

RESEARCH ARTICLE

A melting cryosphere constrains fish growth by synchronizing the seasonal phenology of river food webs

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Abstract

Mountain watersheds often contain a mosaic of glacier-, snow-, and rain-fed streams that have distinct hydrologic, temperature, and biogeochemical regimes. However, as glaciers diminish and precipitation shifts from snow to rain, the physical and chemical characteristics that make glacial or snowmelt streams distinct from rain-fed streams will fade. Among the unforeseen consequences of this hydrologic homogenization could be the loss of unique food webs that sustain aquatic consumers. To explore the impacts of a melting cryosphere on stream food webs, we parameterized an aquatic food web model with empirical physicochemical data from glacier-, snow-, and rain-fed streams in southeast Alaska and used the model to simulate the seasonal biomass dynamics of aquatic primary producers and consumers and the growth of juvenile salmon. Model results suggest that glacier-, snow-, and rain-fed streams exhibit seasonal asynchronies in the timing of biofilm and aquatic invertebrate abundance. Although warmer rain-fed streams were more productive during the summer (June through September), colder glacial and snowmelt streams provided enhanced foraging and growth opportunities throughout the remainder of the year. For juvenile salmon that can track peaks in resource abundance within river networks, the loss of meltwater streams strongly constrained modeled growth opportunities by removing spatially and temporally distinct foraging habitats within a watershed. These findings suggest that climate change induced homogenization of high latitude river networks may result in the loss of unique food web dynamics, which could diminish the capacity of watersheds to sustain mobile consumers.

KEYWORDS

climate change, food webs, glaciers, mobile consumers, Pacific salmon, resource phenology, river networks

1 | INTRODUCTION

Glacier and snowmelt contributions to streams and rivers are decreasing and will eventually disappear from many watersheds as the climate warms (Huss et al., 2017). This loss of meltwater is predicted

to reduce freshwater biodiversity in many high-latitude and high-elevation watersheds (Cauvy-Fraunié & Dangles, 2019; Jacobsen et al., 2012; Milner et al., 2009). Effects on species diversity are relatively well-studied in proglacial streams and suggest that some organisms may be extirpated, such as certain species of aquatic

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insects adapted to cold water (Brown et al., 2007; Finn et al., 2013). However, loss of meltwaters could also alter the structure and phenology of river food webs that support aquatic consumers (Clitherow et al., 2013; Fell et al., 2017; Milner et al., 2017).

Glacier- and snow-fed streams may support food webs with distinct seasonal dynamics compared with non-meltwater-fed streams (i.e., rain-fed) due to strong differences in light, temperature, discharge, and biogeochemical regimes (Milner et al., 2017). For instance, glacier-fed streams in temperate regions generally have high, cold, and turbid flows in the summer, whereas summer flows in rain-fed streams are typically lower, warmer, and more amenable to light penetration (Fellman, Hood, et al., 2014; Fellman, Nagorski, et al., 2014; Hood & Berner, 2009; Malard et al., 2000; Moore et al., 2009). These pronounced physicochemical differences may create unique seasonal cycles in the production and availability of aquatic resources such as primary (algae) and secondary producers (aquatic insects). In turn, this phenological diversity could provide seasonally distinct foraging opportunities that promote the growth and population stability of mobile consumers (Abrahms et al., 2019; Armstrong et al., 2016), such as fishes, that can move across heterogeneous river networks tracking sequential peaks in food availability (Jardine et al., 2012; Ruff et al., 2011). Although prevailing research suggests that cold meltwater-fed river networks will become more biologically productive as meltwaters diminish (Milner et al., 2017; Pitman et al., 2020), a potentially unforeseen consequence could be a shrinking portfolio of seasonal forage and growth windows for mobile organisms as peaks in resource availability occur more synchronously (Sarremejane et al., 2021).

Here, we explore how meltwaters impact resource phenology in watersheds along the Gulf of Alaska (GOA), which support some of the most productive Pacific salmon (*Oncorhynchus* spp.) fisheries in the world (Johnson et al., 2019). Coastal watersheds in this region frequently contain a mosaic of glacier-, snow-, and rain-fed tributaries

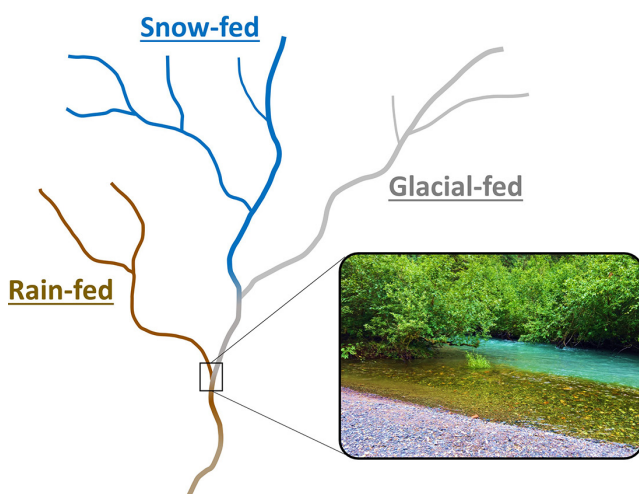


FIGURE 1 Coastal Gulf of Alaska watersheds can contain a mosaic of glacier-, snow-, and rain-fed streams that frequently co-occur in close proximity, creating visually and hydrochemically striking contrasts, such as when tannin-stained rain-fed streams merge with cold and turbid glacier-fed streams (inset photograph)

