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Water Temperature, Prey Concentration and Salmonid Density Influence Daily Growth of Wild Juvenile Salmonids in Tributaries of the Upper Salmon River, Idaho (USA)

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ABSTRACT

1. Theory, experiments and field studies indicate that the somatic growth rate of freshwater consumers is shaped by the individual, additive and multiplicative effects of multiple factors, including consumer size and condition, temperature, prey resources and biotic interactions. While our understanding of how these factors affect wild populations of freshwater consumers is improving, the topic remains poorly studied, especially with respect to mobile species.

2. Here, we report on an 8-year, seven-stream ($n = 49$ stream-year combinations) observational study examining the individual and interactive effects of invertebrate prey concentration (F, mg/m^3), mean daily water temperature (T, °C) and juvenile Chinook salmon (*Oncorhynchus tshawytscha*) density (D, fish/100 m^2) on summer daily growth rates (%/d) of mobile, anadromous, juvenile Chinook salmon (age-0+, $n = 382$) and sub-yearling (age-0+, $n = 61$) and yearling (age-1+) steelhead trout (*O. mykiss*, $n = 70$) rearing in cold (mean daily summer: 12.1°C, range: 4.2°C–16.7°C) mountain tributaries of the Salmon River basin in central Idaho (USA).

3. AIC_c model selection indicated that daily juvenile salmonid growth positively correlated with water temperature, prey biomass concentration, local juvenile Chinook density and the interaction between water temperature and food but with species and age-specific differences. Water temperature was a covariate in all top-ranked models, with daily growth (%/day) rate increasing (0.05%–0.23%/d) linearly with mean daily summer water temperature. In addition to a direct positive relationship with daily growth rate, there was evidence that prey concentration positively interacted with water temperature to accelerate daily growth (F×T). The positive relationship between juvenile salmonid daily growth rate and juvenile Chinook density is difficult to explain and could result from confounding factors.

4. The individual success observed in these streams may contribute to population-level benefits for the focal consumers, as prey-rich, warm summers may result in larger individuals with higher energy reserves at the end of the summer/autumn growing season, contributing to improved overwinter survival.

5. Our results, taken in combination with evidence from models, experiments and observational studies, have climate change implications. Current and predicted increases in water temperature will necessitate higher rates of prey consumption by aquatic ectothermic consumers to offset accelerated metabolic demands.

6. Thus, to improve the resilience of mobile freshwater consumers in a warming climate, we suggest that natural resource managers not only consider physical and chemical habitat conditions but also biotic conditions, including the spatiotemporal quantity and quality of prey resources.

1 | Introduction

Somatic growth is an important component of consumer fitness influencing a variety of fitness-related traits such as age and size at maturity (English et al. 2014). Theory, bioenergetic models and small-scale experiments indicate multiple abiotic and biotic factors, individually and interactively, influence somatic growth of freshwater fish including temperature, prey concentration and population density (Brett, Shelbourn, and Shoop 1969; de Barros, Villacorta-Correa, and Carvalho 2019; Naman et al. 2020; FitzGerald et al. 2022).

While our understanding of environmental factors influencing freshwater fish is improving, observational studies, especially of mobile species in the wild, like stream salmonids, remain relatively rare (DeMott, Edington, and Tessier 2004; Edmundson and Mazumder 2001; Ward, Nislow, and Folt 2009; Rhoades et al. 2023). There are likely many factors contributing to this lack of knowledge including the logistical constraints associated with such an effort at scales relevant to the organism. However, increasing our understanding of how mobile freshwater fish respond to environmental gradients (e.g., food concentration) in the wild could improve conservation effectiveness in a changing climate by directing management actions that increase species resilience to higher temperatures (Lusardi et al. 2020; Rossi et al. 2023). Salmonids, the focus of our study, are freshwater fishes that are declining in abundance and spatial distribution across large portions of their native range (e.g., Chaput 2012). They also display a range of mobility and are culturally, economically and ecologically important to subarctic and temperate systems in native and non-native habitats (Quinn 2005).

Temperature—both the mean and variance—is a master variable controlling ectothermic growth by regulating biochemical and physiological rates (e.g., assimilation efficiency) and behaviour (Gibson 1978; Sauter, McMillan, and Dunham 2001; McConnachie and Alexander 2004; Björnsson, Steinarsson, and Árnason 2007; Bozinovic et al. 2011; Steel et al. 2012). Growth–temperature relationships are established for some aquatic organisms, especially economically important fish species (e.g., anadromous salmonids) from laboratory experiments where water temperatures, body size and stock origin and density are tightly controlled and consumers are fed artificial food at varying levels (e.g., Elliott 1975; except see Hogg and Williams 1996). The fish growth response to gradients of water temperature in laboratory experiments is typically unimodal. Specifically, growth increases with temperature at a rate dependent on species, ration and body size, until reaching a maximum and then declining abruptly as thermal stress disrupts biochemical and physiological functions (Brett, Shelbourn, and Shoop 1969; Elliott 1994; Jobling 1997).

While these experiments are highly informative, in nature, environmental conditions, such as fish size, condition and density; prey concentration and quality; and local consumer density can be highly variable, likely modifying how individual growth responds to water temperature. Thus, from a management and conservation perspective, there is a need to assess how fish growth–temperature relationships established in the laboratory are supported in the field with wild, mobile populations, including the identification of modifying factors.

Along with temperature, prey concentration is a key determinant of consumer individual growth, with several studies indicating food limitation is relatively common in freshwater ecosystems due to both natural and anthropogenic factors (Wilzbach, Cummins, and Hall 1986; Richardson 1991; Sterner 1997; Ward, Nislow, and Folt 2009). Not only does prey quantity and quality (e.g., fatty acid composition) influence individual growth, they also affect growth by modifying the physiological effects of water temperature. In laboratory experiments, where juvenile sockeye salmon (*Oncorhynchus nerka*) were exposed to a gradient of water temperature (1°C, 5°C, 10°C, 15°C, 20°C, 24°C) and food ration (0%, 1.5%, 3.0%, 4.5% and 6% of dry body weight per day), higher food rations increased both the temperature range where an individual grew and the optimum temperature for maximum growth rate (Brett, Shelbourn, and Shoop 1969). Results from a recent field experiment and select observational studies are mostly consistent with these laboratory results (Weber et al. 2014; Lusardi et al. 2020; Rhoades et al. 2023).

Competition for food or space is another environmental factor that can influence the consumer growth rate (Edmundson and Mazumder 2001; Jackson, Peres-Neto, and Olden 2001; Schindler et al. 2005), although there is some uncertainty regarding the extent and strength of competition in shaping natural ecological communities (Houlahan et al. 2007). Theoretically, at a given food concentration, more competitors reduce individual energy intake by modifying energy budgets via exploitative and agnostic interactions (Fausch 1984; Fausch, Nakano, and Kitano 1997; Railsback and Rose 1999). A recent review of 199 published studies focusing on salmonids (21 species) found 71% of them showed density dependence on individual growth (Grossman and Simon 2020). In contrast, recent observational studies found little evidence of a compensatory response by resident rainbow (*O. mykiss*) or cutthroat trout populations (*O. clarkii clarkii*), either at the individual- (e.g., individual growth rate) or population-level (e. g., density), to variation in juvenile coho salmon (*O. kisutch*) density (Buehrens et al. 2014; Martens and Dunham 2021; Kiffney et al. 2023). Furthermore, Houlahan et al. (2007) found no evidence of negative compensatory changes in species in 41 natural communities including plants, invertebrates, reptiles, fish and mammals. In fact, species tended to

positively covary. These contrasting results indicate the need for additional evaluation of how the population size of one species influences the demography of the same or similar species.

Besides competitive interactions affecting growth directly, a reduction in energy intake resulting from competition might also indirectly influence individual growth by increasing sensitivity to other stressors. For example, the individual growth of wild juvenile Chinook salmon rearing in tributaries of the Salmon River in central Idaho, USA declined with water temperature at high conspecific densities, while increasing at low densities (Crozier et al. 2010). It was hypothesised that this differential growth response to water temperature resulted from a 'bioenergetic constraint' due to invertebrate prey limitation at high juvenile Chinook densities (Crozier et al. 2010).

Thus, the daily growth rate of mobile freshwater consumers is likely a result of multiple interacting factors including water temperature, food or invertebrate prey concentration and local density of putative competitors. Here, we examine the relationships between daily growth rates (percent increase in length per day or %/d) of two freshwater fish – anadromous juvenile Chinook salmon (age-0+, *O. tshawytscha*) and sub-yearling (age-0+) and yearling (age-1+) steelhead/ trout (*O. mykiss*) – rearing in seven cool (mean summer daily ~12.0°C) mountain tributaries of the Salmon River, Idaho (USA) and invertebrate prey biomass concentration, mean daily water temperature and density of juvenile Chinook salmon over an 8-year period. Empirical studies that explore how mobile freshwater consumers, such as stream salmonids, are influenced by multiple environmental conditions simultaneously over multiple years and streams in the wild are rare but necessary in order to inform ecosystem management and species recovery (Rossi et al. 2023).

Based on previous research, we expected that daily growth rate would:

1. positively covary with summer water temperature (T) and invertebrate prey concentration (F), while possibly declining with juvenile Chinook salmon density (D);

2. increase at higher rates in warm, food-rich relative to warm, food-poor years (F × T); and

3. decline at higher rates in warm, high juvenile Chinook salmon density years relative to high density, cool years (D × T).

2 | Methods

2.1 | Study Details

This study is part of a long-term monitoring effort exploring how environmental conditions, such as water temperature, prey populations, competitor density and non-native species influence movement, growth and freshwater survival of wild populations of juvenile Chinook salmon and steelhead trout rearing in montane (1100–2100 m. a. s. l.) wilderness tributary streams of the South Fork, Middle Fork and main stem of the Salmon River (Achord, Levin, and Zabel 2003; Zabel and Achord 2004; Sanderson et al. 2009; Macneale et al. 2010; Crozier et al. 2010).

