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RESEARCH ARTICLE

Habitat modulates population-level responses of freshwater salmon growth to a century of change in climate and competition

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Abstract

The impacts of climate change are widespread and threaten natural systems globally. Yet, within regions, heterogeneous physical landscapes can differentially filter climate, leading to local response diversity. For example, it is possible that while freshwater lakes are sensitive to climate change, they may exhibit a diversity of thermal responses owing to their unique morphology, which in turn can differentially affect the growth and survival of vulnerable biota such as fishes. In particular, salmonids are cold-water fishes with complex life histories shaped by diverse freshwater habitats that are sensitive to warming temperatures. Here we examine the influence of habitat on the growth of sockeye salmon (*Oncorhynchus nerka*) in nursery lakes of Canada's Skeena River watershed over a century of change in regional temperature and intraspecific competition. We found that freshwater growth has generally increased over the last century. While growth tended to be higher in years with relatively higher summer air temperatures (a proxy for lake temperature), long-term increases in growth appear largely influenced by reduced competition. However, habitat played an important role in modulating the effect of high temperature. Specifically, growth was positively associated with rising temperatures in relatively deep (>50 m) nursery lakes, whereas warmer temperatures were not associated with a change in growth for fish among shallow lakes. The influence of temperature on growth also was modulated by glacier extent whereby the growth of fish from lakes situated in watersheds with little (i.e., <5%) glacier cover increased with rising temperatures, but decreased with rising temperatures for fish in lakes within more glaciated watersheds. Maintaining the integrity of an array of freshwater habitats—and the processes that generate and maintain them—will help foster a diverse climate-response portfolio for important fish species, which in turn can ensure that salmon watersheds are resilient to future environmental change.

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KEYWORDS
climate change, competition, conservation, freshwater growth, habitat, Pacific salmon, temperature

1 | INTRODUCTION

Recent changes in the Earth's climate are both unprecedented and intensifying, with some changes likely to be irreversible over hundreds to thousands of years (IPCC, 2022). Human activities are responsible for more than 1°C of warming over the last century, and global temperatures are expected to increase on average by an additional 0.5°C in the coming decades (Allen et al., 2018). While the impacts of such change are widespread and threaten natural systems and associated biodiversity globally (Parmesan & Yohe, 2003; Pecl et al., 2017), specific regions and ecosystems will be affected differently. For example, northern latitudes are warming faster than the global average (O'Reilly et al., 2015); marine animal biomass is projected to decline in the Pacific, Atlantic, and Indian Oceans, yet increase in the Arctic and Southern Oceans (Bryndum-Buchholz et al., 2019); rangeland primary productivity is projected to increase in North America but decline in western Africa and Australia (Boon et al., 2018).

Within regions, climate can be differentially filtered by heterogeneous physical landscapes, giving rise to variability in local responses (commonly referred to as *response diversity*; Elmqvist et al., 2003). For instance, a metapopulation of house sparrows (*Passer domesticus*) occupying nearby island habitats experienced divergent environmental conditions that resulted in fledgling rate variation (Ringsby et al., 2002). Discrete sockeye salmon (*Oncorhynchus nerka*) populations exposed to similar regional climatic conditions in different habitats showed asynchronous temporal trends in population productivity (Brennan et al., 2019; Rogers & Schindler, 2008). Freshwater lakes also can exhibit a diversity of thermal responses to climate owing to their unique morphology (Winslow et al., 2015; Woolway & Merchant, 2017). Even within a single watershed, the growth of fish from two adjacent freshwater lakes that differed in morphology showed contrasting responses to shared increases in air temperature (Griffiths et al., 2014). Certain lake characteristics—such as depth, area, and water clarity—can modulate the effect of warming temperatures and climatic stress on the growth of aquatic life (Massie et al., 2021; Read et al., 2014). In this way, the physical landscape filters regional climate to shape environmental conditions that are unique to the characteristics of an organism's habitat, which can produce distinct responses of organisms to those conditions. The value of such response diversity among aggregate systems is that it can spread risk against climate variation, and thus be more resilient to future change (Elmqvist et al., 2003; Munsch et al., 2022).

Freshwater lakes are responding rapidly to climate change and the associated warming of air temperatures. Surface water temperatures have increased globally (O'Reilly et al., 2015), seasonal duration of ice cover has shortened (Sharma et al., 2019), and the strength and duration of seasonal stratification has increased (Woolway et al., 2021). These changes can affect ecological processes and influence the growth and survival of sensitive freshwater biota. Growth is a useful indicator of an organism's response to climate as filtered by their habitat and the interactions with their biotic community. For fishes, water temperature is a key driver of growth (Sharma et al., 2007), which can influence individuals indirectly though the availability and abundance of prey (Adams et al., 1982; Edmundson & Mazumder, 2001), and directly via metabolism (Brett, 1971; Fry, 1947). As water temperatures warm, growth rates of fish tend to rise as energy and food consumption increase. However, as temperatures reach beyond a species' thermal optimum, growth will decrease due to greater metabolic demands (Neuheimer et al., 2011). Generally, warmer rearing temperatures associated with climate change are predicted to increase the body growth of juvenile fish, yet lead to smaller-bodied adults (Lindmark et al., 2022; Ohlberger, 2013). Different species have diverse thermal tolerances, with cold-water fishes being particularly sensitive to warming temperatures (Massie et al., 2021).

Salmonids are an ecologically, culturally, and economically important group of cold-water fishes that have complex life histories shaped by diverse freshwater habitats (Montgomery, 2000; Waples et al., 2008). Sockeye salmon have many populations of conservation concern in Canada (COSEWIC, 2017; Price et al., 2019), which are particularly sensitive to warming temperatures (Martins et al., 2012). Juveniles live for up to 3 years in freshwater lakes before emigrating to the ocean, and their response to future warming during this life stage may include an increase in growth due to enhanced conditions (e.g., Schindler et al., 2005), or a decrease in growth and survival resulting from greater thermal challenges and reduced prey abundance (e.g., Henderson et al., 1992; Melack et al., 1997). Predicting how the freshwater growth of juvenile sockeye will respond to warming regional temperatures is complicated by lake-specific morphology and competition for food resources. Fish routinely show reduced growth in the year after a large number of adults return to spawn because of the resulting high density of lake-rearing juveniles (i.e., high intraspecific competition; Burgner, 1991; Foerster, 1944; Goodlad et al., 1974). Conversely, growth of juvenile sockeye often is higher in years following low numbers of spawning adults and warmer temperatures (Rich et al., 2009; Schindler et al., 2005). However, it is not known whether these patterns are modulated by lake habitats. Such density-dependent and climate-driven growth of juveniles is important as it can affect population age-structure, size at maturity, and the survival to adulthood (Gregory et al., 2019; Koenings et al., 1993; Wilson et al., 2021). More broadly, variability in responses among salmon populations to environmental change can provide insight into future resilience.