(Figure 1) that have distinct flow, temperature, and biogeochemical regimes and provide accessible year-round habitat to salmon (Figure 2; Edwards et al., 2013; Fellman, Hood, et al., 2014; Hood & Berner, 2009). Juvenile salmon live up to 2 years in these streams before migrating to the ocean and can move long distances within watersheds to track favorable conditions for growth and survival (Armstrong et al., 2013; Sethi et al., 2021). Thus, the close spatial juxtaposition of meltwater and non-meltwater streams could enhance juvenile salmon productivity by providing an intra-watershed portfolio of streams with different resource phenologies (Moore et al., 2015). However, the contribution of meltwater to this portfolio is changing as the climate warms. The mountain glaciers that surround the GOA have some of the highest rates of mass loss on Earth (Larsen et al., 2015), and winter precipitation is rapidly shifting from snow to rain (Littell et al., 2018). As glacier and snowmelt contributions to runoff diminish, the physical and chemical characteristics of meltwater streams will become more similar to those of rain-fed streams (O'Neel et al., 2015). This loss of meltwater is predicted to have important implications for mobile consumers such as salmon at watershed scales (Jones et al., 2020; Pitman et al., 2020), however the impact of these changes on the resource portfolios that sustain mobile consumers has not been evaluated.

Using a food web simulation model (Bellmore et al., 2017), we explored how the distinct physicochemical properties of glacier-, snow-, and rain-fed streams (Figure 2) influences seasonal resource dynamics, and the capacity of watersheds to support juvenile salmon growth. Our model mechanistically linked the dynamics of river food webs to empirical flow, temperature, nutrient, and turbidity regimes for glacier-, snow-, and rain-fed streams in the GOA. For each stream type, we simulated the seasonal availability of benthic biofilm, aquatic macroinvertebrates (primary prey for juvenile salmon), and juvenile salmon growth potential (i.e., food assimilation minus metabolic costs). We then constructed a heterogeneous river network model comprised of one glacier-fed, one snow-fed, and one rain-fed tributary, and a downstream mainstem that integrated these tributaries. We examined the potential for this “mosaic” river network to support fish growth using an individual-based model (Railsback & Grimm, 2019), where individual fish varied in their propensity to move between stream types. Finally, we manipulated watershed heterogeneity by removing meltwater streams from the model to explore how juvenile salmon growth may be affected by the loss of cryospheric reserves from watersheds.

2 | METHODS

2.1 | Physicochemical conditions of glacier-, snow-, and rain-fed streams

The physicochemical conditions used to parameterize the food web model were collected monthly from November 2004 to December 2008 from 12 streams surrounding Juneau, Alaska. The 12 watersheds range in area from approximately 1 to 231 km² and extend from near sea level to the western margin of the Juneau Icefield (max elevation ~2100m; Figure S1), and all support salmon rearing except one (due to human

