

## RESEARCH ARTICLE

# Effects of climate on salmonid productivity: A global meta-analysis across freshwater ecosystems

Brian K. Gallagher  | Sarah Gergeoura | Dylan J. Fraser

Department of Biology, Concordia University, Montreal, Quebec, Canada

**Correspondence**

Brian K. Gallagher, Department of Biology, Concordia University, 7141 Sherbrooke Street West, Montreal, QC H4B 1R6, Canada.

Email: [brian.kenneth.gallagher@gmail.com](mailto:brian.kenneth.gallagher@gmail.com)

**Present address**

Sarah Gergeoura, Environment and Climate Change Canada, Gatineau, Quebec, Canada

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**Abstract**

Salmonids are of immense socio-economic importance in much of the world, but are threatened by climate change. This has generated a substantial literature documenting the effects of climate variation on salmonid productivity in freshwater ecosystems, but there has been no global quantitative synthesis across studies. We conducted a systematic review and meta-analysis to gain quantitative insight into key factors shaping the effects of climate on salmonid productivity, ultimately collecting 1321 correlations from 156 studies, representing 23 species across 24 countries. Fisher's *Z* was used as the standardized effect size, and a series of weighted mixed-effects models were compared to identify covariates that best explained variation in effects. Patterns in climate effects were complex and were driven by spatial (latitude, elevation), temporal (time-period, age-class), and biological (range, habitat type, anadromy) variation within and among study populations. These trends were often consistent with predictions based on salmonid thermal tolerances. Namely, warming and decreased precipitation tended to reduce productivity when high temperatures challenged upper thermal limits, while opposite patterns were common when cold temperatures limited productivity. Overall, variable climate impacts on salmonids suggest that future declines in some locations may be counterbalanced by gains in others. In particular, we suggest that future warming should (1) increase salmonid productivity at high latitudes and elevations (especially  $>60^\circ$  and  $>1500$  m), (2) reduce productivity in populations experiencing hotter and dryer growing season conditions, (3) favor non-native over native salmonids, and (4) impact lentic populations less negatively than lotic ones. These patterns should help conservation and management organizations identify populations most vulnerable to climate change, which can then be prioritized for protective measures. Our framework enables broad inferences about future productivity that can inform decision-making under climate change for salmonids and other taxa, but more widespread, standardized, and hypothesis-driven research is needed to expand current knowledge.

**KEYWORDS**

abundance, data synthesis, freshwater fish, growth, population dynamics, systematic review

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## 1 | INTRODUCTION

Climate change is strongly impacting biodiversity throughout the world (Parmesan & Yohe, 2003; Woodward et al., 2010). These effects are likely to intensify in the future (Urban, 2015), but estimates of effect size can vary considerably depending on the design, location, and focal organism of different studies (Haddaway, 2015; Koricheva et al., 2013). Understanding how and why climate change affects biodiversity in natural systems is critically important for improving predictions of biodiversity loss (Mouquet et al., 2015; Urban et al., 2016), as well as for developing adaptive conservation and management strategies (Reside et al., 2018). Although the ecological consequences of climate change can be affected by evolutionary history, spatial scale, and other factors (Nadeau et al., 2017a, 2017b), data synthesis approaches offer a way to disentangle these confounding influences to gain a more integrated understanding across multiple studies. Indeed, data synthesis plays a prominent role in explaining patterns and changes in biodiversity more broadly, and while conclusions can still be disputed (e.g., Dornelas et al., 2014; Vellend et al., 2013, but see Gonzalez et al., 2016), this process can help identify key knowledge gaps that motivate further study.

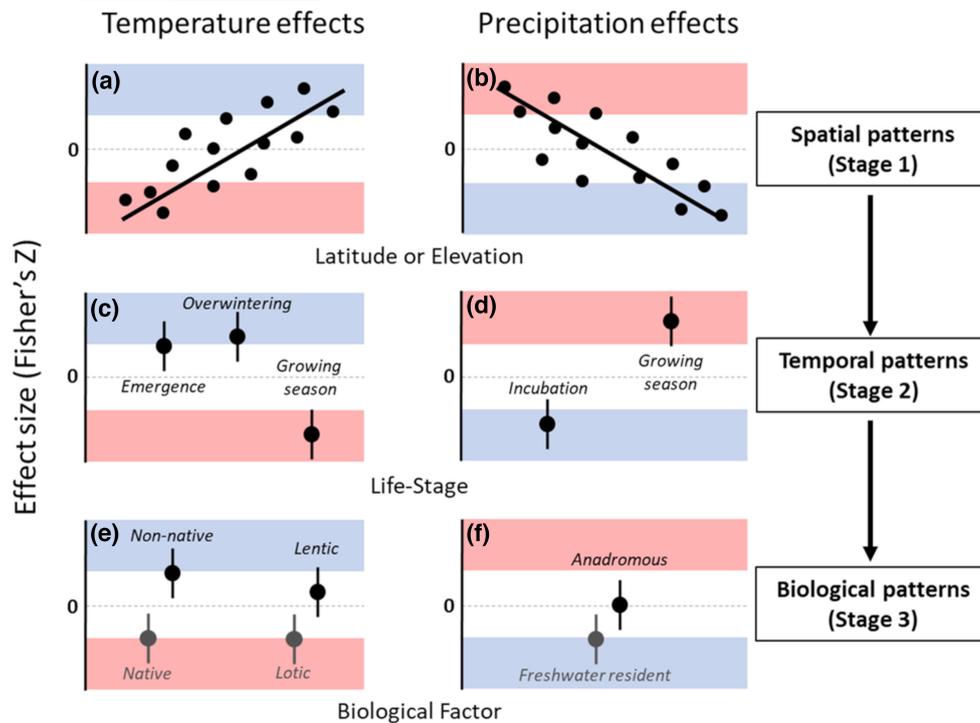
A growing body of research has focused on synthesizing effects of climate change on fishes (Comte et al., 2021; Comte & Olden, 2017; Kovach et al., 2016; Krabbenhoft et al., 2020; Myers et al., 2017), which are culturally and economically important to communities around the world. Salmonids in particular support valuable commercial, recreational, and subsistence fisheries in many regions (ASF, 2011; PSC, 2017) and are thought to be sensitive to climate change, driving fears of future declines in productivity (defined herein as the rate of population biomass production, which we assume to increase with higher abundance, individual growth, or both). However, there is considerable uncertainty in how different species and populations will respond to future warming, while the factors shaping vulnerability to climate change are thought to be complex and difficult to disentangle (Irvine & Fukuwaka, 2011; Kovach et al., 2019). As a result, previous syntheses have not explicitly quantified spatial, temporal, and biological variation in salmonid responses to climate across many empirical studies. Our research attempts to fill this knowledge gap by synthesizing the effects of climate variables (temperature and precipitation) on a wide range of salmonid populations, providing timely insight into the broad patterns influencing current and future productivity.

Spatial variation likely plays a dominant role in structuring salmonid responses to climate. Salmonids occupy an enormous native and non-native range across the globe (Crawford & Muir, 2008), and often exhibit strong gradients in productivity based on latitude and elevation. Previous research suggests that populations at low latitudes (Ayllón et al., 2019; Carlson & Satterthwaite, 2011) are expected to respond to climate change differently than those at high latitudes (Campana et al., 2020; Pitman et al., 2020), with similar contrast expected between low-altitude and high-altitude populations (Isaak et al., 2016; Kanno et al., 2015). Specifically, declines in salmonid productivity are expected in areas where temperatures regularly exceed upper thermal

limits, and should decline further if low precipitation reduces the volume and thermal buffering capacity of water (Kovach et al., 2016). Therefore, in the warmest areas at low latitudes and elevations, higher temperature is expected to reduce salmonid productivity and increased precipitation should enhance productivity, whereas opposite patterns are expected at high latitudes and elevations (Figure 1a,b). Despite the importance of spatial variation in moderating responses to climate, no quantitative research to date has tested these predicted effects at a global scale across salmonid species.

