

Linking climate change projections for an Alaskan watershed to future coho salmon production

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Abstract

Climate change is predicted to dramatically change hydrologic processes across Alaska, but estimates of how these impacts will influence specific watersheds and aquatic species are lacking. Here, we linked climate, hydrology, and habitat models within a coho salmon (*Oncorhynchus kisutch*) population model to assess how projected climate change could affect survival at each freshwater life stage and, in turn, production of coho salmon smolts in three subwatersheds of the Chuitna (Chuit) River watershed, Alaska. Based on future climate scenarios and projections from a three-dimensional hydrology model, we simulated coho smolt production over a 20-year span at the end of the century (2080–2100). The direction (i.e., positive vs. negative) and magnitude of changes in smolt production varied substantially by climate scenario and subwatershed. Projected smolt production decreased in all three subwatersheds under the minimum air temperature and maximum precipitation scenario due to elevated peak flows and a resulting 98% reduction in egg-to-fry survival. In contrast, the maximum air temperature and minimum precipitation scenario led to an increase in smolt production in all three subwatersheds through an increase in fry survival. Other climate change scenarios led to mixed responses, with projected smolt production increasing and decreasing in different subwatersheds. Our analysis highlights the complexity inherent in predicting climate-change-related impacts to salmon populations and demonstrates that population effects may depend on interactions between the relative magnitude of hydrologic and thermal changes and their interactions with features of the local habitat.

Keywords: Alaska, Chuitna watershed, climate change, coho salmon, hydrology modeling, life-cycle modeling, *Oncorhynchus kisutch*, salmon life-cycles

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Introduction

Climate models project significant increases in air temperature (2.4–6.3 °C) and precipitation (14–28%) across Alaska by the end of the twenty-first century (Christensen *et al.*, 2007). If realized, these changes could cause substantial changes in the structure and function of freshwater ecosystems (Hinzman *et al.*, 2005; White *et al.*, 2007; Kittel *et al.*, 2010). In southcentral Alaska, where five species of salmon inhabit rivers across 100 000 km² of coastal watersheds, these climate-induced changes are projected to include increased actual evapotranspiration, decreased annual snow depth and soil moisture, increased winter streamflow, earlier spring runoff, smaller magnitude of spring runoff events, and lower summer streamflow (Prucha *et al.*, 2012). Understanding and anticipating the effects of these changes on salmon populations is an important

task for fisheries biologists and managers (Rogers & Schindler, 2011).

Alaska's coho salmon (*Oncorhynchus kisutch*) typically rear for 2 years in streams (Sandercock, 1991), potentially making them more susceptible to changing hydrologic regimes than other Pacific salmon populations. The greatest direct impacts on coho salmon are expected to occur through elevated water temperature and changes in flow regimes (Bryant, 2009), and changes beyond the historical range of variability during freshwater life-stages can negatively impact salmon productivity (Beacham & Murray, 1990; Cramer 2001; Scheuerell *et al.*, 2006; Battin *et al.*, 2007). Approximately half the variability in coho salmon recruitment success (i.e., survival to adulthood) has been attributed to the freshwater stage (Holtby *et al.*, 1989; Bradford, 1995).

While the potential impacts of climate change on salmon and their habitat have been examined in other regions (Battin *et al.*, 2007; Crozier *et al.*, 2008; Bryant, 2009; Mantua *et al.*, 2010; Ruesch *et al.*, 2012; Hedger *et al.*, 2013), there is relatively little information on

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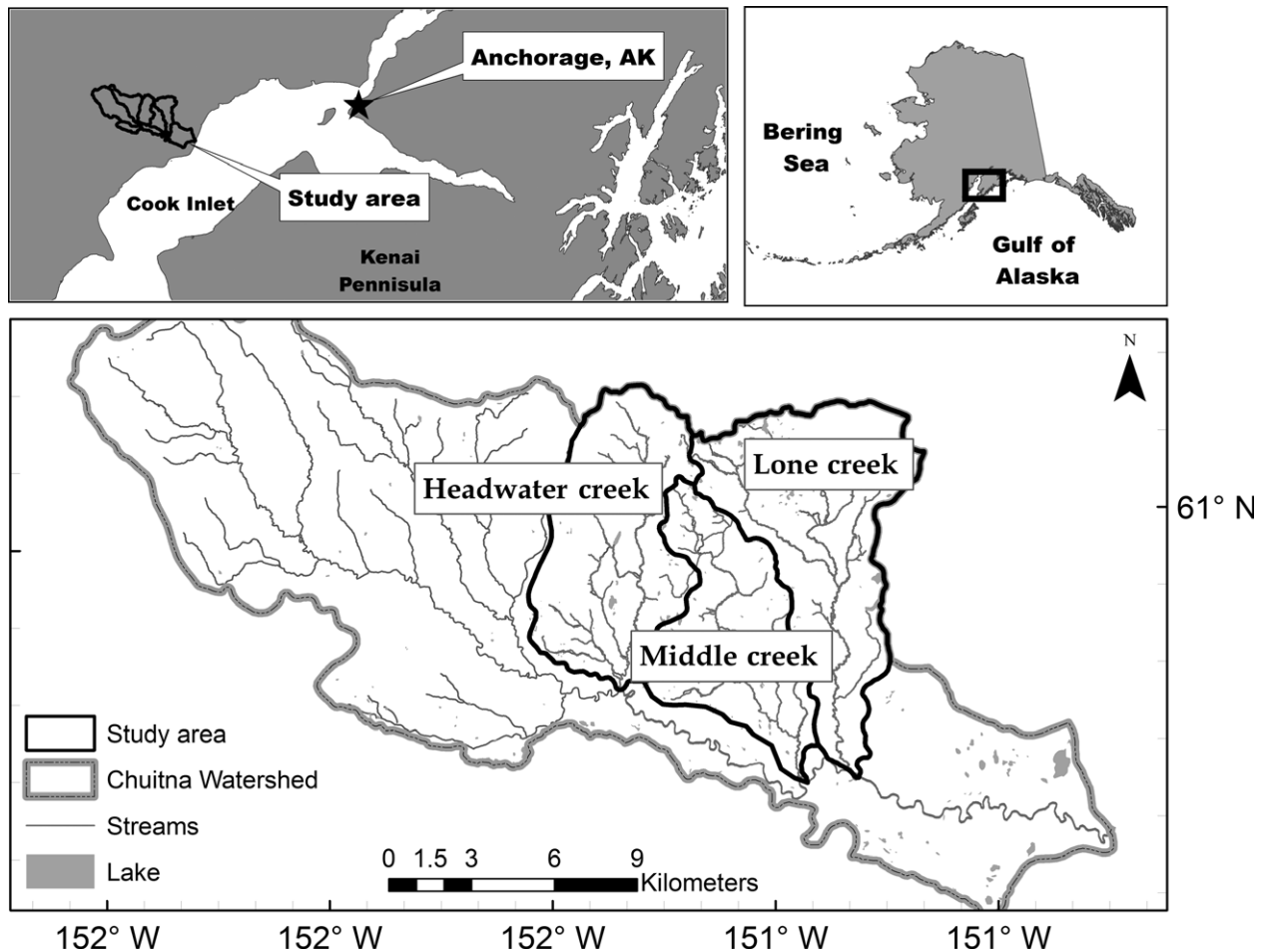