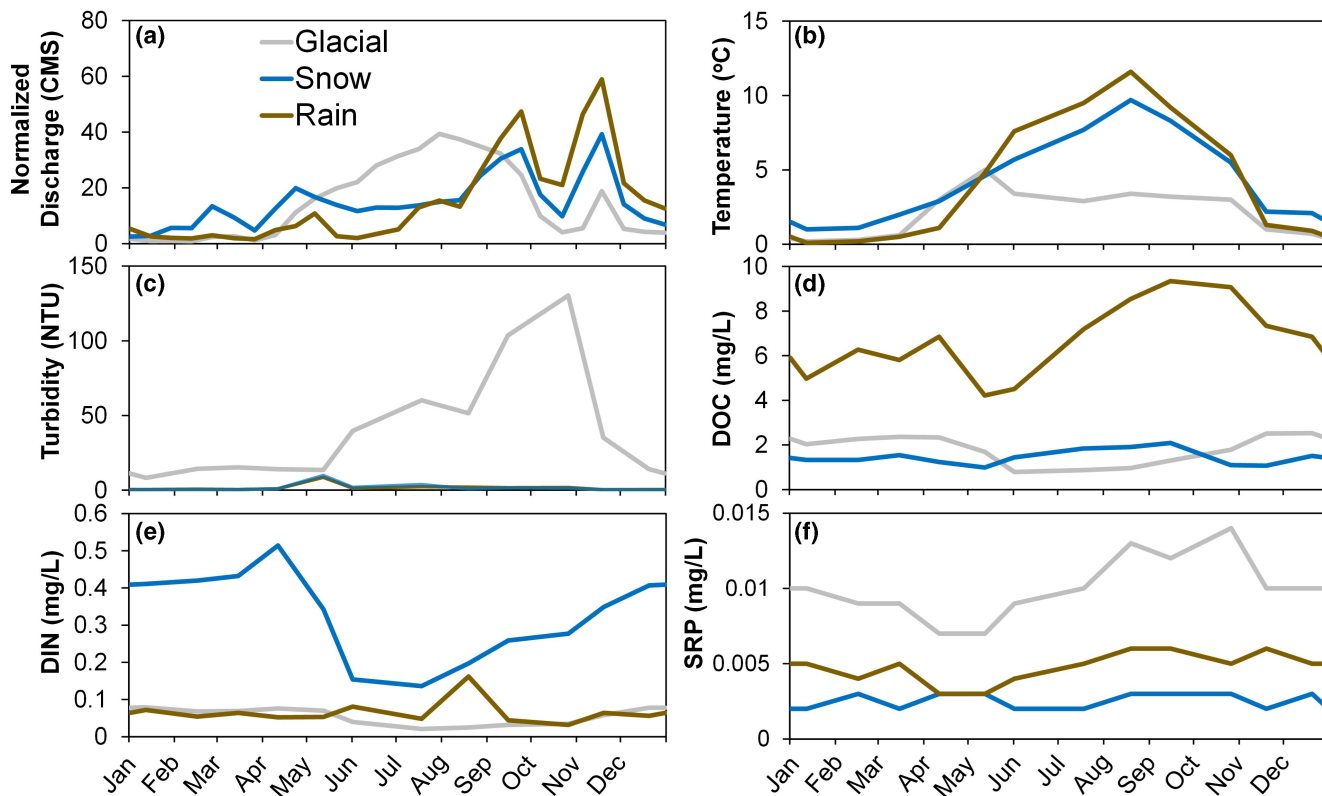


FIGURE 2 Physicochemical characteristics of glacier-, snow-, and rain-fed streams near Juneau, Alaska used to parameterize the food web model: (a) normalized discharge, (b) water temperature, (c) water turbidity (nephelometric turbidity units [NTU]), (d) dissolved organic carbon (DOC) concentration, (e) dissolved inorganic nitrogen (DIN) concentration, and (f) soluble reactive phosphorus (SRP) concentration. Mean monthly physical and biogeochemical data by stream type from monthly sampling of 12 streams (4 glacier, 4 snow, and 4 rain-fed) over a 4-year period of record. Discharge values from stream gauges located on one glacier-, snow-, and rain-fed stream, and were normalized to account for differences in stream size across the gauged systems (see Section 2)

modification). Watersheds were categorized into three broad stream types based on their dominant watershed characteristics and annual hydrographs (Sergeant et al., 2020): lower elevation rain-fed streams (forest and wetland-dominated, $n = 4$), higher elevation snow-fed streams (largely forest and alpine, $n = 4$), and glacier-fed streams (that are predominately fed by the Juneau Icefield; $n = 4$). The physicochemical heterogeneity among these 12 watersheds was used as a proxy for the heterogeneity that exists in single watersheds where glacier-, snow-, and rain-fed stream co-occur. Collecting this physicochemical data from a single watershed (or multiple watersheds) that contained a mosaic of glacier-, snow-, and rain-fed tributaries (see Figure 1) was restricted by a lack of access to the upper reaches of these remote river basins.

We collected three replicate 250 ml water samples monthly at approximately midday (9 a.m. to 3 p.m.) from each stream for biogeochemical analysis. All water samples were filtered in the field through pre-combusted, glass fiber filters (nominal pore size 0.7 μm) and placed in acid washed polyethylene bottles that were stored in the refrigerator at 4°C until analyzed. From each 250 mL sample, subsamples were taken to estimate nutrient concentrations. Concentrations of dissolved organic carbon (DOC) were analyzed by high temperature combustion on a Shimadzu TOC-V-CSH analyzer. Nitrate- and nitrite-nitrogen ($\text{NO}_3\text{-N}$ and $\text{NO}_2\text{-N}$) was measured using a Dionex DX600 ion chromatograph with an AS18A anion column, and

ammonium-nitrogen ($\text{NH}_4\text{-N}$) was measured using a Dionex ICS-1500 with a CS16C cation column. Soluble reactive phosphorus (SRP) was measured colorimetrically using the ascorbic acid method (Murphy & Riley, 1962) with a 10 cm quartz flow-through cell to enable the detection of low SRP concentrations (lower detection limit $\sim 1 \mu\text{g P/L}$). A handheld YSI (Model 85) meter was used to measure water temperature in the field for each sample date, and turbidity was measured in the laboratory using a HACH (2100P) turbidimeter.

