Reviewers' comments:

Reviewer #1 (Remarks to the Author):

This manuscript describes an effort to use a state-of-the-art life-cycle model to quantify the risks of extinction for 8 populations of Chinook salmon in the Pacific Northwest of the USA. The model relies heavily on an extraordinary dataset of individually tagged fish to estimate various functional relationships that describe the processes that affect survival throughout the life-cycle of this species. The model is used to simulate the potential effects of climate change on the viability of these 8 populations. The primary conclusion reached by these efforts is that climate warming is likely to doom this group of populations and that the primary survival bottleneck is during the fish's first year of life in the sea. While the model development is commendable and the data used are impressive, the conclusions that are drawn are not particularly new and have been appreciated for some time. Thus, it is not really clear what the main contribution from this paper actually is.

My concerns for the current manuscript are given below.

1) The manuscript attempts to grasp at jargon to increase its general appeal, but these attempts are often a bit off-target. For example, there has been a lot of interest in 'non-stationarity' in ecology and in fisheries science recently and this manuscript attempts to link in to these interests. However, while this term does refer to a changing variable (in the strictest statistical sense), use of this term in ecology typically is referring to changes in a relationship between variables (i.e. the relationship or correlation among variables is non-stationary). Thus, why call climate change 'stationary' or 'non-stationary'? We have known for decades that climate is non-stationary; what is interesting is that the relationships between climate conditions and ecological processes are non-stationary. Thus, use of non-stationary/stationary in this manuscript is somewhat distracting. While this is just a semantic issue, I don't think the paper benefits from the current use of these terms.

2) Similarly, the manuscript refers to 'aggressive' warming scenarios. This also seems misplaced. Typically we refer to aggressive scenarios of curtailing carbon emissions (i.e. it's not the climate that is aggressive, it's the policy actions to reduce emissions that are aggressive).

3) The key results are expressed as the time to quasi-extinction for each of these populations. In general, I do not think this is the best way to present the key results. When a modeled population goes extinct in these simulations is based on arbitrary population thresholds that probably don't apply well when populations are reduced to very low numbers where stochastic processes are more likely to ultimately determine whether they go extinct or not. Thus, the primary results of these simulations would be more useful if the population growth rate was the response variable used to explore the consequences of different climate scenarios (i.e. the posterior distribution of lambda). The result could then be focused on how much of the posterior distribution was <1, thereby leading to population decline, etc. Time to extinction is too arbitrary and too 'loaded' a variable that is easily misinterpreted that it shouldn't be used in these types of analyses.

4) Line 24, 'species' should be 'populations'

5) ~ Line 121, it is not clear what the goals of the paper are. Is it to construct this model? The paper would benefit from some clear statements about what the primary objectives of this exercise are.

6) It is surprising that the model suggests that the populations are essentially at no risk of going extinct given the ‘stationary’ climate scenario. This does not seem realistic given the current status of these populations.

7) I think the ‘Caveats’ section should be part of the Discussion of the paper.

8) The Discussion highlights the weakness of the paper. Here the text basically runs through what is known about different processes or conditions that affect salmon survival. Nothing is particularly novel in this summary, nor does it highlight the main contributions of this specific modeling effort. Thus, it reinforces the lack of clarity about what this specific research activity contributes to our general understanding of Chinook salmon ecology and conservation.

Reviewer #2 (Remarks to the Author):

I found this paper to be exceptionally well written and the topic to be of broad international interest as a study of the impact of climate on a commercially valued species that is now at risk. This work explores the population dynamic of 8 populations of Chinook salmon in the Snake River watershed. This paper uses a life cycle model and two climate change scenarios to model the potential population trajectories of these populations. It effectively tells the risks of changing climate, particularly at sea, to all these populations but especially the smaller ones. It is sobering in its assessment of the viability of these populations- not a happy story. However, it effectively looks at the fact that these fish persist in highly altered systems and actions in freshwater might mitigate or at least slow population declines and localized extinction. These findings are novel for the populations of interest and findings (and solutions) will they be of interest to not only the fisheries biology community but ecologists and also to the public. This work is a tangible story of the impact of change upon a species that captures the imagination of a broad spectrum of society. The species also has rich cultural importance to first nations in this watershed. These conclusions are supported by appropriate modeling and add to not only Pacific salmon literature but will be of great interest to Atlantic salmon conservationists. The sea-run nature of this species also will inform understanding of challenges in freshwater and marine systems. I found this paper to be extremely convincing and the conclusions are strengthened by a rice use of citations and the addition of allied related manuscripts on the stream temperature model and wild/hatchery marine survival. This work is cutting edge and current. I firmly believe that this paper will influence thinking in the field due to its clarity of message and exceptional graphical presentation of results. I am generally familiar with salmon life cycle models and the overall use was both appropriate and added novel methods. I noted in one part of the paper where I am less familiar with one of the statistical analyses used. I would defer to you and others there. The open nature of the models, data and coding would allow not only the researchers to reproduce the work but add on to a toolkit of models that could be used for other species and habitats.

I have included comments in the margin of the manuscript as well as made some direct in-text suggestions to improve clarity. This was a pleasure to read.

John F. Kocik

Reviewer #3 (Remarks to the Author):

In this paper the authors apply a stage-based life history model to 8 populations of Chinook salmon in the Columbia River/Snake River basins and show strong associations between warming (particularly warming SST) during the marine stage of the life history and probability of population extinction/extirpation. I accepted the review with considerable excitement of seeing something truly new, insightful, or transformative. Unfortunately I was underwhelmed, not by the statistical rigour, but rather with the interpretation of the results. The claim is essentially that warming is bad and that smolts need to survive the ocean better for populations to avoid extinction. The authors all but said, and perhaps should have, that this analysis provides strong evidence that these populations are doomed and that restoration/conservation is a fools-errand (that would indeed have been provocative at least).

What I was hoping to see more of was a more holistic linkage between different stages of the life history and a quantitative appreciation that what happens in freshwater may lead individuals down trajectories that result in the ocean life history being the proximate stage of mortality. I was hoping and expecting to see discussion that warming SSTs may be detrimental to southern Chinook populations, but Alaska populations may fare better during warming temperatures (and indeed the authors did not cite the obvious paper to suggest so).

So in the end I am left wanting the authors to make a better case for novelty and insights that can be gleaned by this very complex modelling exercise that goes beyond what is already firmly established.

Although the reference section is extensive, I do suggest the authors incorporate information from populations beyond their focal range to broaden the discussion of SSTs and to also contrast their work to other very similar approaches.

Cunningham, Curry J., Peter AH Westley, and Milo D. Adkison. "Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model." Global change biology 24.9 (2018): 4399-4416.

And a new paper just out led by Leslie Jones (open access)
https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15155

Iconic species in peril: Chinook salmon face climate change across multiple life stages

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Keywords

Columbia River Basin, Snake River salmon, spring/summer Chinook salmon, conservation, biological impacts of climate change, ecological modelling

Abstract:

Widespread declines in salmon have tracked recent climate changes. But managers still lack quantitative projections of population viability in response to future climate change. We addressed this gap by assembling a vast database of survival and other data for eight wild populations of threatened Chinook salmon. We evaluated climate impacts at all life stages, and modeled future population trajectories forced by global climate model projections. Populations rapidly declined in response to increasing sea surface temperatures and other factors across a wide range of model assumptions and climate scenarios. Strong density dependence in freshwater habitat limits the number of salmon that survive early life stages, suggesting a potential target for conservation effort. Other potential solutions require a better understanding of the factors that limit survival at sea. We conclude that dramatic increases in the number or survival of smolts are needed to overcome the negative impacts of climate change for this threatened species.

Introduction

The worldwide decline of wild salmon [1-3] has negatively affected fisheries, cultural heritage for indigenous tribes [4], and other marine species, including endangered Southern Resident Killer Whales [5]. Currently the majority of Atlantic and Pacific salmon and steelhead in the conterminous U.S. are threatened with extinction [6]. Overfishing, migration barriers, water diversions, habitat loss, salmon farms and hatcheries drove much of the decline, as well as previous regime shifts in marine ecosystems [7]. Climate change has increasingly become an additional threat, as remnant small populations in overly simplified habitats may lack the adaptive capacity necessary to cope with it [8,9]. Quantifying the impacts of climate change is a high priority for salmon management, driven by legal requirements [10] and national guidelines on science strategy [11]. Despite these needs and despite the vulnerability of Atlantic and Pacific salmon to climate change through freshwater and marine forces [12,13], quantifying these threats throughout their life cycles with future climate projections has been problematic.

Previous population models that have used global climate model (GCM) projections have focused on freshwater life stages only (e.g., stream temperature, winter flooding, and drought) [14-16]. GCM projections related to marine survival, on the other hand, have primarily been used to inform niche-based models that forecast future habitat for salmon generally rather than for specific populations [17,18]. Although marine climate indices have been tightly linked to survival (e.g., Pacific Decadal Oscillation (PDO), [19]Atlantic Multidecadal Oscillation (AMO)), many cannot readily be used in projections of future climate because GCMs have low confidence for these metrics [20]. Moreover, ocean stratification may change their characteristics, leaving biological impacts uncertain [21]. Our analysis was focused on climate drivers with more reliable

GCM performance that are also closely correlated with fish survival to produce a more robust analysis of the impacts of climate change.

A second limitation of previous models is that they often did not account for large-scale climate forcing that affects multiple life stages and food webs simultaneously, and thus could have compounding effects across developmental stages. Accounting for the correlation structure of climate effects over the full life cycle is especially important for migratory species with complex life histories [22,23]. For example, freshwater processes affect salmon arrival timing to the estuary, which in turn affects marine survival. We acknowledge that relationships between survival and climate are often non-stationary [24], so we made the correlation structure of the environmental drivers explicit, and in principle, flexible enough to incorporate future changes.

We used a stochastic age-structured life-cycle model [25,26] with both density-dependent and density-independent climate effects. Salmon survival was forced by environmental drivers where future climate trends were based on ensemble projections from GCMs (Fig. 1). We used a simulation framework to explore model assumptions and quantify different aspects of model uncertainty, including the functional form of the model, covariate selection, and life stage-specific sensitivity.

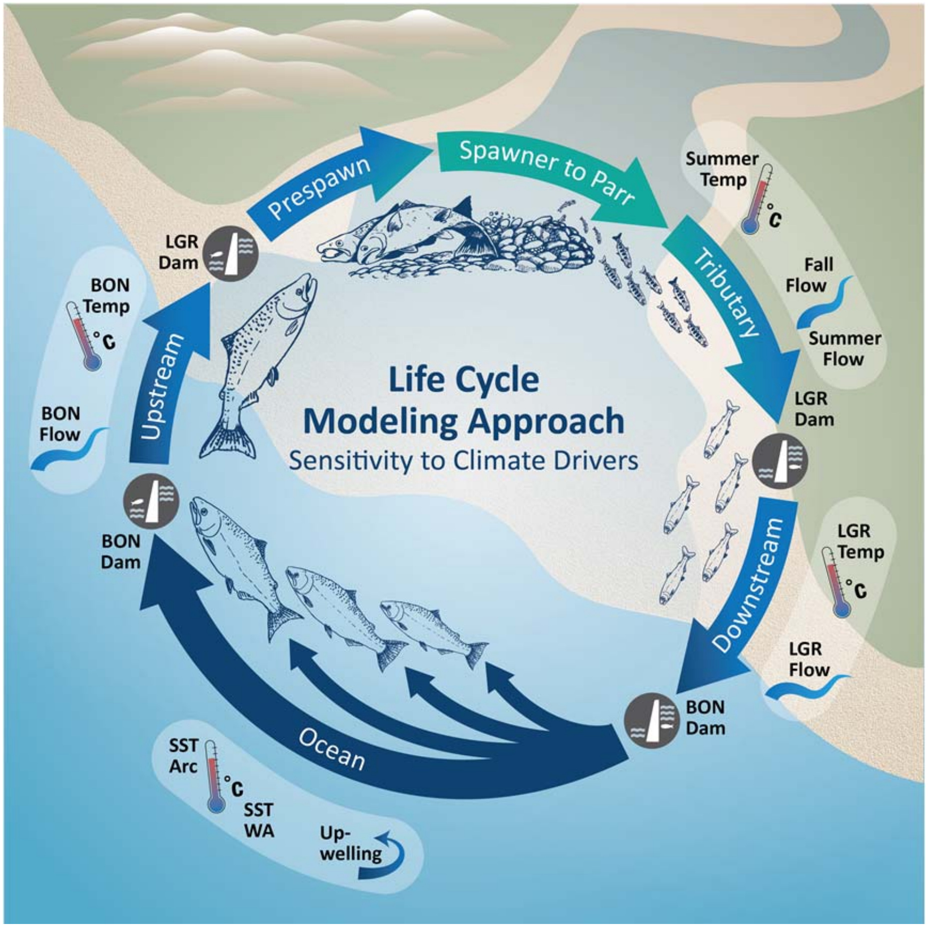

Fig. 1. Life cycle model diagram showing the life stages and climate drivers that influenced each stage. The freshwater stages include upstream migration and holding, spawning, rearing in tributaries, and migrating downstream. The migration passes through the Columbia River hydrosystem, bracketed by Lower Granite Dam (LGR) and Bonneville Dam (BON). The freshwater stages were influenced by stream flows (Flow) and temperatures (Temp). The marine stage, which has variable duration represented by multiple arrows, was influenced by ocean temperatures across the northeastern Pacific (SSTarc) and along the Washington coast (SSTwa). Other influences on ocean productivity are represented by Upwelling. Figure courtesy of Su Kim (NOAA Fisheries) and illustrations by Blane Bellerud (NOAA Fisheries).