Responses to climate in salmonids also likely depend on the time-period under consideration, as most salmonids occupy temperate regions where temperature and precipitation vary seasonally and may disproportionately affect some life-stages more than others (Bassar et al., 2016; Jonsson & Jonsson, 2009; Nislow & Armstrong, 2012). Moreover, because salmonid productivity can also be limited by cold temperatures, warming can be beneficial for most of the year but harmful during summer months (Armstrong et al., 2021). Despite a large volume of research on these topics, the vulnerability of specific life-stages to increasing temperatures is still debated (Dahlke et al., 2020; but see Pottier et al., 2022), and the severity of the threat posed by warming temperatures to species persistence remains unresolved (Muñoz et al., 2015; but see Mantua et al., 2015). Similarly, although some research shows that climate impacts can vary based on the size- or age-class being affected (Letcher et al., 2002, 2015), these can differ among systems within studies (e.g., Xu et al., 2010a). Nonetheless, increased temperatures and reduced precipitation should be associated with declines in productivity during the warmest time-periods, with opposite effects expected during the coldest periods, especially for temperature (Figure 1c,d). More complex influences of temporal variation should also be considered, as negative impacts of flooding could be observed during vulnerable life-stages such as egg incubation, and timing of key events across the life cycle can vary considerably within and among species (Kovach et al., 2016, 2019). Data synthesis can test these predictions, thereby informing debates and uncertainties about the factors shaping salmonid vulnerability to climate change.

Finally, biological differences among populations have the potential to modify the effects of climate on salmonid productivity (Figure 1e,f), but these too await quantification across many studies. For example, effects may differ based on whether salmonids occupy lotic (streams and rivers) or lentic environments (lakes and ponds) due to the prevalence of stratification in lakes, which is expected to increase the availability of coldwater habitat (Blair et al., 2013) and reduce sensitivity to warming in lentic populations. Additionally, some research has suggested that non-native salmonids may respond more favorably to warming than their native counterparts by exhibiting higher thermal tolerance or outcompeting them for suitable habitats (Al-Chokhachy et al., 2016; Bell et al., 2021), leading us to expect more severe climate-induced declines in productivity within native species. In addition, because our work focuses on salmonids in freshwater environments, migration behaviors may play a role, as anadromous populations could respond to climate variation differently than freshwater residents due to their shorter periods of residence and exposure to ocean conditions (Mueter et al., 2002).



**FIGURE 1** Summary of predicted patterns in effects of temperature (a, c, e) and precipitation (b, d, f) on salmonid productivity. Predictions are structured according to spatial (a, b), temporal (c, d), and biological (e, f) patterns that were of most interest, and stages 1–3 (boxes and arrows) correspond to the order variables were inputted into models during the stepwise model selection process (see Section 2). All panels have a shaded background to highlight expected climate effects when temperatures exceed upper thermal limits (red shading), or when low temperatures limit productivity (blue shading; see Introduction). Note that predicted effects on productivity were expected to be largely similar for measures of abundance and growth.

Specifically, temperature and precipitation are expected to impact productivity in freshwater resident populations more strongly than anadromous ones. Finally, observed climate impacts could be influenced by methodological differences, as studies can vary widely in sampling design, the exact salmonid or climate data measured, and how data were transformed and analyzed. Taken together with the spatial and temporal variation discussed previously, it is clear that broad patterns should be detectable in salmonid responses to temperature and precipitation. A simplified overview of a priori predictions for the influence of spatial (latitude, elevation), temporal (age-class, time-period), and biological (range portion, habitat type, anadromy) factors is shown in Figure 1. Rigorously testing these predicted patterns will help clarify key drivers underlying variation in climate impacts, thereby addressing an important knowledge gap in salmonid biology (Kovach et al., 2016, 2019).

We conducted a global systematic literature search and quantitative meta-analysis to illuminate key patterns in the effects of climate variables on salmonid productivity. This research is timely because it can leverage a vast body of past research to inform the future of salmonids in a changing world—a topic that remains rife with uncertainty and disagreement (Dahlke et al., 2020; Kovach et al., 2016; Mantua et al., 2015; Muñoz et al., 2015; Pottier et al., 2022). Our objectives were to (1) conduct a systematic review to build a database of standardized effect sizes describing the influence of climate variation on salmonid productivity, (2) identify a parsimonious

set of covariates that best explain variation in effect sizes and test predicted spatial, temporal, and biological patterns, and (3) assess publication bias and potential taxonomic, methodological, and geographic influences that may limit current knowledge. This is the first study to carry out these objectives at a global scale for salmonids, providing the most in-depth analysis to date of climate impacts on these iconic coldwater taxa. Our structured and hypothesis-driven approach allowed us to identify broad patterns in salmonid-climate relationships, which can then support inferences about future productivity. Such patterns can inform conservation and management decisions by helping agencies identify populations that are likely to be most vulnerable to climate change. More broadly, we believe this approach can be adapted to a host of other taxa to predict and test key drivers of variation in responses to climate change.

## 2 | METHODS

### 2.1 | Literature search and screening criteria

Throughout this study, we used PRISMA-EcoEvo criteria to guide decision making and reporting (O'Dea et al., 2021). We sought to identify studies reporting correlations between climate variables (temperature or precipitation) and the individual growth or relative abundance (growth or abundance hereafter) of wild salmonid

populations in freshwater environments. To increase consistency and maximize focus on natural contexts, we targeted observational studies of populations that did not receive hatchery supplementation during the study period. Correlations were preferred because they are the simplest measure of standardized relationships between continuous variables, and can easily be used to calculate effect size and its sampling variance (see below). Although this decision may have reduced data availability, it is paramount to standardize effect sizes for rigorous quantitative analysis (Koricheva et al., 2013). Measures of relative abundance (e.g., density, population size, biomass, survival) and individual growth (e.g., length-at-age, somatic growth rate) were interpreted as surrogates for productivity, but past research has shown that rates of salmonid biomass production are often more sensitive to abundance than growth (Lobón-Cerviá, 2009). Similarly, all surrogates of temperature and precipitation were treated equally, although a previous review argued that direct measures of aquatic habitat conditions (e.g., water temperature, streamflow) are preferable to indirect proxies (e.g., air temperature, rainfall; see Kovach et al., 2016). It would have been ideal to quantify differences between the many proxies used to describe climate and salmonid productivity, but we felt this was impractical because relationships between these proxies and the processes of interest varied and were often unknown or unreported.

A comprehensive literature search was conducted during the first week of July 2020 through the Web of Science advanced search portal, including all available collections since 1900. Search terms were adapted from Kovach et al. (2016) but expanded to include more salmonid taxa, yielding 2989 studies. The specific search string was:

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TS = (trout* OR char[r] OR salmon* OR whitefish* OR grayling*) AND TS
    = (streamflow OR stream temperature OR lake temperature) AND TS
    = (abundance OR survival OR growth).
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where TS denotes a set of search topics, AND/OR are Boolean operators, and asterisks enable truncated word searches (e.g., salmon\* identifies salmon, salmonid, salmoninae, etc.). Web of Science was the only literature search method used and may not be exhaustive, but we chose to avoid other methods (e.g., alternative search engines, compiling studies from past reviews) to maximize consistency and save time.

Titles and abstracts were screened for relevance based on whether relationships between salmonid data and climate variables were mentioned, or if it seemed plausible that relevant raw data could be reported. Title and abstract screening was first conducted by S.G. and followed up in full by B.K.G. for verification. All studies deemed relevant by one or both authors were collated, yielding 700 studies for subsequent screening. Google Scholar was used to retrieve full-texts, which were available for 603 relevant studies. Each study was subsequently scanned to determine whether the study design was suitable (review papers and modeling studies without empirical data were excluded), and whether correlations (with sample sizes) or raw data were reported. Overall, 182 studies satisfied these criteria and were subjected to data extraction. If not directly

reported by authors, correlations and sample sizes were calculated in a spreadsheet from raw data extracted manually from tables, or from figures with the *Digitize* package in R (Poisot, 2011). Non-linear relationships were ignored unless they were shown in figures, in which case the data were extracted and used to calculate linear correlation coefficients. This practice was uncommon (10 observations from six studies), and did not strongly impact effects (correlation between linear and non-linear  $R^2$  values = .94). In total, this process yielded 1735 observations. We were satisfied with this outcome and, therefore, decided not to allocate more time toward increasing the number of observations or studies (e.g., contacting authors for missing data).