Stream discharge was only available for three of the 12 watersheds (one of each type) where gauge data was available, but which represent the generalizable flow pattern of each stream type in the GOA (Sergeant et al., 2020). Discharge was measured in Peterson Creek (rain-fed) using a stilling well equipped with a pressure transducer (Solinst model 3001) and a rating curve was built using the stage-discharge relationship. Discharge for Montana Creek (snow-fed) and Mendenhall River (glacier-fed) were obtained from the US Geological Survey (site numbers 15052800 and 15052500, respectively).

2.2 | Food web model

We used the Aquatic Trophic Productivity (ATP) model to explore how physicochemical conditions found in these glacier-, snow-, and

rain-fed streams influence the seasonal availability of aquatic resources and growth of juvenile salmon (Bellmore et al., 2017; Whitney et al., 2019). The ATP model is a dynamic river food-web simulation model that represents the generalized trophic structure of river food webs. At the base of the food web are biomass stocks of biofilm (e.g., attached algae and heterotrophic microbes) and terrestrial detritus (e.g., leaf litter from riparian vegetation) that are consumed by aquatic invertebrates, which along with terrestrial invertebrates that enter the stream from the riparian zone, are consumed by fish. Fish and aquatic invertebrate consumption rates are a function of both: (1) density dependence, whereby foraging rates decrease as fish/invertebrate densities increase; and (2) food availability, whereby foraging rates increase as resource availability goes up following a type II functional response (see Bellmore et al., 2017). In turn, consumers deplete the availability of resources when consumption by fish/invertebrates exceed the rate of resource renewal, which can result in density-dependent resource limitation. The model also includes the multiple trophic pathways by which adult spawning salmon influence the food web, including: consumption of salmon eggs by fish, consumption of post-spawned salmon carcasses by aquatic invertebrates, and incorporation of labile dissolved nutrients (nitrogen and phosphorus) by biofilm (Bellmore et al., 2017). The model runs on a daily time step and tracks the biomass of biofilm, terrestrial detritus, aquatic invertebrates, and fish through time in units of grams of ash-free dry mass per square meter (g AFDM/m^2). For an annotated description of the model structure see Whitney et al. (2019).

The biomass dynamics of the food web and the performance of specific trophic groups (biofilm, aquatic invertebrates, and fish) are mechanistically linked to the physicochemical conditions of rivers. Concentrations of dissolved inorganic nitrogen (DIN ; $\text{NO}_2 + \text{NO}_3 + \text{NH}_4$), SRP, and DOC influence the production of biofilm at the base of the food web in the model. Water temperature mediates the metabolic rates of organisms and decay rates of organic matter. Stream discharge controls seasonal patterns of stream depth, width, velocity, and shear stress, which in turn influences the retention and export of organisms and organic matter, as well as the amount of wetted habitat available to support biological production. Water turbidity along with water depth influences biofilm production by attenuating light before it reaches the stream bed.

The ATP model has been described in detail elsewhere, including a comprehensive list of parameter values, sensitivity analyses, coding, and comparisons with empirical data, and we refer the reader to those references for additional model details (Bellmore et al., 2017; Whitney et al., 2019). However, two important modifications were made to the ATP model for this analysis. First, we added an explicit linkage between DOC bioavailability and biofilm production (in addition to DIN and SRP) to account for the strong differences in DOC observed among GOA stream types (Figure 2) and the importance of DOC to instream heterotrophic biofilm production (Fellman et al., 2015). The assumed relationship between DOC concentration and biofilm production was a type II functional response curve, described by a DOC half-saturation value of 5 mg/L. Second, instead of

having one fish stock that represents the entire population, we converted the fish biomass stock into an individual based model (IBM; Railsback & Grimm, 2019) that tracks the size and growth of individual fish that can move between different modeled river segments. Thus, the modified model represents a food web model linked to an IBM for fishes. The Wisconsin Bioenergetics Model (Deslauriers et al., 2017) was used to calculate metabolic rates (consumption, respiration, and specific-dynamic action) for each fish; which accounts for allometric changes in mass-specific consumption and respiration as fish grow. The model was parameterized to represent juvenile coho salmon (*Oncorhynchus kisutch*), which are one of the most abundant salmon that reside year-round in GOA rivers.

2.3 | Model scenarios and parameterization

We parameterized the ATP model with generalized flow, temperature, turbidity, and nutrient regimes for glacier-, snow-, and rain-fed streams, constructed by averaging empirical data across watersheds ($n = 4$ for each stream type) and years ($n = 4$ years). This approach was preferable to parameterizing the model for each of the 12 watersheds across all 4 years because stream flow data was only available for three of the watersheds, and turbidity and temperature data were missing for some dates. Furthermore, this approach allowed us to examine how generalizable physicochemical differences among glacial-, snow-, and rain-fed streams common in GOA rivers (Edwards et al., 2013; Fellman, Hood, et al., 2014; Hood & Berner, 2009), influences aquatic food webs and mobile aquatic consumers. That said, we also parameterized the model across our 4 years of data (2005–2008) to examine how interannual variability in physicochemical conditions (averaged across watersheds) influences model outcomes. This required estimating the value of missing temperature and turbidity data assuming linear interpolation between known data points.