Here, we focus on seven of these streams including Lake Creek (LAK), South Fork of the Salmon River (SFS), Valley Creek (VAL), Elk Creek (ELK), Bear Valley Creek (BVA), Cape Horn Creek (CHO), Marsh Creek (MAR) and Valley Creek (VAL) (Figure 1).

The Salmon River basin encompasses 36,000 km² and is one of the largest contiguous undammed main stem rivers in the continental United States. The river flows into the Snake River, a tributary to the Columbia River and the Pacific Ocean (Achord, Levin, and Zabel 2003; Thurow, Copeland, and Oldemeyer 2020). Outgoing smolts (life stage emigrating to ocean) and incoming adults must migrate from 1100 to 1500 km between their natal streams and the Pacific Ocean, navigating eight dams and associated reservoirs on the main stem Columbia River (Crozier et al. 2010).

The Salmon River is part of the Northern Rocky Mountain Ecoregion but has important features in common with the High Desert and Basin and Range ecoregions (Omernik 1987; Minshall et al. 1992). The climate is continental but strongly influenced by the Pacific Ocean over a 1000 km away, elevation and aspect. Summers are short and cool and winters cold. Minshall et al. (1992) reported a mean annual air temperature of 4°C in Stanley, Idaho (lat. 44.216642, lon. −114.930176, altitude = 1872 m above mean sea level). Precipitation amounts increase with elevation, with Stanley receiving 23 cm of precipitation annually, mostly as snow (Minshall et al. 1992). The composition and structure of upland and riparian vegetation vary with elevation and aspect. Trees include both evergreen conifers (Douglas fir, *Pseudotsuga menziesii*; Ponderosa Pine, *Pinus ponderosa*) and deciduous broadleaf species (Aspen, *Populus tremuloides*; black cottonwood, *Populus trichocarpa*; Rocky Mountain maple, *Acer glabrum*). The semiarid climate, rocky terrain and poor soil development limit the density of the forest and upland shrubs and restrict the riparian deciduous vegetation and wetland grasses and sedges to a relatively narrow band adjacent to the stream channel (Minshall et al. 1992).

Fire is a major source of disturbance in the region where it can modify nutrient and sediment budgets; algal, bacterial and invertebrate productivity; and biotic assemblages (e. g., Minshall, Robinson, and Lawrence 1997). As far as we know, there are no published studies focusing on the ecological effects of forest fire on the study streams. However, a comparative study in the nearby Boise River, ID did not observe statistical differences in invertebrate drift biomass concentration (mg AFDM/m³) between burned and unburned streams (Rosenberger et al. 2011).

The seven study streams are generally low-gradient, unconfined, sunlit channels (5 to 21 m wetted width at summer base flow), characterised by low concentrations of nitrogen (median dissolved $NO_3^- - N = 1.7 \mu g/L$) and phosphorus (dissolved $PO_4^- p = 5.4 \mu g/L$), cool to cold water (mean daily summer temperature ~12.0°C) and gravelly substrates (Sanderson et al. 2009). The annual stream hydrograph is characterised by a single major runoff period from early April to late July, with the baseflow extending from mid-August to March (Minshall et al. 1992).

Stream fish assemblages are represented by five families (Catostomidae, Cottidae, Cyprinidae, Petromyzontidae
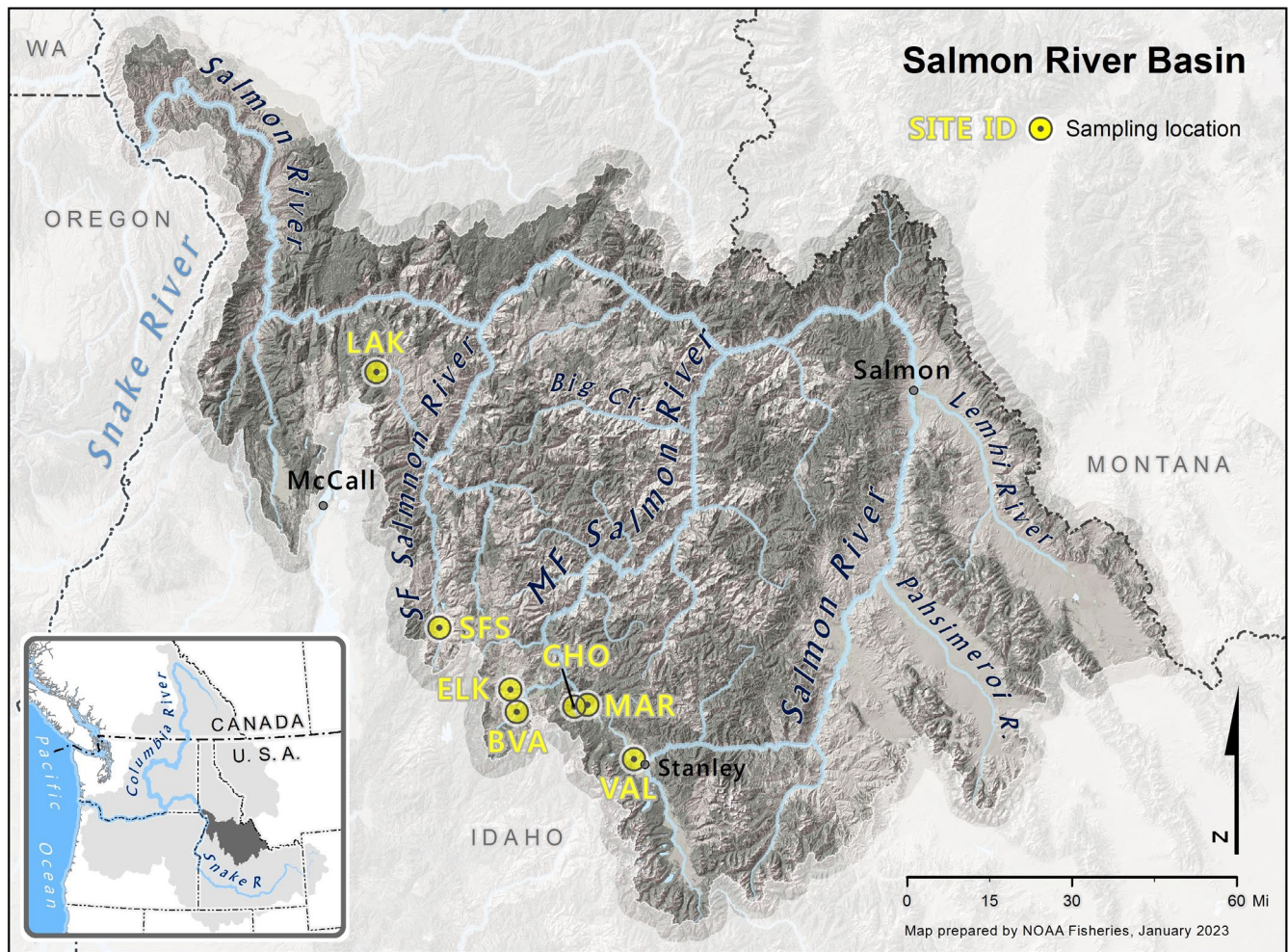
FIGURE 1 | Map of study streams represented by yellow dots (BVA, Bear Valley Creek; CHO, Cape Horn Creek; ELK, Elk Creek; LAK, Lake Creek; MAR, Marsh Creek; SFS, South Fork Salmon; VAL, Valley Creek).

and Salmonidae), with brook trout (*Salvelinus fontinalis*) being the only non-native species (Thurow, Copeland, and Oldemeyer 2020). Hatchery origin resident rainbow trouts (nonanadromous *O. mykiss*) are planted in one tributary, Valley Creek, for recreational purposes. We focus on sub-yearling (age-0+) Chinook salmon (hereafter juvenile Chinook salmon), the most abundant salmonid in the study streams, and sub-yearling (age-0+) and yearling (age-1+) steelhead trout (anadromous *O. mykiss*). Adult Chinook salmon typically spawn in Salmon River tributaries in late August to early September. Juvenile Chinook salmon rear in tributaries for 1 year before migrating seaward to the Pacific Ocean, where they mature after 1–3 years before returning to spawn. Adult steelhead trout typically spawn from March to May, while juveniles rear in streams for 2–3 years before migrating seaward (Crozier et al. 2010). Both species are listed as threatened under the US Endangered Species Act (1973).

Before European settlement, anadromous fish populations in the basin were robust, and prey resources supporting stream-rearing salmonids likely consisted of a diverse assemblage of terrestrial and aquatic invertebrates in addition to eggs and flesh resulting from adult salmon reproduction and subsequent carcass decomposition. However, current anadromous populations and their associated nutrients are much reduced (Gresh,

Lichatowich, and Schoonmaker 2000; Thurow, Copeland, and Oldemeyer 2020); therefore, on an annual basis, invertebrates are likely the dominant source of energy supporting salmonids in the basin. Based on our observations, the invertebrate assemblage supporting stream-rearing salmonids during summer include a variety of stream insects, especially Diptera, Ephemeroptera and Trichoptera, while spiders (Araneae), beetles (Coleoptera), true flies (Diptera) and grasshoppers (Orthoptera) are common terrestrial prey (Macneale et al. 2010).

2.2 | Sampling Logistics

We sampled one to two streams a day over several weeks between July and early September for 8 years (2003–2004, 2007–2011, 2014) for water temperature, invertebrate prey biomass concentration and juvenile salmonid density and daily growth rate. Not all streams were sampled for all elements in all years, resulting in 49 unique stream-year combinations.

