

Individual-based simulations suggest mixed impacts of warmer temperatures and a nonnative predator on Chinook salmon

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Abstract. As the climate changes, warmer water temperatures may stress populations of native coldwater fishes. Simultaneously, nonnative warmwater predators may expand their ranges and interact with already at-risk native fish populations. To explore the independent and combined effects of these two stressors on threatened salmon, we present a case study of simulated Chinook salmon *Oncorhynchus tshawytscha* and largemouth bass *Micropterus salmoides* interacting under two thermal regimes in the Snoqualmie River, Washington, USA. We applied an individual-based and spatially explicit model that tracks fish movement and growth. We evaluated changes in Chinook salmon emergence date, outmigration date, mass, and survival. We ran simulations for four scenarios: (1) Baseline, run without either stressor, (2) Warm, run with warmer temperatures, (3) Predator, run with largemouth bass, and (4) Warm-Predator, run with both stressors. We assessed outcome metrics relative to the Baseline scenario. In the Warm scenario, salmon emerged 37 d and outmigrated 55 d earlier. There were 61% more subyearling migrants that were 31% smaller, and 72% fewer yearlings. In the Predator scenario, salmon survival decreased 64% for subyearlings and 69% for yearlings, and subyearlings were 7% smaller. In the Warm-Predator scenario, salmon emerged 39 d and outmigrated 59 d earlier, subyearling survival increased 22%, subyearling mass decreased 37%, and 93% fewer yearlings survived. Our results suggest that warmer temperatures shift emergence and outmigration; predation by nonnative species is a threat to salmon survival; and life history strategies experience these stressors in different ways. Whereas subyearling production benefited from warmer temperatures more than it was hurt by predation, yearling production was depressed by both stressors independently and combined. Managers can use our individual-based and spatially explicit approach to identify key times and areas to address exposure to extreme temperatures, overlap with nonnative species, and their interactive effects on threatened salmon. Our case study addressed three pressing needs identified in the literature: investigate impacts of nonnative species on threatened native salmon, build tools to evaluate management options where bass and salmon overlap, and explore how freshwater fishes will contend with multiple interactive stressors.

Key words: Chinook salmon; climate change; individual-based model; invasive species; largemouth bass; nonindigenous species; protected species; threatened species.

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INTRODUCTION

As climate change alters freshwater thermal regimes (Kaushal et al. 2010, Orr et al. 2015), coldwater fish species are predicted to experience phenology shifts (Otero et al. 2014, Peer and Miller 2014); altered physiological processes, growth, and survival (Lynch et al. 2016, Whitney et al. 2016); changes in food webs (Albouy et al. 2014, Rosenblatt and Schmitz 2016); and range reductions (Isaak and Rieman 2013, Radinger et al. 2017). Simultaneously, warmwater and potentially invasive nonnative fish species may proliferate as habitats that were previously thermally unsuitable become habitable (Rahel and Olden 2008, Diez et al. 2012). The combined impacts of climate change and nonnative species on native coldwater fishes are still unclear.

Pacific salmon and steelhead (*Oncorhynchus* spp.) are economically, culturally, and ecologically important coldwater species in the Pacific Northwest, USA. Due to stressors such as habitat loss, commercial harvest, hydropower, and hatchery practices, seventeen population segments are listed as threatened or endangered under the Endangered Species Act (ESA; Nehlsen et al. 1991, Ford et al. 2015). These already-threatened salmonids are expected to be further impacted by continued climate change (Crozier et al. 2008b, Mantua et al. 2010, Ford et al. 2015).

Nonnative predators are an additional and understudied threat to imperiled salmonids (Carey et al. 2011). For example, largemouth bass have been documented consuming Chinook salmon in Lake Washington, Washington (Tabor et al. 2007); the Lower Columbia River, Oregon (Poe et al. 1994); and the San Joaquin River, California (Grossman 2016, Michel et al. 2018). Carey et al. (2011) reported that another nonnative bass, smallmouth bass (*M. dolomieu*), consumed up to 35% of outmigrating wild Chinook salmon in reservoirs of the Snake and Columbia river basins in the Pacific Northwest, USA. Salmon may be particularly susceptible to these nonnative predators, because they have no previous exposure to them (Kuehne and Olden 2012).

To weigh the independent and combined effects of climate change and nonnative predators on native juvenile salmon, we used an individual-based model (IBM). IBMs simulate the states and behaviors of individuals in order to

evaluate emergent population-level responses (DeAngelis and Grimm 2014). We evaluated Chinook salmon emergence, outmigration, mass and survival using an IBM set in the Snoqualmie River, Washington, USA. Our aim was to explore how increasing temperature and predation by nonnative largemouth bass might affect native and threatened Chinook salmon. We chose the Snoqualmie River watershed for our case study because the watershed has both ESA-listed salmonids and nonnative largemouth bass (Thompson et al. 2011). The lower watershed contains salmon habitat that is already considered temperature impaired (Stohr et al. 2011), and there exists a rich water temperature dataset on which to build a model.

Our specific objectives were to evaluate how Chinook salmon emergence, outmigration, mass, and survival were affected by: (1) warmer temperatures, (2) predation by nonnative largemouth bass, and (3) the combined effects of warmer temperatures and largemouth bass predation. Our findings can help resource managers to identify conditions under which bass may present additional stress to this threatened population of Chinook salmon, and to plan conservation actions accordingly.

METHODS

Study area

The Snoqualmie River drains ~1800 km² on the west side of the Cascade Range, Washington, USA (Fig. 1). Three main forks (North, Middle, and South) run through mostly forested public land owned by the United States Forest Service and the Washington Department of Natural Resources, before meeting near the city of North Bend and combining to form the mainstem Snoqualmie River. The river flows over Snoqualmie Falls, an anadromous fish barrier, and continues flowing northwest where human land use (agriculture, residential, and commercial) becomes more prevalent. The Tolt River, which provides drinking water to the city of Seattle, then joins from the north. The Raging River joins from the south and is a relatively warm tributary used by salmonids. Finally, the Snoqualmie River joins the Skykomish River to form the Snohomish River near Monroe, Washington, and enters Puget Sound shortly downstream. Streamflow

peaks in winter (from rain) and again in spring (from snowmelt).

The river supports wild populations of Chinook, chum (*O. keta*), coho (*O. kisutch*), and pink salmon (*O. gorbuscha*), as well as steelhead (*O. mykiss*), rainbow trout, and cutthroat trout (*O. clarkii*). Bull trout (*Salvelinus confluentus*) may have been present historically, but they have not been observed recently. The Snoqualmie population of Chinook salmon is considered ocean-type, with a mix of subyearling and yearling migrant life history strategies. The yearling life history strategy is slightly more prevalent in the Snoqualmie River population than other Puget Sound populations now, although the prevalence of yearling migrants in many Puget Sound populations was likely higher in the past (Beechie et al. 2006). Largemouth bass have been stocked in ponds and lakes throughout the basin, and

they have been observed in oxbows and slow-moving sections in the mainstem below Snoqualmie Falls (Thompson et al. 2011, <https://wdfw.wa.gov/fishing/washington/Species/1738>; K. Higgins, King County Water and Land Resources Division, *personal communication*).

Thermal regimes

To represent thermal regimes across the stream network (i.e., thermal landscapes) that influences fish behavior in the IBM, we used estimates of stream temperature located every 1 km throughout the Snoqualmie watershed during 2014 and 2015. Stream reaches were from the National Hydrography Dataset (McKay et al. 2012), pruned to reaches of Strahler order ≥ 3 . Stream temperature predictions were made twice daily to represent daily minimum (6 am) and maximum (6 pm) temperatures. Details about the