## 2.2 | Database description

In addition to correlations and sample sizes, a wide range of other data were collected in the initial database, including relevant spatial, temporal, biological, and methodological covariates. Study coordinates and elevation data directly reported by authors were preferred, but georeferencing was conducted in Google Maps and elevations were inferred using the *Elevatr* R package (Hollister et al., 2021) when necessary. A detailed account of the methods used and data recorded in this process can be found in the (see Appendix S1, section S.1), whereas details about covariates, their usage, and categorical levels are in Table 1. Once the initial database was completed, it was subjected to critical appraisal to ensure the validity and comparability of observations (Haddaway, 2015), while filtering out duplicates and observations with insufficient sample size ( $n < 5$ ; Appendix S1, section S.2). After six critical appraisal and filtering steps, the final database contained 1321 correlations from 156 studies, featuring 23 species within six genera, and spanning 24 countries across five continents. Overall, our database (see Gallagher et al., 2022 on Dryad) had considerably greater sample size, taxonomic breadth, and geographic contrast than a previous systematic review by Kovach et al. (2016). A summary of the study filtering process is provided in Figure S1 (after Haddaway, 2020), the final database is publicly available, and we have cited all of the included studies (see Data Sources). Note that repeated measures within studies were often present (range: 1–102 correlations per study), and this non-independence was accounted for during data analysis.

## 2.3 | Statistical analysis

The filtered database was imported into R, and analyzed using the *Metafor* package (Viechtbauer, 2010). The *escalc()* function was used to calculate Fisher's Z based on the formula:

$$Z = \frac{1}{2} \ln \left( \frac{1+r}{1-r} \right) \quad (1)$$

where  $\ln$  is the natural logarithm and  $r$  is the correlation coefficient. This transformation alleviates problems with correlations becoming

**TABLE 1** List of all potential covariates, plus their abbreviations (abbrev.), usage during quantitative meta-analysis (model selection stages 1–3, or post-selection tests; see Section 2), and number of levels (categorical variables only). Note that variables used in stages 1, 2, and 3 of model selection correspond to spatial, temporal, and biological or methodological covariates, respectively, and were tested in a stepwise forward selection framework. Details for data collection protocols can be found in the (Appendix S1, section S.1), while the full database, metadata, and R code are freely accessible online (see Gallagher et al., 2022 on dryad)

Covariate	Abbrev.	Usage	N levels	Description or levels
Latitude	L	Stage 1	Cont.	Absolute value of latitude (° from the equator)
Elevation	E	Stage 1	Cont.	Elevation (meters above sea level)
Age-class	AC	Stage 2	4	Age-0, age-1, age-2+, or multiple
Season	SE	Stage 2	5	Fall, spring, summer, winter, or multiple
Life-stage	LS	Stage 2	7	Incubation, emergence, growing season, overwintering, migration, reproduction, or multiple
Life-stage*Age	LSA	Stage 2	10	Same as Life-stage, but growing season is broken up by age into growing season_0, growing season_1, growing season_2+, and growing season_multiple levels
Study design	S	Stage 3	2	Spatial or temporal
Anadromy	A	Stage 3	2	Anadromous or resident
Range portion	N	Stage 3	2	Native or non-native
Habitat type	H	Stage 3	2	Lotic or lentic
Publication year	YR	Publication bias	Cont.	Year when study was published
Response type	RT	Robustness tests	7	Abundance, population growth, stock-recruitment, survival (abundance only), length, weight, or growth rate (growth only)
Predictor type	PT	Robustness tests	6	Average, maximum, minimum, percentile, PCA (temperature or precipitation), or degree-day (temperature only)
Data transformation	DT	Robustness tests	2	Yes or no
Extraction method	DM	Robustness tests	2	Direct reporting or manual extraction

skewed as they approach  $\pm 1$ , while retaining the magnitude and direction of effects. The asymptotic variance ( $v_z$ ) for each Fisher's Z estimate was calculated by:

$$v_z = \frac{1}{n-3} \quad (2)$$

where  $n$  is the sample size. In all subsequent analyses, Fisher's Z was used as the standardized effect size, while the inverse of the variance was used to weight observations (Koricheva et al., 2013).

The database was then divided into four data sets based on the type of response and predictor variables used within each correlation: Abundance–Precipitation ( $n = 362$ ), Abundance–Temperature ( $n = 610$ ), Growth–Precipitation ( $n = 66$ ), and Growth–Temperature ( $n = 283$ ). Abundance and growth were both assumed to be positively related to population productivity. Each data set was analyzed separately using the *rma.mv()* function, which allows for linear mixed-effects models to be built with a nested random effect structure (Viechtbauer, 2010). Across all models in this analysis, response variables from each correlation (which were assigned unique within-study codes) were nested within study to create a consistent random effect structure. When appropriate, variances were partitioned among studies, within studies, and due to sampling variance, which were used to calculate indices of heterogeneity and test their statistical significance (Nakagawa et al., 2017; Senior et al., 2016). Variance components also influenced weights for each effect size

by downweighting repeated measures within and among studies according to the variance observed at each level, thereby alleviating pseudoreplication. An explicit demonstration of this random effect structure and its handling of repeated measures can be obtained through R code that we have made publicly available (see online Data Availability Statement).

## 2.4 | Model selection

Due to the large number of potential covariates in our data, we sought to test competing models in a stepwise forward selection framework that reflected the structure of our data and was guided by mechanistic hypotheses (see Figure 1). Model selection was conducted separately for each data set, but we ensured the same framework was applied consistently to all data sets. All covariates were incorporated as fixed effects, with models fit using maximum likelihood and compared based on AICc values. The model with the lowest AICc was selected in each stage, although the most parsimonious model was preferred in cases where AICc values differed by less than two (Johnson & Omland, 2004). Note that taxonomic variation was not explicitly considered during model selection due to unbalanced sample sizes and concerns that estimating species-specific coefficients would yield over-parameterized models, so this was addressed in subsequent analyses (Section 2.6).

The first stage of model selection sought to identify the best set of spatial covariates (latitude, elevation, and their interaction; Table 1) because these effects are of considerable biological interest, and were expected to be relatively strong and consistent across data sets. In all analyses, latitude was expressed as an absolute value for simplicity, but 98% of observations were from the northern hemisphere (Figure S2). There was limited spatial contrast in the Growth–Precipitation data set due to low sample size, so the interaction between latitude and elevation was not explored.

The selected model from the first stage was then used as the base model for the second stage, where temporal covariates based on age-class (four levels), season (five levels), life-stage (seven levels), or life-stage\*age (10 levels; see Table 1; Appendix S1, section S.1 for details) were added individually and compared. Note that most levels of life-stage\*age were identical to life-stage, but estimates from the growing season were broken up by age-class (Table 1). These factors were of interest because they could suggest differential vulnerabilities to climate change based on size, age, or specific events in the life cycle. However, the relative importance of each temporal covariate may vary across data sets, especially since model selection penalized more complex covariates. There were few observations during the growing season in the Growth–Precipitation data set ( $n = 35$ ) such that age differences were unlikely to be informative, so we chose to omit life-stage\*age from model selection. For all other temporal covariates and data sets, there was sufficient contrast ( $n > 10$  within two or more levels) to proceed with model selection, but we noted all cases where sample sizes did not meet this threshold for specific levels (see Section 3).

Finally, the selected model from the second stage moved forward to the third stage, wherein four binary covariates (two levels) denoting biological (range portion, habitat type, anadromy) and methodological differences (study design; see Table 1; Appendix S1, section S.1) were added in all possible combinations. These factors were expected to have less consistent effects across data sets, but could nonetheless help explain variation. Covariates were excluded from model selection if they lacked contrast within a given data set ( $n < 10$  for one of two levels), which ruled out habitat type in Abundance–Precipitation and Growth–Precipitation, and range portion in the Growth–Precipitation and Growth–Temperature data sets. The selected model from the third stage was considered the best-fit model overall for each data set.

## 2.5 | Best-fit models

After identifying best-fit models, we summarized model performance using  $\Delta\text{AICc}$  scores, likelihood ratio tests, and pseudo- $R^2$  values (based on proportional reduction in variance components) relative to alternative models with no covariates. Mean effect sizes and their 95% confidence intervals were estimated from each best-fit model, while variance components were used to run omnibus tests for residual heterogeneity (Viechtbauer, 2010) and calculate total heterogeneity within and among studies (Nakagawa et al., 2017). Finally, estimated coefficients for all covariates (or contrasts for

categorical levels) were reported and used to make summary plots, while an omnibus test across all covariates was performed for each best-fit model (Viechtbauer, 2010).

