ocean entry locations will likely enhance early marine survival rates.

Our study also highlights the fact that phenological match-mismatch between timing of ocean entry and projected change in coastal upwelling make it difficult to infer cumulative growth from conditions at time of entry. Under the assumption that the window of ocean entry times will remain the same in the future, our results show that projected changes in temperature and prey will have both spatial and seasonal match-mismatch effects on juvenile salmon growth potential, with end-of-the-century conditions favoring increased growth potential for early and late entry fish in the north. In contrast, end-of-the-century conditions indicate reduced growth potential for late entry fish in the south. In the north, ocean conditions are projected to become more productive around peak entry time and in the months following, leading to a situation where future changes in growth potential at the time ocean entry are representative of changes in cumulative growth over a 90-day period. In the south, the largest projected changes in upwelling occur 2–3 months after peak entry time, leading to a situation where future changes in growth potential at ocean entry are not matched by changes in cumulative growth over the first 90 days. This temporal mismatch also results in conditions where outmigration time becomes an important determinant of early marine growth, whereby the size at age for fish entering the ocean late will decline in response to the projected decrease in growth potential. Empirically, changes in ocean entry size and timing have been shown to impact the size and age structures of spawners later in the Chinook salmon life cycle, indicating the potential for changes in phenology as climate changes to have prolonged impacts on cohorts [84]. By looking at the spread between ensemble members (downscaled earth system models, eq 5.), we can compare the magnitude of the climate change signal relative to projection uncertainty. As the projected differences in daily growth potential between present-day and end-of-the-century conditions largely exceed the ensemble spread, the scenarios examined here predict a robust increase in cumulative 90-day growth for all entry times in the Klamath region and a robust decrease in cumulative growth for late entry times in the CV salmon ocean entry region. Interannual variability in the phenology of ocean conditions is also high in the Klamath region, indicating the importance of anomalous and extreme events relative to the long-term trend (S2 Fig, S3 Fig).

Overall, our findings provide guidance for how future management strategies could promote adaptation to the impacts of climate change on freshwater stages, while at the same time increasing the probability that out-migrating fishes encounter favorable marine conditions during their first period at sea. For instance, advanced juvenile Chinook salmon outmigration timing is expected for the Columbia River under climate change scenarios in response to warmer freshwater conditions, and has already been modeled in CV nursery areas [36,51]. If the same response were to happen for fall run CV Chinook salmon, our results suggest that early entry juvenile salmon would remain within the expected present-day range of growth conditions after ocean entry. Hence, a natural adjustment to climate change during the freshwater phase may also act as a mitigating factor in the ocean. Such cascading effects emphasize the importance of climate change management strategies that consider potential synergistic adaptations in freshwater and ocean environments. For example, identifying a release time that concurrently optimizes the freshwater and ocean survival of hatchery fish may become an important future priority for CV Chinook salmon. Management of salmon populations is complicated, balancing release timings, habitat management, and both fresh water and ocean stages. For example, as a strategy favorable for fall-run Chinook salmon could be detrimental to winter- and spring-runs that have different outmigration timing, and vice versa [85,86].

Frequency of cohort failures with poor growth years

We project an increase in the number of anomalously poor growth years in the southern part of the domain as the century progresses. A prolonged period of poor ocean productivity and growth potential, such as 2005–2007 off central California, can point at poor survival of several consecutive cohorts and ultimately resulting in fisheries closures, thus compounding the impacts that would be experienced on a year-to year basis [87]. These low productivity and growth potential years directly preceded the 2008 closure of the salmon fishery in California. Similarly, several anomalously low growth potential years preceded the salmon fishery closure in 2023. This suggests that multiple poor years of growth in a row can cause consecutive cohort failures. Further, an increase in duration and recurrence of prolonged periods of anomalous conditions in the future could have long-lasting impacts on commercial and tribal salmon fishing communities.