Here we explore the influence of habitat on the freshwater growth of sockeye salmon rearing in 13 lake systems of Canada's

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Skeena River watershed over a century of change in regional climate and competition. Since 1913, summer air temperatures have been variable with no clear trend, whereas salmon abundances have declined. We use genetic tools to assign specific populations to century-old fish scales sampled from a mixed-population fishery to: (a) reconstruct annual freshwater growth of fish inferred from scales from each population, (b) examine shared temporal patterns in growth among these populations, and (c) quantify the influence of regional climate and its interaction with intraspecific competition and local habitats on freshwater growth. Our results demonstrate that the growth of fish in fresh water has increased broadly over the last century. While body growth tended to be higher in years with higher temperatures and lower intraspecific competition, habitat played an important role in modulating the effect of high temperature.

2 | METHODS

The Skeena watershed in British Columbia, Canada, has 31 sockeye salmon Conservation Units (CU; Holtby & Ciruna, 2007), which are grouped broadly into 13 population complexes (hereafter referred to as *populations*; Price et al., 2019), each associated with at least one nursery lake (Figure 1). These freshwater lakes vary widely in their geomorphology and productive capacity. For example, mean depths range from 4 m (Slamgeesh) to 81 m (Kalum), elevations range from 30 m (Alastair) to 1373 m (Sustut), and primary productivity varies from 20 mgC/m^2/day (Motase) to 265 mgC/m^2/day (Kitwanga; Table 1). Commercial fishing began at the mouth of the Skeena River in 1877 (Wood, 2008), and an annual scale-collection program for adult sockeye caught in commercial fisheries occurred from 1912 to 1947 (e.g., Gilbert, 1914)—known as the Gilbert/Clemens collection. A similar scale collection program resumed in 2000 at the mouth of the Skeena River from fish caught in the Tyee Test Fishery, which uses a gill net composed of multiple mesh sizes. Additional scale collection programs for sockeye have occurred at terminal locations (i.e., from source populations) since 1950. Fish (scales) from the Gilbert/Clemens and Tyee Test Fishery collections were first identified to population as part of a broader scientific investigation (Price et al., 2019; Price, Moore, et al., 2021), where DNA was extracted from scales, genotyped at up to 12 microsatellite loci, and individuals were assigned to population via genetic stock identification (Appendix S1). We included only those scales from fish assigned to population with ≥90% probability; scales from fish sampled near spawning locations were assumed to be from the local population. We sampled up to 30 scales per population per year over the last century from these various collections to obtain annual growth data from as many years and populations as possible, representing a total of 2477 fish (Table SI-1). This research was exempt from Simon Fraser University's Animal Care Protocol because all fish scales were from existing collections and Indigenous fisheries programs.

Each fish scale was examined for age at maturity using a Leica DMS1000 digital microscope at 25× magnification, and had a digital image captured for subsequent growth measurement analyses (Appendix S2). The digital image analysis software, Image Pro Premium 9.1 64 bit (Media Cybernetics Inc.; www.mediacy.com), was used to measure annual growth of each scale, which proceeded using the following steps. First, each scale was calibrated using a metric micrometer slide measurement, then positioned with a measurement axis on each scale by superimposing XY axes lines onto the scale image. Second, digital markers were placed on the outside edge of the circulus denoting the end of each annual growth zone (hereafter referred to as a *life stage*) and the length between each freshwater stage was measured. Life stages included the first freshwater annulus (FW1) and the second freshwater annulus (when present; FW2). All scales were aged and measured by one individual with extensive experience reading salmon scales to minimize the potential for among reader variation observation error (D. Gillespie).

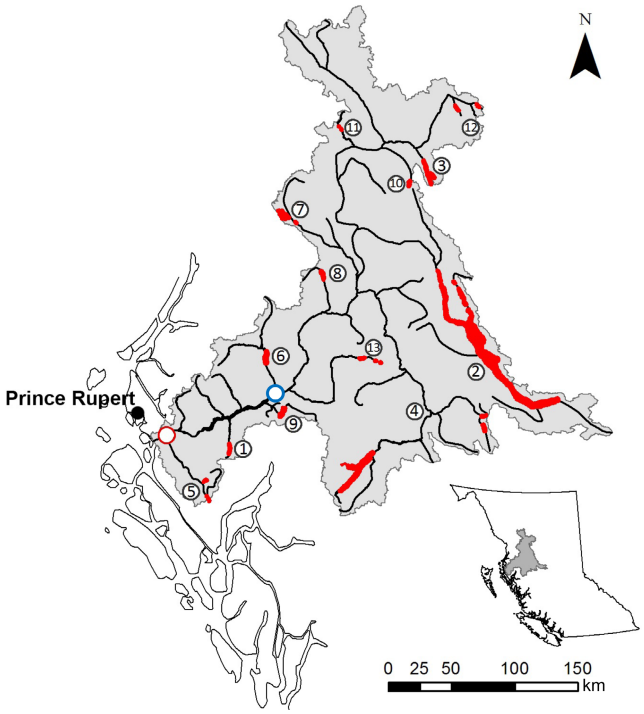

FIGURE 1 Skeena River watershed showing the location of each sockeye salmon (*Oncorhynchus nerka*) population complex (numbers 1–13, detailed in Table 1) identified in genetic analyses, and associated freshwater nursery lakes in red. White-filled red circle denotes the approximate location of historical scale sample collection and current Skeena Tyee Test Fishery. White-filled blue circle denotes the location of air temperature records at Terrace.

We examined changes in the body growth of fish inferred from scales between time periods for each freshwater life stage and population by grouping growth years into historical (1908–1959) and recent (1960–2014) periods and calculating arithmetic mean growth for each. There is a consistently strong linear relationship between body size (length) and scale growth for juvenile sockeye across freshwater years (Clutter & Whitesel, 1956; Fukuwaka & Kaeriyama, 1997). To explore differences in growth between freshwater life stages, we compared the arithmetic mean annual growth

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#	Population	Elevation (m)	Depth (m)	Area (km^2)	Glacier cover (%)	Productivity ($mgC/m^2/day$)
1	Alastair	30	24	7	7.02	209
2	Babine	711	55	461	0.00	140
3	Bear	805	13	18	0.28	144
4	Bulkley	764	69	98	5.96	92
5	Ecstall	100	45	2	12.05	210
6	Kalum	122	81	19	10.29	33
7	Kispiox	522	34	16	0.00	93
8	Kitwanga	376	5	8	0.00	265
9	Lakelse	137	8	14	0.25	74
10	Motase	1021	13	4	29.94	20
11	Slamgeesh	616	4	1	0.00	71
12	Sustut	1373	9	2	0.15	77
13	Zymoetz	830	8	2	0.00	65

TABLE 1 Freshwater lake habitat characteristics for each sockeye salmon (*Oncorhynchus nerka*) population complex in the Skeena River watershed (numbers correspond to Figure 1).