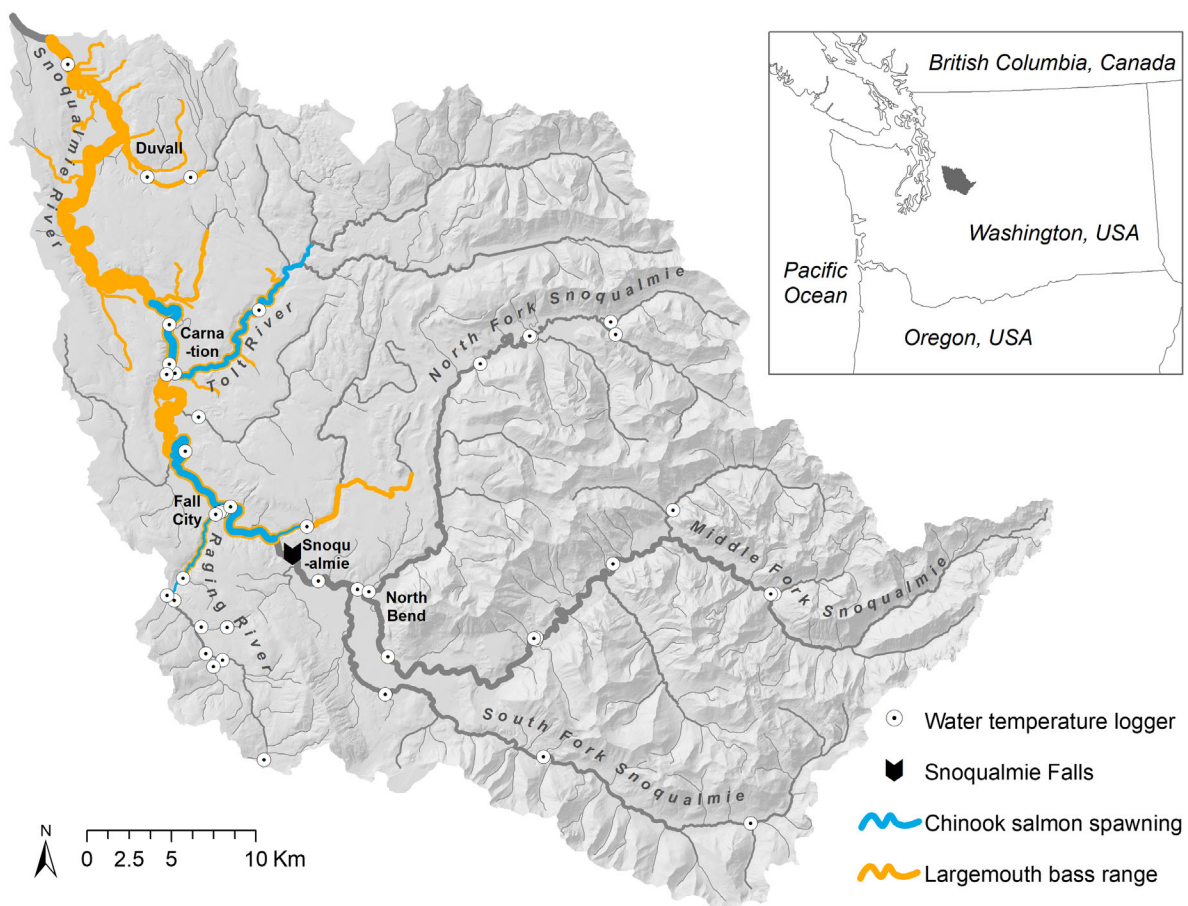


Fig. 1. Map of the Snoqualmie River watershed, Washington, USA.

empirical data and model construction are provided in Steel et al. (2016) and Marsha et al. (2018), and summarized here. Predictions were based on observations of water temperature monitored every 30 min at >40 locations throughout the mainstem, the three forks, and other tributaries (Fig. 1) using Tidbit loggers by Onset (Bourne, Massachusetts). Predictions were made using a spatial stream network (SSN) model (Ver Hoef et al. 2006, Ver Hoef and Peterson 2010), which incorporates the spatial covariance present in water temperature data, the unique branching structure of the river network, flow direction, and volume. Applications of SSN models have found significantly improved prediction accuracy at unsampled locations compared to other approaches (Isaak et al. 2010, Peterson and Ver Hoef 2010). The SSN model was fit to stream temperature observations using three covariates: elevation, mean annual discharge, and percent commercial area in the contributing watershed. Steel et al. (2017) provide animations in their supplementary information that visualize how water temperature predictions change over time and across the entire Snoqualmie watershed (Fig. 2).

Individual-based model

Overview and assumptions.—The IBM developed here was adapted from a spatially structured IBM that tracked Chinook salmon from egg deposition through outmigration (Fullerton et al. 2017). The original model included sub-models for movement, growth (via bioenergetics), and survival, and summarized population-level responses that emerge from individual fish behaviors. Movement decisions and growth were governed by water temperature and fish density; survival was driven by body size and recent growth. Our version of the model (Fig. 3) differed from the original in multiple ways (Appendix S1: Table S1). Key changes made to answer our research questions were (1) we applied it to a real watershed, the Snoqualmie River, (2) we incorporated empirical water temperature data, and (3) we added predation by largemouth bass. Below, we describe the model, focusing on the modifications from the original version, especially the updated movement rules and the addition of predation. All model parameters are provided in Appendix S1: Table S2;

model initialization data are provided in Appendix S1: Table S3; model validation data are provided in Appendix S1: Table S4; model code (in R) is provided on GitHub (<https://github.com/brooke-l-hawkins/salmon-simulations>) and in Data S1.

Our model made several assumptions about stream habitat and fish behavior. These simplifying assumptions may have resulted in predictions that do not perfectly reflect reality, but they allowed us to make relative comparisons among scenarios while controlling for variability that could mask effects.

We made two key assumptions about habitat. First, we did not explicitly model flows, and assumed that thermal landscapes in 2014 and in 2015 reflected associated flow regimes during those years. Second, we assumed that food availability varied throughout accessible habitat, increasing with stream order and decreasing with distance from the base of the network. We reasoned that this representation of larger and lower elevation streams as more productive was plausible given the temperature dependence of prey production (Brown et al. 2004, Patrick et al. 2019) and given that temperature, nutrient input, and primary production are often higher in lower regions of watersheds (Wipfli and Baxter 2010, Petty et al. 2014, Huntsman et al. 2016, Kaylor et al. 2019).

We also made several assumptions about how fish responded to their environment. First, we assumed that movement was driven by growth potential, which is a direct measure of fitness influenced by fish mass, water temperature, and food availability. Second, we assumed that growth was driven by growth potential and adjusted to account for intraspecific competition, represented as reduced food availability based on biomass of nearby conspecific fish. Third, we assumed that predation was influenced by predator temperature, proximity between predator and prey, and ratio of predator to prey mass. Finally, we assumed that size-based stochastic survival was based on fish size and growth. We return to the potential impacts of these assumptions on our findings in the *Discussion*.

The model used superorganism concepts to reduce computation cost (Scheffer et al. 1995, Railsback et al. 2013). For instance, we simulated 2241 Chinook salmon in each scenario. This