Fig. 1 Map of the Chuitna watershed (Alaska, USA) showing the location of three subwatersheds within the study area (thick black lines) and Chuitna streams (thin grey lines) as well as the location of the watershed in southcentral, Alaska.

anticipated changes to the freshwater life-stages of coho salmon across the northern portion of their range. Predicting impacts to salmon is particularly complicated due to their long migrations, use of a diverse range of marine and freshwater habitats throughout their lives, and their variable life histories types (Crozier *et al.*, 2007). Furthermore, most of Alaska's watersheds are remote and have no hydrologic, salmon, or climate monitoring programs, limiting our baseline understanding of these systems.

Our objective was to project how a population of coho salmon in southcentral Alaska's Chuitna watershed might be affected by climate-induced changes in streamflow and temperatures during early freshwater life-stages and, in turn, how these changes affect smolt production over a 20-year period. We chose this study area because, in contrast to the scant environmental data coverage over much of Alaska, a range of climatic, stream habitat and fish data have been collected in three of the Chuitna's subwatersheds as envi-

ronmental baseline work for a proposed mining project (Oasis, 2006, 2008; Nemeth *et al.*, 2009, 2010; Riverside, 2009; Williams & Burrell, 2010). In addition, the watershed is physiographically similar to many non-glacial salmon streams in the region. We used output from an existing hydrologic model developed for the watershed to predict how parameters such as stream flow and temperature might change under Intergovernmental Panel on Climate Change (IPCC) future climate scenarios (see Prucha *et al.*, 2012; Loinaz *et al.*, In review). We then linked these changes to a population model developed for coho salmon to estimate population responses.

Materials and methods

Study area

The Chuitna watershed is located approximately 65 km west of Anchorage, Alaska on the northwestern side of Cook Inlet

(Fig. 1). The watershed consists of a large network of streams (ca. 320 km) that drain about 240 km² into Cook Inlet. We focused on three of the Chuitna's six subwatersheds: Lone Creek, Middle Creek, and Headwater Creek. The topographic relief in these subwatersheds is small, creating low gradient sinuous streams that intermingle through wetland complexes connecting numerous shallow ponds. Headwater Creek subwatershed has the highest average elevation (285 m) followed by Middle Creek (175 m) and Lone Creek (155 m), respectively. Lone Creek has the largest drainage area (53 km²) and the longest stream length (62 km). The vegetation lower in the subwatersheds is generally dominated by mixed spruce (*Picea* spp.) and birch (*Betula papyrifera*) forests, with a shift toward ericaceous shrubs, willow (*Salix* spp.), and alder (*Alnus* spp.) in the upper reaches of the subwatersheds. Precipitation ranges from approximately 76–152 cm annually with major precipitation events occurring as rain in fall and snow in the winter. These three subwatersheds support five species of Pacific salmon: coho, Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*), although coho and Chinook are the dominant species (Nemeth *et al.*, 2009). Additional fish species found in the Chuitna Watershed include rainbow trout (*O. mykiss*), Dolly Varden (*Salvelinus malma*), coast range sculpin (*Cottus aleuticus*), slimy sculpin (*C. cognatus*), pacific lamprey (*Lampetra tridentata*), Arctic lamprey (*Lethenteron camtschaticum*), ninespine stickleback (*Pungitius pungitius*), and threespine stickleback (*Gasterosteus aculeatus*) (Nemeth *et al.*, 2009).

Future climate scenarios and hydrology

Historic and five future climate scenarios were incorporated into the coho life-cycle model through data derived from an integrated hydrologic model for the Chuitna Watershed (see Prucha *et al.*, 2012; Loinaz *et al.*, In review). Climate change projections for Alaska were extracted from a suite of 21 general circulation models run using the A1B emissions scenario (medium to low cumulative carbon dioxide emissions) from the IPCC's Fourth Assessment Report (Table 11.1 in Christensen *et al.*, 2007). To evaluate how salmon populations respond to changes in hydrology, we chose scenarios that included

combinations of the maximum and minimum predicted changes in air temperature ($T_{\max}$, $T_{\min}$) and precipitation ($P_{\max}$, $P_{\min}$), as well as the median changes in both (T_{50}/P_{50}) (Table 1). Future climate scenarios for the Chuitna watershed were prepared using the delta method (Hamlet & Lettenmaier, 1999; Hamlet *et al.*, 2010) in which IPCC seasonally specific changes in temperature and percent changes in precipitation were applied, for each of the five scenarios outlined earlier, to the baseline (1980–2000) subdaily North American Regional Reanalysis (NARR) data (Mesinger *et al.*, 2006; Prucha *et al.*, 2012). To simulate local hydrology within the subwatersheds, an integrated hydrological model system MIKE SHE was used which required sub-daily temperature, precipitation, radiation, wind speed, dew point, and soil heat flux variables and necessitated the use of a reanalysis such as NARR (see Prucha *et al.*, 2012). Our scenarios fell within the range of the down-scaled monthly climate projections provided by the Scenarios Network for Alaska and Arctic Planning (<http://www.snap.uaf.edu>), which were also produced by applying the delta method to select global climate models. Although Walsh *et al.* (2008) suggest that selecting models on the basis of skill in simulating historical climate will improve projections, other studies have shown that quality ranking varies substantially on the basis of criteria used and that, in most situations, it may be more important to use a wide range of scenarios than attempt to select the best models according to subjectively defined criteria (Brekke *et al.*, 2008; Pierce *et al.*, 2009).

Salmon model

Predicting coho salmon responses to future hydrologic changes required a flexible population model framework capable of incorporating subwatershed-scale hydrologic model output, future climate scenarios, specific habitat requirements, and stream habitat measurements. We followed an existing framework for incorporating these various model components (Scheuerell *et al.*, 2006; Battin *et al.*, 2007) and built a model in the R statistical platform (R Development Core Team, 2011) parameterized for Alaskan coho salmon life cycles. We ran the model for a 20-year period at the end of the century (2080–2100) and tracked changes in smolt abundance

Table 1 Projected change in air temperature and precipitation used in the simulations based on the Intergovernmental Panel on Climate change (IPCC) scenarios for southcentral Alaska

Scenario	Season									
	Change in air temperature °C					Change in precipitation %				
	Winter	Spring	Summer	Fall	μ	Winter	Spring	Summer	Fall	μ
$T_{\max}/P_{\max}$	10.5	7.3	5.4	4.9	7.0	53.0	36.0	29.0	34.0	38.0
$T_{\min}/P_{\max}$	4.2	2.2	1.2	2.2	2.5	53.0	36.0	29.0	34.0	38.0
T_{50}/P_{50}	6.0	3.3	2.3	4.3	4.0	27.0	16.0	13.0	18.0	18.5
$T_{\max}/P_{\min}$	10.5	7.3	5.4	4.9	7.0	6.0	−2.0	1.0	6.0	2.8
$T_{\min}/P_{\min}$	4.2	2.2	1.2	2.2	2.5	6.0	−2.0	1.0	6.0	2.8

Winter = December, January, February; Spring = March, April, May; Summer = June, July, August; Fall = September, October, November; μ = Annual mean of scenario.

