Simulated juvenile salmon growth and phenology respond to altered thermal regimes and stream network shape

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Abstract. It is generally accepted that climate change will stress coldwater species such as Pacific salmon. However, it is unclear what aspect of altered thermal regimes (e.g., warmer winters, springs, summers, or increased variability) will have the greatest effect, and what role the spatial properties of river networks play. Thermally diverse habitats may afford protection from climate change by providing opportunities for aquatic organisms to find and use habitats with optimal conditions for growth. We hypothesized that climate-altered thermal regimes will change growth and timing of life history events such as emergence or migration but that changes will be moderated in topologically complex stream networks where opportunities to thermoregulate are more readily available to mobile animals. Because climate change effects on populations are spatially variable and contingent upon physiological optima, assessments of risk must take a spatially explicit approach. We developed a spatially structured individual-based model for Chinook Salmon (*Oncorhynchus tshawytscha*) in which movement decisions and growth were governed by water temperature and conspecific density. We evaluated growth and phenology (timing of egg emergence and smolting) under a variety of thermal regimes (each having a different minimum, rate of warming, maximum, and variability) and in three network shapes of increasing spatial complexity. Across networks, fish generally grew faster and were capable of smolting earlier in warmer scenarios where water temperatures experienced by fish were closer to optimal; however, growth decreased for some fish. We found that salmon size and smolt date responded more strongly to warmer springs and summers than to warmer winters or increased variability. Fish in the least complex network grew faster and were ready to smolt earlier than fish in the more spatially complex network shapes in the contemporary thermal regime; patterns were similar but less clear in warmer thermal regimes. Our results demonstrate that network topology may influence how fish respond to thermal landscapes, and this information will be useful for incorporating a spatiotemporal context into conservation decisions that promote long-term viability of salmon in a changing climate.

Key words: Chinook Salmon; climate change; individual-based model; network topology; thermal heterogeneity.

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INTRODUCTION

Climate change is expected to alter the dynamics of riverine thermal regimes, causing warmer temperatures, and potentially increased thermal variance (Isaak et al. 2012, Arismendi et al. 2013). These changes could have biological implications for stream biota, because temperature regulates metabolism, influences growth, phenology, and survival, and drives food webs and community structure (Caissie 2006, Steel et al. 2017). Pacific salmonids (*Oncorhynchus* spp.) are expected to be vulnerable to changes in hydrologic and thermal regimes caused by climate change (Crozier and McClure 2015, Falke et al. 2015). As environmental conditions become less tolerable (Mantua et al. 2010, Arismendi et al. 2012), salmon can either adapt (Reed et al. 2011), shift their spatial distribution (Isaak and Rieman 2013), or bear potential consequences. Future thermal landscapes will likely alter growth, survival, and phenology in multiple life stages (Kovach et al. 2013). Altered phenology may be problematic if it results in mismatches between evolved life history strategies and environmental conditions. For instance, fish emerging (hatching) earlier, growing faster, and smolting (migrating to sea) earlier may find inadequate food resources or increased susceptibility to predators in the marine environment. It remains unclear what component of altered thermal regimes might most influence growth and phenology of salmon. For instance, are elevated temperatures during winter, spring, or summer more influential to the date at which smolts migrate to sea? Does growth differ in stable and variable thermal regimes?

Although it is clear that future climate will challenge salmon, we do not know how spatial properties of thermal habitat in streams will influence salmon responses. Diverse thermal habitats, if accessible within life stage-specific movement ranges, should afford more opportunities for salmon to find optimal growing conditions. This, in turn, could promote life history diversity and reduce long-term risk, thereby bolstering the portfolio of populations capable of responding to climate change (Waples et al. 2008, Anderson et al. 2015). Stream networks with complex topology afford a diversity of habitats to stream biota. Benda et al. (2004) proposed that the spatial arrangement of tributaries in a network

(i.e., as measured by basin size, shape, drainage density, and network geometry) interacts with stochastic watershed processes to regulate the spatial diversity of stream habitats throughout a river basin. Their work focused on physical processes, but Kiffney et al. (2006) and Torgersen et al. (2008) subsequently found effects of tributary confluences on water temperature, habitat quality, and fish distribution. Olden and Naiman (2010) state, "The management of riverine landscapes for thermal integrity will require a broad perspective that recognizes the heterogeneous nature in which the topology of the drainage network controls the physical processes shaping spatial and temporal variability in stream temperatures." Network topology has been implicated in colonization dynamics and species distributions (Martin and Petty 2009, Della Croce et al. 2014) and may be important for other aspects of population ecology. Here, we focus on three stream network shapes as described by Benda et al. (2004) and common in the Pacific Northwest: a long network, which has a long mainstem and numerous short low-order tributaries; a compact network, which has a short mainstem and hierarchically nested tributaries packed into a tight space; and a typical pear-shaped network, which is intermediate in shape.

Evaluating how salmon will respond to climate-altered thermal regimes in different stream networks would be difficult to test empirically, given the broad spatiotemporal extent, complexity of variables, and feasibility of tracking growth and movement of individual salmon protected by the Endangered Species Act. Individual-based models (IBMs) are well suited to evaluating how fish may respond to potential future climates because interacting processes can result in emergent properties not observable with models that do not track individuals. Individual-based models have been developed for evaluating consequences of environmental conditions experienced by fish in one or several stream reaches (Van Winkle et al. 1998, Railsback and Harvey 2002, Piou and Prévost 2012, Penaluna et al. 2015). The role of stream network topology was investigated by Leibowitz and White (2009) in a life cycle model to better understand Coho Salmon (*Oncorhynchus kisutch*) population dynamics, but they did not consider effects of decisions made by individual fish.

Here, we present an individual-based model for subyearling Chinook Salmon (*Oncorhynchus*

tshawytscha) that explicitly considers how individuals respond simultaneously to components of altered thermal regimes and to spatial variance in thermal habitat across a whole stream network. Subyearling Chinook Salmon spawn in the autumn, eggs incubate over winter, juveniles rear in freshwater during spring and early summer, and smolts generally migrate to sea before the onset of winter. Our objectives were to evaluate (1) how juvenile salmon growth and phenology may respond to different aspects of climate-altered thermal regimes, and (2) whether responses differ for fish in stream networks having different shapes. A better understanding of the interaction between thermal regimes and network shape will contribute to informed conservation planning by providing guidance on activities that will maximize climate resilience.

Methods

We used simulation experiments to evaluate our two objectives. We first describe the experiments and the thermal regimes and stream networks used in each. We then describe the individual-based simulation model and how we evaluated results.

Experiment 1: altered thermal regimes

Our objective for this experiment was to evaluate how juvenile salmon growth and phenology may respond to different aspects of climate-altered thermal regimes. Warmer temperature accelerates physiological processes and development rates. We therefore hypothesized that if existing water temperatures were below physiological optima, warmer future water temperatures would increase growth rates, whereas if water temperatures were already optimal, warmer water temperatures may depress growth due to increased metabolic costs or altered ecological interactions. If fish grow faster, they may smolt earlier; however, if growth is compromised by stressfully high water temperature, smolt outmigration may be delayed.

We evaluated the relative influence on juvenile salmon of four different elements of a thermal regime that might be expected to change in a future climate: (1) minimum temperatures during winter, (2) the rate at which water temperature warms during spring, (3) maximum temperatures during summer, and (4) how variable temperature

is from one day to the next. To do this, we constructed a contemporary thermal regime and a variety of altered thermal regimes in which one of the four elements was increased by either a moderate or extreme amount (Fig. 1). We compared fish responses in each altered thermal regime to responses in the contemporary thermal regime (Appendix S1: Table S1).

The contemporary thermal regime was generated to represent a common pattern observed in streams of the Pacific Northwest, USA (Steel et al. 2016), and had a cool winter, slow spring warming, cool summer, and stable variance (hereafter referred to as cscs). The altered thermal regimes were designed to capture various aspects of regime change, including magnitude, rate of warming, and variability of the annual cycle (Maheu et al. 2016), and to represent conditions that could occur within approximately 100 yr, should recent rates of warming in the Pacific Northwest (USA) of about 0.22°C per decade continue (Isaak et al. 2012). Each thermal regime began on 1 October, ended on 30 September, and included diel variation. See Appendix S1 for details about creation and implementation of thermal regimes across locations within a network. For Experiment 1, we used a stream network with a typical shape, which is described in the following section.

Experiment 2: network shapes

Our objective for this experiment was to evaluate whether fish responded differently to altered thermal regimes in stream networks having different shapes. We hypothesized that effects of altered thermal regimes would be smaller in networks having more spatial structure (e.g., dense tributary junctions). Under suitable thermal conditions, growth may be highest and fish may smolt earliest in networks of low spatial complexity due to more consistent access to optimal thermal habitats. Under thermally stressful conditions, however, fish growth may be highest in spatially complex networks where distances to thermal refuges are shorter.