Water temperature was measured continuously using Hobo temperature loggers (Hobo, Bourne, USA) between July and August/September. We also measured stream invertebrate prey concentration at these time points. Juvenile salmonid fish density was estimated once between July and August as part of a

long-term fish tagging project. Fish used to estimate instantaneous daily growth were collected as a result of incidental mortalities during this fish tagging effort and an additional effort in August/early September when we sampled drift and collected temperature loggers.

Although we controlled for some sources of sampling variation, we note a number of potential biases associated with the field approach. Because we sampled multiple streams that were remote and not easily accessible, our sampling effort lasted from mid-July until mid-August to early September. This difference in timing from the first to the last sampling event likely resulted in temporal differences in prey resource abundance and composition and rates of fish metabolism, feeding and growth that were not accounted for. In addition, captured fish may have emigrated into the sample reach just prior to capture. We expect such movement was limited by small home ranges during summer and steep channel gradients in MAR and BVA at their respective confluences. Previous research in nearby streams indicated juvenile (age-0+ and 1+) steelhead trout displayed low levels of movement during summer, with 86% of juvenile steelhead trout moving less than 6 m (Edmundson, Everest, and Chapman 1968).

2.2.1 | Water temperature

Due to temperature logger malfunction and disturbance events, there were periods, ranging from weeks to months, when temperature data were not collected. The amount of missing data varied by stream with a continuous record at Valley Creek (VAL: mean daily = 13.5°C, minimum = 11.0, maximum = 16.8), a nearly continuous record at South Fork of the Salmon (SFS: 11.7°C, minimum = 8.3, maximum = 15.0) and Marsh Creek (MAR: 10.4°C, minimum = 4.9, maximum = 13.1) and continuous, but more relatively short, interrupted records at the remaining streams, primarily between 2003 and 2008. To address these temperature gaps, individual stream data were combined into one assuming a single overall temperature regime to estimate missing mean daily data using the MARSS package in R (Holmes, Ward, and Wills 2012). We used the mean daily water temperature from this model to determine the site-specific mean daily water temperature over a 14-day period prior to fish capture. Mean temperature was used as a predictor of daily growth rate rather than the maximum or 90th percentile, as the mean integrates across the entire day capturing both minima and maxima, and thus may better reflect daily growth conditions.

We recognise stream discharge (m^3/s) is a key variable that can influence both invertebrate drift and fish foraging behaviour and success (Naman, Rosenfeld, and Richardson 2016; Caldwell et al. 2018; Rhoades et al. 2023). Stream discharge was measured during the sample years in only one tributary (SFS, https://water data.usgs.gov/monitoring-location/13310700/#parameterC ode=00065&period=P7D&showMedian=false); therefore, we did not include discharge as a predictor in the statistical analysis. However, to provide a general context for the stream discharge regime in the area during the study, we calculated median, minimum and maximum instantaneous daily discharge data (m^3/s) from the SFS gauge measured between 15 June and 1 September each year.

2.2.2 | Invertebrate Prey Concentration

Invertebrate prey concentration was defined by the ash-free dry mass (mg $AFDM/m^3$) of drifting aquatic and terrestrial invertebrates captured by nets (Leung, Rosenfeld, and Bernhardt 2009). Drift samples were collected between 0800 and 1500 in a standardised way in July and August/September each year by placing two rectangular nets ($99 \times 45 \times 30.5$ cm, 363 µm mesh net) (Forestry Suppliers, Jackson, USA) side by side in a riffle habitat perpendicular to stream flow for approximately 30 min. Nets were placed perpendicular to the flow so that water was directed to the back of the net without backfill, the top protruded above the surface to capture drifting terrestrial and emerging aquatic invertebrates and the bottom of the net was a few centimetres above the stream bottom to prevent invertebrates from crawling into the net. Captured material was transferred to a 350 µm mesh sieve then a plastic jar containing 95% ethanol. Invertebrates were picked from each sample and identified to genus or species for aquatic insects and family or order for terrestrial invertebrates using a dissecting microscope and common keys (e.g., Merritt, Cummins, and Berg 2019) by the same laboratory over the course of the study (Rhithron Associates Inc., Missoula, MT).

After identification, invertebrates were added to a dried, ashed and preweighed glass fibre filter (Whatman, type GF/A, 47 mm diameter, 1.6 µm pore size) (Fisher Scientific, Bothell, USA). These filters were placed in preweighed aluminium tins and dried to a constant weight at 105°C for 4 h and allowed to cool in a desiccator before weighing. Dried samples were then baked in a muffle furnace at 500°C for 1.5 h to combust all organic material. Samples were cooled in a desiccator before weighing to the nearest 0.0001 g (ash mass). Invertebrate prey biomass (mg AFDM) was the difference between the dried and ashed weights (https://www.nemi.gov/methods/method_summary/9326/). To calculate biomass concentration (mg $AFDM/m^3$, hereafter mg/m^3), drift biomass was divided by the volume of water flowing through net over the sample period (Smock 2007). Water volume through the net was determined according to the methods by Pringle and Ramírez (1998). Drift samples from July and August/September sample events were pooled before analysis.

It is important to note that prey resources supporting stream salmonids and other freshwater consumers are highly variable in space and time because of variability in species phenology and the environment (e.g., temperature) (Wipfli and Baxter 2010; Rashidabadi et al. 2022; Rossi et al. 2023). Further, we recognise our sample methods captured snapshots of this variability. However, for four reasons, we suggest invertebrate drift biomass concentration is a reasonable proxy for the overall prey resource availability experienced by juvenile salmonid populations during our study. First, previous research showed that stream salmonid growth, biomass and density positively covaries with invertebrate drift biomass or abundance (Wilzbach, Cummins, and Hall 1986; Rosenfeld and Raeburn 2009). Second, stream salmonids in the study tributaries mostly forage on invertebrates drifting in the water column and on the water surface (Macneale et al. 2010). Third, drift samples were collected at the same location by trained individuals using a standardised method and processed by the same laboratory ($n = 49$ sample events,

$n = 224$ samples), thus limiting some sources of sampling variation. Fourth, drift samples were collected twice per sample season and across 8 years and seven streams, thus capturing a range of environmental conditions, including temperature and prey concentration, which can lead to a more robust and reliable regression model.

2.2.3 | Juvenile Salmonids

To estimate instantaneous daily growth rate (%/d) and density of juvenile Chinook salmon and steelhead trout, we used a Smith-Root backpack electrofisher (Model 12b) (Smith-Root, Vancouver, USA) (Achord et al. 1996; Achord, Levin, and Zabel 2003). Fish density (fish/100 m²) was estimated by dividing the number of fish captured per area of stream habitat sampled each summer. Steelhead trouts were categorised into age-0+ or sub-yearlings (40–80 mm fork length) and age-1+ or yearlings (81–140 mm) based on a combination of size–frequency histograms and otolith markings (Chittaro et al. 2015).

To estimate instantaneous daily growth, we used the otolith (ear bone) from sub-yearling ($n = 61$) and yearling steelhead trout ($n = 70$) and juvenile Chinook salmon ($n = 382$) (e. g., Chittaro et al. 2015). Fish used to estimate daily growth were either incidental mortalities resulting from fish tagging efforts or captured opportunistically (see Sanderson et al. 2009). The latter fish were overdosed with tricaine methanesulfonate (MS-222) according to recommended protocol (https://fisheries.org/doi/9781934874394-ch8/) (Sanderson et al. 2009). In the field, sacrificed fish were wet-weighed to the nearest 0.1 g, measured to the nearest 1 mm (fork and total length) and then placed on dry ice. Once back in the laboratory, fish were frozen at −20°C until processing the otolith (Chittaro et al. 2015).

To estimate daily growth rate, we captured digital images of extracted otoliths using a camera (Leica DFC450) mounted to a compound scope (Carl Zeiss Microscopy, White Plains, USA). Using Image Pro Plus (Media Cybernetics Image-Pro Software, Version 7.0, Rockville, USA), we took two measurements from each otolith image: Distance from the otolith core to edge (i.e., otolith radius at time of capture, Oc) and distance from the otolith core to 14 daily increments away from the otolith edge (i.e., otolith radius measured at 14 days before capture, Oa) (Chittaro et al. 2015). These measurements (Oc and Oa) allowed us to estimate individual juvenile Chinook salmon and steelhead trout fork length 14 days prior to capture (FLa).

For each Chinook salmon, we estimated FLa using the quadratic equation with a biological intercept reported in Zabel, Haught, and Chittaro (2010), which is specific to Snake River spring/summer Chinook:

$$FLa = ((0.096 \times (Oa - Ointercept)) + (0.000053 \times (((Oa - Ointercept)))))$$
$$\times (Oa - Ointercept) + FLintercept$$

where fish length (FLintercept) and otolith radius (Ointercept) at hatching were 21.6 mm and 95.8 μm, respectively. To constrain the models to pass through these intercepts, we first subtracted the intercept from each individual′s fork length and otolith radius.

To estimate individual steelhead fork length prior to capture, we used the Fraser–Lee equation (Fraser 1916; Lee 1920):

$$FLa = d + (Lc - d) / Oc\ Oa$$

where d is the intercept (−2.53) of the regression between the fork length and otolith radius at capture, and Lc represents the fork length (mm) at capture.

After estimating FLa, we then calculated instantaneous daily growth rate (% increase in length mm/d) for each Chinook salmon and steelhead for the last 14 days of life (a):

$$\text{Instantaneous growth (mm / day)} = \left(\frac{LN(Lc) - LN(FLa)}{t} \right)$$

where LN equals the natural log, FLc represents fish fork length (mm) at the time of capture, while FLa represents fork length 14 days (t) prior to capture (Shoup and Michaletz 2017). We multiplied this value by 100 to express instantaneous growth rate as a percentage. We used a 14 days growth period because we hypothesised it would be more likely to capture some of the natural variability in prey concentration and availability, such as adult insect emergence events, than a shorter interval.