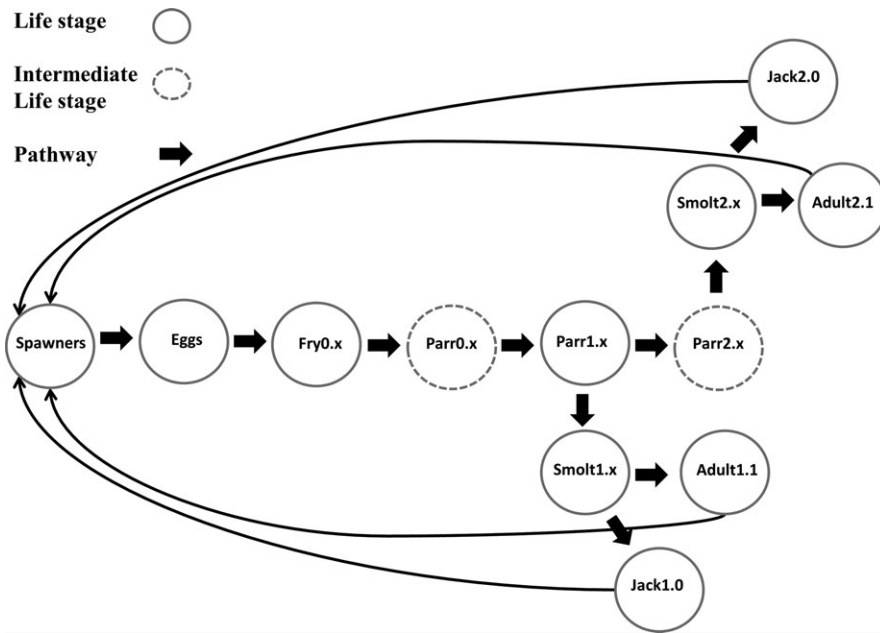


Fig. 2 The Chuitna coho life-cycle model flow diagram showing the possible life histories. Solid gray circles represent life stages modeled, dashed gray circles represent intermediate life stage not modeled and black arrow signifies the different individual pathways.

because this final freshwater life stage integrates mortality across the entire freshwater period. The coho model was built upon the Shiraz model framework (Scheuerell *et al.*, 2006) and uses the multistage Beverton–Holt model to determine the number of individuals transitioning into each life stage at each time step (Moussalli & Hilborn, 1986). Within the asymptotic density-dependent model, the number of fish surviving to the next stage is determined by the number of fish at the current stage, the survival rate to the next stage, and the capacity of the habitat to support individuals at a specific stage. The model tracks the number of individuals across life stages (egg stage – adult stage) at annual time steps while taking into account different life-history strategies and different estimates of survival, habitat capacity, and fecundity at each life stage (Fig. 2). Specifically, the model allows spawner-to-egg survival and egg-to-fry survival to vary with projected environmental conditions in freshwater, but survival rates after the fry stage are randomly selected from a realistic distribution of survival values and are used to estimate the numbers of spawners returning from a given cohort of eggs. We parameterized the model by reviewing literature on coho salmon and consulting with life-cycle modeling and coho fisheries experts. References for all parameters are documented in Table 2.

In the model, we allowed individuals to be within seven different life stages (Fig. 2): (1) Eggs, individuals in the gravel between October 1 and April 30; (2) Fry 0.x individuals in freshwater from May 1 of year 1 to May 31 of year 2; (3) Parr 1.x, parr after 1 year in freshwater; (4) Smolt 1.x and 2.x, individuals that smolt after one or two years in freshwater, respectively; (5) Jack 1.0 and 2.0, precocious males that return to spawn during the same year as smolting after one or two years in freshwater, respectively; (6) Adult1.1 and 2.1, individ-

uals that spend one full year at sea after one or two years in freshwater, respectively; and (7) Spawners, individuals that return to fresh water between July 15 and September 30. Within the model, the different combinations of life stages translate to the four major life-history paths (Fig. 2). Alternative life histories have been documented elsewhere in Alaska (Koski 2009), but evidence for different paths (i.e., estuarine rearing) has not been documented in the study area. The majority of coho salmon in the Chuitna watershed are thought to rear for 2 years in freshwater and then spend one winter in the ocean before returning to spawn (Nemeth *et al.*, 2009).

We used habitat-based functional relationships to drive survival during the prespawning and egg incubation periods. These were similar to those defined by Scheuerell *et al.* (2006) for Chinook salmon but modified to account for different thermal tolerances of coho salmon (Murray & McPhail, 1988; McCullough, 1999). According to our functional relationship, spawner-to-egg survival, which captures the impact of water temperature on spawners during the freshwater migration period (July 15–September 30), decreased linearly with stream temperatures ≥ 15.9 °C, falling to a defined minimum of 0.01 at temperatures above 21 °C (Eqn S1; Cramer, 2001). Egg-to-fry survival was modeled as the product of survival for three functional relationships (Eqns S2–S4) related to water temperature, peak flood streamflow, and fine sediment coverage during the egg incubation period (October 1 to April 30). According to these relationships, fry survival was highest (0.8) at temperatures between 5 and 11 °C and decreased linearly above and below this range (Eqn S2; Murray & McPhail, 1988). To estimate the flow volume that initiated movement of streambed materials and an associated decrease in egg-to-fry survival, we calculated 2-year peak streamflow values for each

Table 2 Fixed productivity values and the functional relationships used to estimate survival at each life stage in the model. Capacity equations used to estimate the Eggs-Smolt stages and fixed values for Parr – Adult stages

Life-stage transition	Productivity	Capacity	Life stage
Spawners-eggs	(temp) ^d _p	(fec) (spawning habitat) ^{kl}	Egg
Egg-fry0.x	(temp, flow, sediment) ^{eq}	(Fry habitat) ^m	Fry0.x
Fry0.x-parr0.x-parr1.x ^a	0.10 ^f	(parr habitat) ⁿ	Parr1.x
Parr1.x-smolt1.x ^b	0.05 ^g	(Smolt habitat) ^o	Smolt1.x
Parr1.x-parr2.x-smolt2.x	0.5 ^h	(Smolt habitat) ^o	Smolt2.x
Smolt-jack1.0 & 2.0 ^c	0.47 ⁱ	∞	Jack
Smolt-adult1.1 & 2.1	0.13 ^j	∞	Adult