To isolate how differences in seasonal flow, temperature, turbidity, and nutrient regimes between glacier-, snow-, and rain-fed streams influence modeled resource dynamics, other model parameters were held constant between stream types, which included: channel gradient (0.01 m/m), channel hydraulics and substrate, stream shading and riparian vegetation cover, and the number and timing of returning adult salmon (see Figure S2). In southeast Alaska channel morphology and vegetation structure can be similar among glacier-, snow-, and rain-fed streams, especially at lower elevations where these stream types come together (although snow- and glacier-fed streams often have different morphology and vegetation at higher elevations and in outwash basins (Lisi et al., 2013; Sergeant et al., 2020). Furthermore, flow data was normalized to account for differences in the size of the three gauged watersheds. For each stream, we first calculated the proportion of total annual discharge that occurred each day and then multiplied these proportions by the average of the total annual discharges across the three streams to convert the proportions back to cubic meters per second. This procedure retained the differences in flow seasonality among glacier-, snow-, and rain-fed streams that influence other physicochemical

conditions (e.g., nutrient concentrations, turbidity), while keeping the total annual discharge the same in each stream.

We first used the model to simulate daily and average annual biofilm and aquatic macroinvertebrate biomass (g AFDM) for a calendar year in one glacier-, one snow-, and one rain-fed stream. Our aim was to explore seasonal biofilm and aquatic invertebrate availability in the absence of top-down pressures from consumers. Thus, no juvenile salmon were included in these simulations. We also calculated the average annual amount of biofilm and aquatic invertebrate biomass that would be available to mobile consumers that could perfectly track seasonal differences in food resource availability; that is, by instantaneously moving to the stream type with the greatest food availability at any point in time. The model also tracked the availability of terrestrial (i.e., leaf litter and insects) and marine (carcasses and eggs from spawning adult salmon) subsidies that we assumed entered each stream at the same time, but we focus on results for in-stream producers and consumers that are directly influenced by the distinct physiochemical regimes of glacier-, snow-, and rain-fed streams.

Using these modeled resource asynchronies, we examined the daily mass-specific "growth potential" for juvenile coho salmon in each stream type (g/g/day), where growth potential is the balance of metabolic gains (food assimilation) minus metabolic costs (respiration and specific-dynamic-action; Warren & Davis, 1967). Daily growth potential values were used to model the annual growth (g AFDM) that an individual juvenile coho salmon could accrue by residing year-round in the glacier-, snow-, and rain-fed streams (assuming coho fry emerge from their gravel nest on May 1). We then calculated the total annual growth of a single juvenile coho salmon that could move among the three stream types, perfectly tracking differences in fish growth potential through time without any energetic costs. Given these assumptions, we interpret modeled growth as the theoretical potential to grow a single fish.

To examine how the loss of meltwater fed streams influences the growth of juvenile coho salmon, we constructed a model river network comprised of one glacier-fed stream, one snowmelt-fed stream, one rain-fed stream, and a mainstem that integrates these tributaries (Figure 4a). We assumed that each stream reach was 10 m in length, which allowed for tractable model run times relative to larger reaches that contained more individual fish (which slowed model simulations) without influencing modeled outcomes. The physicochemical conditions of the mainstem reach were weighted by the amount of discharge coming from each upstream tributary. For instance, water turbidity in the mainstem reach was the average of turbidity values in the glacier-, snow-, and rain-fed tributaries, weighted by the amount of flow coming from each stream type at a given time step. We then created three additional river networks where we removed the glacier and snow-fed tributaries, including networks where: (1) the snow-fed tributary was replaced with a rain-fed tributary; (2) the glacier-fed tributary was replaced with a snow-fed tributary; and (3) both the glacier and snow-fed tributaries were removed creating an entirely homogeneous rain-fed network.

We examined the capacity of each of these river networks to grow juvenile coho salmon. First, we simulated the annual growth trajectory

of an individual juvenile coho salmon that could perfectly track seasonal asynchronies in growth potential across each of the river networks without energetic costs or density-dependent limitations (theoretical potential for growth). Second, we examined the growth trajectories of a population of coho salmon that varied in their propensity to move. To do this, we seeded river networks with 200 juvenile coho salmon (50 in each tributary and mainstem reach) and gave each individual fish a randomly selected movement propensity that represented their ability to track differences in growth potential (ΔGP) between river network locations. Each fish was randomly assigned a ΔGP value between 0 to 0.1 (uniform distribution), which represented the difference in growth potential among stream reaches necessary to initiate movement. Fish with ΔGP values close to 0 move to capitalize on small differences in growth potential among stream reaches, and fish with larger values of ΔGP require larger growth potential discrepancies before moving (and thus, may never leave their natal stream). For example, a fish assigned a ΔGP value of 0.05 would move once the growth potential of another reach was at least 0.05 g/g/day better than the current reach. We assumed that individuals moved without energetic cost but were susceptible to density-dependent limitations on foraging and growth. This formulation created a range of movement propensities that juvenile coho salmon have been shown to exhibit (Armstrong et al., 2013; Sethi et al., 2021), and is realistic when individuals reside in close proximity to other stream types (e.g., tributary junctions).