3 | Data Analysis

We used linear mixed-effects models to analyse whether variation in individual daily growth rates of juvenile Chinook salmon and sub-yearling and yearling steelhead trouts covaried with predictor variables according to expectations (Bolker et al. 2009). Because of a larger sample size, we used multiple linear regression to conduct a similar analysis for juvenile Chinook salmon after averaging across individual fish within a stream and sample event ($n = 49$). A problematic aspect of aggregating is that inferences about the relationships in the data can change as the level of aggregation changes, and this should be taken into account when interpreting results (Maas-Hebner et al. 2015).

Juvenile Chinook salmon density (4.8 fish/100 m²) was used as covariate in statistical analysis because, on average, they outnumbered juvenile steelhead trout density (sub-yearling and yearling combined = 0.56 fish/100 m²) eightfold. Juvenile Chinook salmon were also about 18% larger than sub-yearling steelhead trout during the sample period. Because of the combination of individual size and abundance, we hypothesised juvenile Chinook salmon were more likely to influence biotic interactions and energy flow within the salmonid assemblage.

To assess the plausibility of models predicting how daily growth (G, %/d) varied as a function of the fixed effects of prey concentration (F, mg/m³), water temperature (T, °C) and juvenile Chinook salmon density (D, fish/100 m²), we used the small sample size Akaike′s Information Criterion (AIC$_c$) and associated metrics (Burnham and Anderson 2002) (Table S1). In the

mixed-effects model, stream was included as a random term to account for unmeasured stream to stream differences (Zuur et al. 2009). For interaction terms, we examined three plausible two-way interactions, including interactions between water temperature and prey concentration (T × F), water temperature and juvenile Chinook density (T × D) and juvenile Chinook density and prey concentration (D × F) in both the mixed-effects and linear regression analysis. An interaction effect indicates that the effect of one causal variable (e.g., prey concentration) on daily growth rate depends on the value of a second causal variable (e.g., temperature). All interactions also included individual main effects (see Table S1). Although plausible, we did not include three-way interactions to avoid overfitting the models. Prior to model selection, we standardised predictors so that their mean was 0 and variance 1. The model with the lowest AIC_c value has more support relative to other plausible models (Burnham and Anderson 2002).

We focus our interpretation on models with a difference in $AIC_c < 2$ ($\Delta AIC_c = AIC_{ci} - AIC_{cmin}$), as they are considered to have substantial support given the data (Burnham and Anderson 2002). Support for each model relative to others in the set was also assessed by Akaike weights (w_i) and evidence ratios (w_i/w_j). Models with higher weights and evidence ratios are more plausible relative to others in the candidate set. To assess model fit for mixed models, we calculated the proportion of conditional variance (R^2_m) of the dependent variable (individual growth rate) explained by fixed factors (F, D, T) and R^2_c, which is the conditional variance explained by both fixed and random factors (stream). The difference between R^2_c and R^2_m shows how much variability is in the random effect, which can range from 0 to 1 (Nakagawa and Schielzeth 2013). To asses model fit of linear models, we used the coefficient of variation (R^2). Plots of residuals versus fitted values, histograms of residuals and quantile–quantile plots indicated assumptions of normality and heterogeneity were largely confirmed.

All analyses were conducted in R-studio (version 1.3; R Development Core Team 2020) using the packages MuMIn (Bartoń 2022) and nmle (Pinheiro and Bates 2000, 2022) for model selection and coefficient estimation, and the effects (Fox and Weisberg 2019), sjPlot for plotting model effects (Lüdecke 2022) and ggplot2 (Wickham 2016) libraries for correlation and graphics.

4 | Results

4.1 | Environmental Conditions

Environmental conditions were variable over the course of the study. Median instantaneous daily stream discharge at SFS over the course of the study was $6.6 \, m^3/s$ with a minimum of 2.2 and maximum of $122.6 \, m^3/s$. Averaged across streams, mean annual daily water temperature was 11.6°C, with a range of 4.5°C (9.4°C in 2003 to 13.9°C in 2009) (Figure 2a). Mean annual invertebrate prey biomass concentration ranged 3.9-fold from 0.08 to $0.31 \, mg/m^3$, with a study mean of $0.20 \, mg/m^3$ (Figure 2b). Juvenile Chinook salmon annual relative density varied 2.8-fold ($2.5–7.1 \, fish/100 \, m^2$) with a mean value of $4.8 \, fish/100 \, m^2$

(SD = 1.4) (Figure 2c). On average, juvenile steelhead trout density was eightfold lower than juvenile Chinook salmon, ranging from $0.41 \, fish/m^2$ in 2004 and 2009 to $0.93 \, fish/m^2$ in 2012 (mean = $0.56 \, fish/100 \, m^2$) (Table S2).

On average, yearling steelhead trout (mean fork length = 96.4 mm) were 45% longer than juvenile Chinook salmon (66.3 mm) and 72% longer than sub-yearling steelhead trout (56.0 mm) (Figure 3a). Because they emerge earlier, juvenile Chinook salmon were 18.4% longer than sub-yearling steelhead trout and were as much as 44% longer in some years. On average, individual daily growth of sub-yearling trout (0.98%/d) was about 2.6 times higher than yearling trout (0.38%/d) and 1.75 times higher than juvenile Chinook salmon (0.56%/d) (Figure 3b). Juvenile Chinook salmon daily growth was the lowest in 2003 and 2014 (~0.42%/d) and highest in 2009 (0.8%/d). Sub-yearling steelhead growth rates were lowest in 2003 and 2004 (0.66%/d), peaking at 1.43%/d in 2008, while the growth rate of yearling steelhead was lowest in 2004 (0.26%/d) and highest in 2011 (0.59%/d) (Figure 3c).

4.2 | Daily Growth Rate

4.2.1 | Juvenile Chinook Salmon

Juvenile Chinook salmon individual daily growth rate (%/d) positively correlated with each covariate. The strongest correlation (Pearson's correlation coefficient) between juvenile Chinook salmon daily growth rate and predictors was observed with water temperature ($r = 0.51$, $p < 0.001$), followed by invertebrate prey biomass concentration ($r = 0.34$, $p < 0.001$), and juvenile Chinook salmon density ($r = 0.13$, $p = 0.01$) (Figure 4a–c).

The best approximating linear mixed-effects model predicting annual variation in juvenile Chinook salmon individual daily growth rate included juvenile Chinook salmon density (D, + slope) and water temperature (T, + slope) as fixed effects (Table 1). The 95th confidence interval for model estimated standardised slope coefficients for water temperature and density did not overlap 0; the standardised coefficient for water temperature was about 2.7 times greater than density (Table 2). Overall, this model explained 61% of total model variance with the fixed effects explaining 47% and the random effect of stream explaining 16%. The second-ranked model, which was 14% less likely than the top-model, included the individual fixed effects of density and temperature and their interaction (T × D). However, the 95% confidence interval for the interaction term coefficient included zero.

The top-ranked linear model predicting variation in juvenile Chinook daily growth rate at the stream level included a positive dependence with both prey concentration and water temperature. This model explained 32% of total variance. Based on standardised coefficients and 95% confidence intervals, the relative effects of water temperature (0.07 [0.03, 0.11]) and food concentration (0.05 [0.007, 0.09]) on individual growth were relatively similar. The 2nd ranked model, which included an interaction between prey concentration and water temperature, also received substantial support. The interaction term indicates that
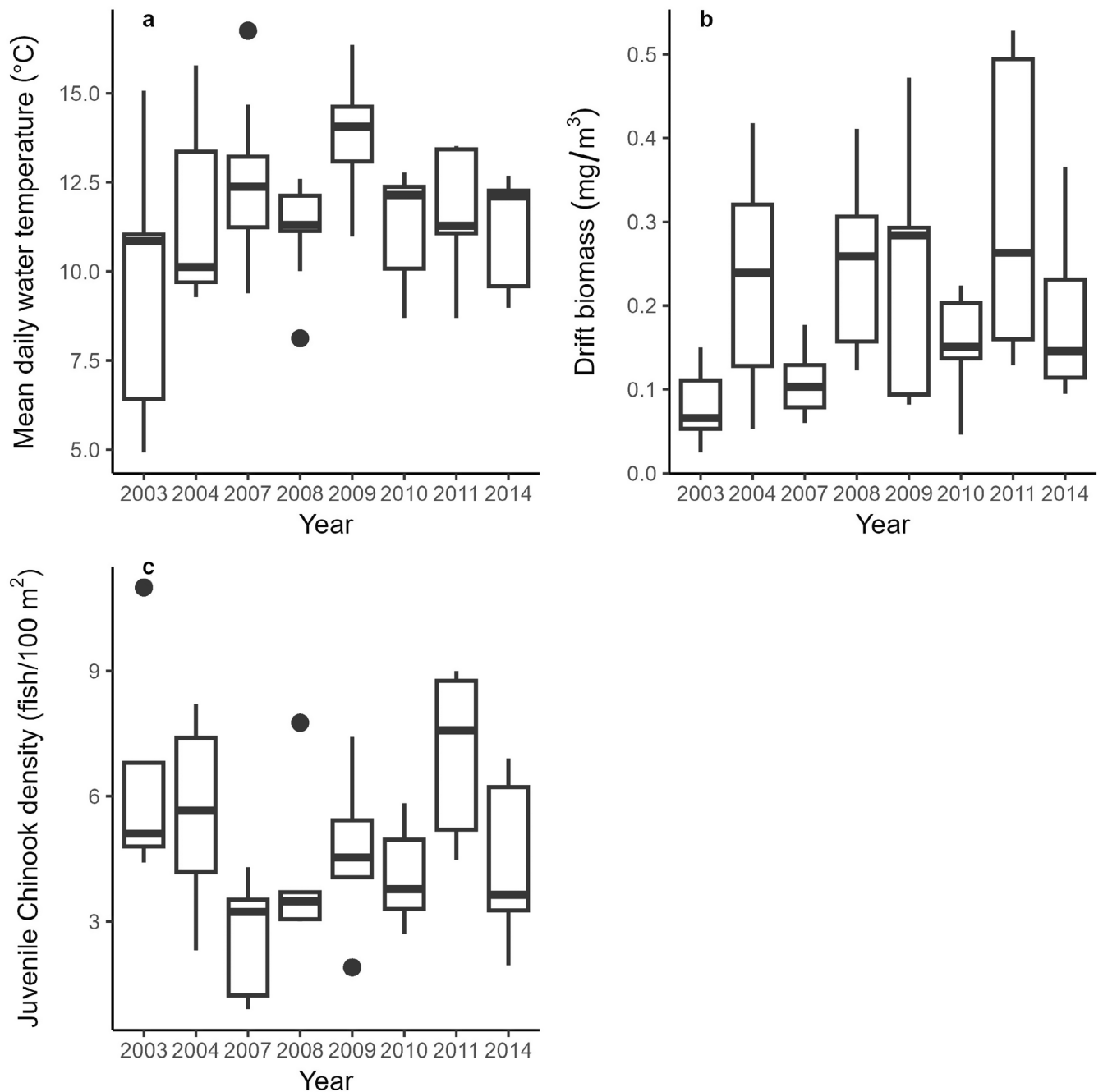
FIGURE 2 | Box plots of (a) mean daily water temperature (°C) 14 day before fish capture, (b) invertebrate prey biomass concentration (mg/m³) and (c) juvenile Chinook salmon density (fish/100 m²) for each year of the study. The box limits indicate the range of 50% of the data, the central line within the box represents the median, the lines or whiskers extending from the box capture the remaining data and the dots outside the whiskers represent outliers.