Sources

^a85% transition to parr1.x (Nemeth *et al.*, 2009).^b15% smolt transition to smolt within a year or move down stream (Nemeth *et al.*, 2009).^c10% of the population transition to Jacks (Shaul *et al.*, 2011).^dPre-spawning mortality is a non-linear function of temperature (Cramer, 2001).^eEgg to fry survival is a non-linear function of stream temperature (Murray & McPhail, 1988), streamflow (Curran *et al.*, 2003; Beamer *et al.*, 2005) and % sediment (Steel *et al.*, 2008).^fParr survival estimated using Eqn S7 (Shaul *et al.*, 1991, 2008).^gSmolt1.x survival estimated using Eqn S5 (Shaul *et al.*, 1991, 2008).^hSmolt2.x estimated using Eqn S6 (Shaul *et al.*, 1991, 2008).ⁱJack survival is based 0.127 monthly mortality rate for Adult1 Eqn S8 (Shaul *et al.*, 2008).^jLong-term average coho marine survival (Shaul *et al.*, 2008).^kFecundity-based Cook Inlet length relationship (Andrews, 1961; Lawler, 1964; McGinnis, 1966; Engel, 1967).^lEgg capacity is estimated based on See Eqn S6 (Bartz *et al.*, 2006).^mFry capacity is a function of egg-fry survival.ⁿParr capacity is based Bartz *et al.* (2006) methods.^oSmolt capacity based on Bartz *et al.* (2006) methods with restricted habitat for smolt.^pSee Eqn S1.^qSee Eqns S2–S4.

temp = water temperature; flow = peak streamflow; sediment = percent sediment coverage; fec = average fecundity.

subwatershed using Alaska-specific methods for ungauged watersheds (Curran *et al.*, 2003). For example, in middle creek subwatershed, egg-to-fry survival was highest (0.65) below 7.16 m³ s⁻¹ (2-year peak streamflow) and fell linearly with increasing flow, dropping to a minimum of 0.01 at flows above 24.45 m³ s⁻¹ (100 year peak streamflow) (Eqn S3; Beamer *et al.*, 2005). Egg-to-fry survival decreased exponentially with fine sediment coverage (Steel *et al.*, 2008), falling below 0.01 at 45% coverage (Eqn S4). Due to limited information on how hydrologic variables influence instream sediment routing, we chose to use field-based estimates of 8% sediment coverage (Oasis, 2008) to set the survival values to 0.64 which remained constant through time.

Life-stage survival values not estimated from functional relationships were obtained or calculated using existing data from southeast Alaskan coho populations (Eqns S5–S9), with the exception of fecundity rates which were obtained from southcentral Alaska-based studies. Exploitation rates were averaged from four streams from the 1982–2010 period (Skanes *et al.*, 2012), long-term marine survival was estimated from seven wild stocks from 1982 to 2007 (Shaul *et al.*, 1991, 2008), and fry survival rates were estimated over a 3-year period (Crone & Bond, 1976). Smolt1.x survival was calculated by using the above information to back calculate the number of smolts and fry required from a given cohort of returning

Table 3 Comparison of survival values between studies across various life stages of coho salmon

Life stage	Study				
	Bradford <i>et al.</i>	Quinn <i>et al.</i>	Shaul <i>et al.</i>	Crone & Bond	Current
Egg-Fry	0.20	0.25	Na	0.21	0.25*
Egg-Smolt	0.01	0.02	0.02	Na	0.01
Fry-smolt	0.08	0.17	0.11	Na	0.06
Smolt- Adult	0.10	0.10	0.13	Na	0.13

*Median value for functional relationships range.

Na = information is not available from source.

adults. The number of smolts was then divided by the number of fry to generate a survival value (Eqn S5). Parr 1.x was calculated by dividing the calculated smolt 1.x survival by the ratio of average juvenile-to-Ocean 1 survival to smolt-to-Ocean 1 survival (Eqn S7). Smolt 2.x survival was calculated using juvenile-to-adult survival rates (Shaul *et al.*, 1991) and smolt-to-adult survival rates for southeast Alaska (Shaul *et al.*, 2008). Jack, adult 1.1 and adult 2.1 survival rates were estimated using long-term (1982–2007) marine survival for several watersheds in southeast Alaska (Shaul *et al.*, 2008), adjusting

survival rates based on the length of time spent at sea. Our fixed survival estimates are comparable with values for coho salmon found in the literature (Table 3; Bradford, 1995; Quinn, 2005; Shaul *et al.*, 2008). Additionally, fecundity (3364) was estimated for adult salmon based on an average length-to-egg relationship developed from four Cook Inlet streams (Andrews, 1961; Lawler, 1964; McGinnis, 1966; Engel, 1967).

Capacity values for adult and juvenile life stages were estimated using site-specific relationships between habitat area and juvenile coho density estimates (Nickelson *et al.*, 1992) following Bartz *et al.* (2006). We estimated egg capacity from 2008 escapement values (Nemeth *et al.*, 2009) with the assumption that ca. 50% of escapement will be female and each female will have one redd. To calculate fry, parr, and smolt capacities, we estimated the areal extent (i.e., length $\times$ wetted width) of pool, riffle, and glide habitats for the whole subwatershed and then multiplied each by habitat-specific rearing densities (Nickelson *et al.*, 1992). To account for the inverse relationship between territory and fish length (Grant & Kramer, 1990), we assigned previously estimated density values (Nickelson *et al.*, 1992) to our respective juvenile life stages (parr1.x and parr2.x). While juvenile densities might differ in the subwatersheds, the summer density values used are similar to values reported in the region (Anderson and Stillwater Sciences 2011). We estimated the length of pool, riffle, and glide habitat using a supervised classification model in ArcGIS's Image Analysis Toolbox based on high-resolution satellite imagery (~1.5 m multispectral imagery) and field data (Oasis, 2006, 2008). We estimated wetted stream width by developing a model that expressed it as a function of streamflow (Eqn S9), which allowed the areal extent of pool, riffle, and glide habitats to change under historic and projected hydrologic regimes in each of the three subwatersheds. Lake rearing habitat was calculated by first estimating the areal coverage of accessible lakes and, due to documented salmon near shore habitat use (Tabor *et al.*, 2006), we multiplied the total area by an assumed usable portion (30% of total lake area).

Sensitivity analysis

We conducted a sensitivity analysis to understand how changes in input parameters affected the predicted number of smolts and spawners. We systematically modified survival or capacity for the different life stages (i.e., spawner, egg, fry, parr, smolt, and adult) by two percent while holding the other variables constant. Because ocean capacity was assumed to be unlimited, we did not include this in the capacity analysis.

Environmental stochasticity

To account for uncertainty in the input parameters, we used Monte Carlo simulation to iteratively derive survival, fecundity, and capacity estimates at each model time-step. Each model was run for a 20-year period and each input parameter was randomly selected from a beta-distribution. Beta-distributions were also created for all input values that were not gen-

erated from functional relationships and assigned a range based on observed values. The process was repeated 1000 times with a new set of randomly selected values for each 20-year iteration.