We chose three hypothetical dendritic network configurations to represent the variety of stream network shapes observed in the Pacific Northwest: a long network, an intermediate typical pear-shaped network, and a compact network as described by Benda et al. (2004; Fig. 2; Appendix S2). These three network shapes were computer-generated

Warmer winter

More rapid spring warming

Warmer summer

Increased variability

using topological rules governing where tributaries were added as the network was grown (e.g., biased toward the base or tips of the network; Som et al. 2014). Each network had 101 tributary-to-tributary reaches; the length of each reach was drawn from a uniform distribution (0.5, 4 km). Total stream length was similar across the three networks. However, each network had different spatial properties such as mainstem length, watershed area, and the density of tributaries and confluences (Fig. 2). These properties provided fundamentally different thermal landscapes, with the compact network providing more thermal heterogeneity because of its high density of tributary junctions. We did not explicitly consider potential effects of elevation or other watershed characteristics. We used the same three networks for all simulations, but conducted a sensitivity analysis to ensure that results using these three networks were representative of the three network shape classes more generally (Appendix S2). For Experiment 2, we considered three thermal regimes: the contemporary regime (cscs), a regime in which change was moderate (wrws), and a regime in which change was extreme (hihs; Appendix S1: Table S1).

Individual-based model

Overview.—Each simulation began with a total of 250 eggs deposited throughout the reaches in a network (see *Initial conditions*) during a spawning event on 1 October (Fig. 3). For each 12-h time step, water temperature at each location

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(Fig. 1. *Continued*)

temperature rises in the spring; (c) summer maximum; and (d) variability. For Experiment 2, we used thermal regimes that combined moderate and extreme increases in winter, spring, and summer temperatures (not pictured). Thermal regimes are named with four letters describing each of these four components: winter minimum (cool, warm, or hot), spring warming (slow, rapid, or immediate), summer maximum (cool, warm, or hot), and regime variability (stable, variable, or irregular). For example, the contemporary thermal regime (cscs), shown with a thick blue line in each panel, has a cool winter, slow spring transition, cool summer, and stable variance. See Appendix S1: Table S1 for further explanation.
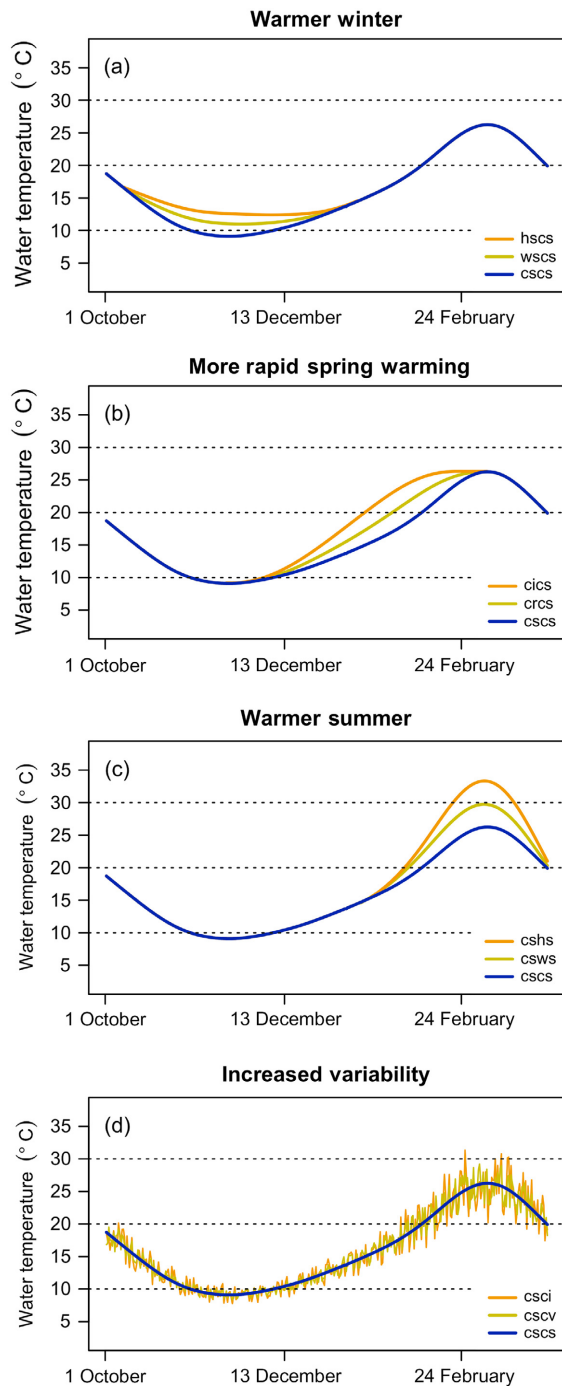
Fig. 1. Annual riverine thermal regimes used in simulations; pictured is the lowest mainstem location (warmest and where change is greatest). For Experiment 1, we evaluated moderate or large increases in each of four elements of potential future thermal regimes: (a) winter minimum; (b) rate at which water

Long

Typical

Compact

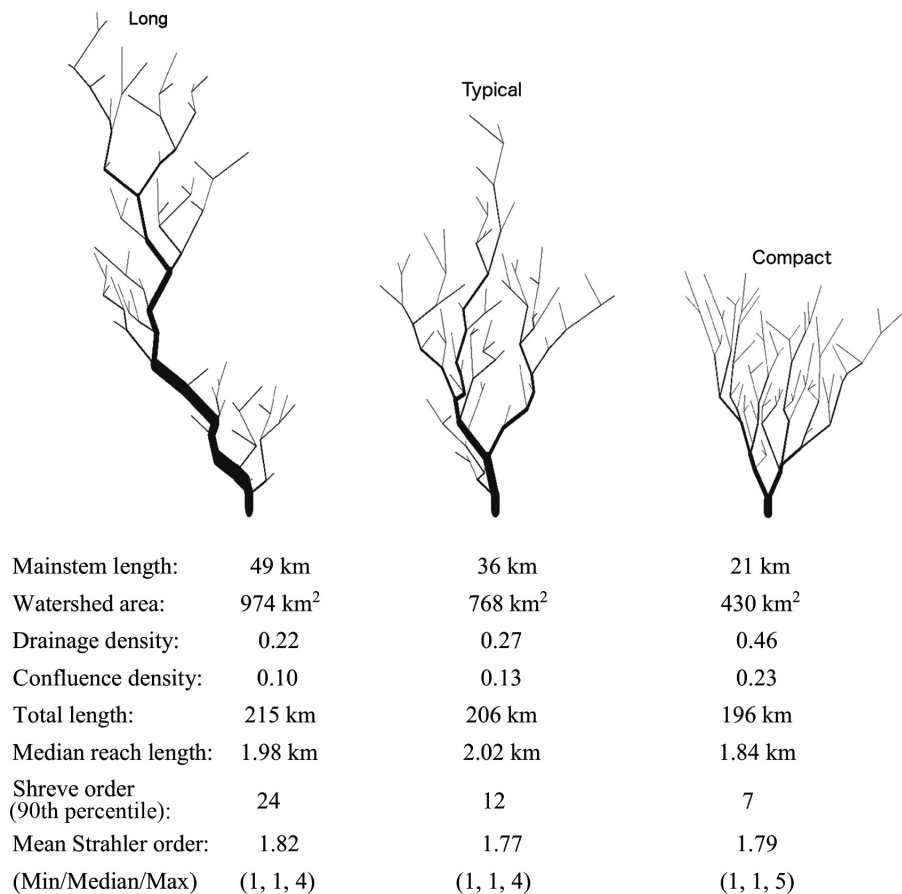|	Long	Typical	Compact
Mainstem length:	49 km	36 km	21 km
Watershed area:	974 km^2	768 km^2	430 km^2
Drainage density:	0.22	0.27	0.46
Confluence density:	0.10	0.13	0.23
Total length:	215 km	206 km	196 km
Median reach length:	1.98 km	2.02 km	1.84 km
Shreve order (90th percentile):	24	12	7
Mean Strahler order:	1.82	1.77	1.79
(Min/Median/Max)	(1, 1, 4)	(1, 1, 4)	(1, 1, 5)

Fig. 2. Three hypothetical networks (long, typical, and compact) used in simulations, and their characteristics (n = 101 reaches per network).

was updated according to the thermal regime scenario (see Appendix S1), and fish eggs were incubated at the temperature corresponding to their location. After sufficient thermal units (i.e., degree-days) had accumulated for any given fish, that fish emerged as an alevin capable of moving and growing. We used median values of accumulated thermal units required for emergence from Steel et al. (2012) for stable and naturally varying thermal regimes (Table 1). Once a fish emerged as a fry, each next 12-h time step began as before by updating water temperatures. Each fish then "decided" how far to move, and in what direction (see *Movement*). Next, fish grew according to the conditions they experienced (see *Growth*). Finally, fish were subjected to size-dependent mortality (see *Survival*). The experiment terminated on 30 September of the same water year,

and we evaluated growth, final size, and potential smolt date as primary responses. For each thermal regime–network combination examined, we performed 100 replicate simulations.