Note: Depth is arithmetic mean lake depth, area is lake surface area, glacier cover is the percentage of a given lake system's watershed covered by glaciers, and productivity is the daily lake photosynthetic rate.

at each life stage within each population and year only for those fish that reared for a combined 2 years to ensure a more accurate test of year-specific differences. Paired-mean differences and resulting effect size were calculated using bootstrap-coupled estimation (5000 bootstrap samples) in the *dabestr* package (Ho et al., 2019) of the R programming language (R Development Core Team, 2022).

3 | COMMON TRENDS IN GROWTH AMONG POPULATIONS

We assessed whether sockeye populations in the Skeena watershed exhibited shared temporal patterns in growth at each freshwater life stage (i.e., year-1 and year-2, separately) over the last century using dynamic factor analysis (DFA; Zuur, Fryer, et al. 2003; Zuur, Tuck, et al. 2003). A DFA can be used to identify underlying common (i.e., latent) trends in multivariate time series, where the relationship between individual time series (in this case, fish growth at each freshwater life stage within individual sockeye populations) and estimated common trends can be assessed using the factor loadings of the individual populations on estimated common trends. A DFA is a form of state-space model where a m number of unknown common trends (X) are modelled as random walks in the state model:

$$X_t = X_{t-1} + w_t, \text{where } w_t \sim \text{MVN}(0, I). \quad (1)$$

The process error, w_t, was assumed to be multivariate normally distributed (MVN), and we set the state variance–covariance matrix, I, to "identity" so that the corresponding random vector has uncorrelated variance components. For each freshwater life stage, the relationship between the observed time series (Y; here, fish growth by population) and the trends (X) is estimated in a Z matrix in the observation model:

$$Y_t = ZX_t + a + v_t, \text{where } v_t \sim \text{MVN}(0, R) \quad (2)$$

and described by the factor loadings. The level parameter, a, was set to zero because data were standardized (i.e., z-scored). The observation error, v_t, was assumed to be MVN distributed, and estimated within the variance–covariance matrix, R. The absolute value of a loading reflects the relative importance of an estimated trend in explaining variance in an observed time series, and the sign indicates whether the time series is positively or negatively related to the common trend. We evaluated models with the following alternative formulations of the R matrix: shared variance and covariance, shared variance but no covariance, or different variances and no covariance between populations. To search for common patterns in growth at each freshwater life stage across the 13 Skeena sockeye populations, we quantified the evidence for all possible numbers of latent trends (i.e., from 1 to 13), including a time-invariant Null model (i.e., an intercept-only model whereby the growth deviate is expected to have no change over time). We used Akaike's information criteria for small sample sizes (AICc; Burnham & Anderson, 2002) to evaluate support for each model and selected the top model with the lowest AICc within each life stage. Model parameters and states were estimated using the *MARSS* package (Holmes et al., 2020) in R (R Development Core Team, 2022).

4 | CLIMATE AND COMPETITION ASSOCIATIONS WITH GROWTH

We used linear mixed-effects models to explain variation in freshwater growth of fish among populations as a function of regional climate and its interaction with intraspecific competition and local habitat characteristics. We included mean monthly air temperatures during the primary growing season (April–August; Rich et al., 2009) for juvenile sockeye salmon as an index of regional climate variation in the Skeena watershed. Monthly air temperatures at Terrace were obtained from the Pacific Climate Impacts Consortium (PCIC;

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https://data.pacificclimate.org/portal/pcds/map/). While Terrace provides the longest continuous air temperature time series (1913–2021) in the Skeena watershed, no single station provide data for all years. We used data recorded at the Terrace Skeena River stations (#623 and #625) for years 1913–1953 and 1968–2014, and at the Terrace airport station (#624) for years 1954–1967. No such continuous records of temperature exist for individual freshwater lakes; however, we assessed how well air temperatures at Terrace may reflect air temperatures at other locations in the watershed (Appendix S3). Geomorphic data at the individual lake and watershed level were obtained from the British Columbia Freshwater Atlas, and those reported in Atlas et al. (2020). We used mean seasonal (i.e., sockeye growing season) photosynthetic rate reported in Shortreed et al. (2001) and Cox-Rogers (2012) as a measure of lake productivity. Because some populations (i.e., Bear, Ecstall, Kispiox, Sustut) are associated with more than one rearing lake in unknown proportions, several variables required additional calculations for each of these populations. To estimate average lake depth, area, and productivity, we quantified the weighted average (i.e., based on each lake's proportion of area within a population) of each metric across all lakes for a given population. For glacier extent, we summed the area covered by glaciers across lake watersheds and divided by the summed watershed area for each population.

We used estimates of the total number of sockeye salmon adults that spawned in the year prior to lake rearing as an index of intraspecific competitor abundance for each population. Annual estimates of spawning adults during the historical (1912–1947) period were derived by multiplying the annual proportions of each population genetically-assigned to scales (Price et al., 2019; Price, Moore, et al., 2021) to aggregate estimates of spawning fish (Shepard & Withler, 1958). We used reconstructed estimates of spawning adults for each population reported in English et al. (2018) for the recent (1960–2013) period. Various years and populations had missing data throughout the time series; thus, we used several approaches to infill years with missing data depending on time period: (i) 1912–1949, we first quantified the decadal average genetic proportion of each population (Price et al., 2019; Price, Moore, et al., 2021), then multiplied these proportions by the aggregate spawning adult estimates reported in Shepard and Withler (1958) for each missing year within each decade; (ii) 1952–1953 (Babine population only), we used data reported in Cox-Rogers and Spilsted (2012); and (iii) 1995–2013, we averaged spawning adult abundance estimates reported in English et al. (2018) over the 5 years before and after each missing year for each population for every year of missing data (Appendix S4).