juvenile Chinook salmon growth rate increased with water temperature but at a higher rate in prey-rich summers (Figure 5). For example, the model predicts juvenile Chinook salmon daily growth is 26% higher (~0.79%/d vs. 0.63%/d) at a mean daily temperature of 11°C and a high prey concentration (0.31 mg/m³) relative to a low (0.07 mg/m³) concentration. Also receiving substantial support was a model including the additive effects of water temperature (+slope) and juvenile Chinook salmon density (+slope). Based on Akaike weights, the top-ranked model was 46% more likely than the 2nd ranked model and 57% more likely than the 3rd ranked model.

4.2.2 | Sub-Yearling Steelhead Trout

Sub-yearling steelhead trout growth rate positively covaried with water temperature ($r = 0.40$, $p < 0.01$) and prey concentration ($r = 0.23$, $p = 0.07$), while negatively covarying with juvenile Chinook salmon density ($r = -0.21$, $p = 0.10$) (Figure 6a–c).

The top-ranked linear mixed effects model predicting variation in sub-yearling steelhead growth rate included the main and interactive effects of prey concentration and water temperature (Table 1 and Figure 7). Similar to juvenile Chinook salmon at
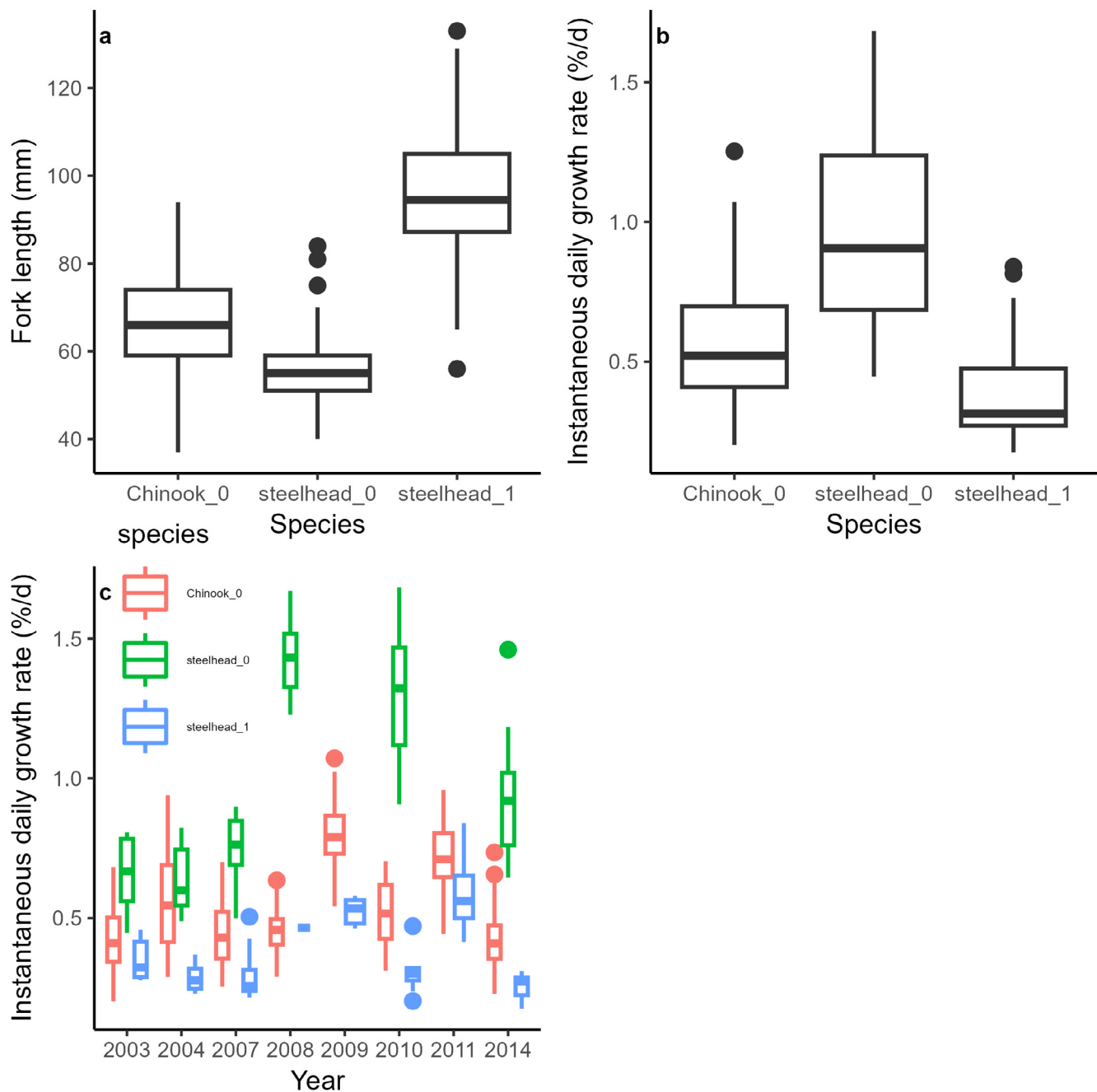
FIGURE 3 | Box plot of (a) fork length (mm) at the time of capture, (b) daily growth rate (%/d) over a 14-day period prior to capture for juvenile Chinook salmon and sub-yearling (steelhead_0) and yearling steelhead trout (steelhead_1), and (c) instantaneous daily growth rate (%/d) 14 days prior to capture for each taxon for each year of the study. The box limits indicate the range of 50% of the data, the central line within the box represents the median, the lines or whiskers extending from the box capture the remaining data and the dots outside the whiskers represent outliers.

the stream-level, this interaction predicts individual growth rate increased with mean daily water temperature but at faster rates at high prey concentrations relative to low prey concentrations. At 11°C, this model predicts sub-yearling trout growth rate is 81% faster (1.81%/d) at a high prey concentration (0.31 mg/m³) relative to a low prey concentration (1.0%/d, 0.07 mg/m³). The fixed effects of this model explained 37% of total variance and the random effect of stream explained an additional 12%. A close second was an additive model, which included food (+slope) and water temperature (+slope); this model explained 7% less total variance than the top-ranked model.

4.2.3 | Yearling Steelhead Trout

Yearling steelhead trout individual growth rate positively co-varied with all predictors. The strongest correlation was with juvenile Chinook salmon density ($r = 0.39$, $p < 0.001$), followed by prey concentration ($r = 0.23$, $p = 0.06$) and water temperature ($r = 0.21$, $p = 0.08$) (Figure 8a–c).