We applied the model to eight populations within the Snake River spring/summer Chinook salmon Evolutionarily Significant Unit (ESU), which migrate downstream from their headwater habitat in central Idaho, past eight major hydroelectric projects in the Snake and Columbia rivers, to grow and mature in the northeastern Pacific Ocean (Fig. 2). They return to freshwater 1-4 years later and migrate upstream for a single spawning opportunity. We simulated population time series for eight exclusively wild populations within this ESU. The model reconstructs historical population dynamics closely for most populations (based on Komogorov-Smirnov diagnostics) and has been relatively stable when confronted with new data over the last 10 years, a period during which it has been used operationally by the National Oceanic and Atmospheric Administration (NOAA Fisheries). This updated version of the model is similar in general characteristics to Crozier et al. [25] but imposes climate influences in more life stages and has stronger validation based on data from over a million individually tagged fish (Supplementary Table S1).

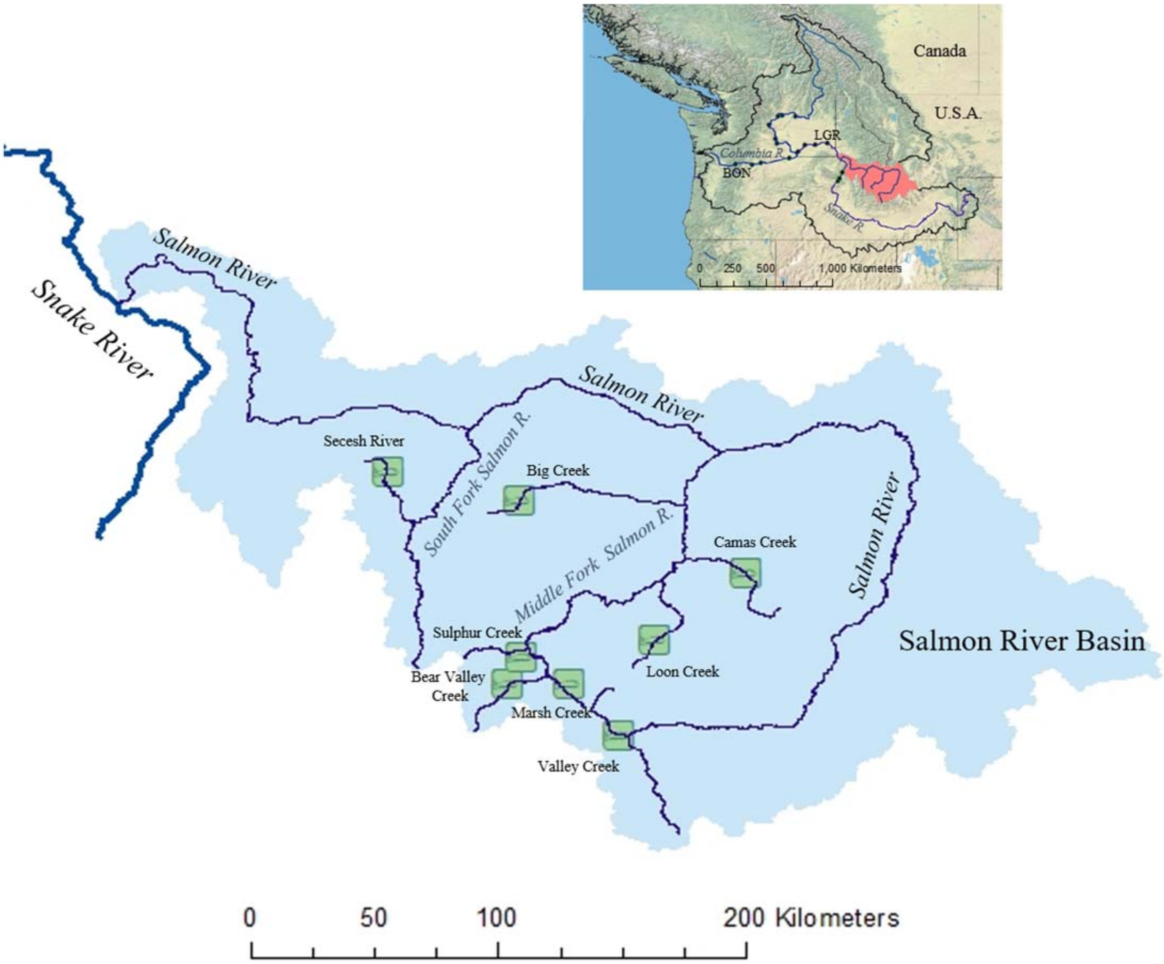

Fig. 2. Map of the Columbia River Basin (top), showing the location of the Salmon River Basin (in red), Bonneville Dam (BON) and Lower Granite Dam (LGR). Modeled populations in the salmon river basin (lower map) are shown by green boxes in the lower map and populations are named after their natal stream.

In our results, climate change in the ocean was particularly catastrophic. We compared multiple alternative covariates in survival models, acknowledging that the best predictor might change over time and thus track different temporal trajectories [24]. Notably, sea surface temperature (SST) is an important component of most relevant indices [27], as it reflects complex interactions between atmospheric forcing, wind strength, upwelling, and mixing of ocean layers, all of which affect productivity throughout the California Current Ecosystem[28]. Although the response of these processes to greenhouse gas forcing will vary, SST will likely continue to be an important indicator, and SST will increase with climate change [29,30].

Results

Quasi-extinction thresholds surpassed in warming climate

We assessed the first year (if any) in which a population in a given simulation fell below a quasi-extinction threshold of adult abundance (QET50). The QET50 is passed when the running mean of spawners, measured at the spawning stream, drops below 50 individuals in any 4-year period [31]. Although small populations drop below this threshold periodically even in a stationary climate, larger populations do not. The proportion of all simulations in which a population dropped below the quasi-extinction threshold (QET50) increased dramatically under a warming climate compared with a detrended (stationary) climate (Fig. 3). Under the representative concentration pathway (RCP 8.5) ensemble mean projection, even the largest populations (Bear Valley Creek and Secesh River) fell below QET50 in over 75% of simulations by 2060. In RCP 4.5, the same milestone was passed a decade later.

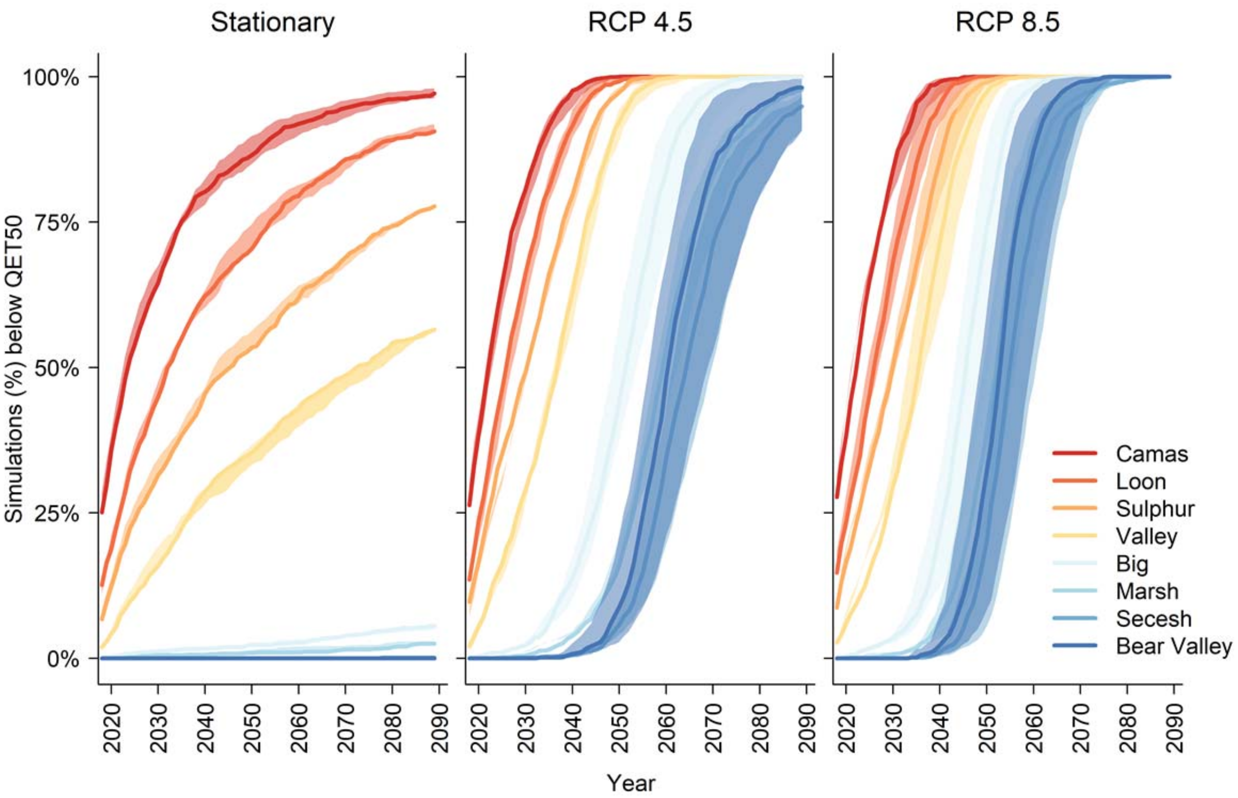

Fig. 3. The percent of simulations in which individual populations reached the quasi-extinction threshold (QET50) by a given year under scenarios assuming extensive interannual and decadal variability but no consistent trends across simulations (a stationary climate) vs. scenarios where trends were superimposed on this natural variability. Trends reflect the median GCM projection (solid lines) and the interquartile range of GCM projections for a given emissions scenario (shading).

Extinction rates increased under the climate change scenarios because population abundances diverged quickly in the climate scenarios compared with the baseline conditions represented by a stable climate (Fig. 4).

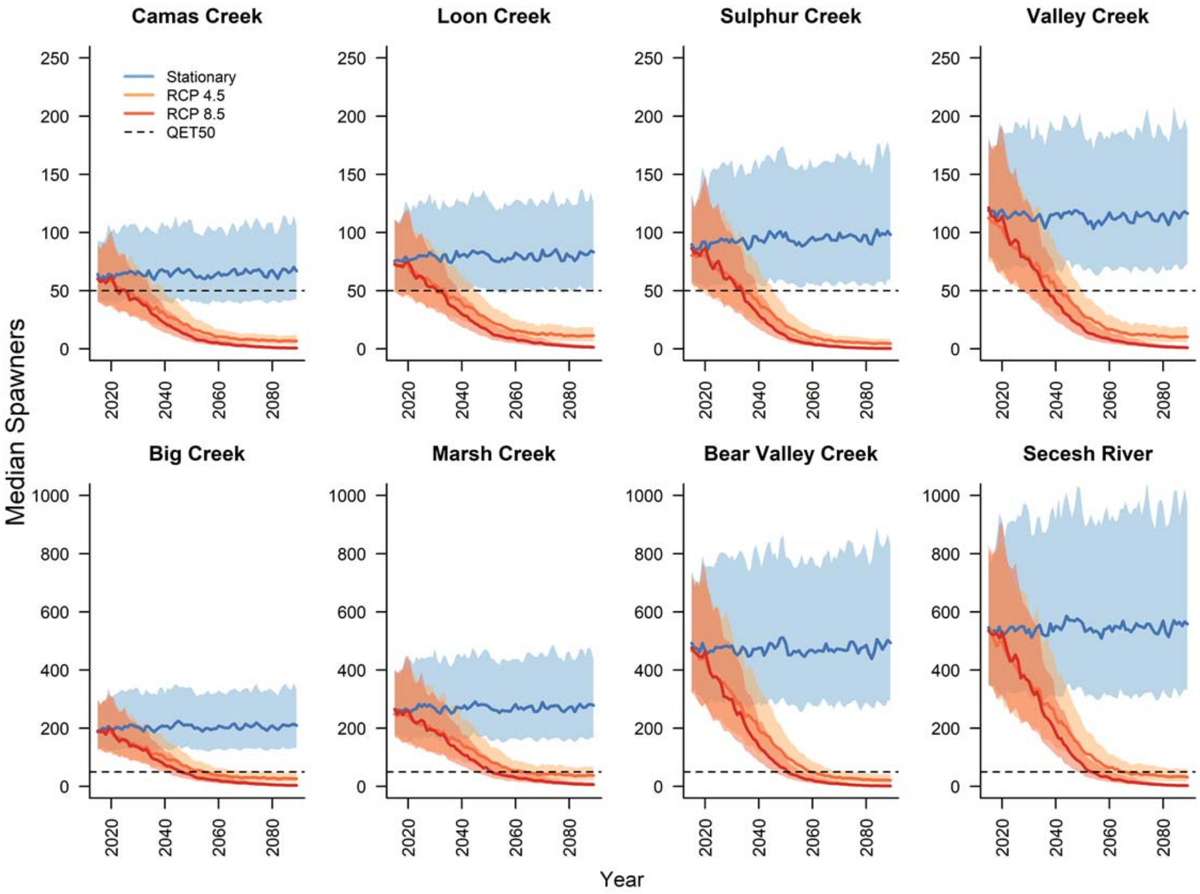

Fig. 4. Population abundance over time. Median (lines) and interquartile range (shading) of population abundance for the ensemble mean GCM projection per RCP in relation to QET50 (dashed horizontal line). Note the different y-axes for small (top row) and large (bottom row) populations.