Annual growth estimates for each fish used in the model were derived from scale measurements that included the area between the nucleus and the outer edge of the first annuli, representing the first year in freshwater; proportions of this life history (i.e., one freshwater year) over the last century for each population ranged from 35% (Bulkley) to 95% (Babine), and averaged 78%. We normalized the response variable (growth) by subtracting the mean growth and dividing by the standard deviation (SD) for each population, so that all growth "observations" ($n = 2291$) were on the same scale and comparable across populations. In addition to the influence of intraspecific competition within populations on fish growth, we considered five lake-rearing habitat characteristics hypothesized to modulate the magnitude of fish growth response to temperature: (1) arithmetic mean depth, (2) surface area, (3) elevation, (4) percent glacier cover, and (5) historical lake productivity. Each covariate was normalized to be on the same scale, which allowed us to compare effect sizes directly. The global model took the form:

$$G_{i,p,y} \sim Z_{p,y}\beta_Z + (T_y Z_{p,y})\beta_Z + b_{p/y} + \varepsilon_i, \quad (3)$$

where the response ($G_{i,p,y}$) is the scale growth measurement for individual i in population p in year y, Z is a vector of lake characteristic covariates including competition, the βs are estimates of the main covariate effects and their interaction with air temperature (T), $b_{p/y}$ is a random effect on the intercept to account for non-independence of observations within populations and year at the scale that the covariates were measured, and ε_i is normally distributed residual error. All covariates were treated as continuous variables. We fit the model in Equation (3) to the data in a Bayesian estimation framework with a uniform prior (all parameter values are equally likely), and with a Gaussian error distribution using four chains, each with 4000 iterations (the first 1000 calibrated the sampler), for a total of 12,000 posterior samples. While we initially considered other covariates—such as latitude, distance to ocean, and watershed area—these variables were strongly correlated with other covariates (cor >.50, $p < .001$), and so were not considered further. We based our inference about the importance of the hypothesized drivers of freshwater growth on the posterior probability distribution of each covariate effect (βs in Equation 3) derived from marginal likelihood estimates (Buerkner, 2017); covariates with posterior probability distributions that had little overlap with 0 (positive or negative) indicate stronger certainty of association with fish growth. We considered the evidence to be *weak*, *moderate*, and *strong*, when posterior probabilities were <75%, from 75% to <90%, and ≥90% from zero, respectively. We performed sensitivity analyses to examine the influence of average Winter (January–March) and extended growing season (April–October) temperatures and its interaction with local habitat features and competition (Appendix S5), as well as to explore the influence of the most data-rich population (Babine; Appendix S6), and small sample sizes (Appendix S7). All analyses and figures were performed and generated using the *boot* (Canty & Ripley, 2021), *brms* (Buerkner, 2017), *corTest* (Yu et al., 2020), *sjPlot* (Ludecke, 2023), and *tidyverse* packages in R (R Development Core Team, 2022). Data available via Skeena Knowledge Trust Data Repository (Price, 2023).

5 | RESULTS

Annual growth of juvenile sockeye salmon in freshwater rearing lakes of the Skeena watershed was highly variable over time, and among life stages and populations. Between 1908 and 2014, growth was highest during the first freshwater year (FW1; median values ranged from 0.26 mm [1965] to 0.49 mm [2011]) compared to the

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second year (FW2; median values ranged from 0.14 mm [1933] to 0.40 mm [1984]; Figure 2). For those fish that reared for 2 years in fresh water, first year growth was higher than second year growth in 75% (77 of 102) of population/year combinations; Figure SI-4). No population consistently exhibited the highest or lowest growth across life stages, except for Motase where average growth was only 68% and 52% of the highest average growth observed in Skeena populations during the first and second freshwater years, respectively (Table SI-2).

Time series of growth showed similarities in trends across freshwater life stages. Based on a Dynamic Factor Analysis, the model with the greatest support estimated a single trend in growth dynamics among the 13 sockeye populations for both first and second year of lake rearing (Figure 3; Table SI-3). The trend for both life stages was characterized by a period of below-average growth from the early 1900s to 1960s, above-average growth over the recent period, with peak growth observed during the late 1990s and a modest decline in growth since then. Population loadings on these trends were modest and broadly similar.

Across all populations, mean growth was higher during the recent (1960–2014) period compared to the historical (1908–1959) period for both freshwater life stages (Figure 4). The average percent change in growth between periods was highest for the FW1 life stage (+22%), compared to FW2 (+14%). Within the FW1 life stage, fish from the Bulkley population showed the highest increase (+35%) in mean growth between time periods; Sustut was the only population not to have changed between periods (Figure 5). Mean air temperature at Terrace, located within the watershed, ranged from 11°C to 16°C during the primary growing season for juvenile sockeye, with no linear trend apparent over time (Figure 6). During this period, there was strong evidence that fish grew more in warmer years (Figure 7), with growth estimated to increase by 8% for every 1°C rise in mean air temperature. Adult spawner abundance in the year prior to juvenile rearing—our proxy for in-lake intraspecific competition—showed the strongest negative effect on fish growth across populations, with an estimated 11% decrease in growth for every 1SD (e.g., 4500 [Slamgeesh] to 534,000 [Babine]) increase in fish abundance. The habitat indices of depth, productivity, glacier extent, and elevation showed at least a moderate positive effect on the freshwater growth of fish, whereas lake surface area showed a weak negative effect.

We found that the influence of regional climate on the growth response of juvenile sockeye was modulated by the characteristics of rearing lakes. Our global model estimated that the negative effect of intraspecific competition on fish growth was greatest at relatively low temperatures (Figure 8). Furthermore, habitat features modulated the influence of high temperatures on fish growth. For example, we found strong statistical support for an interaction between air temperature and lake depth. Specifically, our model estimated that fish in deep (>50 m) nursery lakes increased in growth with rising air temperatures, whereas the growth of fish in shallower lakes remained relatively unchanged with warmer temperatures (Figure 8). The interaction between temperature and glacier extent also had a strong effect on growth, where the growth of fish from lakes situated in watersheds with little (i.e., <5%) glacier cover increased with rising temperatures, whereas growth decreased in warmer years for fish in lakes within more glaciated watersheds. Interactions between temperature and other covariates had weaker and variable effects on growth.