Design concepts.—The IBM (computer code provided in Data S1) ran within the platform for Spatial Modeling on Stream Networks (SSN) package in R (Peterson et al. 2013, Ver Hoef et al. 2014). Code to generate networks having different spatial properties was provided by N. Som, U.S. Fish and Wildlife Service; and P. Monestiez, INRA France (Som et al. 2014). Code implementing the Wisconsin bioenergetics model was provided by M. Nahorniak, South Fork Research Inc. All model parameters are listed in Table 1. Water temperature was simulated at discrete points evenly spaced every 0.5 km throughout the network (see Appendix S1). Fish could occupy any

For each thermal regime and network shape:

I. **Initialize simulation**

1. Assign spatially explicit water temperatures†
2. Spawn (deposit eggs in stream reaches)†

II. **For each 12-h time step:** (twice per day 1 October−30 September)

1. Update water temperature in all reaches according to thermal regime
2. Accumulated thermal units sufficient to emerge (per fish)?

   → no → Incubate eggs in place and accumulate thermal units
   → yes → Fish emerge from redds and become mobile

3. Move fish that are still alive†
4. Grow fish that are still alive
5. Size-dependent survival†

III. **Store results and repeat** (*n* = 100 simulations)

Movement (run for each fish at each time step)

1. Assess fish size and conspecific density in reach
2. Get distance to move (driven by data from step 1) †
3. Move fish in the same direction it was traveling
4. Does fish encounter a tributary?

   → no → Continue moving through the reach and into the next
   → yes → Move fish into the branch with the highest growth potential‡

5. Stop when movement distance reached

‡ Determined by assessing growth in each branch, where only water temperature differed and food availability was assumed equal

Growth (run for each fish at each time step)

1. Get fish size, water temperature nearest to fish, and conspecific density
2. Determine proportion of food consumed (driven by fish density)
3. Predict growth using a bioenergetics model (driven by fish size, water temperature, and food consumption)

Survival (run for each fish at each time step)

1. Compute survival probabilities for each fish (driven by fish size)
2. Adjust survival probabilities to account for growth during previous time step
3. Determine survival by drawing from a binomial distribution using the survival probabilities from above†
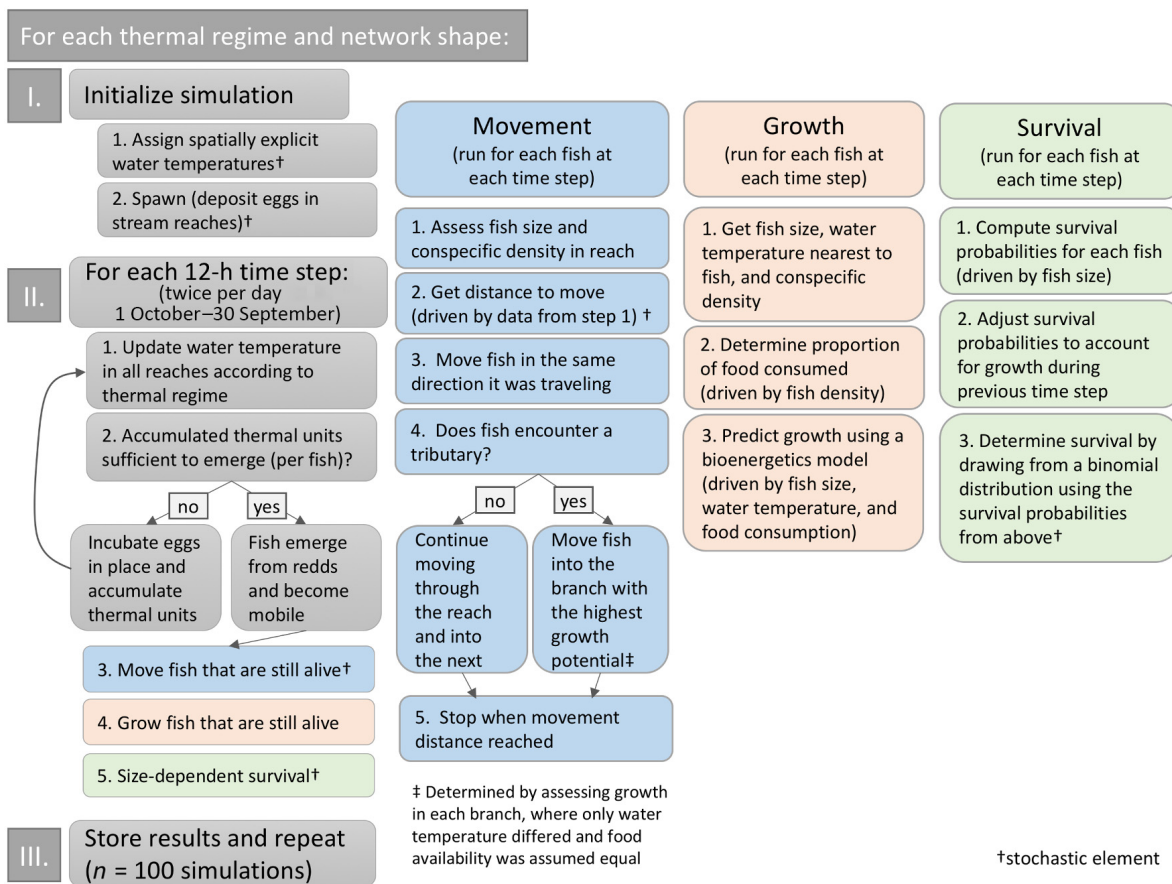
†stochastic element

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

location in the network, but responded to the nearest discrete water temperature point.

There were three primary assumptions in the IBM. First, we assumed that water temperature, conspecific density, and fish size were primary drivers of fish movement and growth and that survival was controlled by fish size. Second, we assumed that individual fish had equal egg sizes, intrinsic metabolic rates, and competitive abilities and that fish were equally influenced by biological interactions (we did not model interactions with organisms other than members of the same cohort). Third, we assumed that our thermal landscapes (i.e., thermal regimes across a network) inherently reflected associated changes in hydrological conditions over time (e.g., warmer locations and times are correlated with low-flow conditions) and that flows, water quality, and physical habitats were similar across network shapes. We chose not to explicitly model flow or

food supply because we do not have sufficient or plausible data for climate scenarios, and because relationships between flow and biota, and between flow and temperature, are not particularly well developed at the spatiotemporal scales we modeled. These simplifications allowed us to compare outcomes across thermal regimes and network shapes while controlling for natural variation present in real stream datasets that could occlude patterns.

Stochastic elements of the model included the initial spatial pattern of water temperature in a network, the distribution of eggs, the distance fish moved in each time step, and survival. Differences among simulations therefore represent natural variability and uncertainty in stochastic processes. To capture the response to these stochastic elements, we ran 100 simulations per network and thermal regime. Conceptually, it may be useful to think of each simulation as one

Table 1. Parameters used in the individual-based model.

Parameter	Value	Description	References
General			
Spawn date	1 October	Date fish eggs are laid	www.fpc.org/adultsalmon/adultqueries/ Adult_Table_Species_Graph_2015.html, Quinn (2005)
No. Fish	250	Number of fish in a network per simulation	Bjornn and Reiser (1991), Jonasson et al. (2000)
Initial weight	0.4	Mass of emerged alevin (g)	Beacham and Murray (1993), Geist et al. (2006)
ATU_{crit}	1140; 1160	Accumulated thermal units (°C-d) required to emerge as alevins for stable and variable thermal regimes	Steel et al. (2012)
Size to smolt	5	Minimum weight (g) to smolt	Denny et al. (2012), Widener (2012)
Movement			
m_{min} in Eq. 1	75	Shortest mean swim distance (m) when alone	Beall et al. (1992), Rodriguez (2002)
m_{max} in Eq. 1	250	Longest mean swim distance (m) when alone	Beall et al. (1992), Rodriguez (2002)
W in Eq. 2	30	Above this weight (g), movement capability does not increase	www.fpc.org/smolt/forklengthqueries/ forklength_query_12.html
D_m in Eq. 1	30	Above this density (virtual fish per linear m), swim distance does not increase	Unknown, but see ISAB (2015)
Growth			
D_g in Eq. 3	15	Above this density of conspecifics (virtual fish per linear m), proportion consumed does not decrease	Unknown, but see ISAB (2015)
P_{min} in Eq. 3	0.2	Lowest proportion consumed, even at high conspecific densities	Arbitrary, to match lower p-values in Beauchamp et al. (2007)
P_{max} in Eq. 3	0.9	Highest proportion consumed when alone	Arbitrary upper limit
Bioenergetics†			
CQ	4.97	Lower temperature (°C) for C_{max}‡	Plumb and Moffitt (2015)
CTO	20.93	Optimum temp. (°C) for C_{max}	Plumb and Moffitt (2015)
CTM	20.93	Maximum temp. (°C) for C_{max}	Plumb and Moffitt (2015)
CTL	24.05	Upper temperature (°C) for C_{max}	Plumb and Moffitt (2015)
CK1	0.09	Proportion of C_{max} at CQ	Plumb and Moffitt (2015)
CK4	0.53	Proportion of C_{max} at CTL	Plumb and Moffitt (2015)
Predator caloric density	5900	Energy density of fish (J/g body weight)	Van Winkle et al. (1998), Railsback and Rose (1999)
Prey caloric density	3500	Energy density of prey (J/g body weight)	Railsback and Rose (1999), Gonzales (2006), Beauchamp et al. (2007)
PFF	0.1	Proportion indigestible prey	Hanson et al. (1997)
Oxygen	13,560	Converts predator mass ($g \cdot g^{-1} \cdot d^{-1}$) to energy ($J \cdot g^{-1} \cdot d^{-1}$) lost to respiration	Hanson et al. (1997)
Survival			
s_{min}	0.997	Probability that an individual fish will survive one time step	Selected so that fish reaching 3 g generally survive