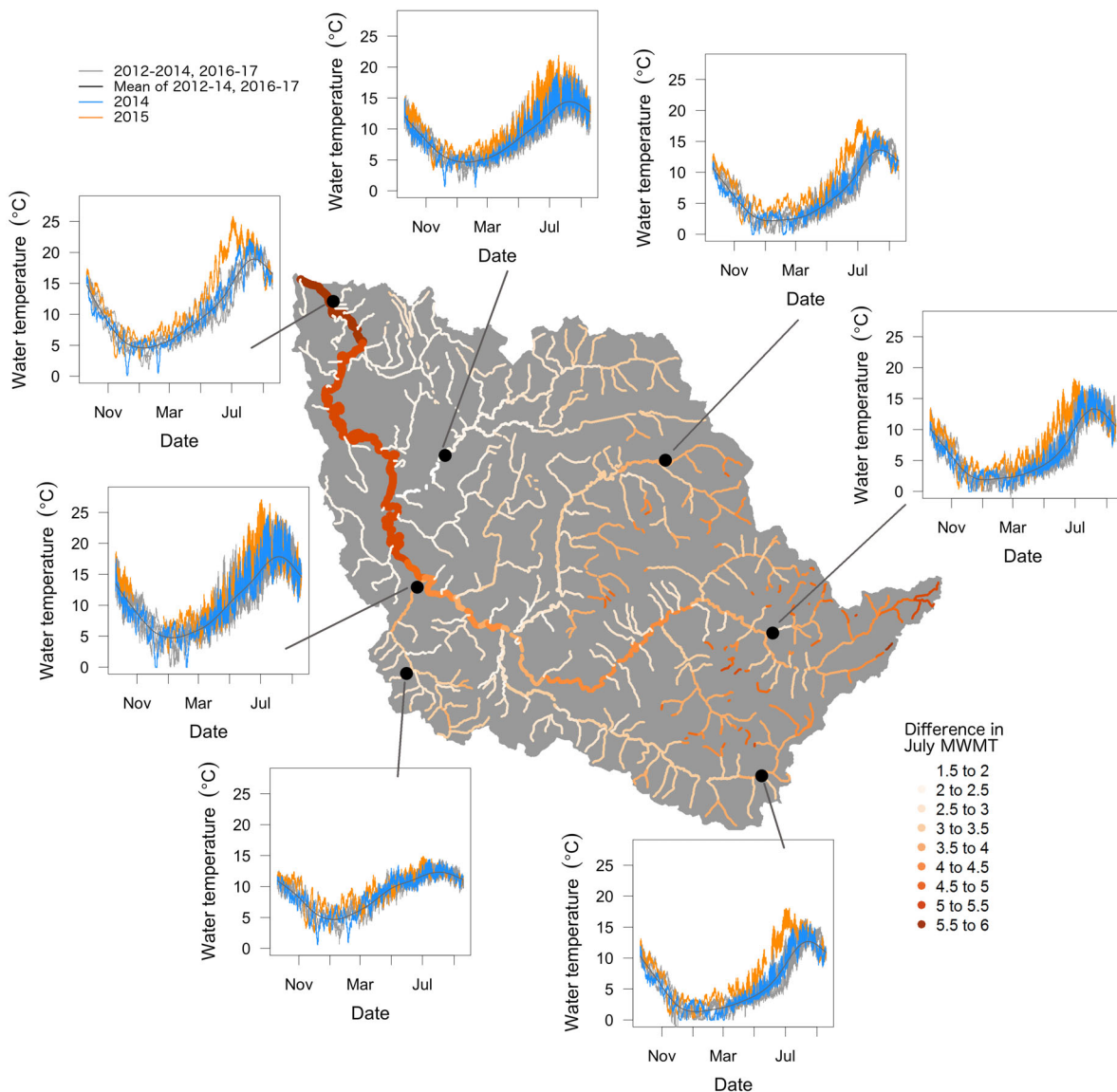


Fig. 2. Map displays the difference ($^{\circ}\text{C}$) between maximum weekly maximum temperature (MWMT) during July in an unusually warm and dry year (2015) and the spatial average of July MWMT during typical years (i.e., 2012–2014 and 2016–2017). The seven plots along the margins show annual time series of water temperature. The gray lines show temperatures from typical years, and the black line displays the mean temperature of typical years. Temperatures used in this study were from a typical year (2014) (blue line), and an unusually warm and dry year (2015) (orange line).

number was the product of the mean number of observed redds in the watershed (851; Kubo et al. 2013), a typical number of eggs per redd (4558; McMichael et al. 2005), and the mean egg-to-fry survival in a nearby watershed (0.578; Pess 2016), divided by a scalar that reduced computation

cost by assuming that one modeled fish represents 1000 real fish. Similarly, each modeled mobile fish represented 1000 real fish in density calculations.

Initial conditions.—At the beginning of each simulation, we calculated food availability and

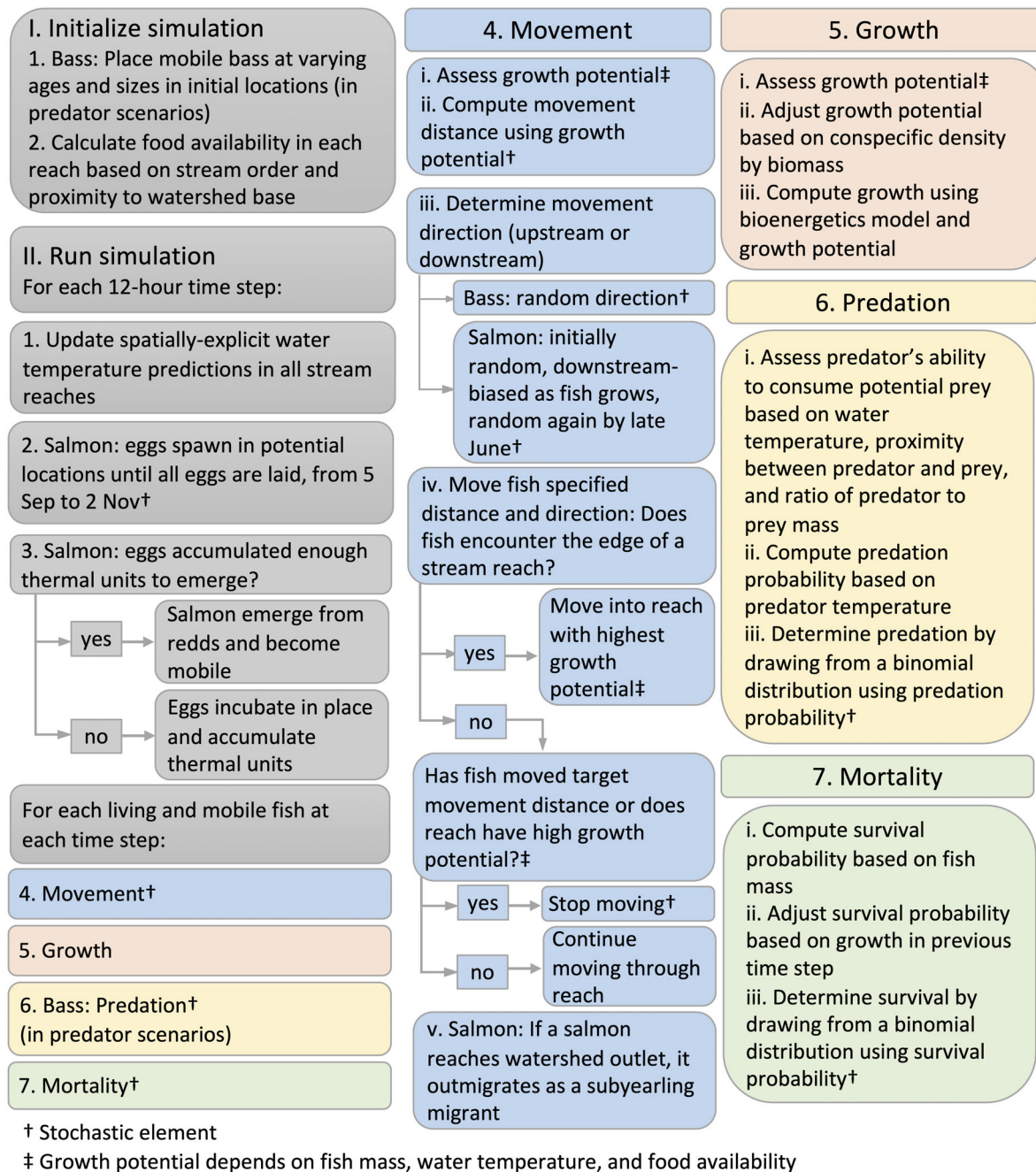


Fig. 3. Schematic describing the sequencing of events during each model simulation.

placed individual fish. We calculated potential food availability in each reach as the product of stream order and distance upstream, which ranged between a maintenance ration and a maximum consumption ration for each species. We

placed 2241 Chinook salmon eggs (Appendix S1: Table S2) in 2241 unique locations, evenly distributed in the stream network where spawning has been observed during annual surveys (Appendix S1: Table S3). This included the

mainstem below Snoqualmie Falls and below confluences with the Tolt and Raging Rivers, as well as lower reaches of the major tributaries accessible to fish below the falls. We placed 500 largemouth bass ranging in size from 1 to 4000 g (Appendix S1: Table S2). Since we did not have survey data for the distribution of largemouth bass throughout the stream network, we distributed them evenly across 188 locations (Michel et al. 2018) in reaches where it was most plausible for them to occur: we selected all stream reaches below ponds where bass have been observed or caught by anglers (<https://wdfw.wa.gov/fishing/washington/Species/1738/>, <https://nas.er.usgs.gov/queries/CollectionInfo.aspx?SpeciesID=401&status=0&fmb=0&pathway=0&HUCNumber=171100>) and mainstem reaches where bass have been observed in adjacent oxbows and off-channel habitats (K. Higgins, King County Water and Land Resources Division, *personal communication*).

Sequence of events.—We ran simulations for one year, beginning on 1 September and concluding on 31 August of the subsequent year. Eggs were deposited during autumn spawning events that occurred between 5 September and 2 November. We tracked development of salmon from egg deposition to outmigration (the point at which juvenile salmon leave the watershed and transition into the saltwater phase of their life history). The outmigration date depended on how rapidly fish reached the river outlet, and generally occurred during spring or summer. Although the model also tracked movement and growth of largemouth bass, we summarized outcome metrics for Chinook salmon only.

For each simulation, we incubated salmon eggs where they were spawned until they were ready to emerge. During this time, bass moved, grew, and survived without interacting with salmon. After salmon emerged, the following sequence of actions occurred twice every day (at 6 am and 6 pm) for all fish in all scenarios: fish moved, grew, and survived size-based mortality. In the predator scenarios, salmon were also exposed to predation by largemouth bass. At each time step, salmon that had moved into the lower mainstem were counted as subyearling migrants and removed from the population of remaining fish. Stochastic elements of the model included spawn date, initial fish position,

movement distance, movement direction at the beginning of each time step, predation, and survival (Fig. 3).

Movement.—Fish moved along the river network and could occupy any one-dimensional position within a reach. Movement rules used growth differential (g_d), which describes how well a fish would grow in its current location relative to other accessible locations, defined as:

$$g_d = \frac{\max(g_e) - g_f}{\text{range}(g_e)} \quad (1)$$

where g_f = growth potential at the fish's current location during that time step, and g_e = growth potential in other accessible reaches during that time step. Growth potential was calculated using the bioenergetics submodel and is a function of a fish's mass, water temperature, and the food available in that reach after accounting for the biomass of conspecific fish in the reach.