6 | DISCUSSION

Our reconstruction of the freshwater growth of sockeye salmon over the past century revealed population-specific responses to intraspecific competition and climate, as filtered by nursery lake

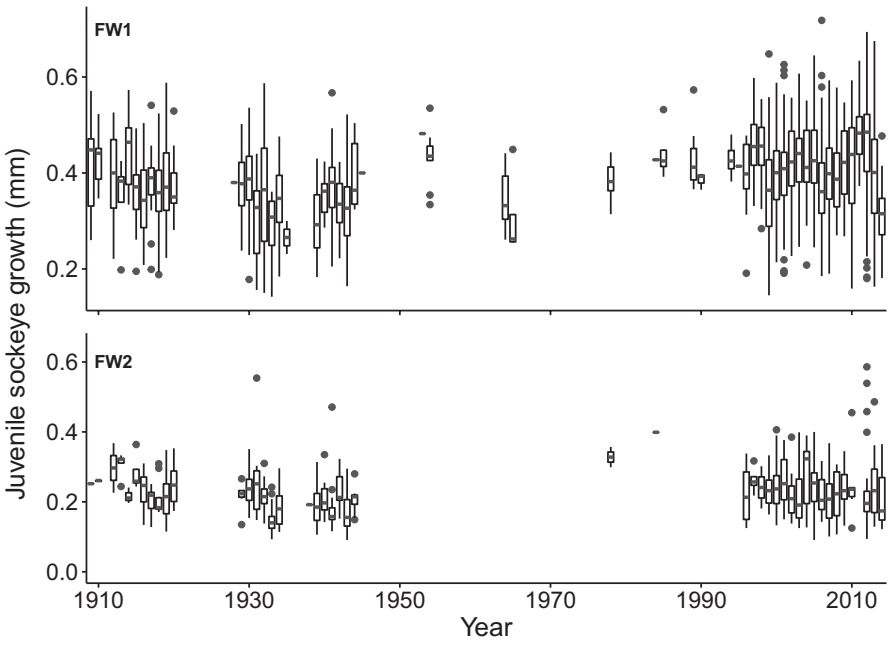

FIGURE 2 Scale growth (mm) during first (FW1, top) and second (FW2, bottom) year freshwater life stages of Skeena River sockeye salmon (*Oncorhynchus nerka*) from 1908 to 2014. The thick black line is the median, the box encapsulates the first and third quartiles, and points are observations that fall outside this quartile range.

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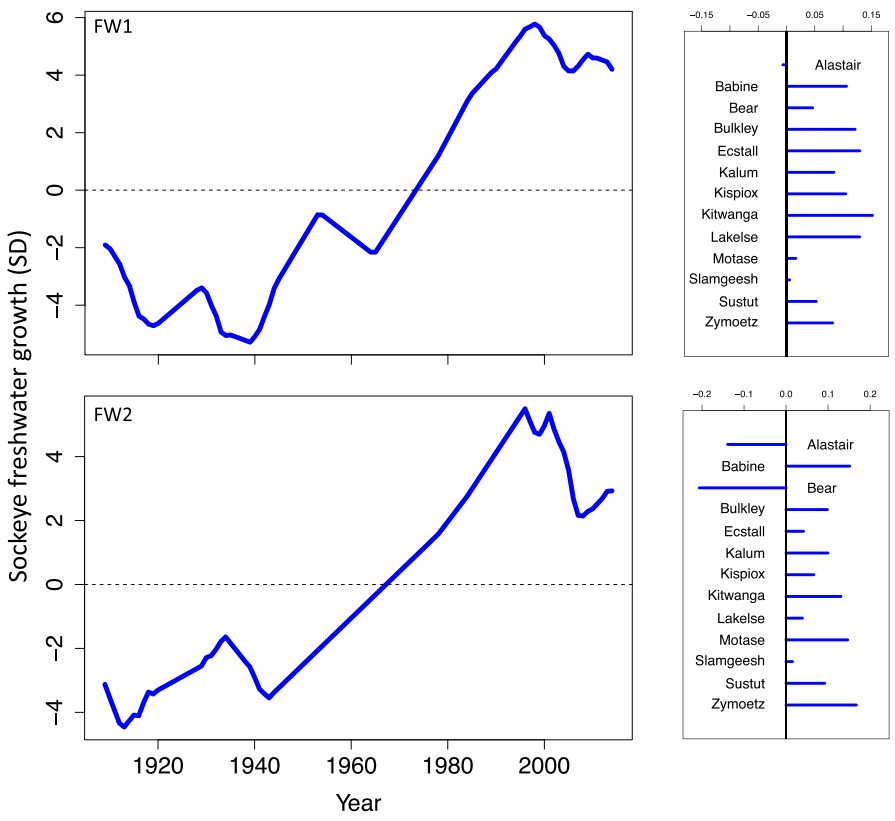

FIGURE 3 Trends and population loadings from the top dynamic factor analysis models to explain first (FW1) and second (FW2) year freshwater growth (in standard deviation (SD) units) of sockeye salmon (*Oncorhynchus nerka*) in the Skeena River watershed from 1908 to 2014.

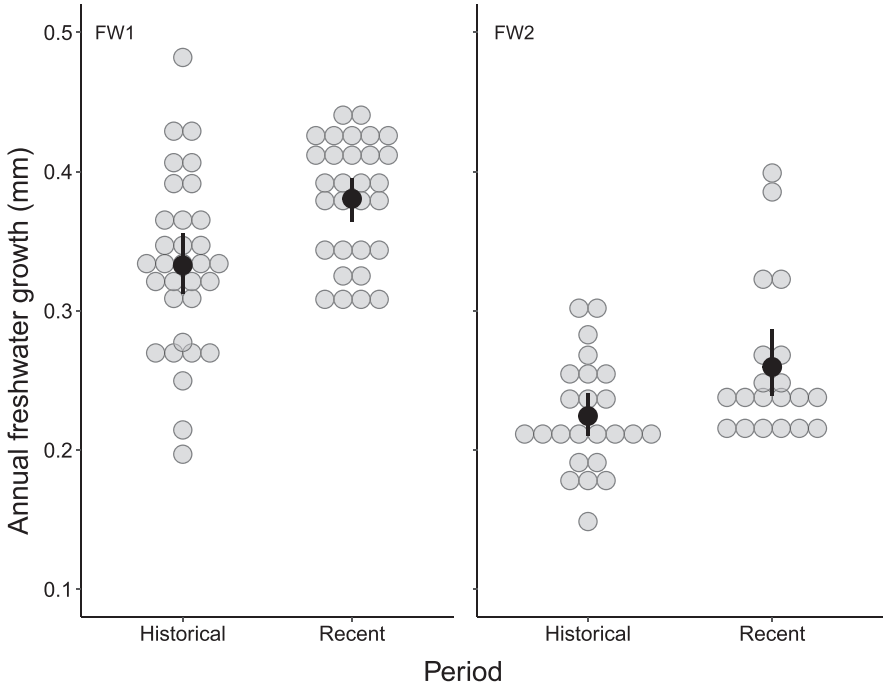

FIGURE 4 Arithmetic mean annual sockeye salmon (*Oncorhynchus nerka*) scale growth (grey dots) for first (FW1) and second (FW2) year freshwater life stages across all populations and between Historical (1908–1959) and Recent (1960–2015) periods. Black dots and vertical lines are the arithmetic mean and 95% confidence intervals, respectively, across all years within each time period and life stage.