Results

Subwatershed physical change

Both historic and future stream temperature and flow simulations were extracted from previous research by Loinaz *et al.* (In review) during ecologically important time periods for each subwatershed. We project stream temperatures during the adult freshwater migration period to generally increase under future climate scenarios at all locations, with the greatest average change (ca. 4 °C) occurring under the $T_{\max}$ scenarios (Fig. 3). The sole exception to this projected warming is Lone Creek under the $T_{\min}P_{\min}$ scenario, where projected temperatures are the same as historic (Fig. 3). Stream temperature during the egg incubation period was also predicted to increase under all scenarios and subwatersheds from a historic <1 °C to more than 5 °C under $T_{\max}$ (Fig. 3). Additionally, peak discharge during the incubation period was predicted to increase in Lone Creek under all climate scenarios except for $T_{\max}P_{\min}$, under which increased precipitation is presumably offset by increased evapotranspiration. The $T_{\min}P_{\max}$ scenario led to the greatest increase in peak discharge for all three streams, while the other scenarios had little effect on peak discharge in Middle Creek and relatively modest increases in Headwater Creek (Fig. 3). The highest peak discharges of ca. 32 m³ s⁻¹ and 26 m³ s⁻¹ were predicted for Lone Creek and Headwater Creek, respectively, while Middle Creek was projected to see smaller maximal peaks flows of ca. 17 m³ s⁻¹ (Fig. 3).

Population response under future climate scenarios:

Increases in stream temperature during adult migration generally had no impact on egg survival, except that both $T_{\max}$ scenarios led to decreases of up to 22% in Middle creek and Headwater creek (Fig. 4). By contrast, increased stream temperature during the egg incubation period led to increased fry survival in all three subwatersheds, with the greatest increases (up to 34%) occurring under the $T_{\max}$ scenarios (Fig. 4). Increased peak flows led to decreased fry survival for Lone Creek under all scenarios and under the $T_{\min}P_{\max}$ scenario in the other subwatersheds (Fig. 4). The greatest impacts were projected for Lone Creek, where a near complete loss of some fry cohorts was projected for the $P_{\max}$ and $T_{50}P_{50}$ scenarios (Fig. 4).

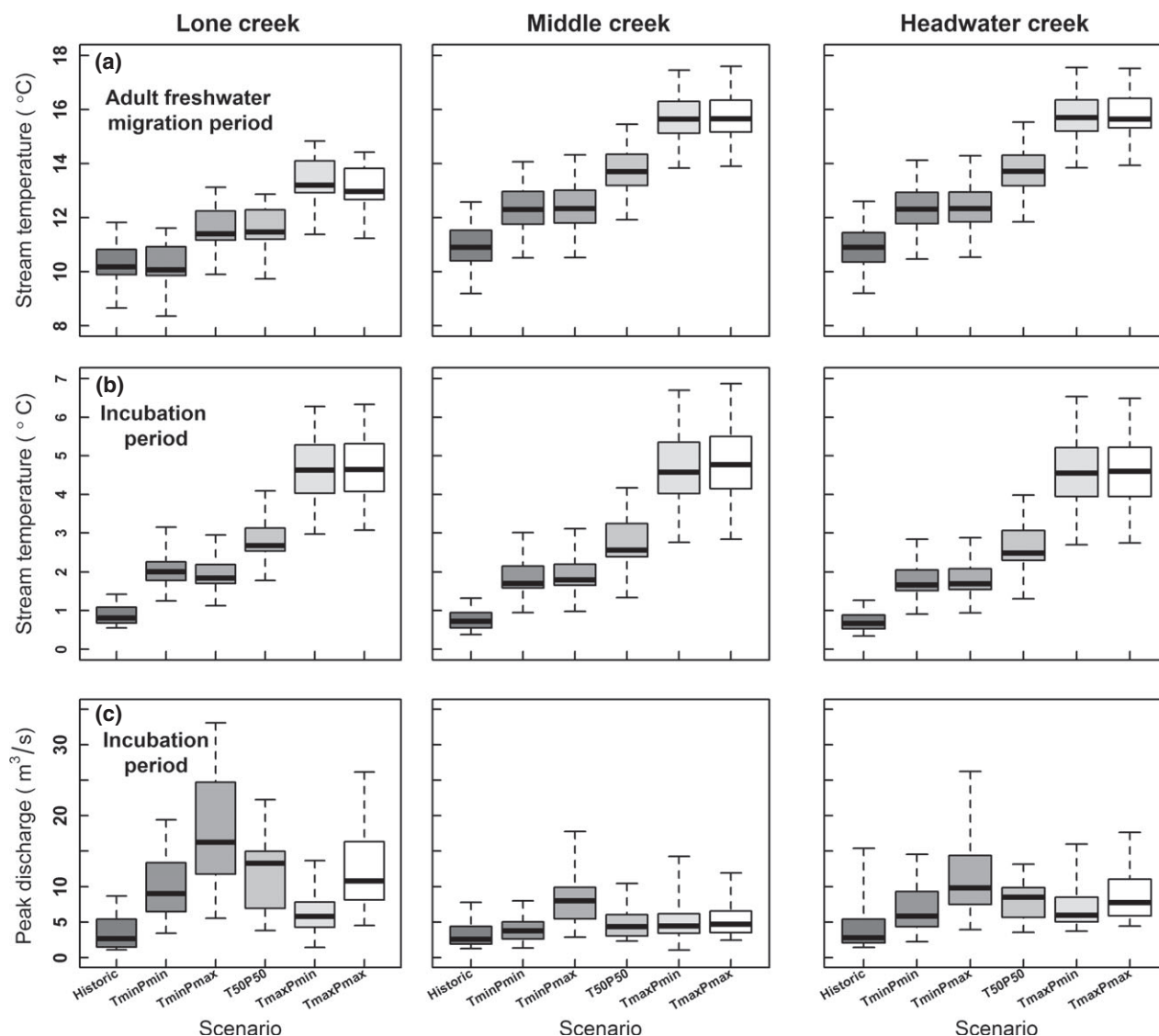


Fig. 3 Summary of the historical and future environmental input data used within the model at each subwatershed. The top row (a) shows the simulated stream temperature values during the adult freshwater migration period (July 15 to September 30). The middle row (b) shows the simulated stream temperature values during the egg incubation period (October 1 to April 30). The bottom (c) row shows the simulated peak discharge values during the incubation egg period. The dark horizontal line shows the median of the 20 annual estimates, the boxes enclose the first and third quartile range and the whiskers show the extreme values.