3 | RESULTS

3.1 | Asynchronies in stream physicochemistry

There were distinct differences in the annual discharge, temperature, and biogeochemical regimes used to parameterize the model for all three stream types (Figure 2). The rain-fed stream had higher flows in autumn (September through November) when precipitation is generally highest, while the glacial stream had higher discharges in the summer during peak glacial melt (June through September). The snow-fed stream had a bi-modal flow pattern with discharge peaks occurring during both spring snowmelt (May) and the autumn rainfall season (September–November). Summer temperatures (June through August) were warmest in the rain-fed streams peaking at $>10^{\circ}\text{C}$, slightly cooler in snow-fed streams ($8\text{--}10^{\circ}\text{C}$), and were always below 5°C in the glacial streams. Glacial streams had the highest turbidity and SRP concentrations, whereas DIN was highest in snow-fed streams (Figure 2c,e,f). In the rain-fed streams, DOC concentrations were more than 2 \times greater than the meltwater stream types and were especially high during the main runoff season from May through November (Figure 2d).

3.2 | Implications for resource availability and fish growth

The measured physicochemical differences among stream types resulted in unique seasonal cycles of modeled biofilm and aquatic

invertebrate biomass (Figure 3a,b). Seasonally, the peaks in biofilm and aquatic invertebrate biomass in the glacial-fed stream occurred earlier in the year (April/May) compared with the snow- and rain-fed streams (July/August). In the glacier-fed stream, biofilm and invertebrate biomass peaked before the onset of glacier melt, followed by a substantial decrease in productivity because of the harsh conditions that dominate glacial streams during the summer melt-season (high flow and consequent scour, and low water temperatures and clarity). In contrast, biofilm and invertebrate biomass in the snow- and rain-fed streams peaked after spring snowmelt due to warmer water temperatures and lower flows. Summer resource peaks were especially pronounced in the rain-fed stream (Figure 3a,b) where temperatures and DOC concentrations were highest. In the autumn and winter (September–January), the snow-fed stream maintained higher modeled resource availability due to slightly warmer water temperatures and lower flows. This phenological variation in resource availability resulted in growth potential for juvenile salmon being highest in the glacier stream in the spring (April and May), the rain-fed stream in the summer (June–September), and the snow-fed stream in the autumn and winter (October–March; Figure 3c). That said, cold water temperatures constrained growth potential benefits, especially in glacier- and snow-fed streams, below what might be expected based on modeled resource availability alone.

These seasonal asynchronies resulted in higher resource availability and growth for mobile consumers that can track favorable foraging and growth conditions across space and through time (Figure 3d,e,f). For instance, seasonal asynchronies in periphyton and aquatic invertebrate biomass resulted in at least 30% higher availability of these resources on an average annual basis, relative to availability in each individual stream type alone (Figure 3d,e). Furthermore, the relatively small seasonal asynchronies in fish growth potential provided by glacier- and snow-fed streams (Figure 3c) allowed juvenile salmon to continue growing—albeit slowly—throughout the entire calendar year in our model simulations. This resulted in modeled annual fish growth that was 1.4, 3.0, and 84 times greater than for fish that permanently resided in the rain-, snow-, and glacier-fed streams, respectively (Figure 3f). However, when we parameterized the model with all 4 years of empirical data, year-to-year variation in physicochemical conditions resulted in growth potential benefits from glacier- and snow-fed streams being large in some years and small in other years (Figures S3 and S4).

The model also tracked the seasonal biomass of terrestrial (terrestrial detritus and insects) and marine resources (salmon carcass and egg), but these resources were less important to fish than in-stream production of biofilm and aquatic invertebrates (Figure S5). Furthermore, because these resources are donor controlled and we assumed they entered each stream at the same time, they generally