## 2.6 | Publication bias and model robustness

Homogeneity of variance was evaluated by inspecting residual plots from all best-fit models. Collinearity was checked in each best-fit model using variance inflation factors (VIFs) calculated across all levels of each covariate, while within-level VIF values were also reported for temporal covariates that had more than two levels. All best-fit models were assessed for publication bias by creating funnel plots in *Metafor*. Currently, Egger regression cannot be implemented in models with nested random effects, so instead we added the standard error as an additional covariate in each best-fit model to test for the effect of precision on residuals (Viechtbauer, 2010). This test (Egger test hereafter) is analogous to an Egger regression, such that a significant effect of the standard error indicates publication bias. If bias was detected, we identified individual studies that contributed to the pattern, removed them from the data set, and re-tested for publication bias in the reduced data. Similarly, temporal publication bias was explored by relating residuals from each best-fit model to publication year (Gurevitch et al., 2018).

Possible taxonomic biases were examined by subsetting the Abundance–Precipitation, Abundance–Temperature, and Growth–Temperature data sets to only include the five species with the largest sample size (Growth–Precipitation was excluded due to low sample size), then re-running the best-fit model with and without species as an additional covariate. The decision to select five species was subjective, but we sought to estimate multiple species effects while retaining sufficient sample sizes within species. Species contrast terms were reported and analyzed for significance in each data set, while 95% confidence intervals for all other coefficients were compared. Support for species-specific intercepts and slopes was assessed using  $\Delta\text{AICc}$  scores relative to the original best-fit model. Additionally, the effects of four methodological factors (response type, predictor type, data transformation, data extraction method; Table 1) were evaluated by adding them individually to all best-fit models and testing their significance. Finally, influential studies were identified in each data set using Cook's distance, and their impact was assessed by comparing 95% confidence intervals of all coefficients from models fitted to data with and without these studies.

## 3 | RESULTS

### 3.1 | Model selection

Table 2 describes all models run and their  $\Delta\text{AICc}$  scores within each stage of model selection, suggesting that each data set had a different set of covariates that best explained variation. Abundance–Precipitation effect sizes differed according to season and study

design, while Abundance–Temperature effects were influenced by latitude, elevation, age-class, study design, and range portion (Tables 2 and 3). Growth–Precipitation effect sizes varied according to life-stage and anadromy, while Growth–Temperature effects had the most complex model that included latitude, elevation, life-stage\*age, and habitat type as covariates (Tables 2 and 3). Across all data sets, best-fit models substantially outperformed models with no covariates ( $\Delta\text{AICc} > 15$ ; likelihood ratio test  $p < .001$ ), but the proportional reduction in variance components suggested that relatively little variation was explained (pseudo- $R^2 = 5\%$ – $41\%$ ; Table 3). Mean effect sizes based on predicted values from the best-fit models were positive and significant for the Growth–Precipitation and Growth–Temperature data sets, while 95% confidence intervals contained zero in the Abundance–Precipitation and Abundance–Temperature data sets (Table 3). Residual heterogeneity within and among studies was significant (Wald-type test;  $p < .006$ ) and accounted for a large percentage of the total variance (40%–74%; Table 3) observed in all best-fit models.

### 3.2 | Best-fit models

In all data sets, omnibus tests showed that covariates had significant explanatory power (Wald-type test  $p < .002$ ; Table S1). Coefficients from the best Abundance–Precipitation model confirmed a significant positive effect of fall precipitation on abundance highlighted in a previous review (Kovach et al., 2016), but this was only evident in temporal studies, which were associated with significantly more positive (or less negative) effect sizes than spatial studies ( $p < .05$ ; Table S1; Figure 2). In contrast, a significant negative effect of spring precipitation on abundance was apparent ( $p < .01$ ; Table S1), but only for spatial studies (Figure 2).

The best Abundance–Temperature model showed that latitude and elevation had a significant positive influence on effect sizes ( $p < .01$ ; Table S1), such that effects of temperature on abundance were predicted to be negative at low latitudes and elevations, but positive at higher values (latitude  $> 60^\circ$ ; elevation  $> 1500\text{m}$ ; Figure 3a,b). Temperature effects did not vary significantly by age-class ( $p > .05$ ; Table S1) but were significantly more positive in temporal study designs ( $p < .05$ ) and non-native ranges ( $p < .01$ ; Figure 3c).

Within the best Growth–Precipitation model, precipitation had significant positive effects during the growing season ( $p < .001$ ) and negative effects during incubation ( $p < .01$ ; Table S1). However, the latter was based on a very low sample size ( $n = 2$ ; Figure 4), and this model should be interpreted with caution due to the low number of observations in the data set ( $n = 66$  total). Effect sizes varied for precipitation during other life-stages, but precipitation effects were significantly more negative in anadromous populations relative to those observed in freshwater residents ( $p < .05$ ; Figure 4).

Finally, estimates from the best Growth–Temperature model suggested that temperature effects became more positive with increasing latitude and elevation (Figure 5a,b). This was only significant for elevation ( $p < .05$ ; Table S1), while temperature effects

were also significantly more negative in lotic than lentic habitats ( $p < .05$ ; Figure 5c). Similarly, effect sizes varied across levels of life-stage\*age, with significant differences observed during incubation (positive effect;  $p < .05$ ), overwintering, and the growing season (negative effects;  $p < .05$ ; Figure 5c). Negative effects during the growing season were weaker in age-0 compared to age-1 or age-2+ salmonids (Figure 5c), but these differences were not significant ( $p > .05$ ). Estimates for incubation ( $n = 8$ ) and overwintering ( $n = 12$ ) were likely impacted by low sample sizes.

### 3.3 | Publication bias and model robustness

Visual inspections of residuals suggested that assumptions of residual homogeneity were satisfied for all best-fit models (Figure S3; Table S2). VIFs suggested that collinearity among covariates in each best-fit model was limited (VIF  $< 5$ ; Table S2). However, there was evidence of collinearity within the “multiple” (VIF = 6.12) and “winter” (VIF = 6.43) levels of the season covariate in the best-fit Abundance–Precipitation model, but not within other seasons or any of the other data sets (Table S2). Funnel plots and Egger tests revealed evidence of publication bias in the Abundance–Precipitation data set only ( $p < .05$ ; Table S2). This bias appeared to be mostly caused by observations with high precision having residual values that were skewed negative (Figure S4). Further investigation identified eleven studies that contributed disproportionately to this bias, which were skewed toward two study areas and correlations based on precipitation data averaged over nine months or more (i.e., season = “multiple”). Removing these eleven studies caused publication bias to become non-significant (Egger test  $p = .064$ ) and reduced collinearity (VIF = 2.70 and 1.87 for “winter” and “multiple,” respectively), while estimated coefficients had overlapping confidence intervals (details in Appendix S1, section S.3). Significant negative relationships between residuals and publication year were detected in the Abundance–Precipitation and Growth–Temperature data sets ( $p < .05$ ; Table S2). However, these patterns were largely driven by positive residuals from very few studies published before 1981, suggesting these trends could be an artifact of the skewed distribution of publication years.

Analysis of the three data sets subsetted by species indicated that results from best-fit models were robust to taxonomic differences. Specifically, whenever species contrasts were added, they were not significantly different than zero, with wide and overlapping confidence intervals (Figure S6). Confidence intervals for all coefficients broadly overlapped in models with and without species contrasts, while models with species contrasts were always outperformed by best-fit models without them ( $\Delta\text{AICc} > 3.5$ ). Interactions between species and intercepts or slopes were also explored for effects of latitude and elevation in the Abundance–Temperature and Growth–Temperature data sets, but these models performed poorly compared to the original best-fit models ( $\Delta\text{AICc}$  range: 8.0–21.5).