The above changes in egg and fry survival translated to increases or decreases in smolt production, depending on the subwatershed and climate scenario. In Lone Creek, the $T_{\min}$ and T_{50P50} scenarios led to decreased smolt production in at least 15 of the 20 years simulated (Fig. 5). The largest and most variable decreases occurred for the $T_{\min}P_{\max}$ scenario, under which annual declines in smolt production ranged from 0.6% to 99% and were greater than 50% for 15 of the 20 years simulated. The $T_{\max}P_{\min}$ scenario, by contrast, led to increased smolt production during each year simulated, with a maximum increase of 53%. The $T_{\max}P_{\max}$

scenario led to no change in median smolt production. Overall, responses were more variable in Lone Creek than in the other two subwatersheds, ranging from an increase in smolt production of 53% to a decrease in 99% (Fig. 5). Likewise, interannual variation in smolt production under each of the five climate scenarios was greater in Lone Creek than in the other two subwatersheds.

Smolt production in Middle and Headwater creeks responded similarly to each of the five climate change scenarios (Fig. 5). Four of the five scenarios ($T_{\min}P_{\min}$, T_{50P50} , $T_{\max}P_{\min}$, and $T_{\max}P_{\max}$) were predicted to yield

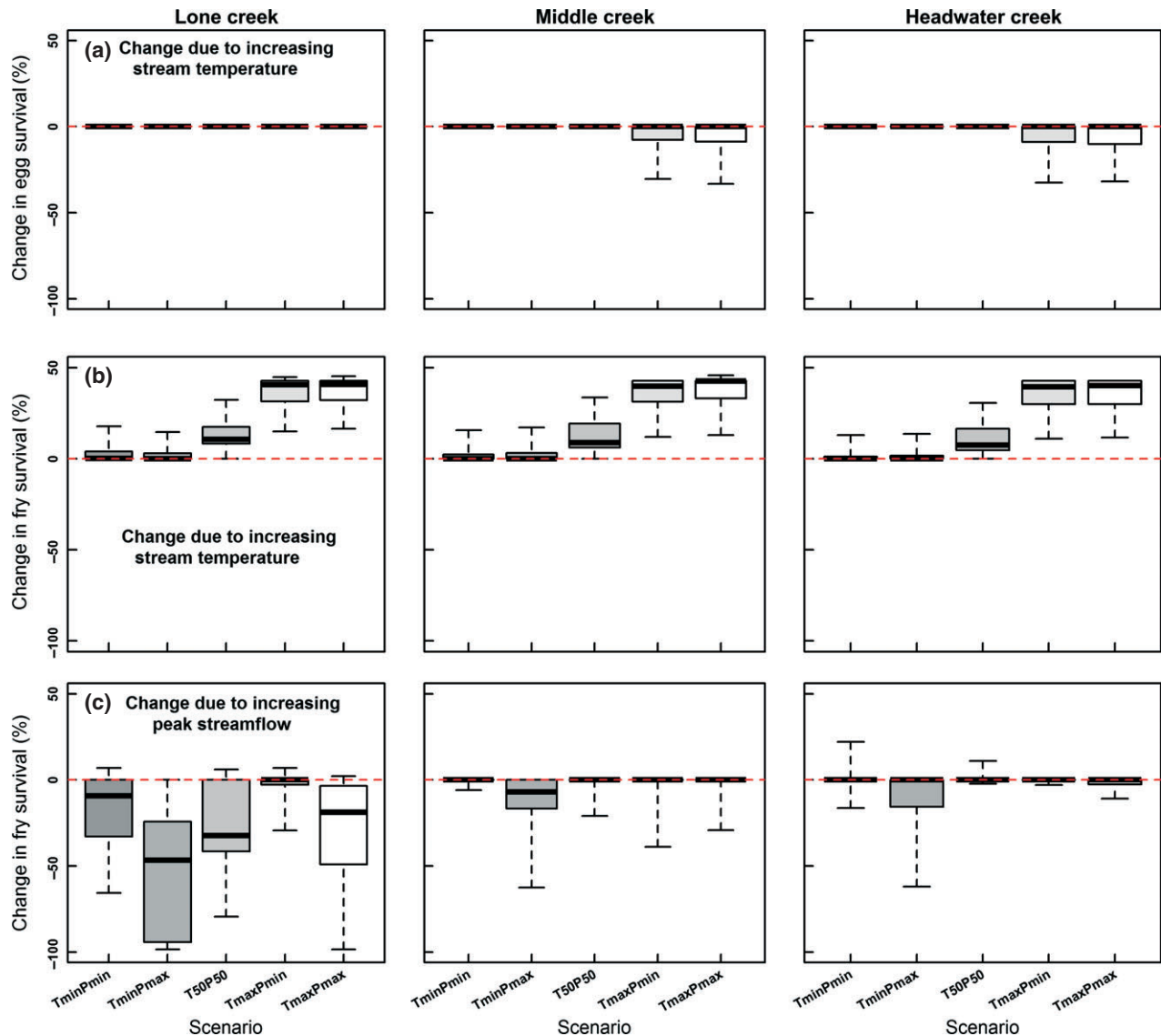


Fig. 4 Percent change in survival parameters for 20 simulated years by climate scenario relative to historical simulations (indicated by horizontal dashed line) for Lone Creek, Middle Creek and Headwater Creek. The top row (a) shows the change in egg survival from elevated stream temperatures during the fall adult migration period (July 15 to September 30), middle row (b) shows the change in fry survival from changes in stream temperatures during the egg incubation period (October 1 to April 30) and bottom row (c) shows the change in fry survival from changes in streamflow during the egg incubation period. The dark horizontal line shows the median of the 20 annual estimates, the boxes enclose the first and third quartile range and the whiskers show the extreme values.

increased smolt production in nearly all of the years simulated. The $T_{\min}P_{\max}$ scenario, by contrast, led to decreased smolt production in 15 of the 20 years simulated. In these subwatersheds, smolt production for all years and climate scenarios was within 50% of the historic levels.

Compared with historical levels of smolt production, climate change scenarios did not necessarily have consistent effects across the three subwatersheds (Fig. 5). The $T_{\min}P_{\max}$ scenario led to decreased smolt produc-

tion for at least 15 of 20 years in all three subwatersheds (Fig. 5). The $T_{\max}$ scenarios, by contrast, led to increased or unchanging production in all three subwatersheds. The remaining two scenarios ($T_{\min}P_{\min}$ and $T_{50}P_{50}$) showed mixed responses, with smolt production generally decreasing in subwatershed Lone Creek and increasing in subwatersheds Middle Creek and Headwater Creek.