Fish movement resulted from four processes: determining initial movement direction (Eq. 2), assigning target movement distance (Eq. 3), selecting which reach to occupy at confluences (Eq. 4), and enabling fish to stop early if suitable growing conditions were encountered (Eq. 5).

For salmon, the initial movement direction in each time step had a downstream bias that increased as fish grew to 1.5 g, tapered off after 1 April (past which observations of fish in smolt traps in the Snoqualmie are rare), and became zero after 30 June (past which no fish are observed outmigrating (Kubo et al. 2013)). The probability of downstream movement p_d was calculated as:

$$p_d = \begin{cases} \frac{m_f}{m_d} \left(1 - \frac{d_t - d_s}{d_1 - d_s}\right) & \text{for } d_s < d_t < d_1 \\ \frac{m_f}{m_d} & \text{for } d_t < d_s \\ 0 & \text{for } d_t > d_e \end{cases} \quad (2)$$

where m_f = mass of the fish, m_d = mass above which a fish was strongly driven to move in a downstream direction, d_t = the date of the current time step, d_s = the date past which fish no longer bias their movements in a downstream direction, d_e = the date past which fish no longer outmigrate, and d_1 = the last day of the simulation.

Target movement distances were drawn from a lognormal distribution with the following properties:

$$\ln(\mu) = g_d c; \ln(\sigma) = s \quad (3)$$

where g_d = growth differential (Eq. 1), c is a constant used to reduce potential movement to match distances reported in the literature, and s is a shape parameter (Appendix S1: Table S2). High growth differentials (i.e., the fish was not in a suitable habitat due to low temperature or crowded conditions) resulted in high target movement distances.

A fish moved in the same direction it was previously traveling, unless it had moved its target distance, encountered a confluence, or stopped early. At each confluence, the fish moved into the reach (r) with the highest growth potential:

$$r = \max(g_i, g_j, g_k) \quad (4)$$

where g_i , g_j , and g_k are growth potential in reaches i , j , and k , respectively.

The probability of stopping early p_s was calculated as:

$$p_s = (1 - g_d) \times (1 - p_d) \quad (5)$$

where g_d is growth differential (Eq. 1) and p_d is the probability of moving in a downstream direction (Eq. 2).

Largemouth bass followed the same rules but were not driven to move in a downstream-biased direction; their initial movement direction (upstream or downstream) each time step was random. The distance a bass moved was reduced further by multiplying the target movement distance by c (Appendix S1: Table S2) to match empirical observations of site fidelity (Warden and Lorio 1975, Copeland and Noble 1994).

Outmigration.—Outmigration only applied to Chinook salmon, which were biased towards downstream movement according to Eq. 2. As soon as a Chinook salmon reached the river outlet, it was recorded as a subyearling migrant. These fish were removed from the rest of the population, for which modeling continued. At the end of the simulation, any Chinook salmon that remained in the watershed were assumed to have chosen to overwinter in freshwater and migrate to sea the following year, and they were recorded as yearlings. The presence of a yearling life history strategy is supported by empirical data (Kubo et al. 2013): 3–46% (8% average) of

smolts captured in the lower mainstem Snoqualmie River from 2002–2012 were yearling migrants (Appendix S1: Table S4).

Growth.—We predicted growth of individual fish at each 12-h time step using the Wisconsin Bioenergetics model (Hanson et al. 1997), with updated parameters governing optimal temperatures for maximum consumption by juveniles (Appendix S1: Table S2). In the bioenergetics model, growth is affected by fish mass, water temperature (we used the prediction nearest to each fish), food availability, and the energy density of predators and prey. In our scenarios, only the first three elements varied. Food availability varied over space and was adjusted based on conspecific biomass in each reach. Crowded conditions decreased the food supply available to fish and reduced growth.

Predation and survival.—Fish of both species were subjected to stochastic size-selective mortality where mortality risk decreased as fish size increased. This mortality represented predation by animals other than bass, harvest by anglers, susceptibility to pathogens, etc. (Fullerton et al. 2017, Eq. 4).

If applicable, salmon were subjected to predation by largemouth bass. Each largemouth bass was assigned a predation probability (p_p , Eq. 6) that was applied to all its potential salmon prey. This probability was used to sample randomly from a binomial distribution for each potential salmon prey (0 = the fish was eaten, 1 = the fish survived). It was possible for the same salmon to be at risk of predation by multiple nearby predators with varying predation probabilities. The probability of predation was calculated as:

$$p_p = p_m \left(\frac{T - T_C}{T_C} \right) \quad (6)$$

where p_m = maximum predation probability (proportion), T_C = critical temperature for predator activity (degrees Celsius), and T = current temperature of predator (degrees Celsius). Largemouth bass could only be predators if they were above a critical temperature of 10°C (Lemons and Crawshaw 1985, Fullerton et al. 2000). Potential prey included salmon that were alive, emerged, within the same segment and within a specified distance, and if the prey: predator size ratio was small enough (Appendix S1: Table S2).

Assessing salmon responses

Simulated scenarios.—We used four scenarios (Table 1) to compare the independent and combined effects of warmer thermal regimes and largemouth bass predation on Chinook salmon. We ran simulations with 2014 water temperatures to represent thermal conditions in a cool, typical year, and 2015 water temperatures to represent an anomalously warm, dry year (Fig. 2). The 2015 thermal regime may be illustrative of conditions more likely to occur in the future as the climate warms (Kubo 2016, Steel et al. 2019). We included largemouth bass to evaluate how Chinook salmon were affected by a nonnative predator.

The Baseline scenario was a simulation with 2014 water temperature and without largemouth bass. This represented a control scenario which we used to compare relative effects of independent and combined stressors, and to validate our model. We calibrated parameters involved in spawning, emergence, movement, outmigration, and survival (Appendix S1: Table S2) by trial and error to match empirical observations in the watershed (Appendix S1: Table S4). The Warm scenario was a simulation run with 2015 water temperatures and without largemouth bass, used to evaluate the independent effects of a warmer thermal regime.

The Predator scenario was a simulation including largemouth bass, run with 2014 water temperature, to evaluate the independent effects of a nonnative predator. The Warm-Predator scenario was a simulation run with 2015 water temperature data and including largemouth bass to evaluate the combined, interactive effects of a warmer thermal regime and a nonnative warmwater predator. We have limited data regarding the abundance and size classes of largemouth bass in the Snoqualmie watershed, so our Predator scenarios represent potential

worst-case scenarios that could occur if largemouth bass expand their range or activity as the climate continues to warm.

For each scenario, we quantified and visualized four outcome metrics for salmon: emergence date, outmigration date, mass, and survival. We compared patterns in salmon responses across scenarios by examining time series and distributions of responses. We also created a predation risk map for the Warm-Predator scenario, identifying key times and places that bass eat salmon. For each scenario, our experimental unit was the mean response by all surviving fish in a simulation. We measured a population-level response emerging from the behaviors of individual fish.

Sensitivity analysis.—To assess the sensitivity of salmon outcome metrics to parameter values (Appendix S1: Table S2), we conducted a global sensitivity analysis (Saltelli 2002). We describe the methods and findings in depth in Appendix S2, and briefly summarize them here. We evaluated the Baseline and Predator scenarios (Table 1). We ran 300 iterations of the model for each scenario, respectively.

For each iteration, we stochastically varied parameters simultaneously by drawing values for each parameter from a normal distribution with a mean set to the nominal parameter value and the standard deviation set to 10% of the nominal parameter value. In the Predator scenario, we fixed Chinook salmon parameters that were never one of the top five most influential parameters in the Baseline scenario. Additionally, we stochastically varied parameters specific to largemouth bass. Due to model structure constraints, we varied the number of salmon and (if applicable) bass in five discrete multiples (0.5, 0.8, 1, 1.2, or 1.5) of the nominal value.

We used random forest regression (Breiman 2001), implemented using the "randomForest" package in R (Liaw and Wiener 2002), to identify which parameters had the greatest influence on outcome metrics because this nonparametric approach does not assume linear relationships between outcome metrics and parameters (Aulia et al. 2019). We grew each forest to 5000 trees and we allowed 10 parameters to be considered at each tree node. We investigated parameter importance using evaluation metrics produced

Table 1. Scenarios evaluated using the individual-based model.

Scenario	Temperature data	Largemouth bass
Baseline	2014	Absent
Warm	2015	Absent
Predator	2014	Present
Warm-Predator	2015	Present

by the "randomForestExplainer" package in R (Paluszynska et al. 2019).