Robustness tests suggested that methodological choices often had significant impacts on effect sizes. The best-fit model for the

**TABLE 2** Full list of unique model numbers and corresponding equations within three stages of stepwise model selection.  $\Delta\text{AICc}$  scores are shown for each model in the Abundance–Precipitation (labeled A–P; 16 models tested overall), Abundance–Temperature (A–T; 24 models), Growth–Precipitation (G–P; 10 models), and Growth–Temperature (G–T; 16 models) data sets. Abbreviations used in model equations are taken from Table 1, with  $Z$  denoting the standardized effect size and  $r$  denoting the nested random effect structure (see Section 2). Some models were ignored (denoted by “–”) due to limited contrast in covariates within some data sets (see Section 2). The selected models in stages 1 and 2 are denoted by \*. All models within 2  $\Delta\text{AICc}$  units of the selected model are highlighted in bold italic text, and the model with the fewest fixed effects was selected in these cases. The best model overall for each data set is denoted by\*\*\*

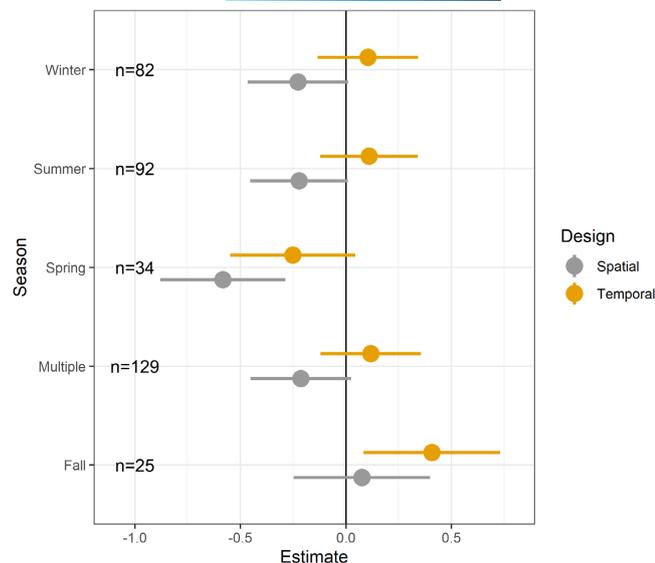
Stage	Number	Model equation	A-P (n = 362)	A-T (n = 610)	G-P (n = 66)	G-T (n = 283)
1	1	$Z = r$	<b>0.00*</b>	9.97	<b>0.00*</b>	3.26
1	2	$Z = L + r$	2.03	8.24	2.10	3.66
1	3	$Z = E + r$	<b>0.59</b>	8.70	<b>1.51</b>	2.16
1	4	$Z = L + E + r$	2.33	<b>1.02*</b>	3.72	<b>0.00*</b>
1	5	$Z = L \times E + r$	<b>1.52</b>	<b>0.00</b>	–	2.08
2	–	Stage 1 (selected)	11.44	2.33	20.03	13.91
2	6	Stage 1 + LS	10.77	10.93	<b>0.00*</b>	2.70
2	7	Stage 1 + AC	7.77	<b>0.00*</b>	23.41	9.57
2	8	Stage 1 + SE	<b>0.00*</b>	7.87	13.13	16.26
2	9	Stage 1 + LSA	14.45	16.59	–	<b>0.00*</b>
3	–	Stage 2 (selected)	4.19	10.96	2.05	2.44
3	10	Stage 2 + S	<b>0.00***</b>	7.57	2.33	3.48
3	11	Stage 2 + A	4.82	10.25	<b>0.26***</b>	4.67
3	12	Stage 2 + N	6.01	2.82	–	–
3	13	Stage 2 + H	–	13.02	–	<b>0.16***</b>
3	14	Stage 2 + S + A	<b>0.06</b>	7.17	<b>0.00</b>	5.72
3	15	Stage 2 + S + N	<b>1.61</b>	<b>0.00***</b>	–	–
3	16	Stage 2 + S + H	–	9.43	–	<b>0.00</b>
3	17	Stage 2 + A + N	6.02	3.04	–	–
3	18	Stage 2 + A + H	–	11.87	–	2.40
3	19	Stage 2 + N + H	–	4.67	–	–
3	20	Stage 2 + S + A + N	<b>0.62</b>	<b>0.45</b>	–	–
3	21	Stage 2 + S + A + H	–	8.13	–	2.24
3	22	Stage 2 + S + N + H	–	<b>1.35</b>	–	–
3	23	Stage 2 + A + N + H	–	4.12	–	–
3	24	Stage 2 + S + A + N + H	–	<b>0.68</b>	–	–

**TABLE 3** Summary of best-fit models for the Abundance–Precipitation (labeled A–P), Abundance–Temperature (A–T), Growth–Precipitation (G–P), and Growth–Temperature (G–T) data sets according to stepwise model selection. Abbreviations used in model equations are taken from Table 1. Each  $\Delta\text{AICc}$  (with  $p$ -values for likelihood ratio tests) and pseudo- $R^2$  value was calculated relative to models with no covariates (number = 1 in Table 2; see Section 2). Heterogeneity tests are based on a Wald-type test statistic, whereas the total heterogeneity (summed within and among studies) was calculated based on variance components. Significant  $p$ -values are marked with an asterisk (\*)

Data set	Best-fit model equation	$\Delta\text{AICc}$	Pseudo- $R^2$	Mean effect	Heterogeneity test	Total % heterogeneity
A–P	$Z = SE + S + r$	15.63 ( $p < .001$ )*	0.05	0.06 ( $p > .05$ )	589 ( $p < .001$ )*	59.3
A–T	$Z = L + E + AC + S + N + r$	22.24 ( $p < .001$ )*	0.10	–0.07 ( $p > .05$ )	1563 ( $p < .001$ )*	70.1
G–P	$Z = LS + A + r$	21.82 ( $p < .001$ )*	0.41	0.23 ( $p < .05$ )*	91 ( $p = .005$ )*	40.2
G–T	$Z = L + E + LSA + H + r$	19.44 ( $p < .001$ )*	0.30	0.26 ( $p < .05$ )*	874 ( $p < .001$ )*	73.8

Abundance–Precipitation data set was robust to all four methodological factors tested ( $p > .05$ ), but the other data sets showed significant effects of one or more variables ( $p < .05$ ; Table S2). Adding

data transformation and extraction method (Table 1) to the best-fit Abundance–Temperature model suggested that correlations based on transformed abundance data (99% of which were log-transformations)



**FIGURE 2** Best-fit model for the Abundance–Precipitation data set, showing categorical coefficients and 95% confidence intervals plotted by season for spatial (silver) or temporal (gold) study designs (see Table S1). Total sample sizes for each level of season are shown for reference.

and data extracted from figures or tables were associated with more positive effect sizes ( $p < .05$ ; Table S3). Similarly, adding response type to both Growth–Precipitation and Growth–Temperature models suggested that correlations based on weight were significantly different ( $p < .01$ ) than those based on length or growth rate (Table S3). Predictor type also affected the best-fit Growth–Temperature model, such that correlations based on minimum temperature were associated with significantly more negative effect sizes than for average temperature, with no significant differences for other predictor types (Table S3). Finally, Cook's distance identified influential studies in each data set ( $n = 3–6$ ), but removing these studies and re-running each best-fit model yielded similar coefficients with substantial overlap in 95% confidence intervals (Table S2).

## 4 | DISCUSSION

We assembled and analyzed the most extensive global database of climate effects on salmonid productivity to date, uncovering substantial variation. This variation exhibited broad spatial, temporal, and biological patterns that often, but not always, aligned with predictions based on salmonid thermal limits (see Figure 1). Specifically, spatial variation in latitude and elevation shaped temperature effects on productivity but, interestingly, did not influence precipitation effects. Generally, increased temperature tended to reduce productivity at low latitudes and elevations where warm and stressful thermal regimes predominate, but increase productivity at high latitudes and elevations where cold temperatures limit salmonid growth and abundance. Similarly, temporal variation structured responses to climate during the warmest time-periods, when higher temperature and lower precipitation were both associated with reduced productivity.