† Default values for Chinook Salmon were used for bioenergetics parameters not defined here (Stewart and Ibarra 1991, Hanson et al. 1997).
‡ Maximum consumption rate.

of 100 possible years in a given network or as one realization of that particular network out of 100 possible realizations (i.e., the topology remains the same, but other processes governing water temperature differ).

Initial conditions.—For each simulation, we generated spatially explicit water temperatures for each time step from a given thermal regime (Appendix S1). This process consisted of two steps. First, at the beginning of a simulation, we

created a spatial pattern of water temperature for the network where headwater reaches were coolest and temperature warmed as it progressed downstream, a commonly observed pattern in the Pacific Northwest, USA (Fullerton et al. 2015). We stochastically added spatial heterogeneity to this pattern at the scale of whole tributary watersheds (i.e., all upstream locations from a given reach) and to individual locations within a reach (each reach had between one and four locations). Water temperature values were scaled across locations in the network to range between 0 and 1; the result was a thermal landscape of relative water temperatures that was maintained throughout a simulation. Second, at each time step, we used the scaled values to spatially distribute the water temperature value for a given time step from the annual thermal regime across the network (Appendix S1).

Fish were initialized by placing 250 fish eggs at locations where scaled water temperatures best matched a pre-determined normal distribution (mean = 0.7, SD = 0.05). This resulted in spawning locations ranging between approximately 15° and 20°C on 1 October. Headwaters and very high-order mainstem reaches were excluded from egg placement. This method ensured that incubation temperatures were nearly identical across network shapes despite different spatial distributions of eggs (Appendix S1: Fig. S1). Because water temperature was distributed differently throughout the network in each simulation, egg locations also differed. Varying initial conditions ensured there were no systematic biases in fish response due to the temperature at locations where fish were initially located.

Movement.—Movement of individual fish was determined by conspecific density, fish size, and water temperature. For the first time step after a fish emerged, it swam upstream. For subsequent time steps, it continued to move in the same direction until it encountered a tributary junction. At the beginning of each time step, a fish first decided how far to move based on the density it currently experienced (farther if conditions were crowded; Eq. 1, below) and its own size (farther as it grew larger; Eq. 2, below). As it encountered tributary junctions, a fish had the option of changing course based on its assessment of the growing conditions in each branch. The fish continued moving until it had completed

the pre-determined distance (i.e., it did not abort movement if it encountered suitable habitat along the way).

Movement distance (k, in m) was drawn from a lognormal distribution with the following properties:

$$\ln(\mu) = \ln(m_{min}) + \frac{\ln(m_{max}) - \ln(m_{min})}{D_m} \times \min(d, D_m); \quad \ln(\sigma) = 0.5 \quad (1)$$

where m_{min} and m_{max} = shortest and longest mean distance (m) a fish can swim when alone, respectively, d = conspecific density (fish per linear km), and D_m = conspecific density above which swim distance remained constant (Table 1). This value was then scaled to fish size:

$$k = k \times \left(1 + \min\left(1, \frac{w}{W}\right)\right) \quad (2)$$

where k = movement distance (m) drawn from the lognormal distribution described in Eq. 1, w = fish weight (g), and W = upper threshold of weight (g) above which movement distance remained constant (Table 1). For example, when a 1-g fish was alone, it moved ≈ 75 m on average (range: 0–600 m); if density reached 30 fish, movement distance ≈ 250 m (range: 0–1.5 km). Mean movement ranges for a 10-g and 20-g fish were ≈ 100 and 125 m when alone, and up to 2 and 2.5 km at high densities, respectively.

As fish encountered a tributary junction, they chose to move into one of three positions: upstream into the left or right tributary or downstream within the same reach. At a confluence, fish sensed temperatures in each of the three reaches, and then moved into the reach where its growth would be highest (*Growth*, below; Railsback and Harvey 2002). Fish density did not influence this decision because a fish presumably could not sense densities in each of the three reaches. This process was repeated for any tributary junctions encountered until the fish had moved its allocated distance for that time step.

Growth.—At a fish's final position for a given time step, it grew according to water temperature and fish densities experienced. Growth was estimated using the Wisconsin bioenergetics model (Hanson et al. 1997). In that model, we used options that are commonly used for salmon (consumption Eq. 3, respiration Eq. 1, and excretion Eq. 3). We used original values for most

parameters, but updated temperature-dependent consumption parameters as defined in recent experiments for subyearling Chinook Salmon (Perry et al. 2015, Plumb and Moffitt 2015; Table 1). We also increased the prey energy-density parameter from the default value of 2500 J/g to 3500 J/g to better match salmon prey (Gonzales 2006, Beauchamp et al. 2007).

Conspecific fish density influenced consumption via a linear relationship with an upper threshold. The proportion of maximum consumption (p-value) for a fish was reduced as the density of conspecifics increased up to a maximum density:

$$p = \begin{cases} p_{max} - \frac{d}{D_g} & \text{for } d < D_g, \\ p_{min} & \text{otherwise} \end{cases} \quad (3)$$

where p = p-value used in bioenergetics consumption equations, d = conspecific density (fish per linear km), and D_g = upper threshold of fish density above which p-value did not decrease. At a density of 1 fish per km, p-value was maximized at 0.83 (i.e., $p_{max} = 0.9$, $d = 1$, and $D_g = 15$), and linearly decreased to $p_{min} = 0.2$ as fish density approached D_g (Table 1).

Survival.—Survival for each fish was assessed stochastically at the end of every time step, based on fish size and recent growth. Each fish was assigned a probability of survival (Eq. 4) that was then used to sample randomly from a binomial distribution (0 = the fish died; 1 = the fish survived):

$$s_{prob} = \left(s_{min} + (1 - s_{min}) \times \left(1 - \frac{1}{e^{w \times \beta}}\right)\right) + g_r \quad (4)$$

where s_{prob} = the probability of a fish surviving; s_{min} (set to 0.997) = the minimum survival probability for the time step; w = fish weight (g); β (set to 1) = a shape parameter for the exponential

curve; and g_r (−0.001 to 0.001) = relative growth during the most recent time step, scaled to the growth of all surviving fish in that time step. The probability of a fish surviving all 730 time steps (two 12-h time steps over 365 d) could be as low as $0.997^{730} = 0.11$ if the fish did not grow large enough (fish generally survived once they reached 3 g). Survival was largely determined by fish size; growth added a slight benefit or drawback for recently experienced conditions.

Sensitivity analysis

To assess sensitivity of results to nominal parameter values, we conducted a basic sensitivity analysis. We selected ten parameters that we believed would be most influential: two that acted on the egg stage, three that influenced movement, four that influenced growth, and one that influenced survival (Table 2). We perturbed the values of each of these parameters individually ±10% in each of the three networks in the contemporary thermal regime (cscs) and an extreme thermal regime (hihs). For each case, we evaluated the effect of parameter perturbation on three metrics: date emerged, final fish weight, and smolt date.

Quantifying results

For each scenario, we quantified (1) water temperatures experienced by fish, (2) date fish emerged from redds, (3) location trajectory (stream order occupied through time), (4) mean daily conspecific densities experienced, (5) daily movement distance, (6) proportion of available food consumed, (7) daily consumption rate, (8) daily growth rate, (9) final fish weights, (10) smolt date (i.e., the date at which fish were large enough to initiate smolting), (11) proportion smolted, and

Table 2. Sensitivity analysis (±10% of nominal values).