habitat. Freshwater growth across populations was highest over recent decades compared to the first half of the 20th century, and several populations that exhibited lower than average historical growth showed the highest recent increase. While freshwater growth tended to be higher in years with relatively high regional air temperatures, long-term growth increases appear to be largely influenced by reduced competition. Habitat played an important role in modulating the effect of temperature, where the growth response of fish was unique to the population and their freshwater habitat. While summer air temperatures are predicted to increase at northern latitudes over the next century (Woolway et al., 2021), which could benefit the growth of fish in freshwater, sockeye rearing in deep-water lakes within largely deglaciated sub-basins likely will display the highest growth response in future years. Such diverse responses

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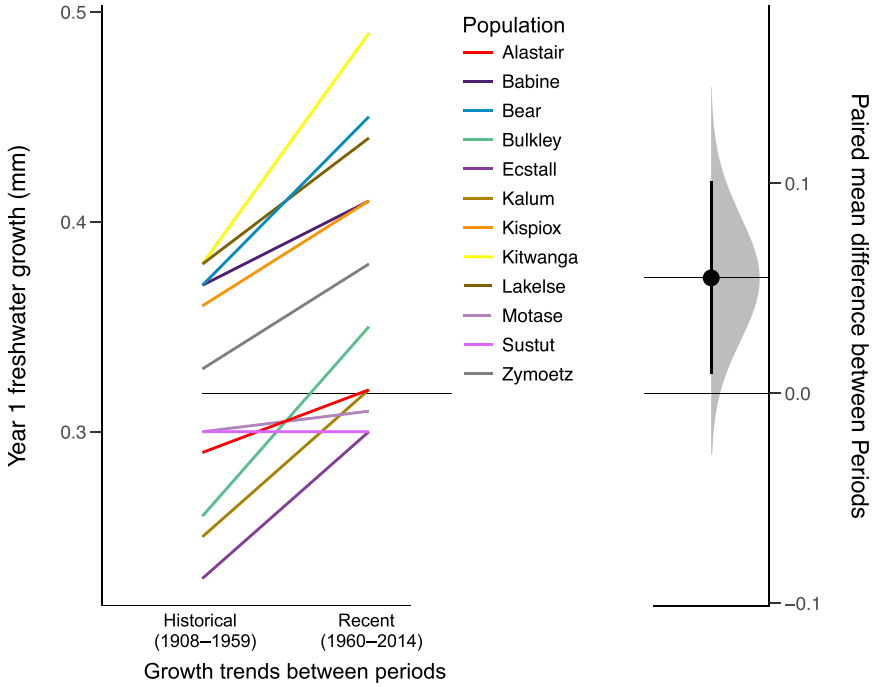

FIGURE 5 Arithmetic mean difference in first year freshwater growth (black dot—including 95% confidence interval and distribution (vertical line and grey shade on right panel, respectively)) for each sockeye salmon (*Oncorhynchus nerka*) population (colored lines) in the Skeena River watershed between historical (1908–1959) and recent (1960–2014) periods. Each colored line denotes the change in growth between time periods for a given population.

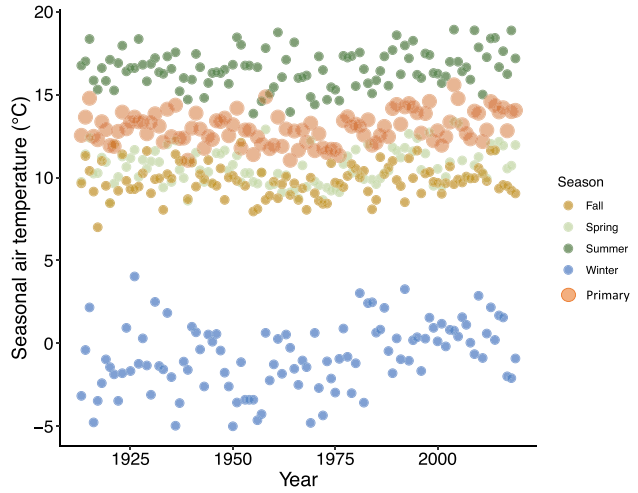

FIGURE 6 Arithmetic mean seasonal air temperature recorded at Terrace, British Columbia, for the period 1913–2019. Large orange dots denote annual air temperatures averaged across the primary growing season (April–August) for sockeye salmon (*Oncorhynchus nerka*) rearing in freshwater lakes.

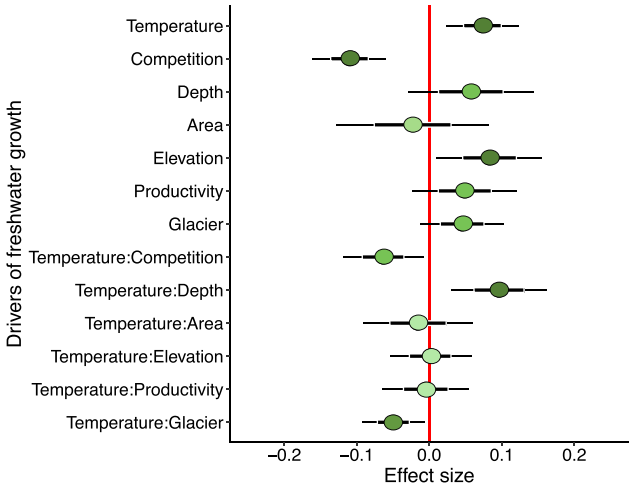

FIGURE 7 Posterior distribution of effect size (green dots), and 50% and 80% credible intervals (thin and thick horizontal lines, respectively) for hypothesized drivers of first year freshwater growth of sockeye salmon (*Oncorhynchus nerka*). Dot colors indicate relative strength of inference for each covariate; we considered the evidence to be *weak* (light green), *moderate* (mid-green), and *strong* (dark green), when posterior probabilities were <75%, from 75% to <90%, and ≥90% from zero, respectively.

of populations and their habitat to a changing climate form a dynamic portfolio that may endow salmon watersheds with resilience to future change (Brennan et al., 2019; Hilborn et al., 2003).