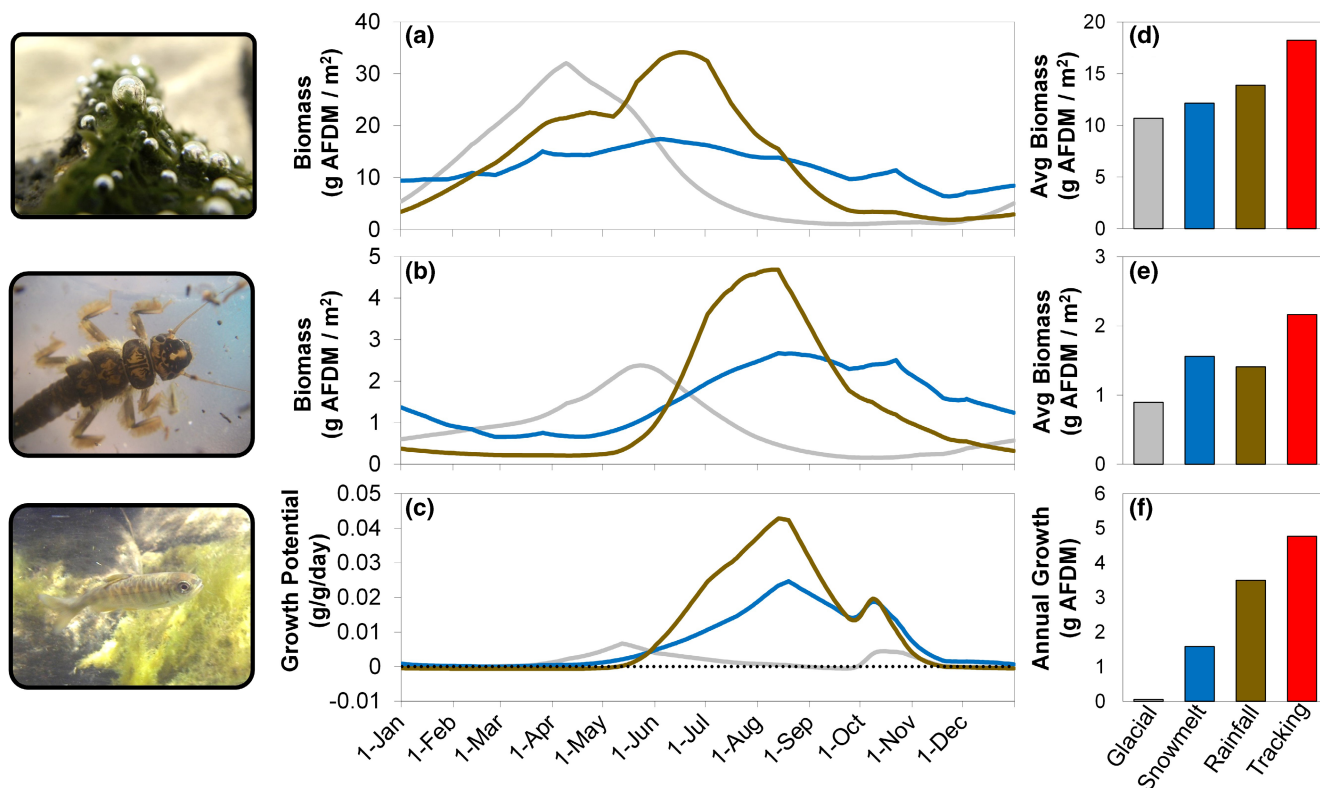


FIGURE 3 Resource asynchronies and fish growth potential in glacial-, snow-, and rain-fed streams. Left panel: Modeled biofilm (a) and aquatic invertebrate (b) biomass, and juvenile salmon mass-specific growth potential (c). Right panel: Average annual biofilm (d) and aquatic invertebrate (e) biomass, and the total amount of growth accrued by a juvenile salmon (f) in each stream. The “tracking” scenario represents the amount of resources available and growth potential for consumers that could perfectly track modeled asynchronies among the three stream types (see Section 2). Growth potential is in of grams of growth per gram of body mass per day (g/g/day). AFDM, ash-free-dry-mass