Similar results with alternative model covariates

We conducted sensitivity analyses to characterize the how population outcomes (extinction risk) varied depending on the covariates that were included in the model, and the extent to which impacts in different life stages predicted population-level responses.

Alternative marine and freshwater covariate models had relatively little effect on overall patterns (Fig. 5). Resulting from the high importance of SST in model comparisons, all three models included combinations of basin-wide and coastal SST indices, which drives much of the overall effect on survival [27]. The freshwater models differed in whether fall (Models 1 and 3) or summer flows (Model 2) limited smolt productivity. We considered both because the data were consistent with both models (Supplementary Table S3). Populations fared slightly worse in the summer-flow models because of projected decreases in summer precipitation, increases in evaporation, and reduced groundwater storage; while fall precipitation (and hence fall flow) is projected to either stay the same or increase (Fig. S2). The models that included upwelling (blue) were more optimistic in more aggressive warming scenarios (GCM_{75}) because some GCMs project a positive trend in spring upwelling later this century in the northern California Current Ecosystem (Fig. S2). Nonetheless, negative effects from SST still drove most populations extinct within the century (Fig. 5).

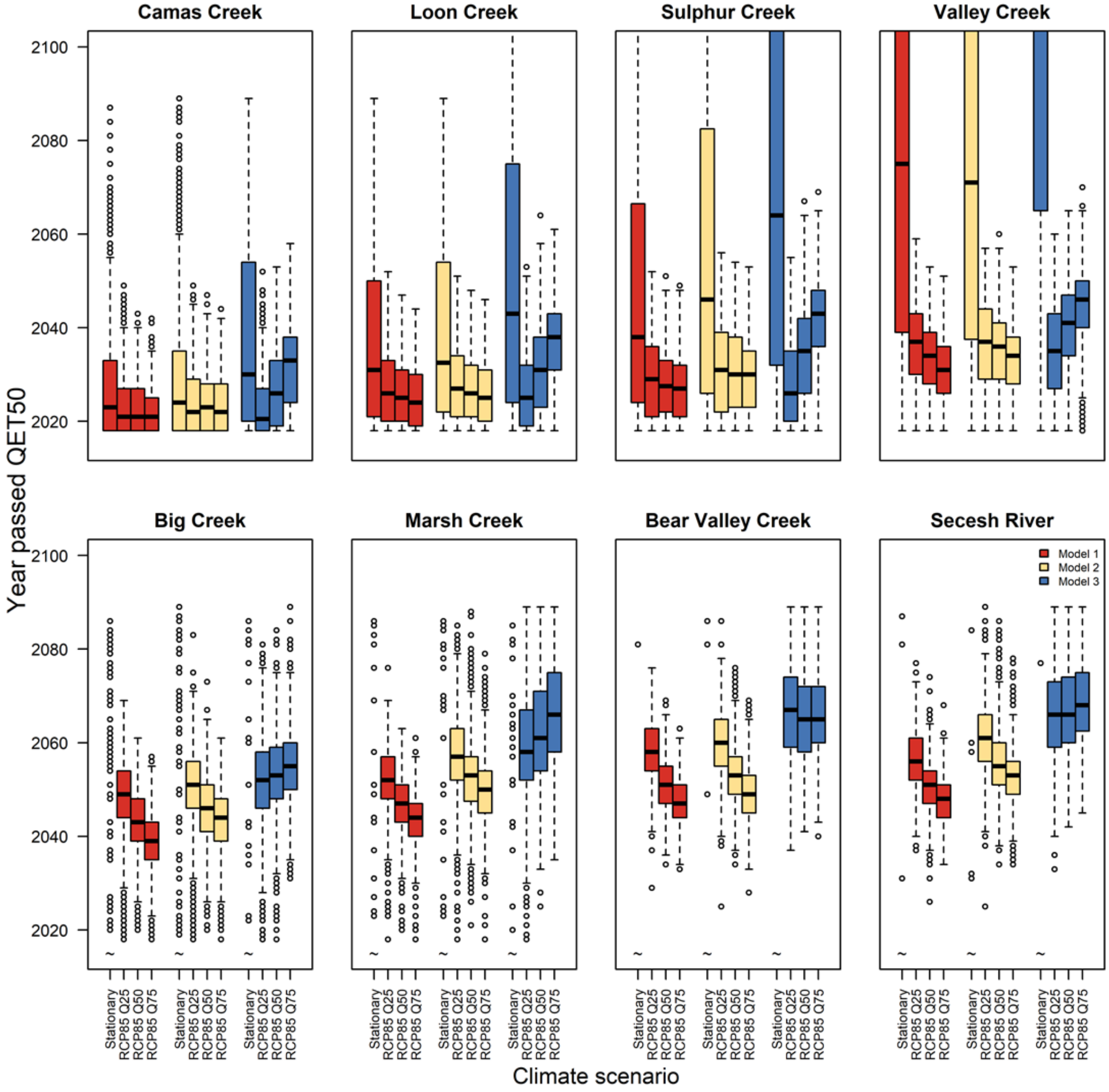
Camas Creek
Loon Creek
Sulphur Creek
Valley Creek
Big Creek
Marsh Creek
Bear Valley Creek
Secesh River
Year passed QET50
2100
2080
2060
2040
2020
Model 1
Model 2
Model 3
Stationary
RCP85 Q25
RCP85 Q50
RCP85 Q75
Climate scenario

Fig. 5. Year that each population fell below QET50 for three models. Different models are shown in different colors (Model 1 (red): covariates include SST and summer flow; Model 2 (yellow): covariates include SST, summer temperature and fall flow; Model 3 (blue): covariates include SST, upwelling, summer temperature and fall flow). Extinction happens earlier in scenarios with more warming (GCM_{75}) in models without upwelling (yellow and red) but later when more intense upwelling ameliorates SST effects (blue). However, in all models extinction happens earlier in the RCP 8.5 scenarios compared with a stationary climate. Note that larger populations (bottom row) often never dropped below QET50 in the stationary climate, indicated with ~.

Marine life stage most vulnerable to warming

The impact of climate change on freshwater life stages was not always negative, but rather depended on population-specific and model-specific sensitivity. In the headwaters, the model with fall flow produced a net benefit to parr to smolt survival, whereas the summer flow model lowered survival (red and blue boxes vs. yellow in juvenile rearing stage in Fig. 6), but produced no difference in effects at other life stages. Thus if climate change affected only the early rearing period and no other stage, there could be a mix of responses across populations depending on local limiting factors such as summer vs. fall flow, similar to the conclusions of Crozier et al. [25].

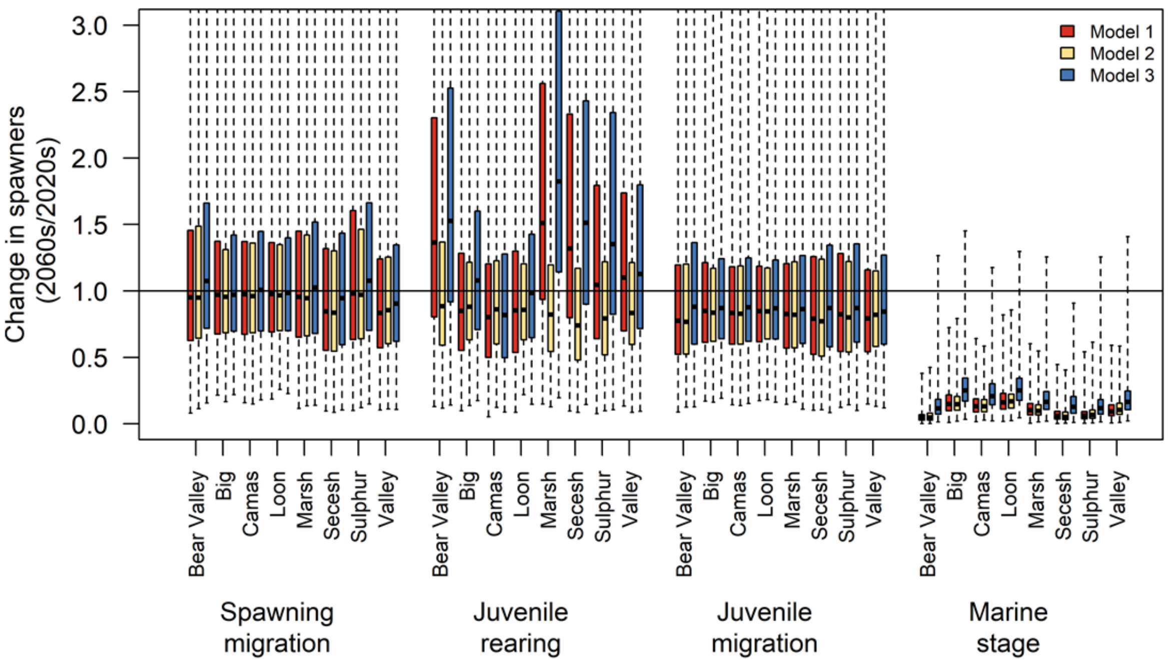

Fig. 6. A three by four factorial experimental design examining the relative loss in spawner abundance from 2020 to 2060 due to the effects climate change. Net trends in population size are shown using the ratio of late abundance (2060-2069) compared with early abundance (2020-2029) when RCP 8.5 ensemble mean climate trends are imposed during a single life stage only, with other life stages under a stationary climate. The horizontal line (Y=1) indicates no change in spawner abundance. Boxes show the interquartile range across simulations, while the whiskers extend to the most extreme values of individual simulations. Model 1 covariates include SST and summer flow; Model 2 covariates include SST, summer temperature and fall flow; Model 3 covariates include SST, upwelling, summer temperature and fall flow.

During the spawning migration, summer-run populations (i.e., populations that returned to their spawning areas in summer, Secesh River and Valley Creek) were more affected by temperature than spring-run populations, with net declines of up to -17% by the 2060s. However, temperature effects on the juvenile, downstream migration reduced populations by about -18% from the 2020s to the 2060s, on average, while climate change effects in the marine stage reduced survival by -83% to -90% (Fig. 6).

It is important to note that the freshwater climate impacts in this study were conservative in some respects. Specifically, we have assumed linear responses to environmental variables, but physiological and ecological thresholds can create non-linear responses, by which future temperatures or flows could have more severe effects. Furthermore, the primary covariate for juvenile survival in two of our models was fall flow, which is the covariate that is least sensitive to climate change [32]. Summer flows could also be limiting (Model 2), which would cause a more negative response. More generally, the high elevation, mostly-wilderness habitat of these populations is unusual for salmon in the region, and partially explains the relatively small effects of climate change on their freshwater life stages. Other populations face more immediate impacts on freshwater productivity [14,33].

Survival through the migration corridor declined for all juvenile migrants and adult summer-run migrants due to rising temperatures. Still, the declines we found were relatively small because of their early run timing compared with other salmon that migrate during peak temperatures. In particular, endangered Snake River sockeye adults experience much higher mortality from heat stress [34,35]. In our analysis, we found relative resilience in freshwater stages and the dominant driver towards extinction was the ~90% decline in survival due to rising SST in the marine life stage. Therefore, closely monitoring ocean survival and directing research into these populations potential response to novel conditions is clearly needed.

Caveats

There are two main caveats to these projections. First, the northeast Pacific might not warm at the rate modeled, despite rising levels of CO_2 in the atmosphere. Over the past century, internal variability in the climate system represented by variation in sea level pressure and natural variability in ocean circulation has been a stronger determinant of coastal SST than global mean temperature [36]. How long this situation will continue is difficult to predict. Warming might occur slower than modeled, which would reduce the rate of population declines. Nonetheless, with the entire ocean warming at all depths [30], at some point this signal will inevitably reach coastal waters.

The second possibility is that the northeast Pacific does warm, but some sort of ecological surprise [37] will reverse the historical relationship between SST and salmon survival. Ocean temperature does not affect salmon primarily through a physiological response, but rather through a combination of bottom up and top down ecological processes that jointly regulate salmon growth and survival [38-40], which explains the non-stationarity of statistical correlations [24]. Warm conditions have been associated with poorer-quality prey and more warm-water predators, likely generating the correlation we have observed. However, it is possible that novel communities will arise with different responses to temperature, or that salmon will adapt to an altered food web in a positive manner. We do see consumption rates increase and unexpected species appear in the California Current Ecosystem when new conditions arise, such as during the marine heatwave of 2013-2015 [41]. For example, anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*) and hake (*Merluccius productus*) showed unusually early and northern spawning behavior, which increased concentrations of larvae in the northern California Current Ecosystem in the winter 2015 and 2016, a shift that could benefit salmon [42].