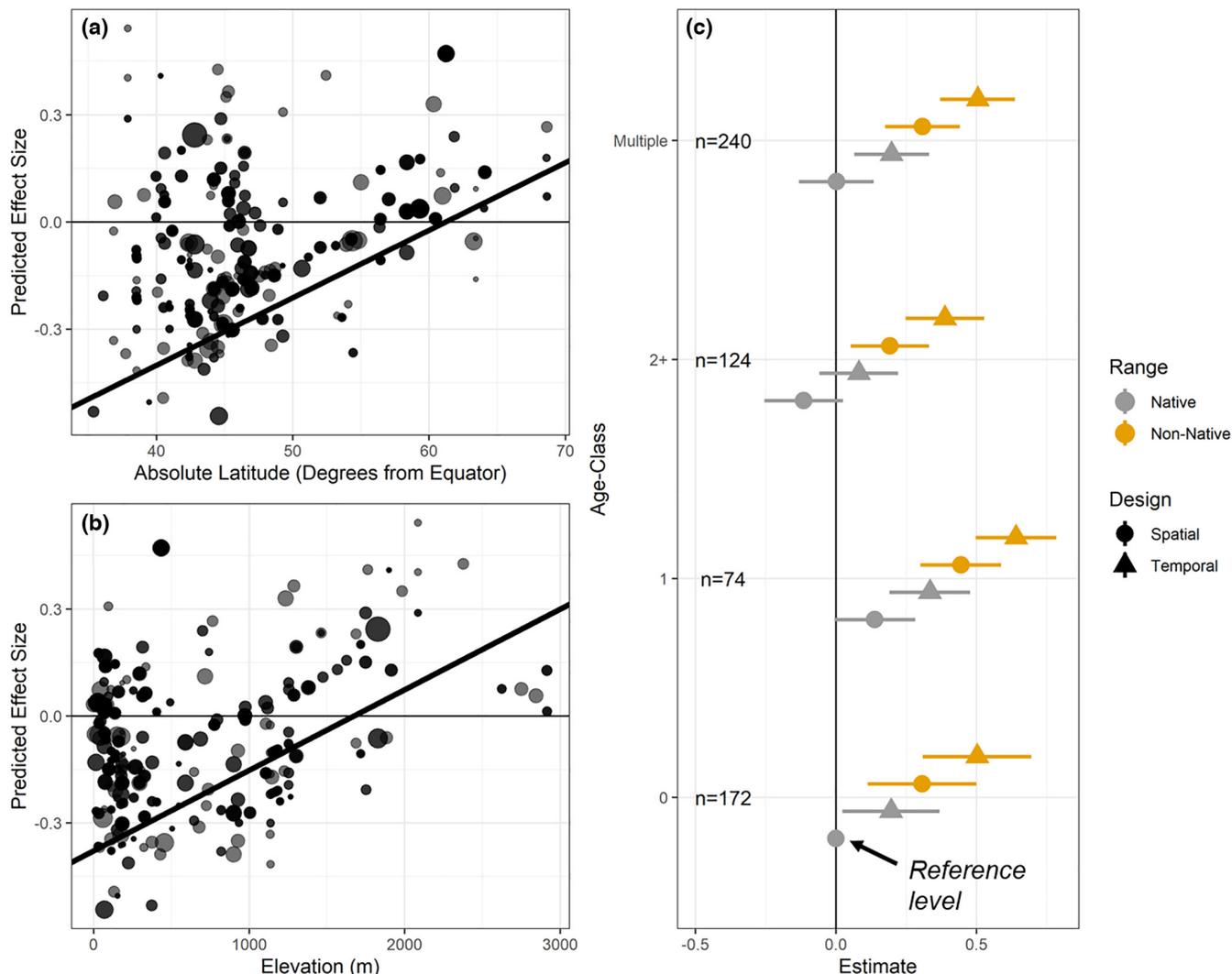
In addition, there was some evidence that increased flooding during egg incubation or the spring could further diminish productivity, but these patterns were inconsistent and sometimes impacted by low sample size. Finally, biological differences were also important, as abundance of non-native populations and salmonid growth in lentic habitats responded more positively (or less negatively) to higher temperatures, relative to native populations and lotic habitats.

Collectively, these patterns imply that future warming should be expected to (1) enhance productivity at polar latitudes ( $>60^\circ$ ) and high altitudes ( $>1500\text{m}$ ), (2) threaten salmonids in areas where precipitation is declining during the warmest months (3) affect native populations more negatively than non-natives, and (4) increase the importance of lentic habitats as climate refugia. These findings can help conservation and management bodies identify and protect salmonid populations that are especially sensitive to climate change, as well as guide future research. However, we also identified key limitations in current knowledge of salmonid responses to climate, as the majority of variation remains unexplained, while geographic bias, methodological inconsistencies, and unbalanced sample sizes likely restricted scope of inference.

### 4.1 | Spatial patterns

The effects of temperature on salmonid abundance and, to a lesser extent, growth were related to latitude, as warming negatively impacted productivity at low latitudes but had positive effects in polar regions, which is in line with previous research. For example, studies of European brown trout (*Salmo trutta*) suggested that higher temperatures and longer growing seasons should increase productivity in high-latitude populations that are currently constrained by cold temperatures (Jensen et al., 2000; Parra et al., 2009), while Mediterranean populations face extirpation due to thermal stress as climate change continues (Almodóvar et al., 2012; Ayllón et al., 2019). Our results suggest that this pattern may be similar across other salmonids, although most species are not well represented in our database across their range. Generally, this latitudinal trend supports predictions that salmonids should become more productive within their native range in the Arctic under climate change (especially  $>60^\circ\text{N}$ ), while declines in productivity will be more frequent in low-latitude regions (Campana et al., 2020; Jonsson & Jonsson, 2009; Reist et al., 2006). However, the Arctic currently has the highest rates of warming on earth and this trend is expected to continue, so many high-latitude areas could be a boon for salmonids over the next few decades but may become less suitable later this century. Moreover, constraints within polar ecosystems could limit increases in salmonid productivity, as primary and secondary production must rise substantially to sustain higher salmonid biomass in the future (Reist et al., 2006), and high-latitude populations can still be negatively impacted by prolonged heat waves and droughts (von Biela et al., 2022).

Similar to latitude, there was a strong trend in temperature effects due to elevation, such that warmer temperatures were linked

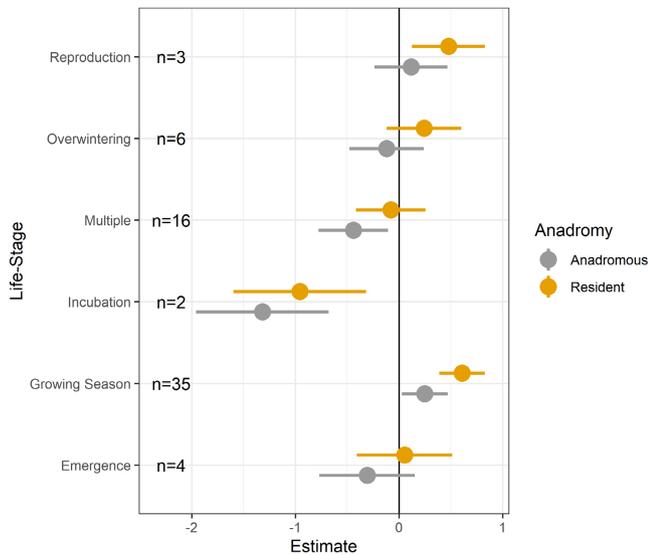


**FIGURE 3** Best-fit model for the Abundance–Temperature data set. Predicted values are plotted by latitude (a) and elevation (b), with fitted slope and intercepts corresponding to a reference level (c; arrow). Intercepts in (a) and (b) were adjusted to reflect the mean elevation and latitude, respectively, while points were sized according to the inverse of their sampling variance. Categorical coefficients and 95% confidence intervals (c) are plotted by age-class for native (silver) or non-native (gold) range portions, and spatial (circles) or temporal (triangles) study designs. Coefficients in (c) were estimated as contrasts relative to a reference level (bottom; see text) while controlling for latitude and elevation (see Table S1). Total sample sizes for each level of age-class are shown in (c) for reference.

to declines in growth and abundance at low elevations, but with increases at high elevations. This pattern supports the notion that high-altitude streams provide a “coldwater climate shield” for salmonids and will serve as important climate refugia in a warming world (Almodóvar et al., 2012; Isaak et al., 2015; Kanno et al., 2015; Nakano et al., 1996). Mountain streams typically exhibit slower climate velocities that help buffer against warming (Isaak et al., 2016), while previous research on cutthroat trout (*Oncorhynchus clarkii*) in the Rocky Mountains showed that productivity at high elevations is limited by cold summer temperatures (Coleman & Fausch, 2007; Harig & Fausch, 2002; Young et al., 2005). Thus, there is considerable scope for warming to increase productivity in high-altitude populations (especially >1500m), and we expect the distribution of productivity to shift toward higher elevations in the future. However, this will be offset by reduced productivity and more

frequent extirpation in low-lying areas (Almodóvar et al., 2012; Nakano et al., 1996). Moreover, there is likely to be considerable variation in the rate of elevation shifts at the local level, especially as warming interacts with changes in snowpack and non-native species (Wenger et al., 2011).