RESULTS

Model performance

We compared simulated emergence date, outmigration date, mass, and survival in the Baseline scenario against field studies. Simulated metrics were within the range of observed data, when available (Table 2). Data for Chinook salmon at the modeled life stage were not always available for the Snoqualmie watershed, which made some direct comparisons difficult. This was especially true for fry-to-smolt survival, and the survival and mass of yearlings at the end of their first summer.

Response to warmer thermal regime

Chinook salmon in the Warm scenario emerged and outmigrated sooner than salmon in the Baseline scenario. On average, salmon emerged 37 d earlier, and subyearling migrants outmigrated 55 d earlier (Fig. 4). The average mass of subyearling migrants was 1.43 g, 31% lower than in the Baseline scenario. The average mass of yearlings was 23.39 g, 41% higher than in the Baseline scenario (Fig. 5). In the Warm scenario, 393,000 fish survived, a 45% increase in

salmon survival. Different life history strategies were affected differently; more subyearling migrants survived (384,000, a 61% increase) and fewer yearlings survived (9000, a 72% decrease; Fig. 6).

Higher winter temperatures accelerated egg incubation, resulting in earlier emergence. Higher spring temperatures increased salmon mass and minimized size-selective mortality. There are countervailing effects in our model structure, however, because growth is driven by both water temperature and food availability. When there are more surviving salmon, there are more fish competing over limited food resources, and growth is consequently limited by density dependence. This combination of increased temperatures and intraspecific competition resulted in more subyearling migrants that were smaller upon outmigration.

Response to largemouth bass predation

Surviving salmon emerged three days earlier and subyearling migrants outmigrated seven days earlier in the Predator scenario than they did in the Baseline scenario (Fig. 4). The average mass of subyearling migrants was 4.40 g, 7% lower than in the Baseline scenario. The average mass of yearlings was 15.76 g, 58% lower than in the Baseline scenario (Fig. 5). Fewer salmon

Table 2. Comparison of values observed in field studies with model predictions for Chinook salmon in the Baseline scenario.

Fish response	Model predictions in Baseline scenario	Field values in the Snoqualmie River	References
Survival	12.0% fry-to-smolt survival, producing 238,000 [†] subyearling migrants and 33,000 [†] yearlings by 31 August	1.7 to 12.6% egg-to-smolt survival, producing 45,000–322,000 smolts	Kubo et al. (2013)
Date eggs emerge	January 12–April 5 (March 1 median)	Approximately December–March [‡]	Beechie et al. (2012); leDoux et al. (2017)
Date subyearling migrants outmigrate	April 3–June 29 (May 21 median)	February 13–June 25 (May 6 median)	Kubo et al. (2013); Pouley and Zackey (2015)
Subyearling migrant mass at outmigration	0.6 to 5.0 g (2.0 g mean)	1.8 to 28.1 g (3.2 g mean)	Field values estimated using a length–weight regression from Denny et al. (2014) and fork lengths from Kubo et al. (2013) and Tulalipsmolt trap data [§]
Yearling mass	6.7 to 29.5 g (16.5 g mean) by 31 August	4.0 to 71.2 g (9.6 g mean) at outmigration at age 1	Same as above

[†] According to our assumption that one simulated fish represents 1000 fish in the field.

[‡] More specific field values for emergence timing were not available for the Snoqualmie River.

[§] M. Pouley and T. Zackey, Tulalip Tribes Natural Resources Department, *personal communication*.

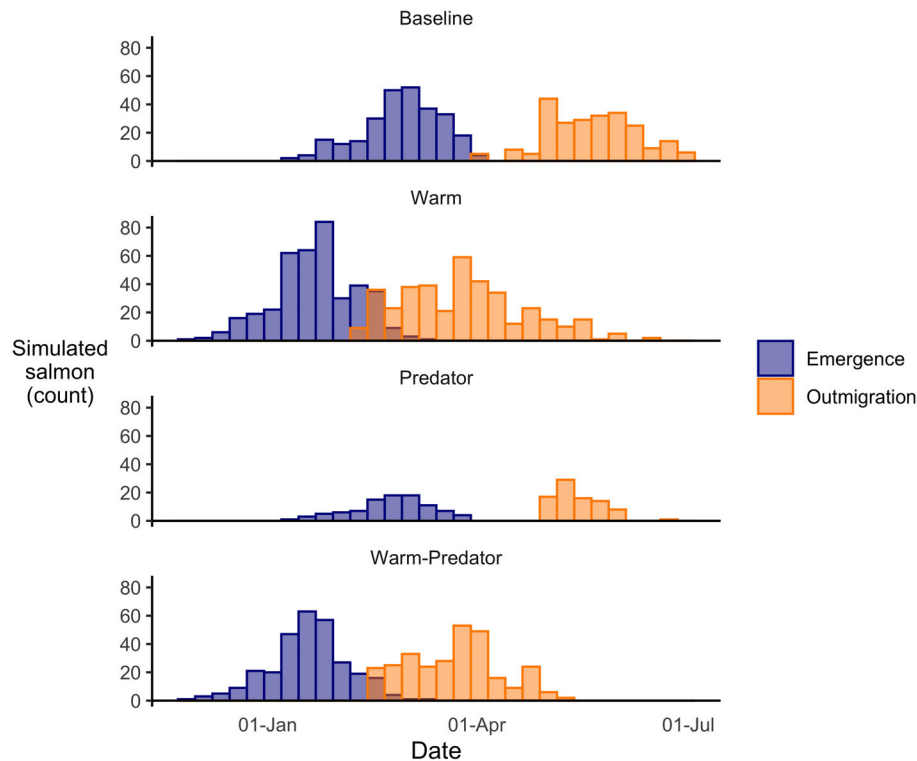


Fig. 4. Chinook salmon phenology in four scenarios. Histograms depict the number of simulated salmon (y -axis) that emerge (blue) and outmigrate (orange) over time (x -axis) across scenarios (rows). Note that although each simulation was initialized with $N = 2241$ salmon, emergence timing is only shown for surviving salmon (Baseline $N = 271$, Warm $N = 393$, Predator $N = 95$, Warm-Predator $N = 294$), and outmigration timing is only shown for surviving salmon that outmigrated as subyearlings (Baseline $N = 238$, Warm $N = 384$, Predator $N = 85$, Warm-Predator $N = 292$).

survived in the Predator scenario relative to the Baseline scenario (Fig. 6). A total of 95,000 fish survived in the Predator scenario, a 64% decrease relative to the Baseline scenario. There were fewer subyearling migrants (85,000, a 64% decrease) and fewer yearlings (10,000, a 69% decrease).

Salmon emergence and outmigration were not driven by predation, so the shift in emergence and outmigration of surviving salmon shows that salmon experiencing these events earlier are more likely to escape predation. Since simulated largemouth bass only fed actively in temperatures above 10°C , predation predominantly affected subyearling migrants at the tail end of the outmigration distribution and yearlings that stayed in the watershed. Still, the additional presence of a nonnative predator depressed both subyearling and yearling survival by over 60%.

Response to combined stressors

Chinook salmon in the Warm-Predator scenario emerged 39 d earlier and outmigrated 59 d earlier relative to salmon in the Baseline scenario (Fig. 4). Surviving subyearling migrants weighed 1.30 g on average, 37% less than in the Baseline scenario, and yearlings weighed 14.23 g on average, 29% less than in the Baseline scenario (Fig. 5). More salmon survived in the Warm-Predator scenario (294,000, an 8% increase). Survival differed by life history; survival increased for subyearling migrants (292,000 fish, a 22% increase) and decreased for yearlings (2000 fish, a 93% decrease) (Fig. 6).