Stage	Parameter	Nominal value	Low (−10%)	High (+10%)
Egg	Spawn date	1 October	4 September	28 October
Egg	ATU_{crit}	1140	1026	1254
Movement	m_{max}	0.25	0.225	0.275
Movement	D_m	30	27	33
Movement	W	30	27	33
Growth	CTO	20.93	18.84	23.02
Growth	D_g	15	13.5	16.5
Growth	Prey caloric density	3500	3150	3850
Growth	Predator caloric density	5900	5310	6490
Survival	s_{min}	0.997	0.980†	1.0†

† These values are reasonable endpoints; −10% would have resulted in 0% of fish surviving, and survival cannot exceed 100%.

(12) survival. We recorded responses through 30 September, as though fish remained in the stream even if they had attained the threshold size for smolting. This metric therefore represents the growth potential given thermal conditions through summer, and was useful for comparing growth opportunities among scenarios and across a consistent timeframe. Fish were assumed large enough to initiate smolting at sizes >5 g. Many factors are believed to influence the date at which fish begin smoltification including size, daylight, temperature, and water quality cues (Sykes et al. 2009, Finstad and Hein 2012, Spence et al. 2014). Mangel and Satterthwaite (2008) proposed thresholds for optimal sizes at which Coho Salmon and Steelhead (*Oncorhynchus mykiss*) smolt that balance the risks and benefits of remaining in freshwater vs. heading to sea.

Our main approach for comparing patterns in fish responses across scenarios was to examine time series and distributions of responses. We also performed a permutation-based analysis of variance (ANOVA) and pairwise comparisons using the "lmPerm" package in R (Wheeler and Torchiano 2016). For a given network shape and thermal regime, our experimental unit was the mean response by all surviving fish in a stream network simulation ($n = 100$ replicate simulations). An individual fish was not an independent sample because fish in the same network could influence one another whereas fish in one simulation did not have the opportunity to interact with fish in another simulation. Thus, we measured a population-level response resulting from the behaviors of individuals.

RESULTS

Approximately half of fish survived each simulation. Predictions of emergence timing, conspecific densities experienced, daily consumption and growth rates, final weight, and smolt outmigration date were generally within ranges observed in the field (Table 3). Temperatures available to

Table 3. Comparison of model predictions (contemporary thermal regime, cscs) with values observed in field studies.

Fish response	Modeled values	Field values	References
Date eggs emerged as alevins	Between late January and early March	83% of fish emerged by 4 March (laboratory)	Steel et al. (2012)
		Late November to early March (Willamette R tributaries)	Schroeder et al. (2015)
Daily movement distance	Median ~250 m; increased over time as fish grew	<50 m to several km, depending on life stage and life history strategy	Bradford and Taylor (1997), Petty et al. (2012), Dugdale et al. (2016)
Conspecific density	From 0.01 to >20 (median ~ 11) virtual fish per linear km	From 0 to >2 fish/m²; means < 1 fish/m² for Chinook Salmon, Coho Salmon, and Steelhead	Bjornn and Reiser (1991), Ebersole et al. (2006), Myrvold and Kennedy (2015)
Specific consumption rate (food consumed daily)	Between 0.02 and 0.15 g·g^{-1}·d^{-1}; medians ~ 0.03 during spring, ~ 0.13 during summer, and ~ 0.08 by October	Mean = 0.11 and 0.07 g·g^{-1}·d^{-1} in mid- and late summer for Chinook; differed among streams	Chittaro et al. (2014)
		0.10 g·g^{-1}·d^{-1} for a 50-g Sockeye; higher for smaller sizes	Beauchamp et al. (2007)
Specific growth rate (daily growth)	Between 0 and 0.11 g·g^{-1}·d^{-1}; medians ~ 0.02 and 0.07 g·g^{-1}·d^{-1} in spring and summer	0.003–0.029 g·g^{-1}·d^{-1} for Chinook in summer	Chittaro et al. (2014)
		0.05 and 0.07 g·g^{-1}·d^{-1} for coho in winter and spring	Ebersole et al. (2006)
Final weight	0.4 g newly emerged; medians ~ 1.5 and 6 g by spring and last day of simulation; range 4–10 g on final day	From 3.5 to 10.5 g for spring Chinook leaving Snake River tribes; estimated weights passing lowest mainstem dam ~ 8–45 g	Achord et al. (2007) www.fpc.org/smolt/forklengthqueries/forklength_query_12.html
Date large enough (>5 g) to smolt	Between late May and early September	Subyearling Chinook generally emigrate between Apr and June; prevalence and timing differ among rivers	Roper and Scarnecchia (1999), Sykes et al. (2009), Schroeder et al. (2015)
Survival (fry to smolt)	Between 25% and 85% (median ~ 55%)	33% in Puget Sound drainages; varies by river	Greene and Beechie (2004), Scheuerell et al. (2006)

fish in the contemporary thermal regime (~ 3–24°C) were within the range of temperatures in rivers of the Pacific Northwest, USA. Incubation temperatures ranged from 5° to 15°C. Mobile fish sought out temperatures between 9° and 13°C during spring, and between 13° and 18°C during summer, which are similar to reported preferences for juvenile subyearling Chinook Salmon (Richter and Kolmes 2005, Tiffan et al. 2009). Fish experienced warmer temperatures than were generally available, but infrequently experienced temperatures of ~21°C where consumption was predicted to be maximized (Perry et al. 2015).

Variance and magnitude of mean final fish weight and mean smolt date stabilized at about 25 simulations whereas variability among individual fish responses remained consistently high as the number of fish included in the sample increased (Appendix S3: Fig. S1). The variance among fish within a given simulation was greater than the variance among simulations for a given fish. The broad range of responses by individual fish reflects the diversity of possible accumulated experiences that could occur throughout a network (i.e., determined by the patchy thermal environment and the particular choices a fish makes as it traverses the stream network).

Experiment 1: altered thermal regimes

Metrics of fish performance responded the most to increases to the rate of spring warming and summer maximum, and least to increases in winter minimum and day-to-day variability (Table 4, Fig. 4). As expected, effect sizes were larger for extreme thermal regimes than for moderate thermal regimes. Emergence occurred earlier with warmer winters, but was not influenced by warmer springs, warmer summers, or increased variability (Fig. 4e–h). Fish growth and final size were largest given warmer springs and warmer summers. Final size was relatively unchanged given warmer winters (Fig. 4q) or additional variability in the thermal regime (Fig. 4t), but was slightly higher in the extreme warmer winter (Table 4). Smolt date occurred earliest with warmer springs, somewhat earlier with warmer summers, and slightly earlier in the extreme warmer winter, but was generally unaffected by increased variability (Fig. 4u–x).

Table 4. Pairwise comparisons of fish responses in each experiment (P-values, computed using permutation-based ANOVA).

Scenario	Pairwise comparison	Final fish weight	Smolt date
Experiment 1: thermal regimes			
Warmer winter	Contemporary vs. Moderate	0.697	0.624
	Contemporary vs. Extreme	*	**
	Moderate vs. Extreme	0.189	**
Warmer spring	Contemporary vs. Moderate	***	***
	Contemporary vs. Extreme	***	***
	Moderate vs. Extreme	***	***
Warmer summer	Contemporary vs. Moderate	***	***
	Contemporary vs. Extreme	***	***
	Moderate vs. Extreme	***	**
Increased variability	Contemporary vs. Moderate	0.661	*
	Contemporary vs. Extreme	0.379	0.771
	Moderate vs. Extreme	0.073	0.135
Experiment 2: network shapes			
Contemporary thermal regime	Long vs. Typical	***	***
	Long vs. Compact	***	***
	Typical vs. Compact	**	**
Moderate thermal regime	Long vs. Typical	***	***
	Long vs. Compact	***	***
	Typical vs. Compact	0.399	*
Extreme thermal regime	Long vs. Typical	*	***
	Long vs. Compact	***	*
	Typical vs. Compact	**	0.0559