The broad spatial patterns in salmonid-temperature relationships we uncovered were in line with our predictions (Figure 1a), and suggest that populations occupying low-elevation habitats near low-latitude range margins are most likely to decline with warming. These vulnerable populations can be targets for conservation interventions or restoration by agencies, especially if they harbor unique diversity that might aid persistence (Carlson & Satterthwaite, 2011). Similarly, if vulnerable populations support fisheries, managers may need to consider reducing future harvests to remain sustainable under climate change. Changes in precipitation could possibly



**FIGURE 4** Best-fit model for the Growth–Precipitation data set, showing categorical coefficients and 95% confidence intervals plotted by life-stage for anadromous (silver) or freshwater resident (gold) populations (see Table S1). Total sample sizes for each level of life-stage are shown for reference.

offset some of these impacts, but model selection did not indicate strong spatial variation in precipitation effects. This is likely because temperature varies more predictably with latitude and altitude than precipitation, which is more influenced by rainshadows, prevailing winds, and proximity to large water bodies (Fick & Hijmans, 2017).

## 4.2 | Temporal patterns

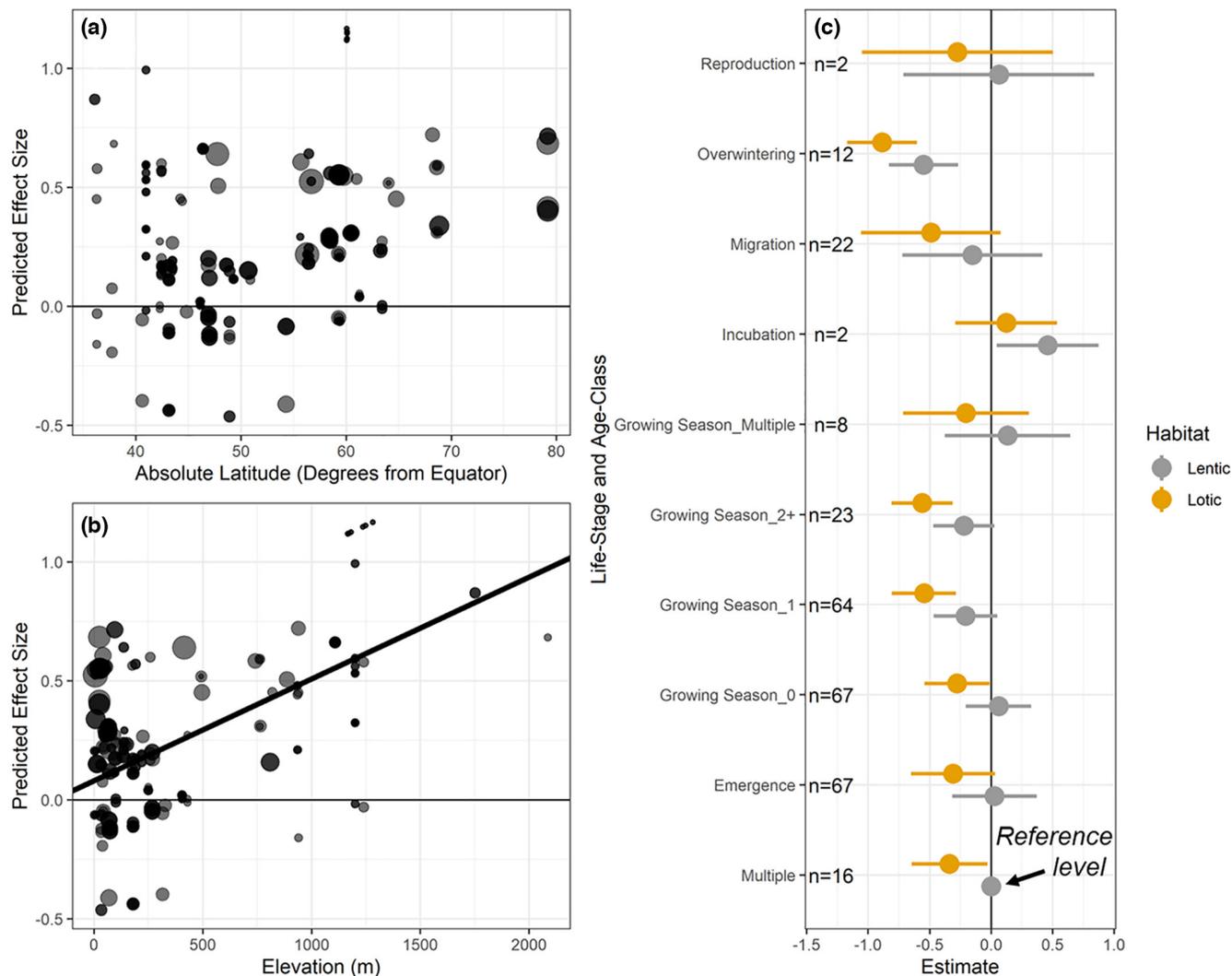
Effects of climate on growth and abundance varied considerably based on the time-period studied, revealing critical periods when climate variation tends to have particularly strong impacts on salmonids. Most notably, warmer temperatures and decreased precipitation during the warmest times of year were both associated with reduced productivity, while increased precipitation during other time-periods (e.g., spring, egg incubation) was also linked to declines in productivity. These patterns largely matched expectations (especially during the growing season; Figure 1c,d) and corroborated previous qualitative reviews that emphasized temporal variation in climate impacts, as well as its utility for improving inferences (Kovach et al., 2016; Nislow & Armstrong, 2012). Indeed, multiple studies of brook trout (*Salvelinus fontinalis*) in eastern North America found that temperature and precipitation have the largest impacts during specific seasons or life-stages (Bassar et al., 2016; Kanno et al., 2015; Sweka & Wagner, 2022). In contrast, model selection in both temperature data sets supported the inclusion of age (age-class in Abundance–Temperature, life-stage\*age in Growth–Temperature), but differences between age-classes varied in direction and were not statistically significant. Thus, the magnitude and direction of future climate change during critical time-periods in the life cycle will be a key determinant

of salmonid persistence, whereas differences among age-classes should be less influential. Continued research on these critical periods should help build upon current knowledge of how temporal climate variation shapes habitat quality (Armstrong et al., 2021), and how this can produce different responses within and among species (Bassar et al., 2016; Kanno et al., 2015, 2017).

The temporal patterns we found in salmonid responses to climate suggest that declines in productivity should be most frequent in areas where growing season conditions are becoming hotter and dryer, as proposed in previous studies (Arismendi et al., 2013). This type of climate change is especially prominent in western North America (Carlson & Satterthwaite, 2011) and Mediterranean Europe (Ayllón et al., 2019), which will create future management and conservation challenges in these regions. However, future responses will likely be complex, as temporal patterns were not always consistent among data sets (e.g., summer precipitation did not show expected positive effects in the Abundance–Precipitation data set), and their significance sometimes depended on other biological and methodological factors. Additionally, some strong effects were based on low sample sizes (e.g., reproduction and incubation in Figure 4, incubation and overwintering in Figure 5) and should thus be viewed as preliminary. The paucity of data during migration, reproduction, incubation, and emergence means we cannot resolve uncertainties about the vulnerability of these life-stages to climate change (e.g., Dahlke et al., 2020; Jonsson & Jonsson, 2009; Pottier et al., 2022). Finally, we believe inferring the impacts of temporal covariates on salmonid productivity is especially hampered by the use of ambiguous time-periods. Specifically, climate data were frequently averaged over 9–12 month periods (e.g., season = “multiple”), which contributed to publication bias and collinearity issues in the Abundance–Precipitation data set (see Appendix S1, section S.3 for details). More broadly, this practice obscures inferences about temporal variation in climate effects (Appendix S1, section S.4) and should thus be avoided, as also suggested by Kovach et al. (2016). Instead, assessments of climate impacts should consistently focus on well-defined periods linked to the life cycle of the focal population.