For Chinook salmon, the risk of negative combined effects of largemouth bass predation during a warm thermal regime was greatest in the mainstem reaches below Snoqualmie Falls and during spring (Fig. 7). Predation intensity was

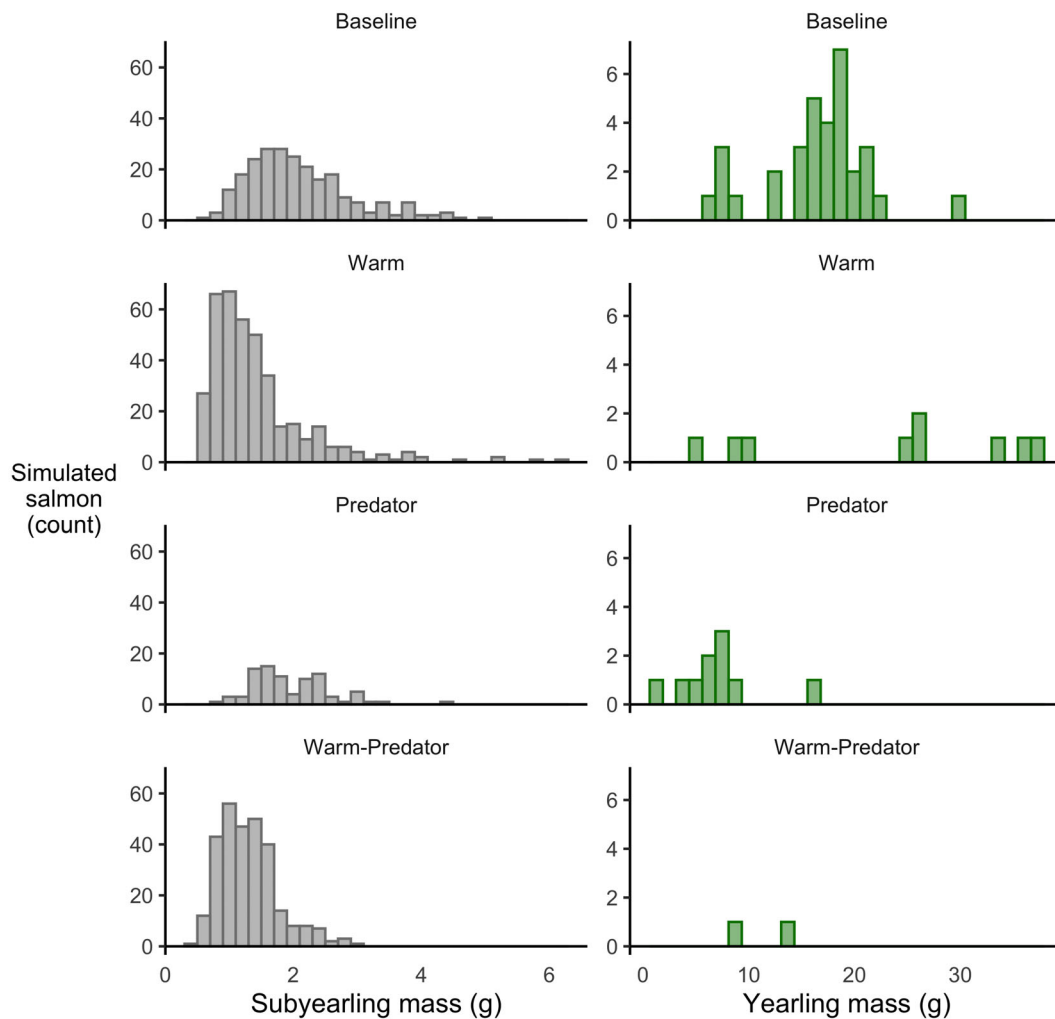


Fig. 5. Chinook salmon mass in four scenarios. Histograms plots depict mass (x -axis) of subyearling (left column) and yearling (right column) migrants across scenarios (rows). Note that although each simulation was initialized with $N = 2241$ salmon, mass is only shown for surviving salmon (Subyearling: Baseline $N = 238$, Warm $N = 384$, Predator $N = 85$, Warm-Predator $N = 292$; Yearling: Baseline $N = 33$, Warm $N = 9$, Predator $N = 10$, Warm-Predator $N = 2$).

especially high surrounding the confluence with the Tolt River, from April to May. These locations and dates coincided with conditions during which bass were actively feeding (i.e., temperatures above 10°C). The majority of subyearlings had outmigrated before May (Fig. 4); therefore, predation predominantly affected subyearling migrants at the tail end of the outmigration distribution and yearlings that stayed in the watershed.

Sensitivity analysis

Salmon outcome metrics were most sensitive to parameters involved in each process directly and indirectly, in the expected directions (Fig. 8; Appendix S2). Emergence date was most sensitive to parameters affecting spawning and thermal exposure. Salmon mass was most sensitive to parameters affecting growth and survival. Outmigration date was most sensitive to parameters affecting thermal exposure, survival, and

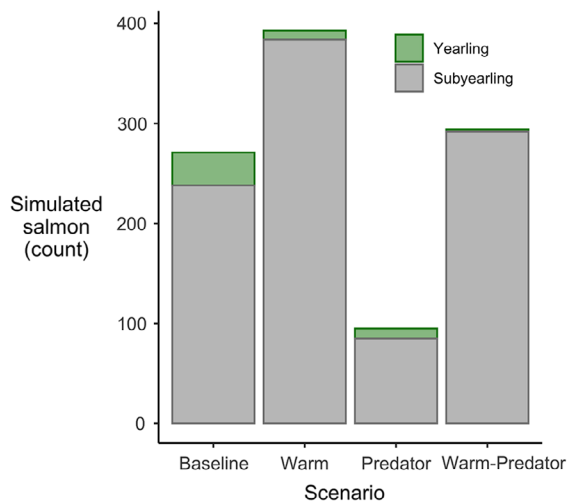


Fig. 6. Chinook salmon survival in four scenarios. Bars depict the number of surviving simulated salmon (y -axis) across scenarios (x -axis). Simulated salmon either outmigrated as subyearling migrants (gray) or stayed in the watershed as yearling migrants (green). Each simulation was initialized with $N = 2241$ salmon.

outmigration. Survival was most sensitive to parameters affecting survival, predation, and growth.

The most influential parameters across outcome metrics in the Baseline scenario were the energy density of prey ("prey.en.dens"), the highest ration available in the stream network ("ration.hi"), the amount of thermal exposure needed for eggs to emerge ("ATU.crit"), the minimum probability that an individual fish will survive one time step ("survival.min"), and the energy density of salmon ("pred.en.dens").

The emergence date and yearling mass outcome metrics had 83.9% and 62.2% of variance explained, respectively, by the random forest models, suggesting that the selected parameters had direct influence on the outcome metric. For the other outcome metrics, the variance explained was <40%, suggesting that relationships between individual parameters and model outcomes were not strong, potentially due to antagonistic interactions or to stochasticity that led to emergent behavior of the model.

For the Predator scenario, four of the most influential parameters across outcome metrics were the same as for the Baseline scenario: "prey.en.dens," "pred.en.dens," "ATU.crit," and

"survival.min." However, the temperature above which largemouth bass could consume salmon ("pred.temp.crit.b") became an important parameter in this scenario. Interestingly, this was the only parameter specific to bass that was influential. Similar to the Baseline scenario, 84.6% of variance was explained by the emergence date model, and variance explained was <50% for other outcome metric models.

DISCUSSION

Impacts of warmer thermal regime

There is ample evidence that climate change poses risks to coldwater species like salmonids (Jonsson and Jonsson 2009, Wade et al. 2013, Wenger et al. 2013). The ways that fish will respond to climate change are likely to be complex and case-specific, varying by species and life stage, as well as by the extent and timing of environmental change. Our model demonstrated that warming temperatures could result in shifted emergence, outmigration, mass, and survival in a life history-specific way for one population of Chinook salmon in one watershed.

Climate change may decrease survival during certain freshwater life stages, especially when flow is low and water temperature is high (Crozier and Zabel 2006, Mantua et al. 2010, Arismendi et al. 2012). In a warmer thermal regime, we observed lower simulated yearling survival, but higher simulated subyearling survival. However, the smolt trap in our study area captured fewer subyearling migrants in warmer 2015 conditions than cooler 2014 conditions (Pouley and Zackey 2015). This discrepancy could be explained if fish outmigrated before the smolt trap was operational in 2015. The most sensitive parameters for survival were the minimum and maximum probability an individual survived each time step, and those parameters were calibrated to match empirical data in a cooler thermal regime. Therefore, this discrepancy could also be attributed to the fact that those parameters did not accurately capture salmon behaviors in a warmer environment.