Application to other species and drivers

The modeling approach described here could be easily applied to other CCE species for which a functioning bioenergetic model with temperature and prey dependence exists. For example, forage fish (e.g., sardine and anchovy), juvenile rockfish, blue whales, and even seabirds (e.g., Common Murre, Brandt's Cormorant, and Rhinoceros auklet) have all been shown to be associated with krill concentrations [45,76,88,89]. Species distribution models for many CCE species, such as Pacific albacore and blue whale, have also identified a strong dependence on temperature [88–90]. Several groundfish species even have fully parameterized bioenergetics models or individual based models that can predict growth as a function of temperature and prey fields [91,92]. An important parallel also exists between Chinook salmon and Pacific hake, a species identified as having moderate to high vulnerability to climate change and life stages with a high degree of dependence on environmental factors [77,93]. Applying a similar analysis to Pacific hake may, for instance, reveal distribution shifts (particularly towards cooler, deeper waters) in response to poorer growth conditions, given hake's moderate to high vulnerability and its potential for distributional shifts. As recruitment variability in hake has been shown to be driven by environmental factors during key life stages such as the yolk sac and late larval stages, and a framework to relate hake recruitment to oceanographic drivers exists, hake is a good candidate for similar climate modeling endeavors to the one we present here [93]. In addition, this or related frameworks could be adapted to include other environmental properties that impact bioenergetics, such as dissolved oxygen and pH [94–96]. By proposing a flexible modeling framework that is adaptable to other species and regions, we aim to better anticipate the ecological and economic implications of climate change in a variety of large marine ecosystems.

As downscaled climate projections become more readily available, researchers will have to choose how they apply these projections to explore potential futures and identify emergent properties (e.g., growth potential of early life stages) in response to shifts in oceanographic processes impacting the drivers and, ultimately, the property itself. Our multi-model framework bridges the gap between the need for robust ecological predictions under climate change scenarios and the necessity of an inclusive and rigorous methodology that explores the nuances of these projections at the relevant spatial and temporal scales.

Supporting information

S1 Fig. Ensemble mean for (a) temperature, (b) krill, and (c) growth potential, change in each driver per decade (ensemble trend) (d-f), and ensemble spread (between downscaled earth system models) (g-i) for projected (2000–2100) nearshore surface temperatures in degrees Celsius, krill concentrations in mmol N/m^3, and juvenile Chinook salmon growth potential in g/day for the month of May. Trends over the entire century are the rate of change (decadal) in growth potential (i.e., the slope).
(DOCX)

S2 Fig. Daily climatological growth potential for the Klamath (a) ocean entry locations for present day (2000–2029; pink) and end of the century (2071–2100; blue) conditions. Historical (2000–2015) modeled number of smolts emigrating to the coastal ocean by year-day at Klamath exit point is overlaid on panel (a) with the solid black line. Error bars represent interannual variability instead of ensemble spread (the variability in the 30 years included in each category, i.e., 2000–2029 and 2071–2100). (b, c) Spatially averaged simulated size at age for juveniles entering throughout the months of May and June for 90 days post ocean entry at the same location by year.
(DOCX)

S3 Fig. (a) Daily climatological growth potential for the Central Valley salmon ocean entry location for present day (2000–2029; pink) and end of the century (2071–2100; blue) conditions. Historical (1976–2015) number of smolts emigrating to the coastal ocean by year-day this exit point is shown by the solid black line (a). Error bars represent

interannual variability instead of ensemble spread. (b) Spatially averaged simulated length at age for juveniles entering throughout the months of May and June for 90 days post ocean entry at the same location by year.
(DOCX)

S4 Fig. Projected growth potential anomalies and extremes for a 100mm fish as a function of latitude for (a) Klamath river ocean early entry, (b) Klamath River ocean late entry (c) CV early entry (d) central valley late ocean entry ensemble mean annual growth potential anomalies relative to the present-day (2000–2030) mean. Black lines delineate negative vs. positive anomalies for.
(DOCX)

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Author contributions

Conceptualization: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Nate Mantua, Steven T. Lindley, David D. Huff, Brian K. Wells.

Data curation: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Brian K. Wells.

Formal analysis: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Brian K. Wells.

Funding acquisition: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Steven T. Lindley, David D. Huff, Brian K. Wells.

Investigation: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Brian K. Wells.

Methodology: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Brian K. Wells.

Project administration: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Nate Mantua, Steven T. Lindley, David D. Huff, Brian K. Wells.

Resources: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Nate Mantua, Steven T. Lindley, Brian K. Wells.

Software: Jerome Fiechter.

Supervision: Jerome Fiechter, Jarrod A. Santora, Nate Mantua, Brian K. Wells.

Validation: Jerome Fiechter.

Visualization: Kelly Vasbinder, Jerome Fiechter, Brian K. Wells.

Writing – original draft: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Brian K. Wells.

Writing – review & editing: Kelly Vasbinder, Jerome Fiechter, Jarrod A. Santora, Nate Mantua, Steven T. Lindley, David D. Huff, Brian K. Wells.

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