Nonetheless, the correlation strength with SST has been increasing rather than decreasing [43], and in fact salmon fared poorly [44] during the recent marine heatwave, with a decadal-low number of adult Chinook returning in many ESUs [45] and the closure of multiple fisheries in 2020. Thus, although the various processes that historically generated the PDO [20] may interact differently in the future, it seems likely that SST will continue to be a negative indicator of salmon survival. Further exploration using our model with a changing correlation structure over time could clarify possible trajectories and when they could be detected.

Other ecological surprises should also be considered, such as increases in competitors such as jellyfish [40] and Humboldt or market squid [46], which could reduce salmon survival in an altered ocean. Predators, such as seabirds that currently concentrate on alternative prey, change behavior when their preferred prey dwindle or alter their distribution, which can increase or decrease predation on salmon [47]. We recommend closely monitoring trophic interactions and salmon growth rates to detect such a possibility.

Finally, our model is conservative in that we have not accounted for any negative effects of ocean acidification. Declines of sensitive species such as crabs and calcariferous zooplankton could have a negative effect on salmon, especially salmon populations that prey extensively on sensitive species [48]. We have assumed that ocean-stage salmon are relatively insensitive to pH, but if there are effects, they will likely be negative [49,50].

Discussion

Our results indicate that rising SST as one symptom of a changing ocean puts all of these populations at high risk of extinction. Small populations have minimal buffer against declining marine survival rates, and are at immediate risk (Fig. 1). The threat to larger populations causes even greater concern because they are the remaining salmon strongholds, which provide genetic and demographic resilience for the ESU as a whole [51]. Moreover, although we have focused on the details for certain populations, strong synchrony across all populations within the ESU [52] and more broadly [53,54] suggests these responses could represent a widespread phenomenon. Salmon populations show coherence at many spatial scales, and synchrony has increased over time in both Pacific and Atlantic populations and climate indicators [3,55,56]. To the extent that negative responses to SST continue as a shared theme in these patterns [57,58], climate change overlaid on other anthropogenic forces [59] could drive salmon declines at a large scale.

There is no easy way to mitigate for increasing SST that produce declines in marine survival of this magnitude. Ecosystem-based fisheries management attempts to consider the complex web of drivers with both direct and indirect links to anthropogenic actions, and track indicators in all sectors [45,60]. Conceptual models of factors that affect salmon marine survival show a large number of interacting processes [61,62]. Importantly, solutions involving management actions could occur in either marine or freshwater realms.

In the marine realm, human activities affect salmon survival through targeted fishing on salmon, their prey (sardine, anchovy, krill, juvenile rockfish, juvenile crab), predators (e.g., marine mammals) and competitors (e.g., hake, Pacific halibut, arrowtooth flounder). Changes in fisheries can have positive or negative effects on salmon. Curtailed salmon harvest since the

1960s reduced one major source of direct mortality. Reduced harvest on top predators, however, led to rebounding marine mammal populations that now consume large amounts of salmon [39,63]. Competition with hatchery fish has complex interactions with climate effects on wild salmon [59], and is an area of active research. Sea level rise combined with coastal development threatens complete loss of intertidal marshes in California and Oregon, and the majority of estuary habitat in Washington [64], which will affect some salmon and their prey.

Other indirect anthropogenic effects on marine habitats are not well quantified, and warrant more research. Increased awareness of the importance of forage fish for the entire food chain [65] led to a ban on the development of fisheries to exploit forage fish, demonstrating a proactive approach that should support salmon. But in sum, we lack key information on the full mechanistic basis of salmon marine survival, which limits the strength of end-to-end models for guiding management [66].

Efforts to mitigate carryover effects from freshwater that could affect marine survival in these populations have primarily focused on dams. Survival through Columbia and Snake River dams generally now meets recovery targets (>96%) [67], and cumulative mortality over 500 km of in-river migrating fish (~50%) is similar to that estimated for unregulated rivers of similar length (i.e., Fraser River [68]). However, slow travel time through reservoirs combined with temperatures that have been elevated by dams[69] can potentially result in lower marine survival [70]. Mitigation efforts to increase smolt body size and advance migration timing could increase marine survival [71,72]. Restoration efforts in freshwater habitat, such as restoring floodplains, riparian planting to reduce stream temperature, reconnecting side-channel habitat [73] or adding nutrients to juvenile salmon rearing areas could also enhance/restore freshwater salmon production.

Our models estimated strong density dependence at the parr to smolt stage, although it is not clear whether summer or winter habitat is constrained. The headwaters have minimum anthropogenic impacts, but the mainstem Salmon River has experienced structural simplification and loss of wood, which could limit both rearing and overwintering capacity. Our results suggest that smolt carrying capacities are currently limited by flow rather than temperature. Higher flows may create more habitat, improve connectivity, or decrease contact with predators. The predator community has also been affected by human impacts, from introduced sport fish (smallmouth bass, *Micropterus dolomieu* and brook trout *Salvelinus fontinalis*) to creation of reservoir habitat more favorable for invasive fish (e.g., American shad, *Alosa sapidissima*).

Throughout salmon watersheds, improving and expanding access to rearing habitat should increase smolt abundance and body condition resulting in improved salmon viability [74]. Intrinsic habitat potential is negatively correlated with current levels of disturbance, so restoring habitat could yield substantial benefits. Specifically, habitat at lower elevation that was historically highly productive has been preferentially lost. Improving individual fish growth by reducing contaminant loads [75], increasing floodplain habitat [74] and habitat complexity in general could boost population productivity [76].

Prospects for saving this iconic keystone species in the conterminous U.S. are diminishing. Resilience to climate change depends on genetic and ecological diversity to adapt to environmental change. Many options have been considered over decades of dedication to salmon recovery, and improvements have been made. However, the urgency is greater than ever to identify successful solutions at a large scale and implement known methods for improving survival. Management actions that open new habitat, improve productivity within existing habitat, or reduce mortality through direct or indirect effects in the ocean are desperately needed.

Methods

Data informing survival estimates

Spawner age and abundance estimates were compiled through large-scale collaborative efforts between states, tribes, and coordinating bodies [77-79]. Stage-specific survival estimates were obtained from multiple sources [27,80-84], originating from tagging and detection records downloaded from PTAGIS.org (Supplementary Table S1). We only used detection records for fish identified as wild from known population sources. Environmental covariates used in the model include air temperature, stream flow and temperature, SST, and coastal upwelling (Supplementary Table S2).

Life cycle model structure

We employed a stochastic, age-structured model modified from [25,26,85]. The model as depicted in Fig. 7 has five annual time steps, based on the five-year generation time of Snake River spring/summer Chinook salmon, which correspond approximately to life-stage transitions. The first time step (“spawner to parr” stage) spans fall spawning(months), incubation and early parr rearing. Survival through the second time step (S_2) includes both tributary rearing ($S_{tributary}$) from summer (July or August) to the following spring (months)when they pass Lower Granite Dam, and migration ($S_{mainstem}$) through the Snake and Columbia River hydrosystem. The third time step includes ocean entry and the first winter and spring in the ocean. Some Chinook salmon return to spawn in their third year (jacks), but most females and “adult” males stay in the ocean for one or two more years, during which ocean survival is represented as S_o. The number of fish in the ocean each year is a latent variable, fit by detections of survivors when they re-enter freshwater (“smolt to adult return”, S_{sar}). Upstream migration survival through the hydrosystem ($S_{upstream}$) and from Lower Granite Dam to spawning ($S_{prespawn}$) are captured in the fourth or fifth time step. Older females tend to lay more eggs, which is reflected in the fecundity parameter, F_5. To calculate "effective spawners", we combined different age classes that returned to spawn in the same year as the weighted sum of 3-y-old (weight=0), 4-y-old (weight=1), and 5-y-old (weight= F_5) fish, which is estimated by an expansion of the number of redds (nests) counted during spawning surveys [31].

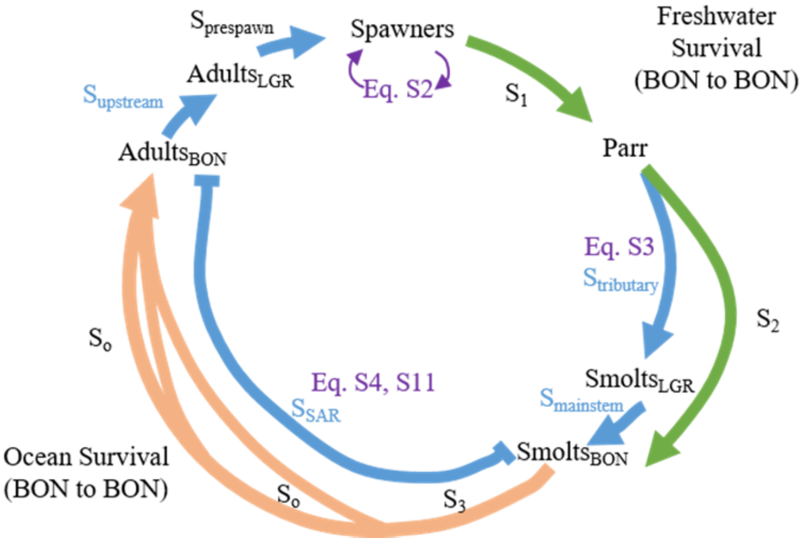

Figure 7. Diagram of life cycle model. Environmental covariate survival models that were fit directly to PIT-tagged data are shown in blue ($S_{tributary}$, $S_{mainstem}$, S_{SAR},$S_{upstream}$). Life stages and fitted transition parameters are in black, with associated equations for reference in the supplementary material.

Model fitting

We fit the life cycle model in two steps. We first fit individual life stage relationships with covariates using a variety of methods in different life stages, generating a posterior distribution for stage-specific parameter estimates. In addition to these parameters, the life cycle model introduces some additional parameters that could not be directly fit to data. We therefore conducted a second step to calibrate the life cycle model using a modified Approximate Bayesian Computing approach [86,87]. In the calibration step, we simulated population time series under recent climatic conditions using the life cycle model, and compared the resulting spawner and smolt time series to those observed, and ranked parameter sets by the deviance from a Kolmogorov-Smirnov test. We selected the top 0.2% of 500,000 sets of parameter combinations. All of the resulting parameter sets met the criterion of producing a spawner distribution that was not statistically different from the observation dataset (p-value>0.05 from the Kolmogorov-Smirnov test). This process maintains the appropriate correlation structure within each parameter set.

Spawner to parr (S_1) and parr to smolt ($S_{tributary}$) stages: We fit adult recruits per spawner for eight populations in a hierarchical Bayesian framework using multiple likelihood equations that reflected stages that could be compared directly with data. Briefly, we fit a 2-stage Gompertz function [88, see Supplementary Methods] to solve the two stages simultaneously, combined with independently-estimated survivals for later stages. Individual population coefficients (productivity and capacity parameters for both stages as well as coefficients for temperature and flow) were assumed to be random samples from an underlying normal distribution [89]. To determine the best environmental covariates, we compared the estimated predictive error of alternative models in a leave-one-out cross-validation method for Bayesian models using the

LOO package [90]. Because of correlations among the climate variables tested, multiple models had similar support from the data. Our primary objective was to identify divergent potential responses to climate change. Therefore, we selected two models with covariates that show different trajectories with climate change (Fig. S2). Model 1 included summer air temperature and fall stream flow, while model 2 included summer stream flow only.

Juvenile survival through the Columbia River hydrosytem ($S_{mainstem}$)**:** We estimated juvenile survival from Lower Granite Dam to Bonneville Dam and arrival day at Bonneville Dam using the COMPASS model [91]. In the COMPASS model, each dam and riverine reach has equations that use hourly flow, temperature, and spill to predict fish survival, migration rate, and the proportion of fish that use the spillway, turbine or bypass passage route at dams. The COMPASS model also tracks the proportion of fish that were loaded into barges to bypass migration through the hydropower system.

Smolt to adult return (S_{sar}**):** We used a mixed-effects logistic regression model [27] to determine the effect of the date of ocean entry and environmental covariates on the probability that an individual fish would return as an adult to Bonneville Dam. The model includes random effects of day and a day by year interaction, which follow an auto-regressive process. Using Akaike Information Criterion, we selected variables with high importance based on model weights, which included a large-scale measure of SST (SSTarc) and a more local, coastal measure of SST (SSTwa), as well as spring upwelling. We applied separate models for fish that had migrated through the mainstem in the river and for fish that had been transported downstream (Supplementary Table S4).

Adult upstream survival ($S_{upstream}$): For the adult upstream survival model, we used generalized additive mixed models (GAMMs) to evaluate the effects of both anthropogenic and environmental covariates on spring/summer Chinook salmon survival [92]. To run the model in simulation mode, all the non-environmental covariates (fisheries catch, the proportion of fish that had been transported in barges as juveniles) had similar distributions to the baseline period 2004-2016. We held survival from the hydrosystem to spawning ($S_{prespawn}$) constant due to the lack of appropriate data for most populations with which to fit a relationship.