There was only one model with a ΔAIC_c score less than 2 (Table 1). This model predicts yearling steelhead trout daily growth rate increases with a unit increase in both water
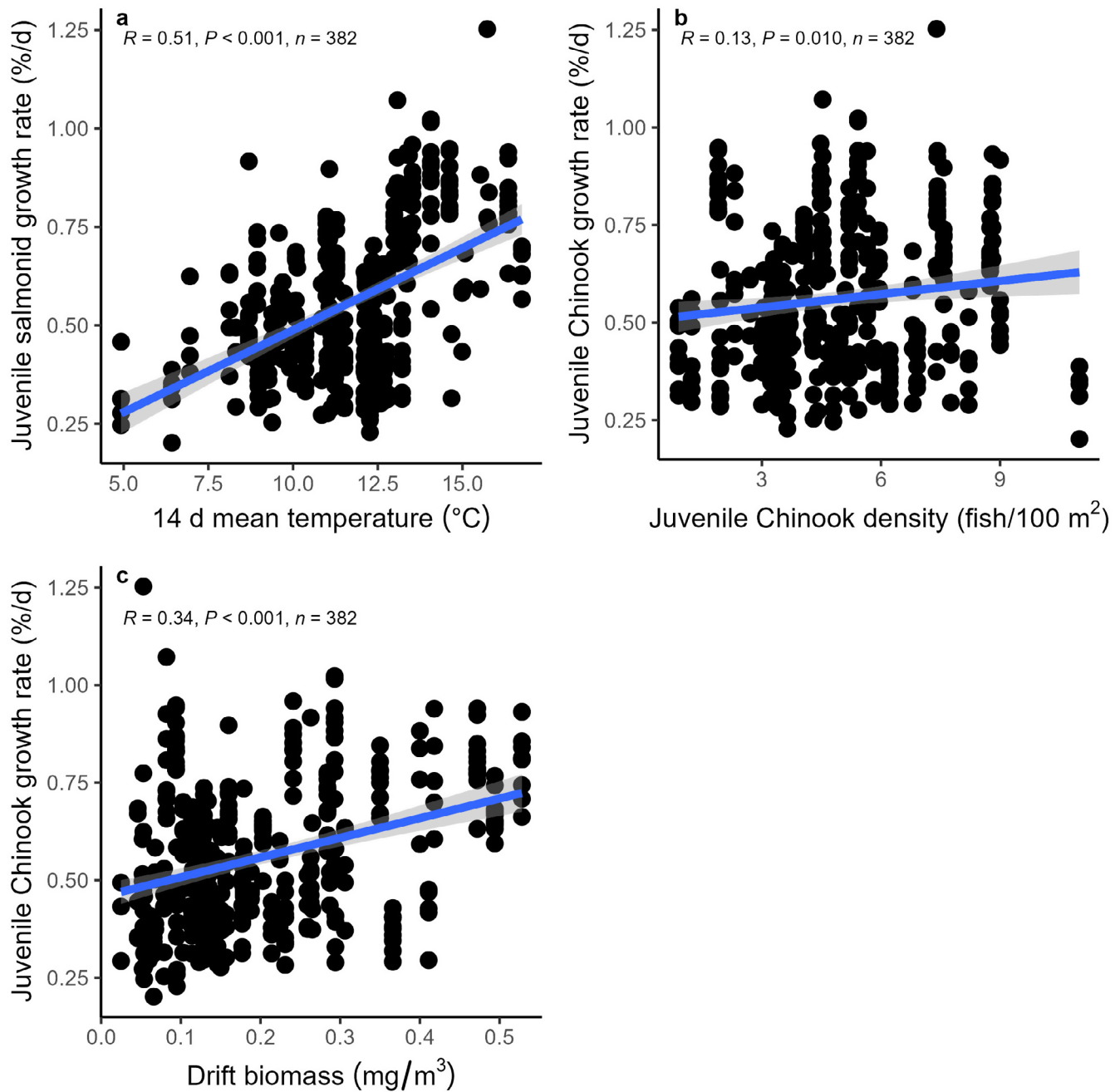
FIGURE 4 | Best fit regression (solid line) and 95% confidence interval (shaded region) representing the relationship between juvenile Chinook salmon individual daily growth rate (%/d) and (a) mean daily water temperature 14 days prior to capture (°C), (b) juvenile Chinook density (fish/100 m²), and (c) invertebrate prey concentration (mg/m³) (R represents Pearson's correlation coefficient).

temperature and juvenile Chinook density; estimated standardised coefficients for density (0.07 [0.02, 0.08]) and water temperature (0.05 [0.04, 0.10]) were similar (Table 2). The fixed effects of this model explained 27% of total variance, while the random effect of stream explained an additional 9%.

5 | Discussion

Individual growth rate is a key component of consumer fitness and can influence a variety of demographic processes (e.g., Boudry et al. 2003). In our study, juvenile Chinook salmon and steelhead trout daily growth rates positively covaried with water temperature, invertebrate drift biomass concentration and local Chinook salmon density, with the nature of these relationships varying by species and age class. Our analysis also indicated that juvenile Chinook salmon and steelhead trout growth increased at a faster rate in warm summers that were food-rich relative to food-poor. We suggest that when making decisions related to the conservation of freshwater consumers and their habitats, natural resource managers not only address degradation of chemical and physical attributes, but also attributes relevant to energy flow, including prey resource biomass and composition (Saunders and Fausch 2007; Weber et al. 2014; Rhoades et al. 2023; Rossi et al. 2023; Ouellet et al. 2024).

TABLE 1 | Results from regression models with an $\Delta AIC_c < 2$ estimating the individual and interactive effects of mean daily water temperature (T, °C), invertebrate prey biomass concentration (F, mg AFDM/m^3) and juvenile Chinook salmon density (D, fish/100 m^2) on juvenile Chinook salmon and steelhead trout (sub-yearling and yearling) daily growth rate (G, %/d).

	Rank	Model	df	AIC_c	ΔAIC_c	W	R^2_m	R^2_c
Juvenile Chinook salmon (individual)	1	$G \sim T + D$	5	−378.7	0	0.538	0.47	0.63
	2	$G \sim T + D + T \times D$	6	−378.4	0.30	0.462	0.47	0.63
Juvenile Chinook salmon (stream)	1	$G \sim T + F$	4	−60.5	0	0.413	0.32	NA
	2	$G \sim T + F + T \times F$	5	−59.2	1.23	0.223	0.33	NA
	3	$G \sim T + D$	4	−58.7	1.73	0174	0.30	NA
Sub-yearling steelhead trout	1	$G \sim T + F + T \times F$	6	30.9	0	0.384	0.37	0.59
	2	$G \sim T + F$	5	31.3	0.31	0.329	0.32	0.52
	3	$G \sim D + F$	5	32.7	1.77	0.158	0.31	0.60
Yearling steelhead trout	1	$G \sim T + D$	5	−80.4	0	0.697	0.27	0.36

Abbreviations: df = model degrees of freedom; $\Delta AIC_c = AIC_{ci} - AIC_{cmin}$ or AIC_c differences; W = Akaike weights; and model variance due to fixed effects alone (R^2_m) and the combination of fixed effects and the random stream effect (R^2_c).

TABLE 2 | Estimated standardised coefficients and 95% confidence intervals from models with $\Delta AIC_c < 2$ predicting the individual and interactive effects of water temperature (T, °C), invertebrate drift biomass concentration (F, mg/m^3), local juvenile Chinook density (D, fish/100 m^2) on juvenile Chinook salmon (individual and stream-level) and steelhead trout (sub-yearling and yearling) daily growth rate (G, %/d).

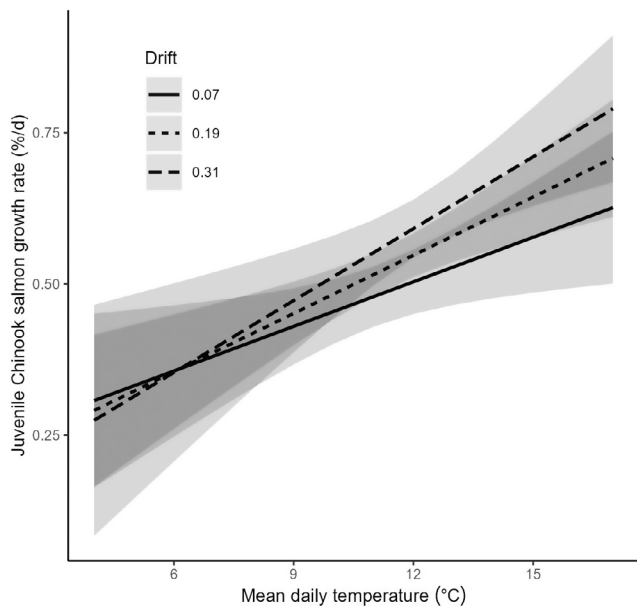|	Intercept	T	F	D	T×F	Random effect
Juvenile Chinook salmon (individual)	0.57 (0.50, 0.64)	0.16 (0.14, 0.18)		0.06 (0.04, 0.08)		0.09 (0.05, 0.16)
Juvenile Chinook salmon (stream)	0.55 (0.51, 0.58)	0.07 (0.03, 0.11)	0.05 (0.007, 0.09)			NA
Sub-yearling steelhead trout	1.0 (0.84, 1.24)	0.23 (0.12, 0.35)	0.15 (0.07, 0.24)		0.08 (−0.01, 0.17)	0.19 (0.09, 0.41)
Yearling steelhead trout	0.37 (0.32, 0.43)	0.05 (0.02, 0.08)		0.07 (0.04, 0.10)		0.05 (0.01, 0.16)

FIGURE 5 | Marginal effects plot displaying juvenile Chinook salmon daily growth rate (%/d) at the stream level in response to the interaction between invertebrate prey biomass concentration (0.07, 0.19, 0.31 mg/m^3) and mean daily water temperature (°C).