Annual growth of juvenile salmon in freshwater rearing lakes was variable over time and population, yet more often higher during the first freshwater year compared to the second year. While growth comparisons across a similar suite of Skeena sockeye populations during a subset of years (1945–1965) did not report a large difference in growth between life stages (Bilton & Smith, 1969), our results concur with those reported elsewhere (Ruggerone & Rogers, 2003). Life-stage differences in growth that we observed are unlikely to be related to climate because comparisons were drawn within growth years and populations. Nor are differences due to an ontogenetic shift in scale growth as fish age (see Clutter & Whitesel, 1956; Fukuwaka & Kaeriyama, 1997). Rather, differences might be due to life-stage specific competitive effects (Burgner, 1987; Ruggerone & Rogers, 2003), although larger cohorts in size-structured populations tend to show increased competitive ability across taxa (Werner & Gilliam, 1984). Or perhaps growth rates simply decrease with age within a given habitat, as occurs during the ocean phase

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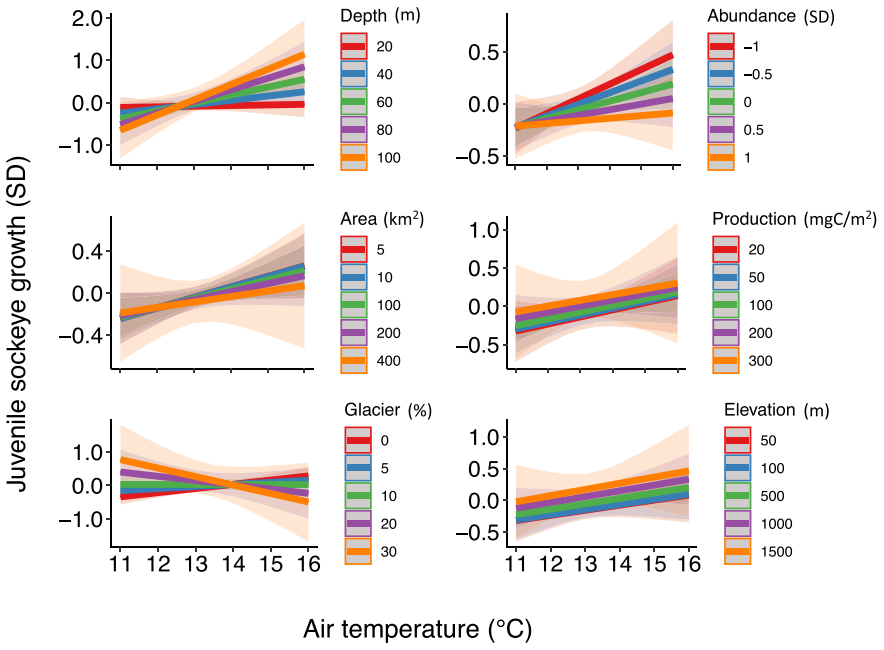

FIGURE 8 Predicted influence of lake habitat covariates on the relationship between air temperature and first year freshwater growth of sockeye salmon (*Oncorhynchus nerka*) in standard deviation units (SD). Predictions are across the observed temperature range, holding other model covariates constant. Colored lines and shades are the posterior predictive 50% and 80% credible intervals, respectively.

(Gilbert, 1914). Whatever the mechanism, we suggest that more attention be given to this 2-year freshwater life stage considering that it may influence later life performance (e.g., Jonsson & Jonsson, 2014).

Temporal synchrony in freshwater growth trends across sockeye populations suggest that widespread salmon-derived nutrient loss over the past century has not led to a systematic decrease in freshwater growth. At a broad scale, our results show that sockeye populations exhibited a shared (positive) growth response from 1908 to 2014 that was watershed wide. Despite a large reduction in the number of spawning adults across the Skeena watershed over the last century (Price et al., 2019; Price, Moore, et al., 2021; Figure SI-8), the widespread increase in freshwater growth of fish suggests that decreased intraspecific competition may have negated any potential effect of lost marine-derived nutrients. While loss in nutrients due to diminished returns of salmon to watersheds has long been a hypothesized driver of productivity decline for sockeye in rearing lakes (Finney et al., 2000; Gregory-Eaves et al., 2004; Martinson et al., 2009; Stockner & MacIsaac, 1996), here we find that other processes are linked to patterns of juvenile salmon growth.

Within the general trend of spatial coherence among time-series of freshwater growth, sockeye populations demonstrate a considerable degree of variability in growth response over time. Population-level increases in first-year freshwater growth between historical and recent periods ranged from 0% to 35%. Historical productivity of lake habitats was not positively correlated with the changes observed (Appendix S8). Instead, populations of fish from lake habitats with low historical productivity responded with some of the highest increases in growth between periods. Similarly, of two sockeye populations rearing in adjacent lakes within the same Alaskan watershed during 1950–1993, fish from the lower productivity (colder) Chignik Lake showed the higher rate of growth increase (Griffiths et al., 2014). Warming temperatures were hypothesized to have increased the scope for growth of fish in Chignik Lake, yet imparted physiological constraints on fish from the warmer Black Lake. Such contrasting responses may indicate that poor-production habitats of the past may become dominant producers in the future under rising temperatures (Hilborn et al., 2003; Rogers et al., 2013) and are evidence of a shifting habitat mosaic operating over broad spatial and temporal scales (Brennan et al., 2019). Importantly, the existing diversity of freshwater habitats in large salmon watersheds like the Skeena form a portfolio of options for fish to adapt to a changing climate (Moore & Schindler, 2022; Schindler et al., 2015).

The growth of lake-rearing sockeye showed a positive response to regional summer air temperature. Air temperatures are highly correlated with surface water temperatures (Read et al., 2014; Sharma et al., 2007), which strongly influence biological processes in freshwater lakes (Kraemer et al., 2021; Woolway et al., 2020). Warming temperatures in northern latitude regions are associated with longer ice-free periods (Smol et al., 2005) and enhanced growing conditions for fish (O'Reilly et al., 2015), which have led to higher growth of sockeye salmon rearing in lakes of Alaska (Edmundson & Mazumder, 2001; Rich et al., 2009; Schindler et al., 2005). We found strong evidence that summer air temperature in the Skeena watershed had a positive effect on juvenile sockeye growth. While Skeena summer air temperatures since 1995 are only modestly higher than the first half century (Figure SI-12), seasonal winter air temperatures have risen substantially (Figure SI-13), and we found strong support for a positive effect of warming winter temperature on fish growth (Appendix S5; Figure SI-10). Whether influenced by seasonal summer (e.g., increased physiological scope for growth) or winter (e.g., longer growing season) temperatures, fish in freshwater lakes of the Skeena generally are growing more now than they had in the past.