Calibration step: The model includes a set of maturation parameters that could not be estimated directly from the data, so we treated them as tuning parameters for the life cycle model as a whole. These parameters partition total smolt-to-adult survival (SAR) to age-specific survivals (S3) for the first year, then S0 for the 2nd and 3rd year), combined with a propensity to return at a given age (jacks: b3, 4y olds: b4, 5 y olds: 1-b4) as follows:

$$S_{SAR} = \frac{b_3 * N_3 + b_4 * N_{4+} + N_5}{N_2} \qquad [S11]$$

Where $N_3 = S_3 * N_2$

$N_4 = (1 - b_3) * N_3 * S_0$

$N_5 = (1 - b_4) * N_4 * S_0$

Fish that stay in the ocean longer have additional mortality (S_0). There is still an advantage to spawning as an older fish because of higher fecundity (F_5). In the model, the effective number of spawners reflects the age distribution of female spawners, which return as either 4 or 5 y olds, and the 5 y olds have the fecundity advantage. A very small percentage of fish return as 6 y olds; these fish were added to 5 y olds.

We fit the tuning parameters (S_0, b_3, b_4, and F_5) using a modified Approximate Bayesian Computing approach [86,87]. We applied this method by first generating a prior distribution for each parameter. The priors for parameters that range between 0 and 1 (S_0, b_3, b_4,) had a beta distribution centered on the mean and including the full range used by Zabel et al. [26, Table 1]. F_5 had a normal distribution with mean from Kareiva et al. [85] and sd=0.1. These values were randomly combined with the freshwater parameter sets from the posterior distribution from the Bayesian analysis to create 500,000 combinations of all 10 parameters.

We ran the life cycle model using each of these parameter sets in a different simulation (500,000 iterations per population). The life cycle model was forced by historical meteorological conditions from 2000 to 2015 (Table S2). For juvenile mainstem survival, we used COMPASS reconstructions of juvenile migration that incorporated actual river management. Note that historical river management was extremely variable over this time period and not comparable to the conditions we projected in the climate simulations (in particular, transportation rates were higher, spill was lower, and dam passage survival was lower than in the action proposed in the Environmental Impact Statement ACOE [93]). We ran the SAR model in retrospective mode, which uses the fitted estimates of historical random effects and observation error. We simulated other life stages in the calibration as we would in future projections.

The parameter values from top 0.2% of these parameter sets compared with their prior distributions are shown in Fig. S1. The resulting models produced Kolmogorov-Smirov p-values from 0.16 to 0.76, which all rejected the null hypothesis that the modeled and observed time series came from different distributions ($p<0.05$).

Climate scenarios

Stationary climate simulations

When creating future climate scenarios, our aim was to maintain the statistical properties of the environmental data driving survival in the various life stages. Large-scale oceanic and atmospheric drivers affect the marine environment and the freshwater environment simultaneously. To account for this, we estimated an unstructured covariance matrix for all the freshwater and marine environmental covariates (Supplementary Table S5) using the TMB libraries for R [94]. We used a multivariate state space model

$$\mathbf{x}_t \sim \mathrm{MVN}(\rho^x \mathbf{x}_{t-1}, \mathbf{Q}) \qquad [3]$$

$$\mathbf{y}_t \sim \mathrm{N}(\mathbf{x}_t, 0.001) \qquad [4]$$

where $\mathbf{x}_\mathbf{t}$, is a vector of the environmental processes at time *t*, ρ^x is the correlation between the vectors from successive time steps, and **Q** is an unstructured covariance matrix. For *n* covariates, the number of estimated correlation coefficients in the unstructured covariance matrix is equal to $0.5 * n * (n - 1)$. The observation error for the observation model was fixed to 0.001, implying the covariate data were measured essentially without error.

Climate change scenarios

Our objective was to explore specifically how the relationships among various climate drivers interacted with population dynamics to shape population trajectories. To do this, we first simulated 1,000 time series of 75 years of stationary environmental conditions that followed the observed covariance relationships in the historical record. Second, we added offsets to these stationary simulations according to GCM projections. Each offset (trend) consisted of a single time series added to all 1,000 stationary simulations. We then input the resulting combinations of stationary-plus-offset environmental conditions for each climate scenario into the life cycle model as forcing factors.

For each model/population/climate scenario, we ran 1,000 iterations. Climate trends were created from the median (GCM_{50}) and interquartile range across 10 to 80 GCM projections, depending on the covariate (Supplementary Table S6). We tracked the geometric mean of population abundance in 10-year intervals. We also assessed the first year (if any) in which a population in a given simulation fell below a quasi-extinction threshold of adult abundance (QET50). The QET50 is passed when the running mean of spawners, measured at the spawning stream, drops below 50 individuals in any 4-year period [31].

We explored projected climate trends from two carbon emissions scenarios, representation concentration pathway (RCP) 4.5 and 8.5 [95,96]. We used time series output from GCMs directly for the marine variables, and output that had been statistically downscaled then processed through hydrological and stream temperature models for the freshwater variables [32,97,98]. For each variable, 10 to 80 time series per emissions scenario were available (Supplementary Table S6). We smoothed each of these individual time series using a 20-y running mean to reduce interannual variation that was already accounted for by the TMB model.

From these resulting time series, we calculated the 25th, 50th, and 75th quantiles each year to generate three trends for each covariate in each climate scenario. These trends represent the spread across climate models of low, medium, and high rates of change in each covariate. Thus in summary, we added each climate trend to the raw simulation of a stationary climate produced by the covariance model. The new time series retained the autocorrelation, variance and covariance of the historical environment with forcing from greenhouse gas emissions added.

Life cycle model simulations

Running the model in simulation mode was relatively straightforward for the stages that were fit on an annual time step (S_1 and $S_{tributary}$) because they only required an annual input of environmental conditions. However, submodels for upstream and downstream survival required daily environmental inputs. We therefore ran a separate step to reproduce numerous representations of daily time series, which were then grouped by their annual spring mean temperatures and flows. For each annual time step, we sampled randomly from the appropriate disaggregated submodel output (Supplementary Methods S2).

We ran the life cycle model from 2015 to 2089, applying climate trends to the stationary climate for each environmental covariate on an annual time step. We repeated 1,000 iterations per population per model per climate scenario. Our first results stem from a single combination of freshwater and marine covariates (Model 1: summer temperature + fall flow for freshwater, SSTarc in winter for transported fish, and SSTarc in winter + SSTwa in summer for in-river fish) to show the full time series of population response to the climate scenarios (Fig. 1-2).

Sensitivity analyses

In our first sensitivity analysis, we compared population outcomes from Model 1 with a different freshwater covariate model (Model 2: summer flow + Model 1 marine covariates). Finally, we exchanged the marine covariates in Model 3: summer temperature + fall flow for freshwater, SSTwa in summer for transported fish, and SSTarc in spring + spring upwelling for in-river fish (Fig 3). Thus, we explored all combinations of the top two models for freshwater and marine stages, respectively.

In our second sensitivity analysis, we applied the climate trends for the ensemble mean of RCP 8.5 to one life stage while the other life stages experienced a stationary climate (Fig. 6). We cycled through parr to smolt, downstream migration, smolt to adult return, and upstream migration. In each case, we reported the extent of population decline as the ratio of geometric mean population size in 2080-2089 divided by mean abundance in 2020-2029. We ran 1,000 simulations per life stage, and calculated the mean change in abundance for each population.

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Author contributions

The primary author contributed to the conception, design, analysis and interpretation of data and writing the paper. BB and RZ contributed to design and interpretation of the work and manuscript revisions; BC contributed to analysis, developing new methods and writing. DW led data acquisition from PTAGIS, design and analysis.

Competing interests

No authors have competing interests in these results. NOAA Fisheries funds the salaries of all authors but has no influence on the results.

List of Supplementary Methods and Materials:

Literature cited

1 Nicola, G. G., Elvira, B., Jonsson, B., Ayllon, D. & Almodovar, A. Local and global climatic drivers of Atlantic salmon decline in southern Europe. *Fisheries Research* **198**, 78-85, doi:10.1016/j.fishres.2017.10.012 (2018).

2 Peterman, R. M. & Dorner, B. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. *Canadian Journal of Fisheries and Aquatic Sciences*, 1255–1260 (2012).

3 Chaput, G. Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science* **69**, 1538-1548, doi:10.1093/icesjms/fss013 (2012).

4 Galbreath, P. F., Bisbee, M. A., Dompier, D. W., Kamphaus, C. M. & Newsome, T. H. Extirpation and tribal reintroduction of Coho salmon to the interior Columbia River basin *Fisheries* **39**, 77-87, doi:10.1080/03632415.2013.874526 (2014).

5 Wasser, S. K. *et al.* Population growth is limited by nutritional impacts on pregnancy success in endangered Southern Resident killer whales (Orcinus orca). *Plos One* **12**, doi:10.1371/journal.pone.0179824 (2017).

6 NMFS, National Marine Fisheries Service. West Coast salmon & steelhead listings. NOAA Fisheries West Coast Region website available at www.westcoast.fisheries.noaa.gov/protected_species/salmon_steelhead/salmon_and_steelhead_listings/salmon_and_steelhead_listings.html (December 2016). (2014).

7 NRC, Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. *Upstream : salmon and society in the Pacific Northwest*. Vol. Board on Environmental Studies and Toxicology. Commission on Life Sciences (National Academies Press, 1996).

8 Katz, J., Moyle, P. B., Quinones, R. M., Israel, J. & Purdy, S. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. *Environmental Biology of Fishes* **96**, 1169-1186, doi:10.1007/s10641-012-9974-8 (2013).

9 Kovach, R. P. *et al.* Genetic diversity is related to climatic variation and vulnerability in threatened bull trout. *Global Change Biol.* **21**, 2510-2524, doi:10.1111/gcb.12850 (2015).

10 Simon, D. J. (2016).

11 Link, J. S., Griffis, R. & Busch, S. (U.S. Department of Commerce, NOAA Technical Memorandum NMFS-F/SPO-155, Silver Spring, MD, 2015).

12 Crozier, L. G. *et al.* Climate vulnerability assessment for Pacific salmon and steelhead in the California Current Large Marine Ecosystem. *PLOS ONE* **14**, e0217711, doi:10.1371/journal.pone.0217711 (2019).

13 Hare, J. A. *et al.* A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *PLOS ONE* **11**, e0146756, doi:10.1371/journal.pone.0146756 (2016).

14 Honea, J. M., McClure, M. M., Jorgensen, J. C. & Scheuerell, M. D. Assessing freshwater life-stage vulnerability of an endangered Chinook salmon population to climate change influences on stream habitat. *Climate Research* **71**, 127-137, doi:10.3354/cr01434 (2017).

15 Battin, J. *et al.* Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 6720-6725, doi:10.1073/pnas.0701685104 (2007).

16 Thompson, L. C. *et al.* Water Management Adaptations to Prevent Loss of Spring-Run Chinook Salmon in California under Climate Change. *Journal of Water Resources Planning and Management* **138**, 465-478, doi:doi:10.1061/(ASCE)WR.1943-5452.0000194 (2012).

17 Cheung, W. W. L., Brodeur, R. D., Okey, T. A. & Pauly, D. Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. *Progress in Oceanography* **130**, 19-31, doi:10.1016/j.pocean.2014.09.003 (2015).

18 Morley, J. W. *et al.* Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLOS ONE* **13**, e0196127, doi:10.1371/journal.pone.0196127 (2018).

19 Burke, B. J. *et al.* Multivariate models of adult Pacific salmon returns. *PLoS One* **8**, e54134, doi:10.1371/journal.pone.0054134 (2013).

20 Newman, M. *et al.* The Pacific decadal oscillation, revisited. *Journal of Climate* **29**, 4399-4427, doi:10.1175/jcli-d-15-0508.1 (2016).

21 Li, S. *et al.* The Pacific Decadal Oscillation less predictable under greenhouse warming. *Nature Climate Change* **10**, 30-34, doi:10.1038/s41558-019-0663-x (2020).

22 Crozier, L. G. *et al.* Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evolutionary Applications* **1**, 252-270 (2008).

23 Healey, M. The cumulative impacts of climate change on Fraser River sockeye salmon (*Oncorhynchus nerka*) and implications for management. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 718-737, doi:10.1139/f11-010 (2011).

24 Litzow, M. A. *et al.* Non-stationary climate-salmon relationships in the Gulf of Alaska. *Proceedings of the Royal Society B-Biological Sciences* **285**, 9, doi:10.1098/rspb.2018.1855 (2018).

25 Crozier, L. G., Zabel, R. W. & Hamlett, A. F. Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. *Global Change Biology* **14**, 236-249, doi:10.1111/j.1365-2486.2007.01497.x (2008).

26 Zabel, R. W., Scheuerell, M. D., McClure, M. M. & Williams, J. G. The interplay between climate variability and density dependence in the population viability of Chinook salmon. *Conservation Biology* **20**, 190-200 (2006).

27 Chasco, B., Burke, B. J. & Crozier, L. G. Differential impacts of freshwater and marine covariates on wild and hatchery Chinook salmon marine survival. *Plos One* (in review).

28 Doney, S. C. *et al.* in *Annual Review of Marine Science, Vol 4* Vol. 4 (eds C. A. Carlson & S. J. Giovannoni) 11-37 (2012).

29 Alexander, M. A. *et al.* Projected sea surface temperatures over the 21st century: Changes in the mean, variability and extremes for large marine ecosystem regions of Northern Oceans. *Elementa-Science of the Anthropocene* **6**, doi:10.1525/elementa.191 (2018).