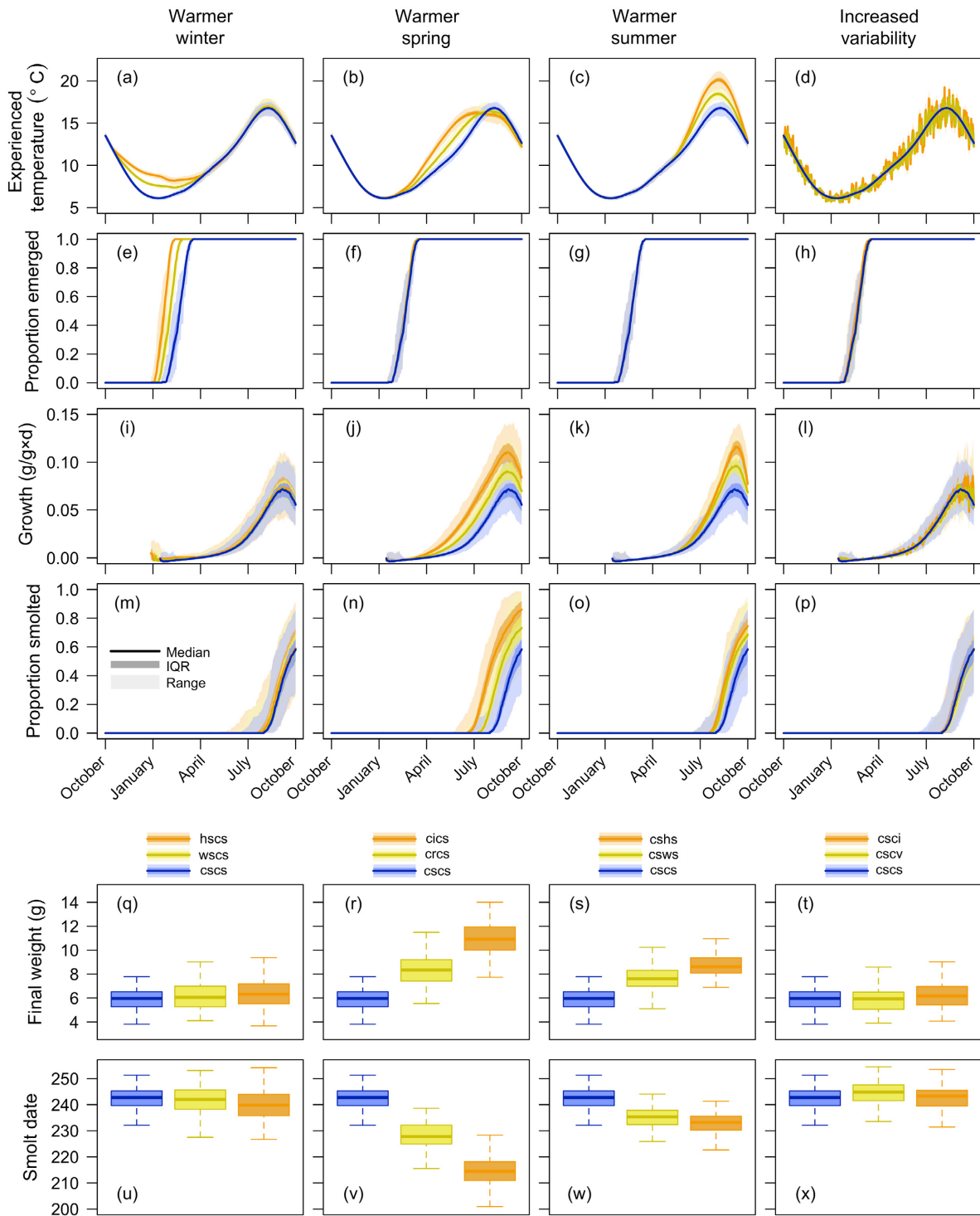$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Fig. 4. Fish response metrics (rows) for the contemporary thermal regime (blue), and for moderate (yellow) and extreme (orange) increases in four components of the thermal regime (columns). The specific thermal regimes compared in each column are identified in the legend (see Fig. 1; Appendix S1: Table S1 for descriptions). Time series plots (top four rows) depict the range (light color bands), interquartile range (IQR; first and

(Fig. 4. *Continued*)
third quartiles, dark color bands), and median (dark colored lines) of responses (*y*-axes) over time (*x*-axes). Box-plots (bottom two rows) depict responses calculated at one point in time. The metric "Experienced temperature" spans the entire experimental year; other metrics include data for surviving fish only. All plots illustrate variance across 100 simulations in mean response of all fish in the typical network.

Earlier emergence during warm winters caused a decrease in survival (Appendix S3: Fig. S2c) because growth was low for fish that emerged early and fish were therefore susceptible to size-selective mortality. More rapid spring warming allowed fish to capitalize on optimal temperatures earlier. As fish grew, they moved farther, which reduced densities and therefore increased the amount of food consumed (Appendix S3: Fig. S3e). In addition to higher final weights and earlier smolt date (Fig. 4r, v), this boost in spring-time consumption and growth led to higher survival (Appendix S3: Fig. S3c). Warmer summers increased consumption and growth during that season (temperatures selected were closer to physiological optima). Larger fish moved more, often into lower-order streams where temperatures were cooler than what was available in higher-order streams (Appendix S3: Fig. S4d). Although final fish weight was higher and smolt date was earlier given warmer summers (Fig. 4s, w), survival was relatively unchanged (Appendix S3: Fig. S4c). Increased variability had surprisingly little effect on any metric of fish performance (Appendix S3: Fig. S5). Overall, the majority of metrics responded most to a warmer spring or summer (Appendix S3: Fig. S6).

Experiment 2: network shapes

Water temperatures seasonally available to fish were similar across network shapes (Appendix S3: Fig. S7). Diel temperature fluctuations were also similar across networks. Median diel variance across locations and time steps under the contemporary thermal regime (cscs) was 1.55°, 1.65°, and 1.58°C in the long, typical, and compact networks (range, all networks: 0.90–5.26°C). Fish in all three networks experienced similar temperatures during egg incubation, but once mobile, fish in the long network experienced slightly warmer temperatures and fish in the compact network experienced slightly cooler temperatures (Fig. 5a–c).

Survival was similar across the three network shapes, but slightly higher in the typical network

(Appendix S3: Fig. S8c). The first fish that emerged in the typical and compact networks experienced higher densities initially than did fish in the long network under the contemporary thermal regime (cscs; Appendix S3: Fig. S8g). They therefore consumed less and moved farther, often into cooler reaches (Appendix S3: Fig. S8d). At least some fish in the long network tended to consume more, grow faster, weigh more, and reach smolting size earlier than fish in the other networks (Fig. 5g, m, p). To ensure similar incubation temperatures across networks, we located eggs in a broader range of stream orders in the long network, which resulted in lower fish densities initially.

We found that final fish weight and smolt date differed between each pair of networks in the contemporary thermal regime (cscs; Table 4). In warmer thermal regimes, patterns remained similar, but differences in responses among networks were smaller. In the moderately warmer thermal regime (wrws), there was no difference in final fish weight and a small difference in smolt date between the typical and compact networks. In the extreme thermal regime (hihs), there was a small difference in final fish weight between the typical and long networks, and in smolt date between the compact and long networks, and no difference in smolt date between the compact and typical networks.

In the moderately warmer thermal regime, median temperatures experienced by fish were closer to those needed to maximize consumption. Correspondingly, fish growth was higher and fish generally reached smolt size earlier in all networks (Fig. 5n, q). Fish moved into lower-order streams during summer to avoid too-warm temperatures, especially in the long network (Appendix S3: Fig. S9d). This behavior was more evident under the extreme thermal regime (Appendix S3: Fig. S10d). In both cases, the result was for fish to experience lower densities and therefore consume more. Overall, relative to the contemporary thermal regime (cscs), fish in
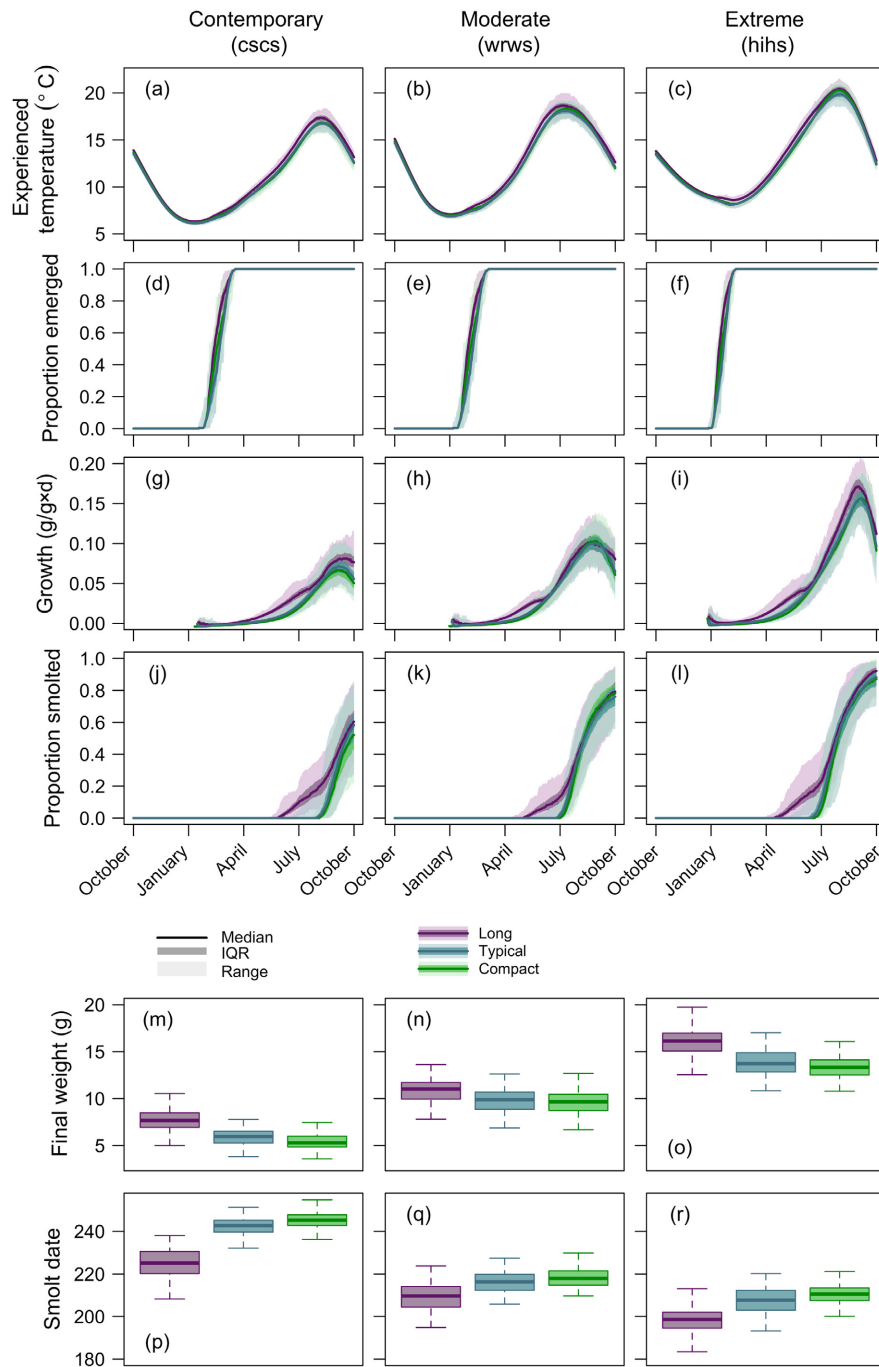
Fig. 5. Fish response metrics (rows) in the long (purple), typical (blue), and compact (green) network shapes and contemporary, moderate, and extreme thermal regimes (columns; see Appendix S1: Table S1 for thermal regime descriptions). Time series plots (top four rows) depict the range (light color bands), interquartile range (IQR; first and third quartiles, dark color bands), and median (dark colored lines) of responses (*y*-axes) over time (*x*-axes). Boxplots (bottom two rows) depict responses calculated at one point in time. The metric "Experienced temperature" spans the entire experimental year; other metrics include data for surviving fish only. All plots illustrate variance across 100 simulations in mean response of all fish in a network.