5.1 | Invertebrate Prey Resources

The positive covariation between juvenile salmonid growth rate and invertebrate drift biomass concentration we observed is consistent with laboratory experiments (Brett, Shelbourn, and Shoop 1969; Elliott 1975), bioenergetic models (Railsback and Rose 1999; Beauchamp 2009; Rhoades et al. 2023), mesocosm experiments (Warren et al. 1964; Kiernan, Harvey, and Johnson 2010), field manipulations (Mason 1976; Johnston et al. 1990) and some observational studies (e. g., Weber et al. 2014). For instance, the addition of marine ephausids (Euphausicea) to a small Vancouver Island stream increased juvenile coho salmon carrying capacity by 6–7-fold, cancelled the negative effect of juvenile coho density, accelerated growth rate and substantially increased the pre-winter lipid preserves (Mason 1976). Similarly, the daily growth rate of juvenile sockeye salmon (*O. nerka*) rearing in Alaskan lakes positively covaried with zooplankton biomass, their main energy source (Edmundson and Mazumder 2001; Schindler et al. 2005). Pink salmon growth in the ocean was also enhanced by prey resource concentration, especially lipid-rich prey (e. g., Aydin et al. 2005). A variety of other freshwater consumers exhibit higher daily growth rates when food is elevated,
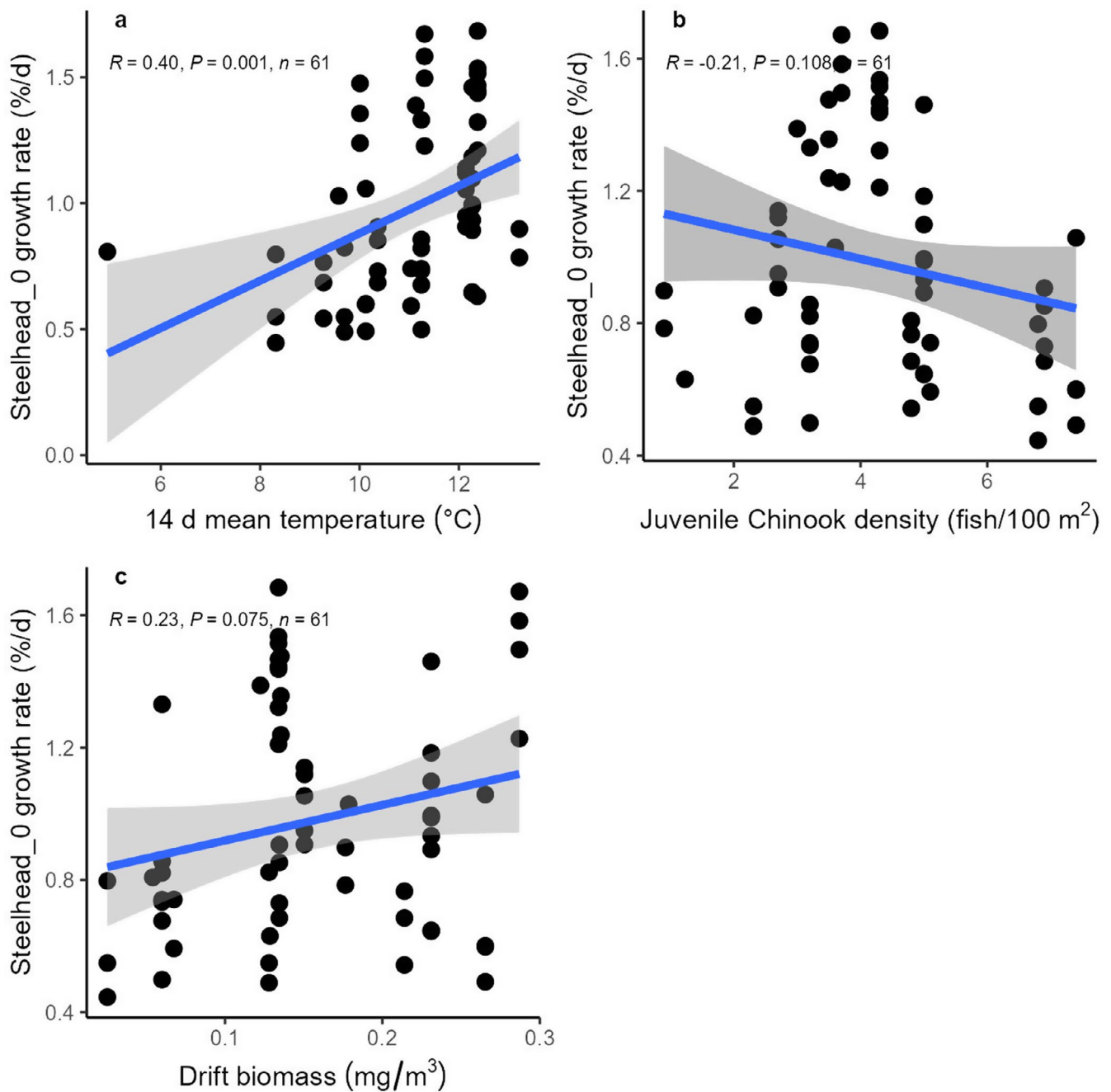
FIGURE 6 | Best fit regression line and 95% confidence interval (shaded region) representing the relationship between sub-yearling (age-0+) steelhead trout individual daily growth rate (%/d) and (a) mean daily water temperature 14 days prior to capture (°C), (b) juvenile Chinook relative density (fish/100 m^2) and (c) invertebrate prey biomass concentration (mg/m^3).

including other species of fish (Leach and Houde 1999; Barriga et al. 2012; Le Pape and Bonhommeau 2015), stream invertebrates (Richardson 1991) and lake zooplankton (DeMott, Edington, and Tessier 2004).

Not only did daily growth rate positively correlate with prey concentration, our analysis indicated that wild sub-yearling steelhead (individual-level) and Chinook salmon (stream-level) daily growth rates were amplified in warm, food-rich summers, relative to warm, food-poor summers. These results are consistent with laboratory experiments (e.g., Wurtsbaugh and Davis 1977), a recent stream enclosure study (Lusardi et al. 2020) and bioenergetic simulations (e.g.,

Beauchamp 2009). We note that the best model predicting juvenile Chinook salmon growth rate depended on the level of data aggregation (individual vs. stream-level). We are unsure of the mechanism causing this difference, but with additional years of data collection, we may resolve some of this uncertainty.

The positive correlation between consumer daily growth and water temperature and prey concentration may depend not only on the mean value but also the variance around the mean. The growth rate of juvenile steelhead trout rearing in enclosures with supplemental prey (larval mealworms, Coleoptera) positively correlated with a principal components axis representing
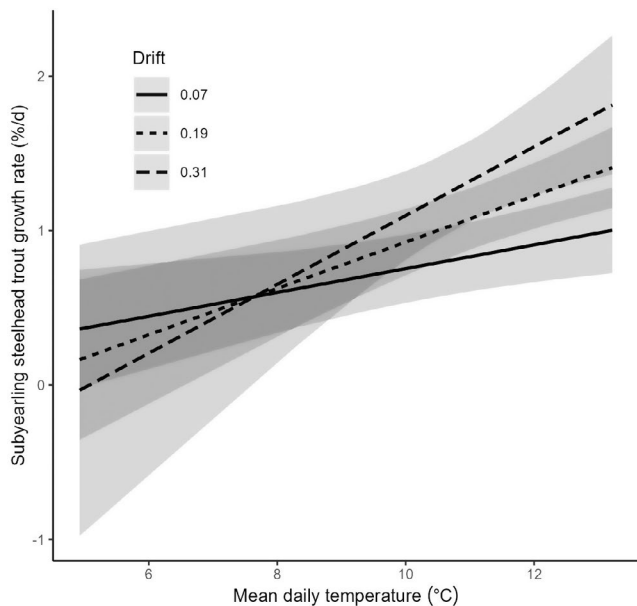
FIGURE 7 | Marginal effects plot displaying sub-yearling steelhead trout daily growth rate (%/d) at the individual-level in response to the interaction between invertebrate prey biomass concentration (0.07, 0.19, 0.31 mg/m^3) and mean daily water temperature (°C).

stream sections that were cool and variable relative to locations that were warm and stable (Boughton et al. 2007). Thus, subtle patterns of temperature and prey resource heterogeneity in aquatic systems are also likely important in determining the individual growth potential for freshwater consumers in the wild (Bozinovic et al. 2011; Armstrong et al. 2010, 2021; Weber et al. 2014; Rossi et al. 2023). We recommend additional research on this topic because climate change is predicted to increase the variance of select environmental attributes, like water temperature and stream discharge, which may have important effects on prey resource heterogeneity and consumer performance (Benedetti-Cecchi 2003; Steel et al. 2012).

Although there is strong empirical and theoretical evidence that food is a vital element of freshwater habitat supporting higher trophic levels, most management efforts to restore or enhance riverine habitats for stream fish, including salmonids, address physical (e.g., connectivity) and chemical (e.g., toxins) habitat limitations (Bernhardt et al. 2005; Nagayama and Nakamura 2010). Addressing these limitations is clearly important for species and ecosystem recovery, and may in fact improve conditions for energetically important prey populations. However, we suggest these conservation efforts may be more effective, especially in a warming climate, with a more holistic, landscape approach that not only explicitly considers chemical and physical conditions, but also biological, including prey biomass, quality and composition at different spatial and temporal scales (Schlosser 1991; Ensign, Strange, and Moore 1990; Rosenfeld et al. 2005; Wipfli and Baxter 2010; Rossi et al. 2023).

5.2 | Temperature

Water temperature is a principal variable determining the individual growth rate of freshwater consumers, including

stream-rearing salmonids, by modulating physiological rates (e.g., assimilation efficiency) and behaviour. We show that juvenile salmonid growth rate in these cool mountain streams positively covaried over the range of observed mean daily summer water temperature (9.4°C–13.9°C). Our results are also consistent with recent field studies examining the effects of water temperature on somatic growth of juvenile salmonids rearing in cool water streams (mean daily range: 5.8°C–14.6°C) in Alaska (Armstrong et al. 2010), Idaho (Crozier et al. 2010) and Norway (Bærum et al. 2013). Similar relationships have been observed in lakes: a 22 year study on Lake Windermere, UK found annual juvenile and adult perch growth increment positively correlated with lake temperature (summer water temperature range ~14°C–22°C) (Le Cren 1958).

Although juvenile salmonid daily growth rate increased with mean daily water temperature in our study, the linear relationship we observed was likely because fish were rarely exposed to physiologically stressful temperatures (≥ 16°C) (Brett, Shelbourn, and Shoop 1969; Elliott 1975; Marine and Cech 2004). The relationship between the juvenile sockeye salmon daily growth rate and water temperature in the laboratory increased non-linearly with water temperature across a range of food rations (> 1.5% of body weight to excess rations) until reaching a maximum between 5°C and 15°C, depending on ration size, after which growth abruptly declines (Brett, Shelbourn, and Shoop 1969).