30 IPCC. (ed D.C. Roberts H.-O. Pörtner, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer) (2019).

31 ICTRT & Zabel, R. W. Required survival rate changes to meet Technical Recovery Team abundance and productivity viability criteria for interior Columbia River basin salmon and steelhead populations., Available at: http://www.nwfsc.noaa.gov/trt/col_docs/ictrt_gaps_report_nov_2007_final.pdf (NWFSC, Seattle, Washington, 2007).

32 Chegwidden, O. S. *et al.* How do modeling decisions affect the spread among hydrologic climate change projections? Exploring a large ensemble of simulations across a diversity of hydroclimates. *Earth's Future* **https://doi.org/10.1029/2018EF001047**, 7, doi:10.1029/2018ef001047 (2019).

33 Justice, C., White, S. M., McCullough, D. A., Graves, D. S. & Blanchard, M. R. Can stream and riparian restoration offset climate change impacts to salmon populations? *J Environ Manage* **188**, 212-227, doi:10.1016/j.jenvman.2016.12.005 (2017).

34 Isaak, D. J. *et al.* Global warming of salmon and trout rivers in the northwestern U.S.: Road to ruin or path through purgatory? *Transactions of the American Fisheries Society* **147**, 566-587, doi:10.1002/tafs.10059 (2018).

35 Crozier, L. G. *et al.* Migration survival of adult Snake River sockeye salmon through the Columbia River Basin. *Research Report for U.S. Army Corps of Engineers, Walla Walla District. Available at https://www.nwfsc.noaa.gov/contact/display_staffprofilepubs.cfm?staffid=1471* (2018).

36 Johnstone, J. A. & Mantua, N. J. Atmospheric controls on northeast Pacific temperature variability and change, 1900-2012. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 14360-14365, doi:10.1073/pnas.1318371111 (2014).

37 Lindenmayer, D. B., Likens, G. E., Krebs, C. J. & Hobbs, R. J. Improved probability of detection of ecological “surprises”. **107**, 21957-21962, doi:10.1073/pnas.1015696107 %J Proceedings of the National Academy of Sciences (2010).

38 Ottersen, G., Kim, S., Huse, G., Polovina, J. J. & Stenseth, N. C. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems* **79**, 343-360, doi:10.1016/j.jmarsys.2008.12.013 (2010).

39 Chasco, B. E. *et al.* Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Sci Rep* **7**, 15439, doi:10.1038/s41598-017-14984-8 (2017).

40 Ruzicka, J. J., Daly, E. A. & Brodeur, R. D. Evidence that summer jellyfish blooms impact Pacific Northwest salmon production. *Ecosphere* **7**, doi:10.1002/ecs2.1324 (2016).

41 Morgan, C. A., Beckman, B. R., Weitkamp, L. A. & Fresh, K. L. Recent Ecosystem Disturbance in the Northern California Current. *Fisheries* **44**, 465-474, doi:10.1002/fsh.10273 (2019).

42 Auth, T. D., Daly, E. A., Brodeur, R. D. & Fisher, J. L. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Global Change Biology* **24**, 259-272, doi:10.1111/gcb.13872 (2018).

43 Ciannelli, Cunningham, Johnson & Puerta. Nonstationary effects of ocean temperature on Pacific salmon productivity. *Can. J. Fish. Aquat. Sci.* **76**, 1923-1928, doi:10.1139/cjfas-2019-0120 (2019).

44 Daly, E. A., Brodeur, R. D. & Auth, T. D. Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. *Marine Ecology Progress Series* **566**, 169-182, doi:10.3354/meps12021 (2017).

45 Harvey, C. J. *et al.* Ecosystem Status Report of the California Current for 2019: A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). *NOAA Institutional Repository: https://doi.org/10.25923/mvhf-yk36*, doi:https://doi.org/10.25923/p0ed-ke21 (2019).

46 Zeidberg, L. D. & Robison, B. H. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. **104**, 12948-12950, doi:10.1073/pnas.0702043104 %J Proceedings of the National Academy of Sciences (2007).

47 Wells, B. K. *et al.* Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *Journal of Marine Systems* **174**, 54-63, doi:10.1016/j.jmarsys.2017.05.008 (2017).

48 Marshall, K. N. *et al.* Risks of ocean acidification in the California Current food web and fisheries: Ecosystem model projections. *Global Change Biol.* **23**, 1525-1539 (2017).

49 Ou, M. *et al.* Responses of pink salmon to CO2-induced aquatic acidification. *Nature Clim. Change* **5**, 950-955, doi:10.1038/nclimate2694

http://www.nature.com/nclimate/journal/v5/n10/abs/nclimate2694.html#supplementary-information (2015).

50 Williams, C. R. *et al.* Elevated CO2 impairs olfactory-mediated neural and behavioral responses and gene expression in ocean-phase coho salmon (Oncorhynchus kisutch). **25**, 963-977, doi:10.1111/gcb.14532 (2019).

51 McElhany, P., Ruckelshaus, M. H., Ford, M. J., Wainwright, T. C. & Bjorkstedt, E. P. Viable salmonid populations and the recovery of Evolutionarily Significant Units. Report No. Technical Memorandum NMFS-NWFSC 42, 156 (National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA, 2000).

52 Jorgensen, J. C., Ward, E. J., Scheuerell, M. D. & Zabel, R. W. Assessing spatial covariance among time series of abundance. *Ecology and Evolution* **6**, 2472-2485, doi:10.1002/ece3.2031 (2016).

53 Ohlberger, J., Scheuerell, M. D. & Schindler, D. E. Population coherence and environmental impacts across spatial scales: a case study of Chinook salmon. *Ecosphere* **7**, doi:10.1002/ecs2.1333 (2016).

54 Zimmerman, M. S., Irvine, J. R., O'Neill, M., Anderson, J. H., Greene, C. M., Weinheimer, J., ... & Rawson, K. Spatial and temporal patterns in smolt survival of wild and hatchery coho salmon in the Salish Sea. *Marine and Coastal Fisheries* **7**, 116-134 (2015).

55 Dorner, B., Catalano, M. J. & Peterman, R. M. Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the northeastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1082-1095, doi:10.1139/cjfas-2017-0197 (2018).

56 Black, B. A. *et al.* Rising synchrony controls western North American ecosystems. *Global change biology* **24**, 2305-2314 (2018).

57 Mills, K. E., Pershing, A. J., Sheehan, T. F. & Mountain, D. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Glob Chang Biol* **19**, 3046-3061, doi:10.1111/gcb.12298 (2013).

58 Litzow, M. A., Ciannelli, L., Cunningham, C. J., Johnson, B. & Puerta, P. Nonstationary effects of ocean temperature on Pacific salmon productivity. *Can. J. Fish. Aquat. Sci.* **76**, 1923-1928, doi:10.1139/cjfas-2019-0120 (2019).

59 Cline, T. J., Ohlberger, J. & Schindler, D. E. Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nat Ecol Evol* **3**, 935-942, doi:10.1038/s41559-019-0901-7 (2019).

60 Andrews, K. S. *et al.* The legacy of a crowded ocean: indicators, status, and trends of anthropogenic pressures in the California Current ecosystem. *Environ. Conserv.* **42**, 139-151, doi:10.1017/S0376892914000277 (2015).

61 Harvey, C. J., Reum, J. C. P., Poe, M. R., Williams, G. D. & Kim, S. J. Using Conceptual Models and Qualitative Network Models to Advance Integrative Assessments of Marine Ecosystems. *Coast. Manage.* **44**, 486-503, doi:10.1080/08920753.2016.1208881 (2016).

62 Wells, B. K. *et al.* Implementing Ecosystem-Based Management Principles in the Design of a Salmon Ocean Ecology Program. *Frontiers in Marine Science* **7**, doi:10.3389/fmars.2020.00342 (2020).

63 Adams, J. *et al.* A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean. *Ecological Informatics* **34**, 44-51, doi:https://doi.org/10.1016/j.ecoinf.2016.04.010 (2016).

64 Thorne, K. *et al.* U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. *Science Advances* **4**, eaao3270, doi:10.1126/sciadv.aao3270 (2018).

65 Kaplan, I. C. *et al.* Impacts of depleting forage species in the California Current. *Environmental Conservation* **40**, 380-393, doi:10.1017/S0376892913000052 (2013).

66 Collie, J. S. *et al.* Ecosystem models for fisheries management: finding the sweet spot. *Fish and Fisheries* **17**, 101-125, doi:10.1111/faf.12093 (2016).

67 Skalski, J. R. *et al.* Status after 5 Years of Survival Compliance Testing in the Federal Columbia River Power System (FCRPS). *North American Journal of Fisheries Management* **36**, 720-730, doi:10.1080/02755947.2016.1165775 (2016).

68 Welch, D. W. *et al.* Survival of Migrating Salmon Smolts in Large Rivers With and Without Dams. *PLoS biology* **6**, 2101-2108, doi:10.1371/journal.pbio.0060265 (2008).

69 Environmental Protection Agency, U. S. A. R. Total Maximum Daily Load (TMDL) for Temperature in the Columbia and Lower Snake Rivers, May 18, 2020 TMDL for Public Comment. (2020).

70 Gosselin, J. L. & Anderson, J. J. Combining Migration History, River Conditions, and Fish Condition to Examine Cross-Life-Stage Effects on Marine Survival in Chinook Salmon. *Transactions of the American Fisheries Society* **146**, 408-421, doi:10.1080/00028487.2017.1281166 (2017).

71 Scheuerell, M. D., Zabel, R. W. & Sandford, B. P. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *Journal of Applied Ecology* **46**, 983–990 (2009).

72 Zabel, R. W. & Williams, J. G. Selective mortality in chinook salmon: What is the role of human disturbance? *Ecological Applications* **12**, 173-183 (2002).

73 Bond, M. H., Nodine, T. G., Beechie, T. J. & Zabel, R. W. Estimating the benefits of widespread floodplain reconnection for Columbia River Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **76**, 1212-1226, doi:10.1139/cjfas-2018-0108 (2019).

74 Herbold, B. *et al.* Managing for salmon resilience in California's variable and changing climate. *San Francisco Estuary and Watershed Sciences* **16**, doi:Retreived from https://escholarship.org/uc/item/8rb3z3nj (2018).

75 Chittaro, P. *et al.* Variability in the performance of juvenile Chinook salmon is explained primarily by when and where they resided in estuarine habitats. *Ecology of Freshwater Fish* **27**, 857-873, doi:10.1111/eff.12398 (2018).

76 Beechie, T. *et al.* Restoring salmon habitat for a changing climate. *River Research and Applications* **29**, 939-960, doi:10.1002/rra.2590 (2013).

77 Idaho Department of Fish and Game, Oregon Department of Fish and Wildlife & Washington Department of Fish and Wildlife. *Snake River ESU Spring Summer Chinook Natural Origin Spawner Abundance Dataset (1949-2017)*, 2018).

78 Nez Perce Tribe East Fork South Fork Salmon River summer Chinook and Secesh River summer Chinook, Natural Origin Spawner Abundance Dataset (1957-2017). (Protocol and methods available at ttps://www.cbfish.org/Document.mvc/Viewer/P165414. Personal communication with Mari Williams, NOAAF NWFSC/OAI 2019, 2019).

79 StreamNet. Fish Data for the Northwest. (http://www.streamnet.org/, accessed Nov 2018, 2018).

80 Faulkner, J. R., Widener, D. L., Smith, S. G., Marsh, T. M. & Zabel, R. W. Survival estimates for the passage of spring migrating juvenile salmonids through Snake and Columbia River dams and reservoirs, 2017. (Draft report of the National Marine Fisheries Service to the Bonneville Power Administration. Portland, Oregon. Available at https://www.nwfsc.noaa.gov/contact/display_staffprofilepubs.cfm?staffid=1524, 2018).

81 Lamb, J. J. *et al.* Monitoring the migrations of wild Snake River spring/summer Chinook salmon juveniles: survival and timing, 2017. (Report of the National Marine Fisheries Service to the Bonneville Power Administration. Portland, Oregon. Available at https://www.nwfsc.noaa.gov/contact/display_staffprofilepubs.cfm?staffid=550, 2018).

82 Crozier, L., Dorfmeier, E., Marsh, T., Sandford, B. & Widener, D. Refining our understanding of early and late migration of adult Upper Columbia spring and Snake River spring/summer Chinook salmon: passage timing, travel time, fallback and survival. (Report of research by Fish Ecology Division, Northwest Fisheries Science Center. Available at https://www.nwfsc.noaa.gov/contact/display_staffprofilepubs.cfm?staffid=1471, 2016).

83 DART. Columbia River Data Access in Real Time. *http://www.cbr.washington.edu/dart/dart.html, accessed June 2019* (2019).

84 NOAA Fisheries. Salmon Population Summary. *https://catalog.data.gov/dataset/sps-abundance-salmon-population-summary-database, accessed July 2018* (2019).

85 Kareiva, P., Marvier, M. & McClure, M. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. *Science* **290**, 977-979 (2000).

86 Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T. & Huth, A. Statistical inference for stochastic simulation models – theory and application. **14**, 816-827, doi:10.1111/j.1461-0248.2011.01640.x (2011).

87 Csillery, K., Blum, M. G. B., Gaggiotti, O. E. & Francois, O. Approximate Bayesian Computation (ABC) in practice. *Trends in Ecology and Evolution* **25**, 410-418, doi:10.1016/j.tree.2010.04.001 (2010).