We observed that simulated salmon emerged and outmigrated earlier in a warmer thermal regime, which is well supported by the literature. Earlier emergence and outmigration are likely to become more frequent since incubation is

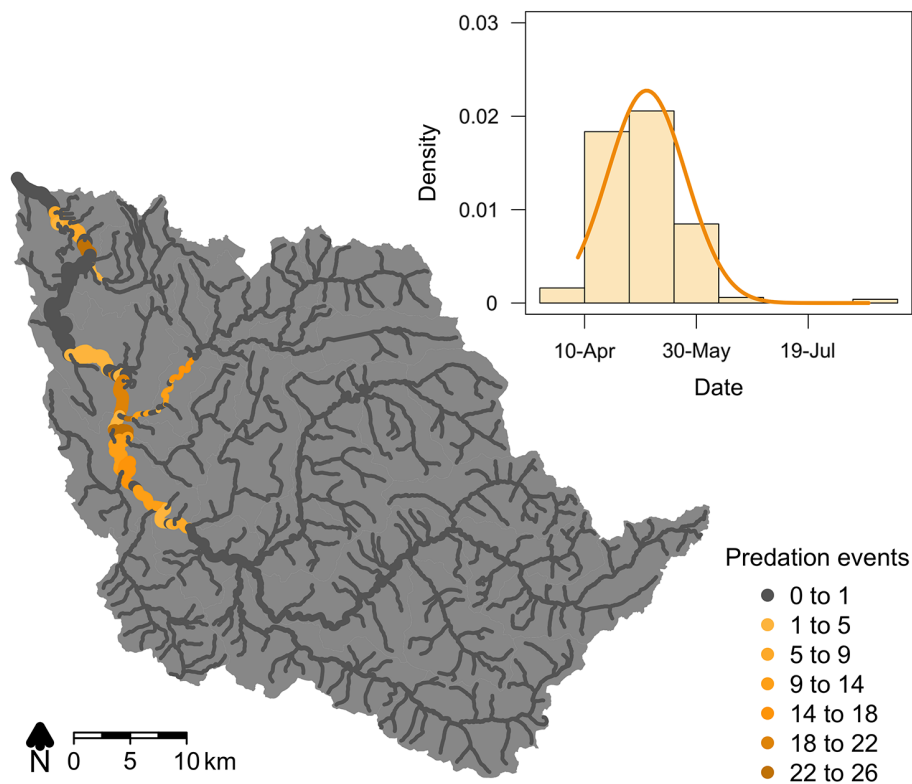


Fig. 7. Intensity of largemouth bass predation on Chinook salmon in the Warm-Predator scenario. Predation is represented over space as the number of predation events per stream reach and represented over time as the probability density of predation events occurring on a particular date (inset).

accelerated during warmer winters (Mundy and Evenson 2011). Multiple studies have found that the median migration date of salmonids shifted earlier as water temperature increased in the migration corridor: spawning Chinook and sockeye salmon in the Columbia River, Oregon (Crozier et al. 2008a); outmigrating Chinook salmon in the Sacramento-San Joaquin River, California (Munsch et al. 2019); outmigrating wild Atlantic salmon (*Salmo salar*) in the River Bush, Northern Ireland (Kennedy and Crozier 2010); and five species of outmigrating salmon in Auke Creek, Alaska (Kovach et al. 2013). The effects of this shift on later life stages are unknown, but could include changes in which year salmon migrate to sea (Beakes et al. 2011), susceptibility to size-selective predation (Weitkamp et al. 2015), mismatched resources (Crozier et al. 2008a, Satterthwaite et al. 2014), altered population age structure (Tattam et al. 2015), and decreased

survival to adulthood (Thompson and Beauchamp 2014).

In addition to phenological shifts in a warmer thermal regime, we observed a decrease in simulated subyearling mass. Although higher temperatures boost simulated growth potential (Falke et al. 2019), this potential may not be realized due to truncated growing seasons; for example, Munsch et al. (2019) found that body size of outmigrating Chinook salmon was directly and negatively related to warmer thermal regimes in a California watershed where salmon outmigrated earlier. Lower mass could also be due to density-dependent impacts on growth. When salmon survival was higher, there were more fish consuming limited shared prey resources, which reduced salmon growth. Such density-dependent impacts are well-documented within salmon species (Greene and Beechie 2004, ISAB 2015). In the Snake River, Idaho, declines in parr-to-smolt

growth and survival of various populations of spring/summer Chinook salmon were partly attributed to density-dependent competition with other salmon (Achord et al. 2007, Walters et al. 2013). Crozier et al. (2010) found that salmon growth had a positive relationship with temperature in habitat with low conspecific density, but a negative relationship in habitat with high conspecific density, suggesting warmer temperatures may intensify density-dependent processes.

Impacts of nonnative predator

In our simulation, the presence of largemouth bass resulted in decreased Chinook salmon survival for both subyearling migrants and yearlings that remained in the watershed. Although data are lacking for largemouth bass predation of Chinook salmon in this watershed and other streams in the Puget Sound, Washington, one study in a Puget Sound lake found that salmonids in general constitute up to 45% of the largemouth bass diets (Tabor et al. 2007). Studies in other locations and with another invasive bass species have found detrimental effects similar to our simulated results. Largemouth bass are known predators of Chinook salmon in the San Joaquin River, California (Nobriga and Feyrer 2007) where Michel et al. (2018) estimates they could consume three to five Chinook salmon per river kilometer daily during peak outmigration periods. Studies of smallmouth bass also found concerning effects on Chinook salmon populations, such as in the lower Yakima River, Washington, where Fritts and Pearsons (2004) found that ocean-type Chinook salmon made up nearly half of the diet of smallmouth bass. Smallmouth bass is a known and substantial risk to native salmon in the Pacific Northwest (Sanderson et al. 2009, Carey et al. 2011, Lawrence et al. 2014), and the diets of largemouth and smallmouth bass overlap considerably (Olson and Young 2003).

Impacts of combined stressors

We found that accelerated emergence and outmigration in warmer temperatures minimized the lethal effects of largemouth bass predation. Warmer winter and spring temperatures shifted the timing of two life history events, and since largemouth bass in our model were only active above a threshold of 10°C, subyearling migrants

that smolted before temperatures reached this threshold escaped predation. Thus, warmer temperatures limited interactions between early migrants and predatory bass. It is worth noting that this finding is sensitive to one specific model parameter: the temperature threshold above which largemouth bass were active predators. This was the only bass-specific parameter that our outcome metrics were sensitive to, with survival being the most sensitive metric. If this threshold was a lower temperature (Fullerton et al. 2000), then largemouth bass would interact with smolts earlier in outmigration and further decrease subyearling survival. In contrast, if this threshold were a higher temperature, then largemouth bass would interact with fewer subyearling migrants, and potentially predate fewer yearling migrants as well. Yearlings would have more time to grow before bass were active predators, and some could potentially grow enough to escape size-selective predation.

We found that yearling survival was lowered by a warm thermal regime and by largemouth bass predation independently, and it was lowest with both stressors combined. A strong phenological shift could result in such a loss of life history strategies (Beechie et al. 2006, Crozier et al. 2008a, Boughton et al. 2015). Furthermore, the Snoqualmie River typically has a snowmelt-driven hydrological peak, but that peak was absent in 2015 (Kubo 2016, Steel et al. 2019), and areas with rainfall-dominated hydrology tend to produce more subyearling migrants (Beechie et al. 2006). Warm thermal regimes, like that observed 2015, may result in fewer salmon remaining instream over winter. If the remaining yearling migrants are additionally stressed by predators, as our model demonstrated, life history diversity may be reduced further. A loss of yearling migrants could be especially problematic for Chinook salmon in the Snoqualmie watershed, which has historically produced a high number of yearling migrants (Kubo et al. 2013) relative to other Puget Sound watersheds.

In addition to concerns about shifted salmon life histories, there is a growing concern that warmwater nonnative species such as bass will expand their range as the climate warms, potentially squeezing salmon out of preferred habitats (Hulme 2007, Lawrence et al. 2014, Cheng et al. 2017). In the Snoqualmie River, Steel et al. (2019)