## 4.3 | Biological patterns

Biological factors such as range portion, habitat type, and anadromy also strongly modified salmonid responses to climate variation. The most striking patterns were the significant differences in temperature effects between native and non-native species, and between lotic and lentic habitats, which both have implications for management and conservation. Specifically, the abundance of non-native salmonids responded more positively to warming on average, relative to native populations. This supports the perception that climate change may allow non-native salmonids to further outcompete or replace their native counterparts in some areas (Al-Chokhachy et al., 2016; Budy et al., 2008), a



**FIGURE 5** Best-fit model for the Growth-Temperature data set. Predicted values are plotted by latitude (a) and elevation (b), with fitted slope and intercept corresponding to a reference level (c; arrow). The relationship with latitude in (a) was not significant, so the fitted line is not shown. Points in (a) and (b) are sized according to the inverse of their sampling variance. Categorical coefficients and 95% confidence intervals (c) are plotted by life-stage\*age for lentic (silver) or lotic (gold) habitat types (see Table S1). Coefficients in (c) were estimated as contrasts relative to a reference level (bottom; see text) while controlling for latitude and elevation. Total sample sizes for each level of life-stage\*age are shown in (c) for reference.

key warning sign given that many management agencies seek to limit or remove non-natives from critical habitats when feasible (Kanno et al., 2016; Kovach et al., 2017). However, such decisions should still be tailored to species- and population-specific data whenever possible, as Bell et al. (2021) showed that competition with non-native salmonids can significantly threaten some native species, but not others. Additionally, the Growth-Temperature model suggested that warming temperatures during the growing season reduced productivity in lotic habitats, but these effects were negligible in lentic habitats. This pattern could be due to lentic environments, especially large lakes, becoming stratified with warming and providing deepwater thermal refugia that can benefit salmonid growth (Blair et al., 2013). Although the role of lentic habitats as potential climate refugia for salmonids has not been extensively studied, protecting or restoring large stratified

lakes may be a worthwhile management and conservation option, especially in areas where lakes are known to be more resistant to warming than other habitats (Reist et al., 2006). Migration behaviors also influenced effects in the Growth-Precipitation data set, such that increased precipitation during the growing season improved growth in non-anadromous salmonids more than anadromous populations. Causes of this pattern are uncertain, given the low sample size in this data set, but could perhaps be due to shorter freshwater residency in anadromous salmonids, which reduces exposure to the warmest time-periods when increased precipitation should be most beneficial. It is also notable that methodological differences in study design, data collection, and transformation influenced patterns in effect size (Figures 2 and 3c; Tables S1–S3), which underscores the need to improve standardization across studies.

#### 4.4 | Limitations and future work

Although our quantitative synthesis now provides the most comprehensive global analysis of salmonid responses to climate change, current knowledge is incomplete and significant uncertainty remains. First, our database does not represent the whole salmonid range, with 85% of observations coming from Canada, the United States, British Isles, and Nordic countries, similar to geographic biases highlighted in critiques of past biodiversity syntheses (e.g., Gonzalez et al., 2016). This bias clearly underrepresents non-English speakers and limits scope of inference, such that applications of our findings beyond these regions must be done with care. Moreover, although covariates were significant overall, the variance explained was low for effects on abundance (pseudo- $R^2 = 5\%$ – $10\%$ ) and modest for effects on growth (30%–41%). This is an important limitation because abundance often has the strongest impact on productivity (Lobón-Cerviá, 2009), and much of the unexplained variation (40%–75%) was attributed to heterogeneity within and among studies. Such variation is typical in ecological meta-analyses (Senior et al., 2016), and suggests that the broad patterns in productivity we uncovered have limited predictive power at the local level and that population-specific monitoring data remain critical for conservation and management planning. The variation we observed also likely reflects the remarkable population diversity of salmonids, which managers should seek to maintain to promote stability and resilience in a changing world (Schindler et al., 2010).

Our analysis was also impacted by the need to use correlations to derive standardized effect sizes, as these simplified relationships cannot account for factors such as density-dependence (Matte et al., 2020), food availability (Railsback, 2022), and species interactions (Wenger et al., 2011). Furthermore, we analyzed growth and abundance separately even though these are often coupled (Lobón-Cerviá, 2022; Zabel & Achord, 2004), and can exhibit complex and variable relationships to actual rates of biomass production (Lobón-Cerviá, 2009). Similarly, interactive (Arismendi et al., 2013; Xu et al., 2010b) or non-linear (Lobón-Cerviá & Mortensen, 2005; Rosenfeld, 2017) climate effects are not adequately captured with correlations, while the linearity of salmonid–climate relationships are likely influenced by choices in study design and data transformation. Further research that standardizes productivity and climate data while accounting for key ecological processes (e.g., density dependence; Matte et al., 2020) would provide more precise and informative effects of climate on salmonids.

Despite some issues with publication bias, collinearity, and unbalanced sample sizes, best-fit models appeared to satisfy assumptions, and were robust to influential studies and taxonomic differences. Although species did not differ significantly in our analyses, divergence in evolutionary histories, habitat preferences, and thermal tolerances within and among species will invariably shape future responses to climate change (Jonsson & Jonsson, 2009; McKenzie et al., 2021). Our data are probably ill-suited to taxonomic comparisons due to skewed species composition (47% of observations were brown trout or brook trout), so more targeted studies of variation

in climate responses within and among species should be a priority for future research. Overall, the patterns our meta-analysis uncovered are not definitive, and more research is needed to mitigate its geographic, taxonomic, and methodological limitations. To this end, we have shared our database (see Gallagher et al., 2022 on Dryad) and encourage others to use it, add more studies, or explore other covariates (e.g., WorldClim data; Fick & Hijmans, 2017). Finally, while we recognize that ecological data are complex and often best analyzed with sophisticated models (e.g., Letcher et al., 2015), we urge researchers around the world to report simple correlations (with sample sizes) between salmonid and climate data believed to be most relevant for their own study systems. Together, broader data sharing and more targeted, hypothesis-driven inquiry should further improve predictions of the future of salmonids under climate change.

## 5 | CONCLUSIONS

Patterns revealed by our meta-analysis suggest that native salmonids occupying lotic habitats at low latitudes and elevations are likely to be most vulnerable to future warming, especially in areas where drought will become more frequent during the hottest time-periods. Conversely, increased temperatures will likely enhance productivity at high latitudes and elevations. In combination, these trends can serve as a point of comparison for future studies and may play an important role in salmonid range shifts over the coming decades (Comte & Olden, 2017). More generally, our framework to predict and test patterns in effects of climate variation on growth and abundance enabled us to translate simple correlations from past research into broad inferences about future productivity, underscoring the value of data synthesis to informing conservation and management decisions (Haddaway, 2015). Although it is imperfect, our structured quantitative approach—centered around simple questions of where, when, and what kind of effects are measured—should be useful for explaining patterns in responses to climate in other organisms. Overall, future impacts of climate change will be complex but are unlikely to be entirely negative, and local responses will exhibit substantial variation around the broad patterns highlighted in this study. Such varied responses to climate change in salmonids imply that, while some populations will inevitably decline, this will be offset by expansion and increased productivity in others (Mantua et al., 2015). For biodiversity at large, this balance between gains and losses in species productivity through time is critically important for the future of life in an increasingly human-dominated world (Dornelas et al., 2014, 2019). Our synthesis suggests that this uncertain balance also applies to salmonids, with far-reaching implications for these coldwater fishes, and the ecosystems and people that depend on them.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data, metadata, and R code used to generate results are openly available on Dryad (DOI: <https://doi.org/10.5061/dryad.t76hdr83z>) and Zenodo (DOI: <https://doi.org/10.5281/zenodo.7071599>).

## ORCID

Brian K. Gallagher  <https://orcid.org/0000-0002-9990-8363>

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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