88 Gompertz, B. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **182**, 513–585, doi:https://doi.org/10.1098/rstl.1825.0026 (1825).

89 Gelman, A., Carlin, J. B. & Rubin, D. B. *Bayesian data analysis*. (Chapman & Hall, 2004).

90 Vehtari, A., Gelman, A. & Gabry, J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**, 1413-1432, doi:doi: 10.1007/s11222-016-9696-4 (2017).

91 Zabel, R. W., Burke, B. J., Moser, M. L. & Peery, C. Relating dam passage of adult salmon to varying river conditions using time-to-event analysis. *American Fisheries Society Symposium* **61**, 153-163 (2008).

92 Crozier, L. G. *et al.* How a changing climate affects survival of Snake River Chinook and Sockeye salmon during their upstream migration: recent extremes and likely futures *Global Change Biology* (in review).

93 U.S. Army Corps of Engineers (ACOE), Northwestern Division Bureau of Reclamation & Administration, P. N. R. B. P. Columbia River System Operations Draft Environmental Impact Statement, February 2020. *DOE/EIS-0529* (2020).

94 Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H. & Bell, B. M. TMB: Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software* **70**, 1-21, doi:10.18637/jss.v070.i05 (2016).

95 NOAA, National Oceanic and Atmospheric Administration,. NOAA Earth System Research Laboratory, Climate Change web portal, CMIP5 maps. Available from esrl.noaa.gov/psd/ipcc/ocn/ccwp.html (November 2018). (2018).

96 Brady, R. X., Alexander, M. A., Lovenduski, N. S. & Rykaczewski, R. R. Emergent anthropogenic trends in California Current upwelling. *Geophysical Research Letters* **44**, 5044-5052, doi:10.1002/2017gl072945 (2017).

97 Yearsley, J. R. A semi-Lagrangian water temperature model for advection-dominated river systems. *Water Resources Research* **45**, W12405, doi:10.1029/2008wr007629 (2009).

98 Brekke, L., Kuepper, B. & Vaddey, S. Climate and Hydrology Datasets for Use in the RMJOC Agencies' Longer-Term Planning Studies: Part 1 - Future Climate and Hydrology Datasets, available at https://www.usbr.gov/pn/climate/planning/reports/index.html. (2010).

Reviewer #1 (conservation ecology and climate change):

This manuscript describes an effort to use a state-of-the-art life-cycle model to quantify the risks of extinction for 8 populations of Chinook salmon in the Pacific Northwest of the USA. The model relies heavily on an extraordinary dataset of individually tagged fish to estimate various functional relationships that describe the processes that affect survival throughout the life-cycle of this species. The model is used to simulate the potential effects of climate change on the viability of these 8 populations. The primary conclusion reached by these efforts is that climate warming is likely to doom this group of populations and that the primary survival bottleneck is during the fish's first year of life in the sea. While the model development is commendable and the data used are impressive, the conclusions that are drawn are not particularly new and have been appreciated for some time. Thus, it is not really clear what the main contribution from this paper actually is.

We revised the introduction to clarify three specific contributions of this model on LN50-126 as follows:

Retrospective analyses also show strong relationships between climate indices and salmon performance (e.g., 8). Looking toward the future, indirect and qualitative assessments point to anthropogenic climate change as an additional overriding threat for salmon in the North Atlantic and California Current (e.g., 9, 10-12). How to mitigate for this threat is therefore a primary concern among conservation organizations and management agencies.

… This is a novel approach to downscaling climate projections in multiple environments.

Thus, there are three reasons why existing approaches for modeling the biological impacts of climate change are inadequate for evaluating potential management actions for salmon. Similar limitations apply to other species that are migratory or have complex life histories. First, proposed management actions are usually focused on conditions in freshwater, so accounting for "carry over" effects from freshwater to marine life stages is essential for their evaluation. Carryover effects occur when an individual's previous history affects its performance in a subsequent life stage (24). For example, the timing of migration from freshwater to the ocean and back again is a key determinant of salmon survival in every life stage, and one of the most sensitive traits in relation to climate (25-28). Timing is also a key element in multiple management actions, especially those involving the hydrosystem (29) and fisheries (30). Quantification of carryover effects that will be affected by climate change is therefore essential for evaluating the net benefits of proposed actions to protect endangered species.

Second, current models of survival in the salmon marine stage rely on climate indices that cannot be linked directly to global climate model (GCM) projections, so it is impossible to conduct formal analyses of how alternative carbon emission scenarios or other anthropogenic actions to mitigate climate change might affect the timing of declines in marine survival. Nor is it possible to quantify uncertainty in modelled projections across GCMs and thus take full advantage of the Coupled Model Intercomparison Project, which represents the major advances of global climate modeling in recent decades (31, 32).

Third, approaches that are currently available for accounting for climate impacts on freshwater and marine life stages use independent downscaling methods for the two environments. Terrestrial downscaling methods usually employ statistical or dynamical downscaling of temperature and precipitation that feed into hydrological models. Statistical downscaling is an efficient way to explore many alternative climate projections and characterize model uncertainty at many steps in the modeling chain (33). A common approach to marine downscaling, on the other hand, is to integrate GCM output into Regional Ocean Models, which in practice are only available for very few GCM projections (32). As a result, these methods often rely on projections from different GCMs and are not consistent in characterizing potential model biases, and thus uncertainty in climate projections. Moreover, they are not temporally linked, which prevents complete accounting for carryover effects from one life stage to the next.

We address each of these difficulties by developing a novel modeling approach with a flexible and explicit mechanism for accounting for the correlation structure among all climate drivers. We also use a multi-model approach to indirectly account for a change in the relationship between climate drivers and ecological responses. Finally, we allowed the timing of the initiation of juvenile migration to vary with environmental conditions, which subsequently affected both smolt migration survival and the probability that fish would be transported in a barge through the hydrosystem (a mitigation action that has fixed start and stop dates). Three factors -- timing, hydrosystem operations and transportation -- subsequently affected arrival timing at the Columbia River estuary, ocean survival, and upstream migration timing and survival. Although the details of the migration models are unique to this system, the need to account for carryover effects and the correlation structure of climate drivers in multiple environments is shared by many migratory species.

My concerns for the current manuscript are given below.

1) The manuscript attempts to grasp at jargon to increase its general appeal, but these attempts are often a bit off-target. For example, there has been a lot of interest in 'non-stationarity' in ecology and in fisheries science recently and this manuscript attempts to link in to these interests. However, while this term does refer to a changing variable (in the strictest statistical sense), use of this term in ecology typically is referring to changes in a relationship between variables (i.e. the relationship or correlation among variables is non-stationary). Thus, why call climate change 'stationary' or 'non-stationary'? We have known for decades that climate is non-stationary; what is interesting is that the relationships between climate conditions and ecological processes are non-stationary. Thus, use of non-stationary/stationary in this manuscript is somewhat distracting. While this is just a semantic issue, I don't think the paper benefits from the current use of these terms.

We acknowledge that we unfortunately used the term 'stationarity' in both of the meanings mentioned ("strictest statistical sense" and "typical ecology" sense). We replaced the former use of the word with the term "detrended" throughout. We also used more specific language for the latter use.

2) Similarly, the manuscript refers to 'aggressive' warming scenarios. This also seems

misplaced. Typically we refer to aggressive scenarios of curtailing carbon emissions (i.e. it's not the climate that is aggressive, it's the policy actions to reduce emissions that are aggressive).

LN 300 We have changed "more aggressive warming scenarios" to "the upper quartile of GCM projections, in which warming occurred at a faster rate"

3) The key results are expressed as the time to quasi-extinction for each of these populations. In general, I do not think this is the best way to present the key results. When a modeled population goes extinct in these simulations is based on arbitrary population thresholds that probably don't apply well when populations are reduced to very low numbers where stochastic processes are more likely to ultimately determine whether they go extinct or not. Thus, the primary results of these simulations would be more useful if the population growth rate was the response variable used to explore the consequences of different climate scenarios (i.e. the posterior distribution of lambda). The result could then be focused on how much of the posterior distribution was <1, thereby leading to population decline, etc. Time to extinction is too arbitrary and too 'loaded' a variable that is easily misinterpreted that it shouldn't be used in these types of analyses.

We respectfully disagree with the reviewer's claim that lambda is an appropriate description of the dynamics in populations that are density dependent, such as these. Lambda changes systematically as density dependence is reduced, which results in changes in lambda being an underestimate and hence misleading representation of deterministic population declines. It also can increase when populations stabilize, but if the new level of abundance is extremely low, then this too is misleading.

So although it is the case that lamda was more negative, and a larger proportion of the posterior distribution was below 1 in the climate change scenarios, we feel this is a trivial point that is much better made with the figure showing changes in abundance.

Extinction is a process that is more closely related to the number of fish in the stream than the rate of a prolonged decline. It is exactly because stochastic processes are so important for small populations (unlike lambda), that we use this quasi-extinction threshold. Although the actual threshold is indeed arbitrary, it is based on evolutionary theory, and in particular the relationship between effective population size and raw abundance in salmon. It was developed specifically in response to the concerns mentioned by the reviewer.

We are not concerned that it is "loaded" because it is one metric that is used in formal management decisions (NMFS 2020). It is related to recovery targets and a large body of work on population viability.

To address the reviewers concerns, we re-ordered the results section to emphasize changes in abundance before introducing the concept of the QET, and modified the presentation of QET as follows:

LN 51 "With a warming climate, deterministic declines inevitably lead to extinction unless some ecological, evolutionary, or climatic rescue effect occurs (38). Climate trajectories did level off in the RCP 4.5 scenarios in the second half of the 21st century, which reduced the rate of population declines in that scenario. However, for the most part populations had already reached very low abundances at that point.

For practical purposes in salmon management, populations that have fewer than 50 spawners on average for 4 years in a row are considered to be at extremely high risk of extinction from chance fluctuations in abundance, depensatory processes, and long-term consequences from loss of genetic variability (39, 40). The evolutionary theory behind this threshold applies to isolated populations, and these populations are not truly isolated. So some small populations may be sustainable within a larger salmon metapopulation. Nonetheless, when the majority of populations within the ESU pass this threshold, the ESU itself is at high risk. This ESU is already threatened with extinction because of historical declines (41), so although this exact threshold is somewhat arbitrary, it is a useful metric for demonstrating the severity of the declines across all of our simulations. We assessed the first year (if any) in which a population in a given simulation fell below a quasi-extinction threshold of adult abundance (QET50). The QET50 is passed when the running mean of spawners, measured at the spawning stream, drops below 50 individuals over any 4-year period (42)."

4) Line 24, ‘species’ should be ‘populations’

LN 23 We replaced “multiple species of Chinook salmon” to “multiple species of salmon”

5) ~ Line 121, it is not clear what the goals of the paper are. Is it to construct this model? The paper would benefit from some clear statements about what the primary objectives of this exercise are.

See the above changes to the introduction

6) It is surprising that the model suggests that the populations are essentially at no risk of going extinct given the ‘stationary’ climate scenario. This does not seem realistic given the current status of these populations.

Text added:

LN 261 Some small populations may be sustainable within a larger salmon metapopulation. Nonetheless, when the majority of populations within the ESU pass this threshold [QET50], the ESU itself is at high risk. This ESU is already threatened with extinction because of historical declines (41), so although this exact threshold is somewhat arbitrary, it is a useful metric for demonstrating the severity of the declines across all of our simulations.

7) I think the ‘Caveats’ section should be part of the Discussion of the paper.

That section was moved to the Discussion, LN 426.

Discussion

8) The Discussion highlights the weakness of the paper. Here the text basically runs through what is known about different processes or conditions that affect salmon survival. Nothing is particularly novel in this summary, nor does it highlight the main contributions of this specific modeling effort. Thus, it reinforces the lack of clarity about what this specific research activity contributes to our general understanding of Chinook salmon ecology and conservation.

We modified the discussion to note the specific benefit of quantifying climate impacts in this study:

LN 399 Our analysis showed relative resilience in freshwater stages, with the dominant driver towards extinction being rising SST, which tracked a ~90% decline in survival in the marine life stage. This occurred despite an advance in smolt migration timing and other changes in hydrosystem management. The modeled carryover effects of changes in timing are likely to be adaptive, but inadequate as compensation for large declines in marine survival.

And

LN 454 The results of our model 3, in which marine survival was driven by upwelling indicated that improved productivity in a warmer ocean could benefit salmon. Nonetheless, the benefit in that case was relatively small compared with overall negative effects.

And

LN 620 Our modeling approach, which accounts for carryover effects across the life cycle, allows systematic exploration of alternative correlation structures among climate drivers and between climate drivers and ecological responses, and a thorough accounting for uncertainty in climate projections lays a path forward for evaluating benefits of proposed actions to protect our critical resources.

Reviewer #3 (Remarks to the Author):

In this paper the authors apply a stage-based life history model to 8 populations of Chinook salmon in the Columbia River/Snake River basins and show strong associations between warming (particularly warming SST) during the marine stage of the life history and probability of population extinction/extirpation. I accepted the review with considerable excitement of seeing something truly new, insightful, or transformative. Unfortunately I was underwhelmed, not by the statistical rigour, but rather with the interpretation of the results. The claim is essentially that warming is bad and that smolts need to survive the ocean better for populations to avoid extinction. The authors all but said, and perhaps should have, that this analysis provides strong evidence that these populations are doomed and that restoration/conservation is a fools-errand (that would indeed have been provocative at least).