As expected, high intraspecific competition reduced the growth of fish in nursery lakes, and the long-term increases in growth across Skeena sockeye populations appear to be largely influenced by reduced competition. The negative influence of competition

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on growth is a well-documented phenomenon for juvenile salmon (Burgner, 1987; Foerster, 1944; Grossman & Simon, 2020). The number of adults returning to spawn in freshwater habitats has declined precipitously for most Skeena sockeye populations over the last half century (Price et al., 2019; Price, Moore, et al., 2021; Figure SI-8), which presumably has decreased the number of juveniles in rearing lakes, and lessened resource constraints for fish. In fact, most sockeye rearing lakes in the Skeena currently are considered below carrying capacity due to the low number of returning adults and subsequent juveniles (Cox-Rogers et al., 2010; Shortreed et al., 1998). Our work also shows that the negative effect of intraspecific competition is dampened during years with higher air temperatures; in other words, freshwater growth is highest in years with relatively low competitor numbers and high temperatures. While anticipated increases in temperature with climate change may weaken competitive effects, ongoing efforts to rebuild diminished sockeye populations in the Skeena (e.g., Cleveland et al., 2006; Price, Finnegan, et al., 2021) will likely enhance such effects; thus, complicating any future growth forecast.

We found that habitat features can modulate the effect of temperature on the growth of fish during the primary growing season. Fish from relatively deep lakes showed an increase in growth with rising temperatures, whereas the growth of fish from shallower lakes did not substantially change. Lakes with shallow depth are thought to be particularly sensitive to changes in air temperature (Winslow et al., 2015), which can have important consequences for fish when optimum temperatures for growth are exceeded (Brett, 1971; Griffiths et al., 2011, 2014). The amount of habitat available as a refuge from high summer water temperatures generally increases with lake depth, where fish can exploit the diverse thermal possibilities offered by a stratified and deep lake (Ficke et al., 2007; Guzzo et al., 2017). While our model predicts that rising summer temperatures will slow growth for fish in shallow lakes—perhaps due to optimum temperatures being reached or surpassed—such temperatures among deeper lakes may become more favorable. Indeed, warming temperatures associated with climate change are predicted to increase the thermal niche for cold-water fishes such as salmonids in deep lakes, yet decrease the thermal niche in shallow lakes (Magnuson et al., 1997).

Rising summer temperatures may reduce growth for fish in glacially-influenced lakes. Most glaciers in North America have been receding since the Little Ice Age Maxima (1600s–1800s; Menounos et al., 2009) and now are retreating more rapidly because of human-caused climate change (Marzeion et al., 2014). While glaciers can be an important source of cold water during summer high temperature events—buffering freshwater fishes from thermal extremes in rivers (Moore, 2006; Pitman & Moore, 2021)—an acceleration of glacier melt associated with higher air temperatures also may increase inorganic turbidity, decouple potential relationships between air temperatures and water temperatures, and lower the productivity of glacially influenced lakes (Barouillet et al., 2019; Koenings & Edmundson, 1991). Our results show that glaciers interacting with summer air temperatures over the last century had an overall negative effect on the growth of sockeye in rearing lakes, with model projections suggesting lower growth for fish in lakes associated with >5% glacier cover as summer temperatures rise. Extant glaciers in western Canada are forecast to shrink by ~70% over the next century (Clarke et al., 2015). Rising temperatures in the short term may decrease biological production of glacially influenced lakes, although once deglaciated, further temperature increases may then enhance lake productivity.

While we identify several factors that may mitigate or magnify the effects of an anticipated rise in temperature on fish growth, there are limitations to our results. For example, our index for competition (lagged number of spawning adults), while a good indicator of intraspecific competition (Burgner, 1991; Goodlad et al., 1974), does not account for annual variation in egg-to-juvenile survival. Nor does it include the full suite of species competing for resources in lakes. Other competitors, such as threespine stickleback (*Gasterosteus aculeatus*) can overlap with juvenile sockeye in their lake distribution and preference for prey (Burgner, 1987), which has affected the growth of fish in at least one Skeena nursery lake (Alastair; Shortreed et al., 2001). Similarly, our measures of lake characteristics are, at best, broad indices for otherwise dynamic thermal habitats. These lake features (and their interaction with temperature) do not exist in isolation, as our models imply; rather, the thermal habitat of a lake is the product of its unique geomorphology influenced by temperature. Such simplification of dynamic ecosystems can nevertheless highlight influential factors—like lake depth—that interact with regional climate to affect fish growth, and thus can broadly inform climate vulnerability assessments for populations at risk. Finally, there is inherent uncertainty in our results given the unbalanced study design that was reliant on opportunistic sampling over the last century. While mixed-effects models implicitly take variable sample sizes within year and populations into account, there are still limits to inference, such as during years with few growth measurements/populations. However, when we re-fit our model after having removed data-limited populations/years, diverse growth responses to temperature and its interaction with habitat features remain evident (Appendices S6 and S7; Figures SI-14–SI-16). Future work would benefit from increased measurements of growth for data-deficient populations.

Future responses of salmon to climate change will be diverse and complicated by lake-specific geomorphology, which can differentially filter regional climate to shape habitat conditions that are unique to each population. Air temperatures are predicted to increase at northern latitudes across seasons over the next century (Woolway et al., 2021), which inevitably will create opportunities and constraints for salmon during freshwater rearing (Iacarella & Weller, 2023). Growth likely will increase for fishes in lakes where thermal environments currently are cooler than their optimum, yet decrease for those that are at or above their optimum (Magnuson et al., 1997); an acceleration of glacier melt under warming temperatures may further suppress fish growth, at least for some populations over the near term. While rising summer

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temperatures may attenuate the negative effect of competition on growth across Skeena populations, such competitive effects may amplify if ongoing rebuilding efforts (e.g., Cleveland et al., 2006; Price, Finnegan, et al., 2021) successfully return more adults to spawning grounds. Finally, erosion of habitat heterogeneity will diminish response diversity, and result in an aggregate system more tightly linked—and less resilient—to shifting climate processes (Moore & Schindler, 2022; Munsch et al., 2022). Thus, maintaining the integrity of an array of freshwater habitats is a proactive way to foster a diverse climate-response portfolio for these important fishes, which in turn can ensure that salmon watersheds are resilient to future global change.

AUTHOR CONTRIBUTIONS

Michael H. H. Price: Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – original draft; writing – review and editing. **Jonathan W. Moore:** Conceptualization; methodology; writing – review and editing. **Skip McKinnell:** Validation; writing – review and editing. **Brendan M. Connors:** Conceptualization; formal analysis; methodology; writing – review and editing. **John D. Reynolds:** Supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available via Skeena Knowledge Trust Data Repository: https://data.skeenasalmon.info/dataset/response-of-salmon-to-a-century-of-climate-and-competition (Price, 2023).

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