Comparing among the different climate change scenarios, however, there is a clear pattern across the three

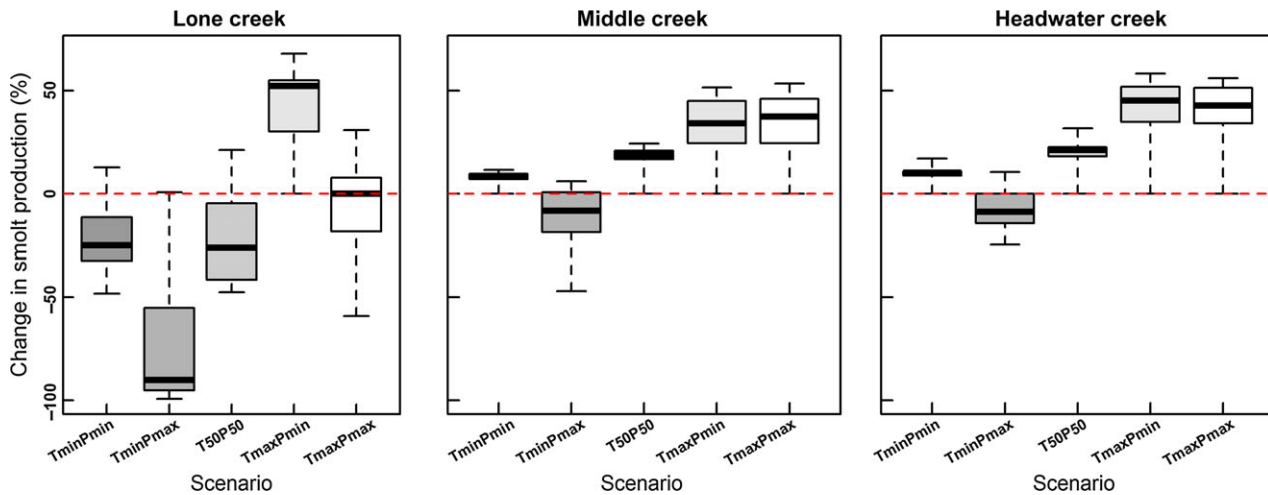


Fig. 5 Percent change in smolt production for 20 simulated years by climate scenario relative to historical simulations (indicated by horizontal dashed line) for Lone Creek, Middle Creek and Headwater Creek. The dark horizontal line shows the median of the 20 annual estimates, the boxes enclose the first and third quartile range and the whiskers show the extreme values.

subwatersheds. The $T_{\min}P_{\max}$ scenario consistently resulted in the lowest smolt production of the five scenarios (Fig. 5). The $T_{\max}$ scenarios, by contrast, generally led to the highest levels of smolt production.

Sensitivity analysis

Variability in survival values for the parr1.x and smolt 2.x had the greatest impact on smolt abundance, and egg survival had the least amount of impact on smolt production (Fig. 6a). Interestingly, decreasing survival rates had a greater impact on smolt production than increasing rates (Fig. 6a). Increasing capacity for all life stages had little effect on smolt production, and decreasing capacity had a somewhat greater impact (Fig. 6b). Egg capacity had a marginally greater impact on smolt production than other capacity parameters (Fig. 6b).

Discussion

Our projections suggest that changing thermal and hydrologic regimes can be positive or negative for the Chuitna River's salmon populations, depending on subwatershed characteristics and the future climate scenario. The predicted changes in smolt production were largely driven by the counteracting effects of warming temperature (positive) and increased peak flows (negative) on egg-to-fry survival. The positive effects of warming temperature, which were greatest under the $T_{\max}$ scenarios, were due to the elevation of winter water temperatures into a range that is more favorable for egg development (Murray & McPhail, 1988; Beacham & Murray, 1990). Egg-to-fry survival in our

functional relationship increased rapidly at low temperatures to a plateau of 80% between 5 and 11 °C (Murray & McPhail, 1988), and the projected increases under the $T_{\max}$ scenarios pushed incubation temperature into this optimal range. A similar analysis for Chinook salmon in Washington state showed no effect of increasing temperature on egg-to-fry survival (Battin *et al.*, 2007), presumably because historic and projected incubation temperatures were both within the Chinook salmon's optimal range (see Scheuerell *et al.*, 2006), demonstrating that improved incubation conditions as a result of global warming may be specific to colder than optimal watersheds found at both higher altitudes and latitudes. Support for enhanced productivity in cooler, high elevation systems under warming scenarios is corroborated by recent applications of bioenergetics models across the northwestern United States which projected increased growth in Chinook salmon and steelhead trout (anadromous *Onchorhynchus mykiss*) (Beer & Anderson, 2011). Similarly, research in high-latitude Norwegian systems projected faster parr growth, earlier smolting, and increased smolt production under future warming scenarios (Hedger *et al.*, 2013). Our research predicts increased survival from elevated stream temperature during egg incubation, but additional factors should be explored to understand the cumulative impacts of stream temperatures on egg-to-fry survival. Our model did not account for earlier coho hatch dates, increased prey production, and shifting prey phenology that may accompany warmer thermal regimes, and we recommend efforts to understand how such climate-driven effects will influence salmon populations.

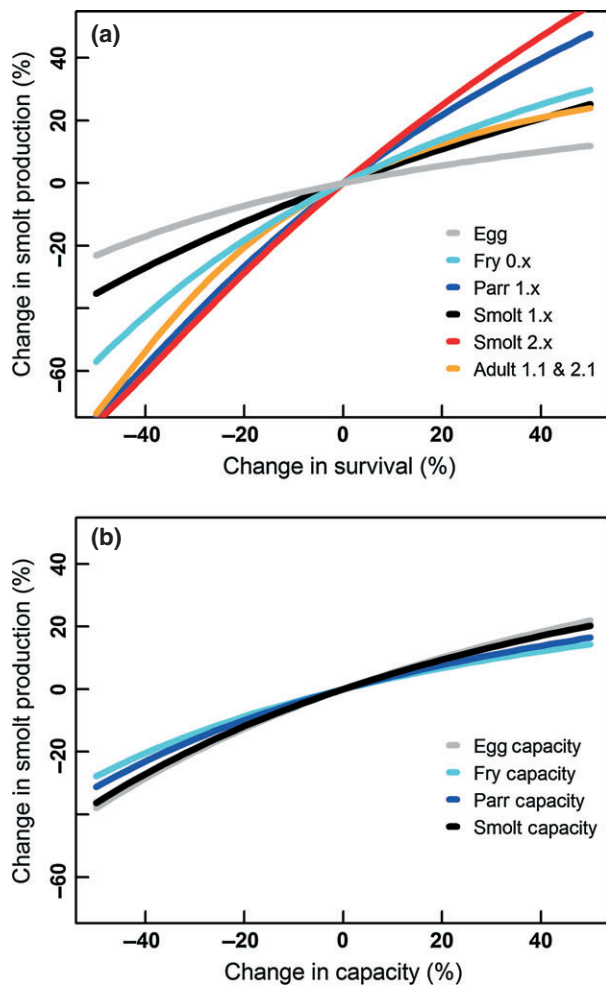


Fig. 6 Sensitivity of smolt change in relation to change in survival (a) and capacity (b) input parameters: the color lines represent the sensitivity of different life-stage survivals (a) and life-stage capacities (b).