In many parts of their range, streams salmonids are regularly exposed to physiologically stressful stream temperatures during summer and early autumn, and the spatial and temporal extent of this exposure will increase with climate change (e.g., Gallagher, Geargeoura, and Fraser 2022). For example, bioenergetic simulations, grounded in detailed field observations, predicted juvenile steelhead trout rearing in northern California coastal streams would lose mass during summer because of energetic bottlenecks created when mean daily water temperature exceeded 17°C, likely due to low invertebrate prey concentrations (McCarthy et al. 2009). Similarly, juvenile steelhead trout in Lapwai Creek, ID experienced poor or negative summer somatic growth as mean daily July water temperature (17.3°C) exceeded the thermal optimum based on energy intake rates (Myrvold and Kennedy 2015). Using a combination of experiments, field studies and models, additional research is necessary to better define water temperature limits for freshwater consumers, including stream salmonids, in the wild. Ideally, these studies would also measure factors that modify a consumer's response to ambient temperature, including habitat complexity, water velocity, biotic interactions, prey resource heterogeneity and pathogen load (Boughton et al. 2007; Armstrong et al. 2010; Crozier et al. 2010; Bruneaux et al. 2017; Twining et al. 2019).

5.3 | Juvenile Chinook Salmon Density

In addition to prey resources and water temperature, consumer daily growth rate can negatively correlate with the local density of putative competitors, due to reduced access to essential resources (Le Cren 1958; Jenkins et al. 1999; Bærum et al. 2013). Some studies report that these negative density-dependent effects can be amplified at higher water temperatures
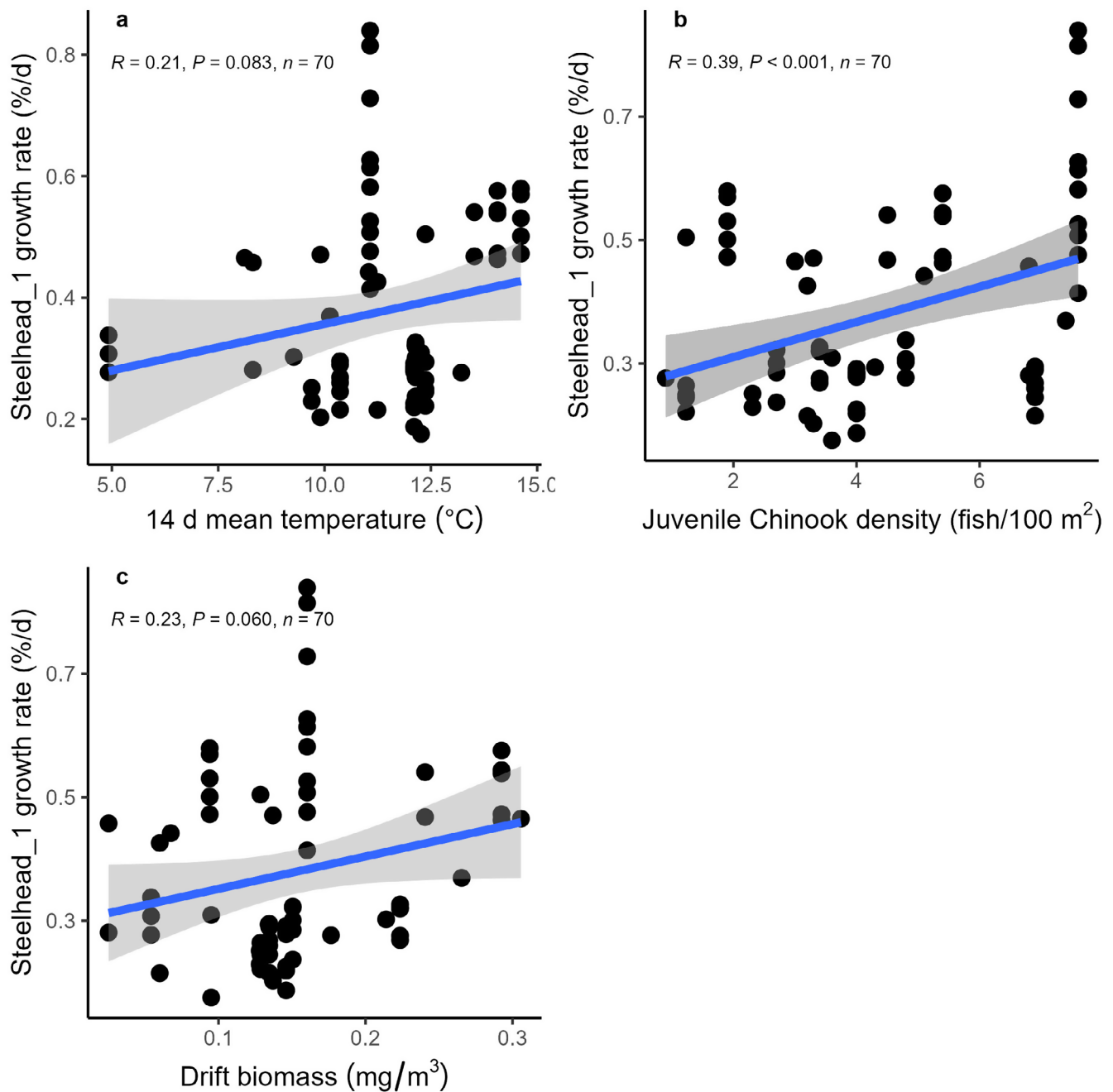
FIGURE 8 | Best fit regression line and 95% confidence interval (shaded region) representing the relationship between yearling (age-1+) steelhead trout individual daily growth rate (%/d) and (a) mean daily water temperature prior to capture (°C), (b) juvenile Chinook relative density (fish/100 m^2) and (c) invertebrate prey biomass concentration (mg/m^3).

because of increased metabolic costs (Crozier et al. 2010; Sloat and Osterback 2013; Myrvold and Kennedy 2018; de Barros, Villacorta-Correa, and Carvalho 2019). Therefore, we anticipated that juvenile steelhead trout and juvenile Chinook salmon growth rates would negatively correlate with juvenile Chinook salmon density, with this relationship enhanced in warm summers. In contrast, we observed that juvenile Chinook salmon and yearling steelhead trout daily growth rate positively covaried with juvenile Chinook salmon density. We are unsure of the mechanism(s) explaining the difference between our study and previous research in the basin Crozier et al. (2010) and elsewhere (e.g., Grossman and Simon 2020). One reason for the

dissimilarity may be sample size: Crozier et al. (2010) sampled several orders of magnitude more juvenile Chinook salmon (131, 286 vs. 382 for our study) from 13 independent streams and populations over a 16-year period, thus capturing a much greater range of environmental conditions (e.g., juvenile Chinook salmon density) than we did.

There are several other possible explanations for the positive covariation between daily growth rate and juvenile Chinook salmon density we observed. This pattern could simply reflect the fact that the study systems can support both relatively high juvenile Chinook salmon densities and daily growth

rates because of suitable physical and chemical conditions and energetically sufficient invertebrate prey biomass. The positive correlation between juvenile Chinook salmon density and invertebrate drift biomass concentration we observed provides partial support for this hypothesis (Pearson's $r = 0.46$, $p < 0.001$). For yearling steelhead, the positive covariation between daily growth rate and local juvenile Chinook salmon density could also result from increased opportunities for predation on smaller Chinook. During field surveys, we observed yearling steelhead, which were 45% larger, prey upon juvenile Chinook salmon.

6 | Caveats and Implications

Common to observational studies, there are a several caveats about our study to note (Morshed, Tornetta, and Bhandari 2009; Lemoine et al. 2016). First, it is possible that fish primarily acquired energy from outside the sample reach before capture, and the invertebrate assemblage and concentration in this habitat were different than the capture location. Second, prey resources and fish foraging behaviour are spatially and temporally heterogenous and our sampling regime only captured a snapshot of this heterogeneity (e.g., Armstrong et al. 2010). Third, equating juvenile Chinook salmon density with competition is complicated by behavioural factors, such as niche partitioning, which can mediate the relationship between density and competition (Hearn 1987). Fourth, there are likely confounding and unmeasured factors, such as predation pressure, stream discharge, habitat volume and complexity and fire disturbance history that can also determine juvenile salmonid growth rates in the study streams (Werner et al. 1983; Rosenfeld and Taylor 2009; Rosenberger et al. 2015).

Despite these caveats, we propose our multi-stream, multi-year observational study is instructive with respect to identifying potential drivers of juvenile salmonid daily growth rate—a key fitness trait—when randomised controlled trials, especially those conducted at relevant temporal and spatial scales, are logistically challenging. Our results are mostly consistent with bioenergetic models, experiments and field studies and imply that natural resource managers focusing on increasing the resilience of stream salmonids and other freshwater consumer populations in a warming climate should consider not only physical and chemical conditions but also prey resources when making conservation decisions (Bellmore et al. 2013; FitzGerald et al. 2022; Rhoades et al. 2023; Ouellet et al. 2024).

To better inform natural resource managers regarding the prey resources supporting stream fish populations, more research is needed to investigate the variability in prey concentration, nutritional quality and composition and how these characteristics overlap with fish foraging behaviour (Rossi et al. 2023). We also must improve our understanding of local (e.g., water temperature) and landscape-scale (e.g., channel form) factors contributing to prey resource variability (Wipfli and Baxter 2010; Ouellet et al. 2024). To better understand the foodscape, defined as the spatial and temporal mosaic of growth potential that consumers exploit across a catchment (Rossi et al. 2023), we suggest taking advantage of both past and future restoration actions (e.g., riparian planting

including density and composition) to investigate how these action influence prey assemblages for stream fish (Rossi et al. 2023; Ouellet et al. 2024). An improved understanding of invertebrate prey resource variability, including the identification of environmental drivers of this variability, is especially imperative for informing future conservation efforts in a warming climate, as increasing temperatures will increase an ectothermic consumer's metabolic rate exponentially (e.g., Crozier et al. 2010).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.