warmer thermal regimes experienced warmer temperatures, emerged earlier, occupied lower stream orders, experienced lower densities, consumed more, grew faster, weighed more, and reached smolt size earlier; however, movement distances and survival did not change (Appendix S3: Fig. S11).

Sensitivity analysis

Responses were most sensitive to changes in parameters controlling egg incubation and those controlling fish growth (Appendix S3: Fig. S12). Results were insensitive to parameters controlling fish movement; possibly, a 10% perturbation may not have been sufficient to detect an effect. Growth, movement, and survival parameters had the greatest potential to influence our conclusions about thermal regimes and network shapes because these parameters were called repeatedly throughout a simulation, whereas spawn date and ATU_{crit} (accumulated thermal units needed to emerge) affected all individuals equally at the beginning of each simulation. The magnitude of effects was slightly larger in the warmer thermal regime in many cases (Appendix S3: Fig. S12). Trends across networks were noticeable for some metrics and were generally consistent with the direction of responses across networks seen with nominal parameter values.

The date fish emerged (Appendix S3: Fig. S12a) was most responsive to changes in spawn date and ATU_{crit}. Final fish weight (Appendix S3: Fig. S12b) was most responsive to changes in prey caloric density, CTO (optimum temperature in the bioenergetics model), predator caloric density, and survival. Smolt date (Appendix S3: Fig. S12c) was generally most responsive to the same parameters that affected final weight with the exception of CTO. Changes were in the direction expected. For instance, decreasing CTO, increasing the ceiling of fish density affecting consumption (D_g), increasing prey caloric density, and decreasing predator caloric density all increased growth and caused earlier smolting. Lower survival (e.g., resulting from lower values of s_{min}) resulted in earlier emergence, higher weights, and earlier smolting for surviving fish, due to decreased density-dependent effects on consumption.

DISCUSSION

Response to climate-altered thermal regimes

The consequences of climate change for salmon are expected to be largely negative (Jonsson and Jonsson 2009, Arismendi et al. 2012). However, the ways that fish will respond are likely to be complex and case-specific, varying by species, life stage, and the extent to which and times when environmental conditions change. Growth rates for most, but not all, modeled subyearling Chinook Salmon increased in our climate-altered thermal regime scenarios, suggesting that temperatures experienced by fish in the contemporary thermal regime (cscs) were below optimal and that our altered thermal regime scenarios were not stressful enough to suppress growth for most fish. Enhanced growth under warmer conditions is not unexpected if fish have been limited by temperatures that were below their physiological optimum. For instance, using a bioenergetics approach, Beer and Anderson (2011) found that in streams where water temperature was cool during summer, warming air temperature and loss of snow were likely to translate into increased growth rates for Chinook and Steelhead, whereas growth decreased in streams where summertime water was already warm.

Although growth was positive for most fish in our virtual experiment, we found reduced and even negative growth for some fish that experienced especially warm temperatures. This may reflect the variability in the way individual fish responded to warmer temperatures (i.e., some finding cooler refuges, some trapped in too-warm reaches and losing weight). Depressed growth might be expected in places where or at times when water warms substantially, for species that have lower thermal requirements such as Bull Trout (*Salvelinus confluentus*), or in the presence of other stressors. Because our model operates on a one-dimensional network that does not reflect stream width or volume, modeled fish densities were calculated as a function of stream length. Therefore, model scenarios that resulted in substantial movements of fish into cooler lower-order stream reaches (e.g., our warming scenarios) likely underestimated density-dependent reductions in consumption and growth that would be expected as fish crowd into a smaller area.

Growth in the field may also be reduced by other factors not considered in our model, such as scarce food resources or the presence of disease.

Life cycle consequences of elevated growth

There can be advantages to higher growth rates. A larger fish has lower relative metabolic costs and therefore more cushion in the amount of weight loss it can sustain (Hanson et al. 1997, Beauchamp et al. 2007), and size confers benefits in competitive ability (Fausch and White 1986), protection from predators (Peterson and Kitchell 2001), and survival and fitness advantages (Duffy and Beauchamp 2011, Thompson and Beauchamp 2014). Conversely, larger fish may spend more energy, which could constrain foraging and predator avoidance capabilities. Moreover, enhanced growth during freshwater life stages does not imply that climate change will have a net positive effect on fish because altered growth can result in subsequent effects later in life. Conditions experienced while rearing can influence the decision to smolt (Beakes et al. 2011), smolt timing (Roper and Scarnecchia 1999), and survival to adulthood (Thompson and Beauchamp 2014). For instance, Reed et al. (2010) observed that Sockeye Salmon (*Oncorhynchus nerka*) in Alaska reared in a warmer lake than other fish from the same genetic lineage grew larger and smolted slightly earlier. Because about two-thirds of fish grew larger in our altered thermal regimes, they were therefore assumed ready to smolt at an earlier date. If higher growth does result in earlier outmigration, phenological asynchrony may ensue whereby smolts entering seawater may experience differences in resource availability or susceptibility to size-selective mortality. Fish size and timing of ocean entry may affect early marine growth (Weitkamp et al. 2015) and subsequent age structure (Tattam et al. 2015). Conversely, fish that do not grow well during early freshwater rearing may delay or abandon smolting (Perkins and Jager 2011). For instance, some fall Chinook migrating out of the Snake River either migrate undetected during winter or choose to spend the winter in the reservoirs and re-initiate smolting the subsequent spring (Widener 2012).

Timing and variability

The timing of thermal exposure may have important consequences for fish. When our modeled fish experienced warmer conditions during incubation, fry emerged earlier, giving them a head start on the growing season. However, this did not translate to differences in final size or smolt timing because fish that emerged early did not grow well and had higher mortality. Finstad and Jonsson (2012) found that Atlantic Salmon (*Salmo salar*) eggs incubated at cooler temperatures resulted in fish that later grew less in warm environments than fish incubated at warmer temperatures. When ecological interactions and variation in spawn timing also occur, warmer incubation conditions could lead to bigger gaps between small and large fish by the end of the growing season, and to a variety of life history strategies depending on size/fitness trade-offs (Lisi et al. 2013).

Modeled fish that experienced warmer summers reached larger sizes and were able to smolt earlier, and these effects were even larger when fish were exposed to warmer spring temperatures. In both cases, effects on fish size and smolt date were unrelated to incubation conditions, because temperatures became warmer after most fish had emerged. In summer, temperatures were too warm in many reaches, and fish either grew less or were restricted to lower-order reaches where temperatures were cooler, whereas warmer springs provided fish with a broader range of reaches at optimal growing temperatures (and summers in these thermal regimes did not get too warm).