What I was hoping to see more of was a more holistic linkage between different stages of the life history and a quantitative appreciation that what happens in freshwater may lead individuals down trajectories that result in the ocean life history being the proximate stage of mortality.

We added more specific details about the changes in timing.

LN 363 Our model predicted that smolts would shift their migration timing about 4.5 days earlier arrival at Lower Granite Dam, which does reduce temperature exposure. Nonetheless, temperature effects on the juvenile migration still grew over time, and reduced populations by about -18% on average from the 2020s to the 2060s.

Climate impacts were most dramatic in the marine stage, where survival was reduced by -83 to -90% (Fig. 6). This occurred despite the fact that smolts arrived at Bonneville Dam, initiating the marine stage, about 6.5 days earlier, which generally improves marine survival (26).

Adult Chinook were predicted to shift their migration ~4 days earlier in response to warmer mainstem conditions with lower flows (43). But again, this was not enough to prevent mortality from increased heat exposure. During the adult migration, populations that returned to their spawning areas in summer (Secesh River and Valley Creek) were more affected by temperature than spring-run populations, with net declines of up to -17% by the 2060s. Still, the declines we found in the mainstem were relatively small because of the early adult run timing of Snake River spring/summer Chinook compared with other run types or species that migrate during peak temperatures.

And in the discussion:
LN 404 The modeled carryover effects of changes in timing are likely to be adaptive, but inadequate as compensation for large declines in marine survival, regardless of entry timing

I was hoping and expecting to see discussion that warming SSTs may be detrimental to southern Chinook populations, but Alaska populations may fare better during warming temperatures (and indeed the authors did not cite the obvious paper to suggest so).

Text added:

LN 419 Some Alaskan populations may fare better in response to ocean warming, but negative responses to warming in freshwater have been observed in other Alaskan populations, highlighting the benefits of an examination of the full life cycle (Cunningham et al. 2018; Jones et al. 2020; Ohlberger et al. 2016).
And
LN 561 Reducing hatchery production could have positive benefits, especially for wild Alaskan salmon which might benefit from warmer conditions in some localities (Cunningham et al. 2018; Jones et al. 2020).

So in the end I am left wanting the authors to make a better case for novelty and insights that can be gleaned by this very complex modelling exercise that goes beyond what is already firmly established.

Text added:
LN 422 Quantitative comparisons of combined climatic and anthropogenic influences and more exploration of changing relationships among drivers are needed to unravel the multiple pressures these populations face

AND

LN 514 Additional changes to the juvenile transportation schedule or faster transit through the mainstem can still be explored, but additional improvements to survival through other mechanisms are needed.

AND

LN 620 Our modeling approach, which accounts for carryover effects across the life cycle, allows systematic exploration of alternative correlation structures among climate drivers and between climate drivers and ecological responses, and a thorough accounting for uncertainty in climate projections lays a path forward for evaluating benefits of proposed actions to protect our critical resources.

Although the reference section is extensive, I do suggest the authors incorporate information from populations beyond their focal range to broaden the discussion of SSTs and to also contrast their work to other very similar approaches.

Cunningham, Curry J., Peter AH Westley, and Milo D. Adkison. "Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model." Global change biology 24.9 (2018): 4399-4416.

And a new paper just out led by Leslie Jones (open access)
https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15155

References added

Reviewer #2 (Remarks to the Author):

I found this paper to be exceptionally well written and the topic to be of broad international interest as a study of the impact of climate on a commercially valued species that is now at risk. This work explores the population dynamic of 8 populations of Chinook salmon in the Snake River watershed. This paper uses a life cycle model and two climate change scenarios to model the potential population trajectories of these populations. It effectively tells the risks of changing climate, particularly at sea, to all these populations but especially the smaller ones. It is sobering in its assessment of the viability of these populations- not a happy story. However, it effectively looks at the fact that these fish persist in highly altered systems and actions in freshwater might mitigate or at least slow population declines and localized extinction. These findings are novel for the populations of interest and findings (and solutions) will they be of interest to not only the fisheries
biology community but ecologists and also to the public. This work is a tangible story of the impact of change upon a species that captures the imagination of a broad spectrum of society. The species also has rich cultural importance to first nations in this watershed. These conclusions are supported by appropriate modeling and add to not only Pacific salmon literature but will be of great interest to Atlantic salmon conservationists. The sea-run nature of this species also will inform understanding of challenges in freshwater and marine systems. I found this paper to be extremely convincing and the conclusions are strengthened by a rice use of citations and the addition of allied related manuscripts on the stream temperature model and wild/hatchery marine survival. This work is cutting edge and current. I firmly believe that this paper will influence thinking in the field due to its clarity of message and exceptional graphical presentation of results. I am generally familiar with
salmon life cycle models and the overall use was both appropriate and added novel methods. I noted in one part of the paper where I am less familiar with one of the statistical analyses used. I would defer to you and others there. The open nature of the models, data and coding would allow not only the researchers to reproduce the work but add on to a toolkit of models that could be used for other species and habitats.

I have included comments in the margin of the manuscript as well as made some direct in-text suggestions to improve clarity. This was a pleasure to read.

John F. Kocik

Thank you!

Specific comments in text:

We edited the text following nearly all of the minor editorial recommendations made in tracked changes, which are not repeated here. I pulled out the comments and discuss how we addressed them.

Ln 54 [19]Atlantic Multidecadal Oscillation (AMO))

Reference added to AMO and Mills et al 2013:

Although marine climate indices have been tightly linked to survival (e.g., Pacific Decadal Oscillation (PDO) (19) and the Atlantic Multidecadal Oscillation (AMO)(20)),…

LN 87 We applied the model to eight populations within the Snake River spring/summer Chinook salmon Evolutionarily Significant Unit (ESU)

The target audience for the introduction consists of people who are not familiar with these specific locations, so the names of populations would not be informative for the general audience. The population names are included in Fig. 2, which is in the introduction and should therefore be quickly accessible when the paper is typeset.

LN 112 interactions between atmospheric forcing, wind strength, upwelling, and mixing of ocean layers, all of which affect productivity throughout the California Current Ecosystem[28]

Added text: ecosystem productivity

LN 121 Although small populations drop below this threshold periodically even in a stationary climate, larger populations do not.

All of these populations are certainly much smaller than they were historically, but we suspect their relative ordering was similar to today.

We modified the text as follows:

Some small populations may be sustainable within a larger salmon metapopulation. Nonetheless, when the majority of populations within the ESU pass this threshold, the ESU itself is at high risk. This ESU is already threatened with extinction because of historical declines (41), so although this exact threshold is somewhat arbitrary, it is a useful metric for demonstrating the severity of the declines across all of our simulations.

LN 125 … even the largest populations (Bear Valley Creek and Secesh River) fell below QET50\

We added a figure showing population dynamics over the past 20 years, including my model simulation of those dynamics, and stated the geometric mean population size at the beginning of the Methods section as follows:

Geometric mean population sizes from 2005-2014 in the populations shown in Fig. 2 ranged from 38 to 474 (39)

We feel that the names and locations of the populations in the figures is sufficient for a general audience. Detailed spawning maps do not seem appropriate for this manuscript.

LN 142 Are data available to have 2000 or 2010 starts with actual abundance metrics for past 10 to 20 years? Would enhance reader understanding of initial states. (Legend for Fig. 4)

We added a figure in the Methods section (fig. 8) showing historical population dynamics, and refer to this section in the first paragraph of the Results section:

For understanding of recent population dynamics and historical population modeling, see Methods.

LN 168 Fig. 5.

We added this information to the introduction:

We simulated population time series for these exclusively wild populations, whose recent mean spawner abundance ranged from 45 to near 600.

LN 218 More generally, the high-elevation, mostly-wilderness habitat of these populations is unusual for salmon in the region, and partially explains the relatively small effects of climate change on their freshwater life stages.

Citation added: Paulsen and Fisher 2001

LN 227 Therefore, closely monitoring ocean survival and directing research into these populations

potential response to novel conditions is clearly needed.

This sentence was removed during general editing

LN 253 closure of multiple fisheries in 2020.

This sentence was removed during general editing

LN 272 Small populations had minimal ability to buffer against declining marine survival rates, and thus were at the most immediate risk (Fig. 1).

Changed to:

Small populations had minimal demographic buffers against declining marine survival rates, and thus quickly dropped below the quasi-extinction threshold in nearly all simulations (Fig. 5).

LN 295 Do these populations use this type of [estuary] habitat? Try not to get too broad and make sure linking to the populations in this paper.

Text added:

Although the populations studied here generally spend relatively little time in the Columbia estuary, smaller, earlier-migrating individuals do utilize these habitats (Weitkamp et al. 2012). As fish outmigrate earlier in the future, they might rely more on estuary habitat. Furthermore, other salmon populations depend heavily on estuary habitat for essential growth and their success has been linked to estuary restoration actions (Diefenderfer et al. 2016).

LN 312 also enhance/restore freshwater salmon production.

Changed as suggested

LN 320 sport fish (smallmouth bass, *Micropterus dolomieu* and brook trout *Salvelinus fontinalis*) to creation of reservoir habitat more favorable for invasive fish (e.g., American shad, *Alosa sapidissima*).

We removed the Latin names here for consistency

LN 326 habitat

The word “prime” was changed to “all critical”

LN 333 However, the urgency is greater than ever to identify successful solutions at a large scale and implement known methods for improving survival. Management actions that open new habitat, improve productivity within existing habitat, or reduce mortality through direct or indirect effects in the ocean are desperately needed.

Text added: However, there are hard choices where human demands on land and water have come at the cost of wildlife. The urgency is greater than ever to identify successful solutions at a large scale and implement known methods for improving survival. Management actions that open new habitat, improve productivity within existing habitat, or reduce mortality through direct or indirect effects in the ocean are desperately needed. We can find new ways to improve salmon habitats while maintaining other benefits for people, like reconnecting floodplains for recharging aquifers, and protection from flooding, storm surge and erosion with floodplains and natural marshes.

Methods section:

LN 339 abundance estimates .

Text added to introduction:

LN 154 We simulated population time series for these exclusively wild populations, whose recent 15-y geometric mean spawner abundance ranged from 45 to near 600 (Ford et al. 2016; NMFS 2020) and shown in new Fig. 8.

wild from known population sources.

Text added:

LN 632 No hatchery fish are released in any of the streams supporting the populations in this analysis.

“effective spawners”,

Thank you

of producing a spawner distribution that was not statistically different from the observation dataset (p-value>0.05 from the Kolmogorov-Smirnov test).

Thank you

The COMPASS model also tracks the proportion of fish that were loaded into barges to bypass migration

through the hydropower system.

Text added to Supplement S2:

LN 58 The COMPASS model predicts the proportion of fish passing a dam that will enter the bypass system as a function of percent spill, flow, and potentially also day of year or water temperature (depending on the dam).

(500,000 iterations per population).

Please note that the formal convergence tests were conducted on the Bayesian mcmc chain output, as described in the supplement S1. We added more information to that section:

LN 105 We assessed convergence of the chains using the Gelman and Rubin’s convergence diagnostic (gelman.diag function in the coda package). The multivariate potential scale reduction factor was <1.0125 for all initial models (6 models, in which covariates included summer temperature and one of spring, summer or fall flow, and covariates were incorporated into either the productivity or the capacity terms). We also examined Heidelberger and Welch’s convergence diagnostics. To ensure all chains were long enough, we re-ran all models with a single chain that was 15 million iterations. All of the parameters in all models passed this diagnostic, except for the two models that included both summer temperature and summer flow. They still had one parameter each that failed the Heidelberger and Welch convergence diagnostic (at eps=0.1 and pvalue=0.05). Although visual examination of the chains and density distributions looked satisfactory, we did not use these models in further analysis.

But for the calibration step, we assessed goodness of fit using the Kolmogorov□Smirov test.

Text added:

LN 770 We selected this number so that we ended up with at least 1000 sets of parameter values for each population that produced spawner distributions similar to that observed.

REVIEWERS' COMMENTS:

Reviewer #2 (Remarks to the Author):

I was quite impressed by the first version of this manuscript. I find this manuscript continued to build upon the existing salmon literature to provide both an expanded and nuanced view of climate impacts on salmon. Results are appropriate and important to share with a broader community. I understand and appreciate some of the concerns relative to focus of the paper raised by other reviews. I believe that the revisions strengthened and further clarified. I would also point out that this paper is of broad geographic reach as some of the findings are applicable to Atlantic salmon and probably other searun fish such as shad and eels. I had no “in-line” comments in this second review and support all the changes made by the authors. All my minor suggestions were either adequately addressed or rebuttal explanations were clear and appropriate. It was a pleasure to reread.

John F. Kocik

Reviewer #3 (Remarks to the Author):

The authors have addressed my most substantive concerns and clarified the novelty of their work (forecasting rather than explanation/hindcasting). This is an important, albeit fairly depressing look into the future, that I predict will shape conversations about conservation/restoration actions given the predictions of warming SSTs.