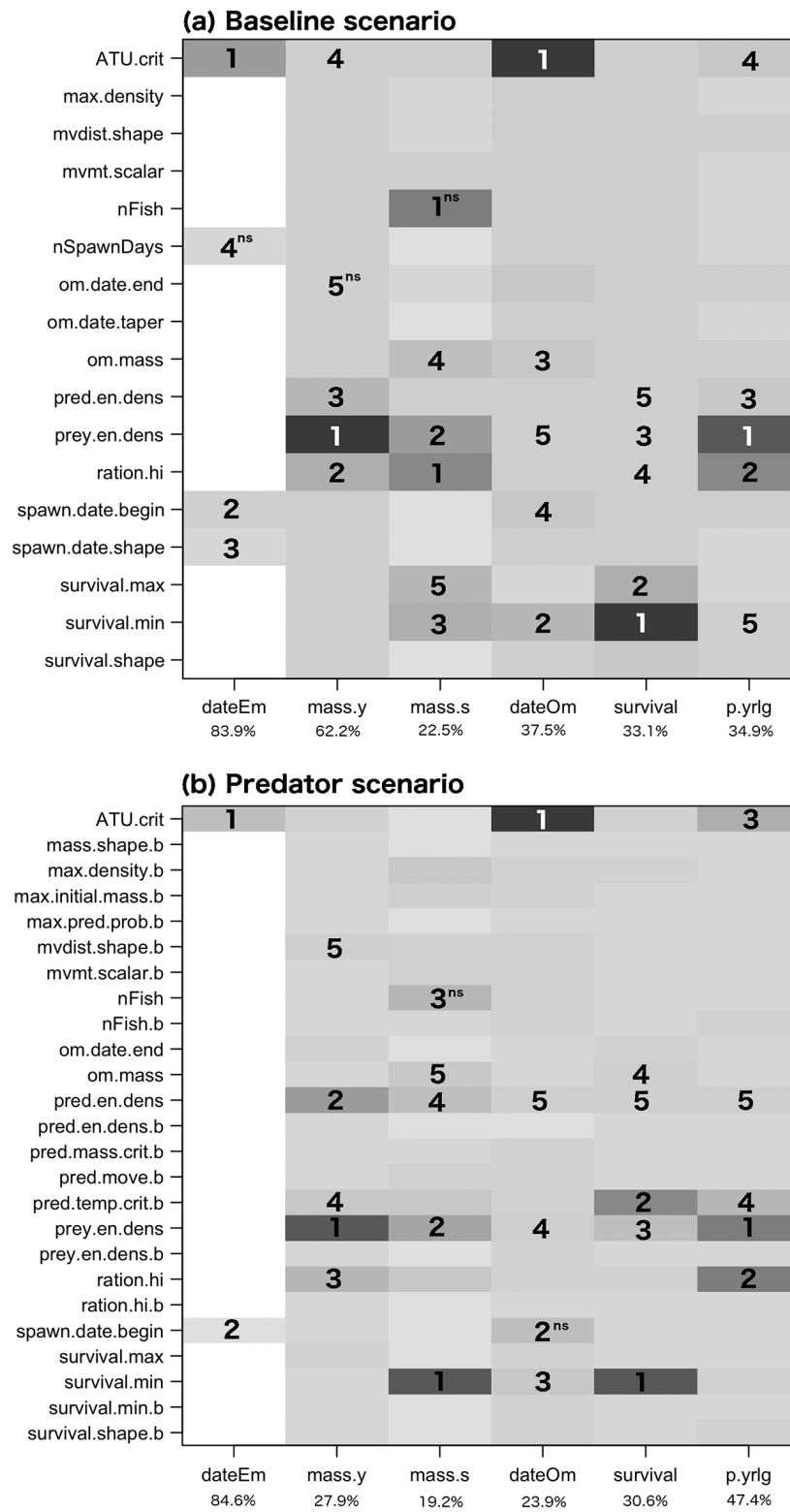


Fig. 8. The relative sensitivity of each outcome metric (x-axis) to parameters (y-axis, defined in

Fig. 8. (Continued)

Appendix S1: Table S1 and in the text) for the (a) Baseline and (b) Predator scenarios. Sensitivity is measured by the increase in mean squared error that would occur in a random forest regression if that parameter was permuted randomly. Darker colors indicate an outcome metric is more sensitive to the parameter, and lighter colors indicate an outcome metric is less sensitive to the parameter. The top five most sensitive parameters for each outcome metric are numbered from 1 to 5. Outcome metric abbreviations are "dateEm" = date of emergence; "mass.y" = mass of yearling migrants; "mass.s" = mass of subyearling migrants; "dateOm" = date of outmigration; "survival" = proportion of salmon that outmigrated or remained in the watershed at the end of the simulation; and "p.yrlg" is the proportion of survivors that remained in the watershed until the end of the simulation. Parameter names with a ".b" suffix were specific to largemouth bass; others were specific to Chinook salmon. The subscript "ns" indicates $P > 0.1$. Percentages below outcome metrics indicate the proportion of variance explained in random forest models. Similar patterns emerged with other evaluation metrics (Appendix S2).

suggested that habitat suitability for adult largemouth bass in warmer years might increase in lower-order streams. However, Lawrence et al. (2015) suggested that growth of juvenile smallmouth bass is more temperature-sensitive than other life stages, and that up-river expansion may be constrained by overwinter energetic constraints. We are beginning to understand the mechanisms controlling range expansion of bass (Rubenson and Olden 2017), and our study contributes to the few existing examples of how interactions with nonnative largemouth bass may affect native salmon.

Caveats and future directions

We did not explicitly model stream flow in our simulations. Flow is an important factor influencing thermal regimes, fish productivity, and largemouth bass predation. Crozier and Zabel (2006) found that flow during fall was the best predictor of survival for certain populations of Chinook salmon in the Snake River Basin, Idaho, whereas survival in other populations was more strongly driven by temperature. Since the estimated thermal regimes used in our model were based on empirical data, effects of flow on temperature were inherently included, but direct effects of flow on fish behavior were not modeled. This simplification enabled us to focus on thermal effects expected under a changing climate in a controlled environment. It is possible that the increases in growth caused by elevated temperatures that we estimated may be counteracted by increased metabolic expenditure navigating high flows, or by increased susceptibility to predators or pathogens during low flows as fish are crowded into smaller areas. Flow could also

affect predation by largemouth bass. In the Snoqualmie River, yearling Chinook salmon predominantly use off-channel habitats and slow-water areas (Kubo 2017) and such slow-water habitats are preferred by largemouth bass. If we accounted for flow in our model, it is possible largemouth bass may overlap more frequently with yearling migrants. It is an important next step to incorporate how native and nonnative species respond to altered flows into our model.

Another simplifying assumption of our model was that habitat quality (other than temperature and prey availability) was homogeneous from one year to another. In nature, prey availability is unevenly distributed in space and over time, and the Independent Scientific Advisory Board (ISAB 2015) notes that limited food resources limit the growth of juvenile Chinook salmon in many locations. Moreover, it is likely that fish assemblages (Pletterbauer et al. 2014) and food webs (Li et al. 2011, Hildrew et al. 2017) will be altered by climate change. Therefore, it is possible that the accelerated growth we estimated in warmer temperatures would not have been possible if preferred prey was no longer available when they were historically used by Chinook salmon.

Other assumptions in our model included the drivers of movement behavior, growth, predation, and survival. We based relationships on established mechanisms such as growth-temperature performance curves (Hanson et al. 1997), density-dependent movement (Railsback et al. 1999, Greene and Beechie 2004), density-dependent growth (ISAB 2015), and size-selective predation (Fryxell and Lundberg 1993). Our outcome metrics were particularly sensitive to the energy density of salmon and salmon prey,

the highest ration available in the stream network, and the amount of thermal exposure salmon eggs needed to emerge. It may be time to revisit and refine the functional form of these relationships and their parameterizations. Responses to stressors may be population-specific (Crozier and Zabel 2006, Crozier et al. 2008a) or evolve over time (Crozier et al. 2008a), and parameters may differ by geographical region (Fullerton et al. 2000).

Informing conservation decisions

Individual-based and spatially explicit simulations can be used to advise effective climate and invasive species mitigation strategies. For instance, understanding potential shifts in phenology caused by a warmer climate may enable managers to proactively alter the window during which salmon are allowed to be harvested by sport and commercial fisheries. Default model outputs could also be used to identify specific conditions under which invasive species expansion could present additional stress. For instance, Fig. 7 illustrates the key reaches where and dates when largemouth bass predation pressure was highest in our simulation of a warmer thermal regime. Maps like these could be examined for locations and/or times that interactions with bass could act as potential bottlenecks for outmigrating or overwintering salmon. This information could be used by managers to help decide where and when efforts at controlling an invasive bass population, through targeted removal or increased recreational fishing opportunities, may be most effective to reduce risks to salmon (Carey et al. 2011).

Similarly, maps depicting when and where salmon growth was lowest may be helpful in identifying potential habitat restoration opportunities. Planting riparian vegetation and increasing connections between mainstem habitat and cooler off-channel habitats could reduce exposure by salmon to warm temperatures (Beechie et al. 2012). Several studies have suggested that riparian restoration may reduce or even ameliorate the potential effects of increased water temperature expected over the next several decades (Bond et al. 2015, Sun et al. 2015, Honea et al. 2016, Justice et al. 2017). Care will need to be taken, however, when increasing connectivity with potentially cooler off-channel habitats to

ensure that these habitats will not become ecological traps due to the presence of nonnative warmwater predators like largemouth bass.

Conclusions

This case study considered how the independent and combined impacts of climate change and a nonnative warmwater predator could affect the early life history of a threatened population of Chinook salmon. Modeling interactive ways that climate change can affect native cold-water species—not simply warmer temperatures, but also interactions with warmwater nonnative species—can provide more information for managers faced with producing effective conservation plans (Beechie et al. 2012, Crozier and Hutchings 2014, Lawrence et al. 2014). Our model demonstrates how a multispecies (Stillman et al. 2015) and spatially explicit individual-based model could be a useful decision support tool for fisheries management (Dudley 2018) at a scale that helps bridge the gap between research and conservation (Fausch et al. 2002). Our model could be applied and calibrated to other watersheds with rich fish and temperature datasets, and it could be expanded to explore interactions among additional native and nonnative species in a changing climate. Our case study addressed three pressing needs identified in the literature: (1) investigate impacts of nonnative species on threatened native salmon (Sanderson et al. 2009), (2) build tools to evaluate management options where bass and salmon overlap (Carey et al. 2011), and (3) explore how freshwater fishes will contend with multiple interactive stressors (Olden 2010).

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Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3218/full>