We did not find much of an effect of increased thermal variability on fish responses. This was surprising because evidence suggests that temporal variability may have important biological consequences (Steel et al. 2017). For instance, emergence timing of Chinook Salmon was related to variability in water temperature in an experimental setting (Steel et al. 2012), and Geist et al. (2010) found that temperature delivery had important consequences for survival of juvenile Snake River fall Chinook Salmon. When Snake River fish experienced fluctuating temperatures, they grew about half as well as those experiencing stable thermal regimes, even when mean temperatures were similar. It is possible that a 12-h time step was not frequent enough to capture the potential effects of thermal variability on fish growth. Our model could also be improved by linking to a thermal exposure-based emergence model (e.g., Beer and Anderson 2001, 2011).

Network shape influence

One of our objectives was to examine whether network topology could influence how salmon responded to climate change. We expected that, given warmer conditions, the compact network would provide a moderating influence to increasing temperature because its topology provided higher spatial diversity in water temperature.

In the contemporary thermal regime, fish generally grew largest and were ready to smolt earliest in the long network. This pattern was not established during the incubation period; rather, results stem from growth of mobile fish in differently shaped networks. One potential explanation is that fish in the long network experienced lower densities of fish initially than in other network shapes because optimal spawning temperatures were more spatially dispersed in the long network. Therefore, fry were able to consume a higher proportion of available food and grow more rapidly initially. By early summer, densities and consumption became similar among networks, and growth even became lowest in the long network during summer. Another potential explanation is that in the compact and typical networks, it was possible for fish to move from one cool branch to another without encountering intervening warm habitat (i.e., not intentionally avoiding it, but not finding it either), whereas in the long network, fish could not avoid passing through warmer mainstem habitat when moving among tributaries. Smoother gradations in water temperature in the long network may also have allowed fish to more quickly find optimal thermal habitat, whereas in other networks, higher thermal heterogeneity may have caused fish to become stuck in local maxima rather than continuing on to a global maximum. This pattern may differ across regions in natural systems. For instance, gradations in water temperature in long networks may be moderated in regions where thermal regimes are strongly influenced by localized cooling influences such as groundwater. Moreover, we assumed mainstem habitats to provide suitable habitat; this may not be the case in some regions.

In warmer thermal regimes, differences in responses of fish among the three networks were less clear. This could be because fish in the long network had lower consumption rates during summer, allowing fish from the other networks to catch up in size. Fish in the compact and typical networks did not appear to exhibit reduced summertime consumption and growth. One possible explanation is that tributaries in the compact and typical networks that had been connected by stretches of cool water in the contemporary thermal regime became separated by stretches of warm water with higher growth potential in warmer thermal regimes. Fish therefore more frequently encountered newly warm habitat than they had in the cooler scenario. In really warm conditions, fish in all networks were more sequestered in low-order reaches to avoid warm mainstem habitats, which may also have contributed to the decreased effect of network shape. In sum, the effect of warmer thermal regimes caused increased growth in all networks, but summertime conditions became most limiting in the long network.

Strengths and limitations of the IBM

Our model provides a novel contribution to the suite of existing tools for evaluating the effects of climate change on Pacific salmon. To our knowledge, this is the first implementation of an IBM that evaluated spatially explicit responses across an entire stream network. Moreover, our model was developed to be able to harness the capabilities of powerful new spatial statistical network models (Peterson et al. 2013), and could be applied to real stream networks that incorporate empirical or modeled water temperature, flow, or food resources. The role of network topology on the response of whole populations has been explored for Coho Salmon, but individual responses were not considered (Leibowitz and White 2009). Bioenergetics and growth are typically evaluated on a daily basis; however, this temporal scale may be too coarse to capture important dynamics (Holsman and Danner 2016). We modeled bioenergetics at a sub-daily time step because thermal regimes can differ enormously between night and day. It is possible that even finer temporal scales are needed.

We considered only water temperature, conspecific density, and size of fish from the same cohort as controls on fish movement and growth (Crozier et al. 2010, Parra et al. 2012, Baerum et al. 2013). By assuming prey quality and other factors were homogeneous across network shapes, our results do not reflect the spatial variation

present in these influences on fish growth in natural stream ecosystems. We recognize that network topology and geomorphological structure of streams are related and that the availability and quality of prey and other factors can be directly influenced by geomorphology (Wipfli and Baxter 2010). This remains an active area of research, and tools such as the IBM described here are ideally suited to address these issues.

There may be countervailing or synergistic pressures associated with climate change that were not captured in our model. Specifically, we did not model changes in flow that are likely to accompany climate change, although this is an aim for future versions of the model. Our objective was to focus on the effect of spatial patterns in water temperature. Yet we know that temperature and flow are related: At lower flows, temperatures are often warmer, and thermal heterogeneity may also be higher. Thus, as flows decrease in future summers, fish may have a more difficult time locating cool thermal refuges and remain effectively trapped in stressfully warm sections of river (i.e., heterogeneity may interfere with the ability of fish to follow the temperature gradient to locate optimal thermal habitat). During winter, if climate change causes increased precipitation and winter flooding, fewer fry may emerge because more redds will be scoured by high flows. The surviving fish may enjoy higher per capita food availability and reduced competition. Even though fewer fish would survive to the smolt stage, these fish may grow large and exhibit higher survival in later life stages. This effect on growth could be exacerbated or nullified depending on how fish respond to future thermal landscapes. Crozier and Zabel (2006) found a negative relationship between water temperature and survival for some but not all populations of spring Chinook Salmon in the Snake River, Idaho. Other populations responded more strongly to flow and fish density, suggesting that climate change will likely have unique impacts on each population in this metapopulation. Similarly, Xu et al. (2010) found that growth of Brook Trout (*Salvelinus fontinalis*) in Massachusetts differed seasonally and depended on water temperature, flow, and fish density. Moreover, unforeseen changes in predator and prey communities as a result of climate change will influence outcomes.

Despite these limitations, our simple IBM produced results that matched field observations reasonably well, and lends insight into the potential mechanistic influence of spatiotemporal temperature patterns during critical early life history stages. Modeled metrics of subyearling Chinook Salmon performance (emergence timing, conspecific densities experienced, daily consumption, final weight, and outmigration date) matched ranges from empirical studies.

Informing spatial conservation priorities

These virtual experiments can inform management decisions during the recovery-planning process for salmonids listed under the U.S. Endangered Species Act as well as conservation of any far-ranging protected species living in habitats constrained as networks (Campbell Grant 2011). For example, given a set of watersheds of varying topology, managers can consider which watershed might afford more protection from expected effects of altered thermal regimes or other stressors. This information can be used to help characterize which populations are most at risk, and to prioritize conservation and restoration activities accordingly. Considering the network shape of a target watershed and associated patterns of connectivity likely under alternate future scenarios may also enable planners to consider the sequencing of appropriate conservation efforts, given the timing of responses expected. For example, in the near future, it may make sense to focus near-term conservation strategies such as planting riparian vegetation aimed at slowing down warming throughout networks with more complex shapes, whereas in the long term, conservation strategies might focus on ensuring adequate thermal refuges and facilitating connectivity within migratory corridors in less complex networks, where fish may experience decreased consumption and growth during summer.

Managers will be best guided by an understanding of the particular spatial arrangement of habitats within their stream networks. This analysis highlights the potential importance of spatial arrangement under current and future scenarios. The particular attributes and spatial properties of any watershed, however, will differ by region, and each watershed will be unique. By illustrating the potential importance of these properties, this study highlights the value of recognizing these patterns and their potential influence on fish.

More broadly, our research suggests that different spatial patterns of water temperature within and among networks may elicit a diversity of responses by animals to altered thermal regimes. Penaluna et al. (2015) found that variability in habitat conditions mediated the response of Cutthroat Trout (*Oncorhynchus clarkii*) to climate change in northwestern Oregon. Boughton et al. (2007) showed experimentally that temperature heterogeneity at local scales influenced growth of Steelhead in California. Although it is possible that some fish will capably adapt to changing conditions (Reed et al. 2011), higher habitat diversity both within and across networks should translate to higher resilience of fish to stressors by strengthening the portfolio of populations capable of responding to change (Anderson et al. 2015, Schindler and Hilborn 2015). For example, Armstrong et al. (2010) found that juvenile coho in the Wood River, Alaska, were able to capitalize on growing opportunities by moving among thermally diverse habitats. Having access to a variety of streams with different topologies and associated thermal patterns can promote diversity in salmon life history strategies, and may enable persistence as the climate changes. Our work adds to a growing body of literature demonstrating that spatiotemporal context (Steel et al. 2016) and stream network relationships (Flitcroft et al. 2012, Mari et al. 2014, Yeakel et al. 2014) are important to salmon and should be explicitly considered during conservation and climate adaptation planning.

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