Our model output suggests that increasing peak flows during egg incubation could substantially reduce egg survival and, consequently, smolt production. Likewise, increased peak flows during incubation have also been identified as an important contributor to projected declines in Chinook salmon populations (Battin *et al.*, 2007). High peak flows can physically disrupt salmon redds, causing eggs to be crushed or displaced (Holtby & Healey, 1986; Montgomery *et al.*, 1996; DeVries, 1997), but egg pocket depth and spawning substrate influence the magnitude of impact (Goode *et al.*, 2013). This may be an important effect over the long term because, compared with temperature changes that can be ameliorated by behavioral responses or natural selection, salmon may have less capacity to avoid or adapt to widespread and unpredictable physical distur-

bance due to specific spawning habitat requirements (Sandercock, 1991).

The projected increases in stream temperatures do not appear to exceed major physiological thresholds (21 °C) for coho salmon (McCullough, 1999), so we do not expect warmer late-summer temperatures (projected at 14–18 °C) to hinder spawning migrations. This contrasts research from historically warmer streams in more temperate climates, where similar temperature increases (up to 7 °C) are projected to push stream temperatures above 21 °C and create migration barriers and widespread thermal stress (Mantua *et al.*, 2010). While Alaskan salmon may have lower thermal thresholds than indicated by literature values from salmon adapted to warmer climates (i.e., McCullough, 1999), we anticipate that spawners have some capacity to mitigate the effects of warmer water by delaying migrations (Quinn & Adams, 1996; Taylor, 2007; Kovach *et al.*, 2012), finding refugia (Torgersen *et al.*, 1999; Goniea *et al.*, 2006) and adapting to new conditions over time (Quinn & Adams, 1996).

Our projected changes in smolt production varied by climate scenario and were mediated by subwatershed habitat conditions. Specifically, we project egg-to-fry survival to increase in proportion to temperature in all three subwatersheds, but in some circumstances, these gains will be offset by higher egg mortality due to increased peak streamflows during incubation. The effects of increased peak flows are especially apparent in Lone Creek, where any climate scenario not accompanied by a maximal temperature increase (i.e., $T_{\min}$ and $T_{50P_{50}}$ scenarios) was projected to negatively impact salmon. We attribute this difference to Lone Creek's larger drainage area and lower elevation which likely causes the subwatershed to collect more winter rain and produce exacerbated peak flow conditions under future scenarios. Geomorphic and physical attributes of watersheds interact with local climate to produce unique stream conditions and our results further support the idea of a heterogeneous watershed response to climate (Lisi *et al.*, 2013). The interplay between temperature and precipitation is demonstrated by comparing the coolest but wettest climate scenario ($T_{\min}P_{\max}$), which was projected to be largely detrimental to salmon in all three subwatersheds, to the warmest and driest scenario ($T_{\max}P_{\min}$), which was projected to be universally beneficial. Increased air temperature likely shifted winter precipitation from snow to rain and, without increased evapotranspiration rates under the $T_{\max}$ scenario, the additional precipitation caused elevated winter peak streamflow events that are thought to reduce egg survival by scouring eggs (Cunjak & Therrien, 1998; Beamer *et al.*, 2005).

Results from our sensitivity analysis reveal that the variability in survival values for the parr1.x and smolt 2.x have the greatest impact on smolt abundance, and it is likely that these life stages are survival bottlenecks (stages when large portions of the population die) for the populations. While little is known about the influence of the environment on the bioenergetics and survival of these later life stages, it is likely that individuals are resilient to most changes due to their ability to move to more suitable locations (Huntingford *et al.*, 1999; Torgersen *et al.*, 1999). We adjusted carrying capacity during the parr and smolt stages to account for changes in streamflow, but we are not aware of existing functional relationships between hydrologic variables and the associated life-stage survivals that could be included in the model, a knowledge gap noted for salmon elsewhere (e.g., Nislow & Armstrong, 2012). While uncertainty exists in our capacity estimates, we found that adjustments to capacity values had little impact on total smolt production. Due to the potential significance that fry0.x-to-parr1.x and parr1.x-to-smolt2.x survival values have on the populations, we recommend that future research be conducted to understand how environmental variables (i.e., streamflow, stream temperature) influence survival at these life stages.

Our results demonstrate that a given climate scenario can have positive effects on salmon production in some habitats and negative effects in others. For example, the $T_{50}P_{50}$ scenario was projected to have negative effects in Lone Creek during most years and positive effects in Middle and Headwater creeks during all years. Additionally, our simulations show that it is possible for a climate scenario to induce dissimilar effects on different freshwater life stages. While climate change has been linked mainly to negative impacts on salmon in other locations (Battin *et al.*, 2007), our results suggest that in colder subarctic environments elevated stream temperatures may enhance productivity during certain life stages.

Our research focuses on the influence of the freshwater environment on coho smolt production and excludes the effects of anthropogenic warming on coastal and offshore marine habitat which could affect marine survival and, in turn, spawner returns to the study area. Research in the marine environment has documented general migratory pathways (Hartt & Dell, 1986), changes in the distribution of suitable habitat (Abdul-Aziz *et al.*, 2011), and impacts to important prey species (Kaeriyama *et al.*, 2004), but to date adequate information is not available to simulate how climate change may affect specific stocks of Alaska salmon during their marine phase. Major processes that control marine survival are thought to be both habitat and species specific (Weitkamp *et al.*, 2011) and more research

on the mechanisms from environmental variability that influence salmon at sea is needed (Hobday & Boehlert, 2001) before it is possible to simulate future survival rates.

These results highlight the complexities involved in modeling climate impacts on salmon and provide additional support for differential effects of climate change (Wenger *et al.*, 2011) on salmon in a subarctic watershed (Hedger *et al.*, 2013). While this research provides valuable insights into plausible population-level responses from climate change, the simplified population model and range of possible outcomes make it difficult to ascertain exactly how populations will respond in the future. Additionally, given the uncertainty inherent in predicting the magnitude of future temperature and hydrologic changes at a fine scale (Christensen *et al.*, 2007) and, in turn, which habitats will be most productive under future climate regimes, our results support the notion that the maintenance of a complex complement of intact and accessible salmon habitats is a sensible strategy for maintaining salmon runs and the fisheries that rely on them (Hilborn *et al.*, 2003; Schindler *et al.*, 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Equation S1.** Equation for egg survival functional relationship (water temperature °C).
- Equation S2.** Equation for fry survival functional relationship (water temperature °C).
- Equation S3.** Equation for fry survival functional relationship (peak flood streamflow $\text{m}^3 \text{s}^{-1}$).
- Equation S4.** Equation for fry survival functional relationship (% fine sediment coverage).
- Equation S5.** Equation used to estimate Smolt1.x survival.
- Equation S6.** Equation used to estimate Smolt2.x survival.
- Equation S7.** Equation used to estimate Parr1.x survival.
- Equation S8.** Equation used to estimate Jack survival.
- Equation S9.** Equation for wetted width functional relationship.