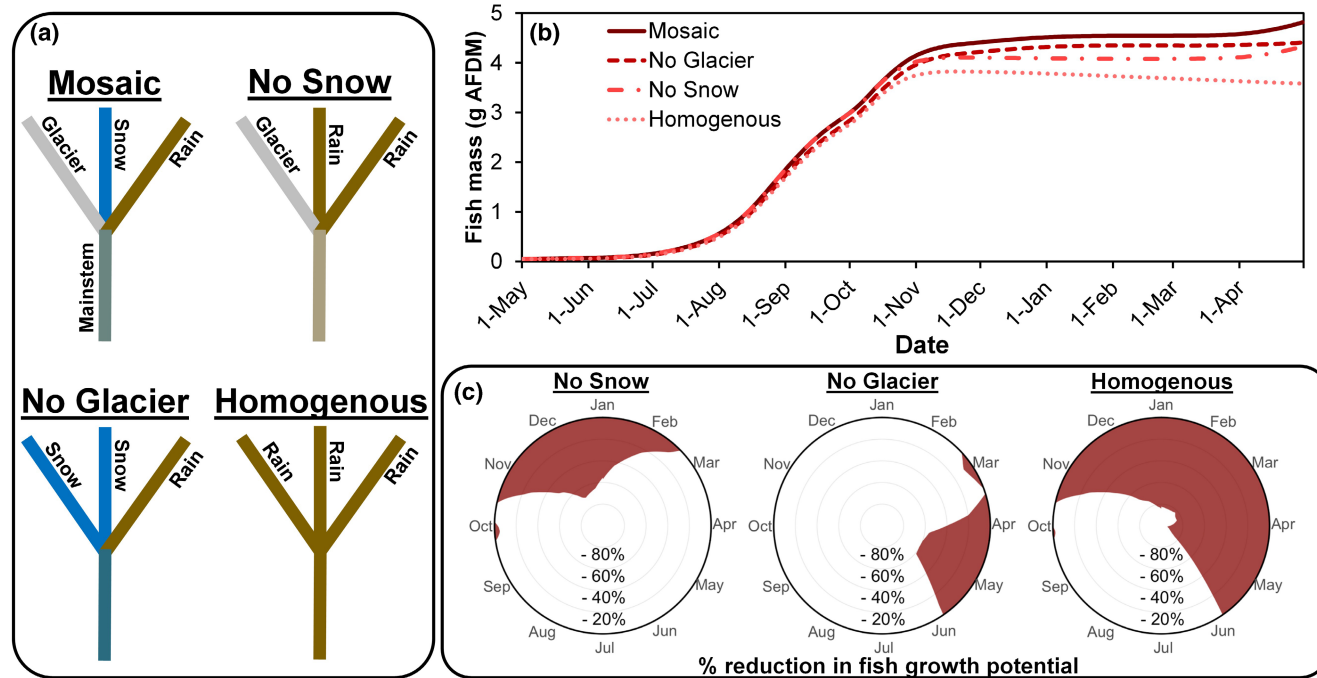


FIGURE 4 Removing glacier- and snow-fed tributaries from the modeled river network diminished juvenile salmon growth during the autumn, winter, and spring. Panel a shows the four river network scenarios that were simulated. Panel b shows modeled fish size for 1 year assuming perfect tracking of growth potential opportunities across the network (starting in May when juvenile salmon emerge from gravel nests); removing the glacier-fed stream reduced fish mass by 9%, removing the snow-fed stream reduced mass by 10%, and removing both glacier- and snow-fed streams reduced mass by 26%. Panel C shows the percent reduction in growth potential by month (shown in red) due to the loss of snow-fed (no snow), glacier-fed (no glacier), and both snow- and glacier-fed streams (homogenous) from the river network

exhibited fewer seasonal asynchronies (Figure S6). For instance, the presence of adult spawning salmon and the associated availability of salmon eggs resulted in a synchronous spike in modeled growth potential in October in each stream (Figure 3c).

3.3 | Implications of snow and glacier loss for juvenile salmon growth

In our model river network that contained all three stream types and a downstream main-stem (Figure 4a), homogenization of the fluvial network through the loss of glacier- and snow-fed tributaries reduced juvenile salmon growth by limiting foraging opportunities during the autumn, winter, and spring (October through May; Figure 4b,c). Juvenile salmon growth was greatest in the mosaic watershed that contained all three stream types, when fish were allowed to perfectly track suitable growth conditions as they shifted across space and time. Removing only the glacier tributary from the river network with its spring resource peak (Figure 3) reduced modeled fish growth from April to June, resulting in a 9% reduction in juvenile salmon mass after 1 year (Figure 4b,c). Similarly, removing only the snow-fed tributary, which had higher resource availability in the autumn and winter, reduced fish mass 10% via lost growth potential from October to March. When both glacier- and snow-fed tributaries were removed, fish mass after 1 year decreased by 26% (Figure 4b,c), which was a result of a 100% decrease in growth

potential from November through May. Thus, removing glacier- and snow-fed streams—despite their low overall growth potential (Figure 3f)—resulted in almost zero fish growth (and at times, negative growth) for over half the year.

The loss of meltwater streams from the modeled fluvial network also reduced the number of unique growth trajectories expressed by juvenile salmon (Figure 5). The mosaic river network supported 63 unique growth trajectories when 200 individual fish—which varied in their movement propensity—were placed in the network; “unique” trajectories represent fish that had a modeled mass >0.01 g AFDM different from all other fish after 1 year. Final fish masses ranged from a low of 0.1 g AFDM (almost no growth), for fish that resided year-round in the glacier stream, to 3.6 g, for fish that perfectly tracked suitable foraging conditions as they shifted seasonally across space. Fish with intermediate propensity for movement fell in-between this size range. When glacier- or snow-fed tributaries were removed, the river network supported 36 and 50 growth trajectories (out of 200), respectively, and the range of fish sizes decreased by 34% (no glacier) and 4% (no snow) from the mosaic network (Figure 5). The homogeneous rain-fed network supported only eight unique trajectories, and the range of fish sizes was reduced by 87% relative to the mosaic network (Figure 5). Average fish size, however, increased with the loss of meltwater streams from 1.6 g AFDM in the mosaic river network to 2.9 g AFDM in the homogenous rain-fed river network, due to the loss of slower growth trajectories.

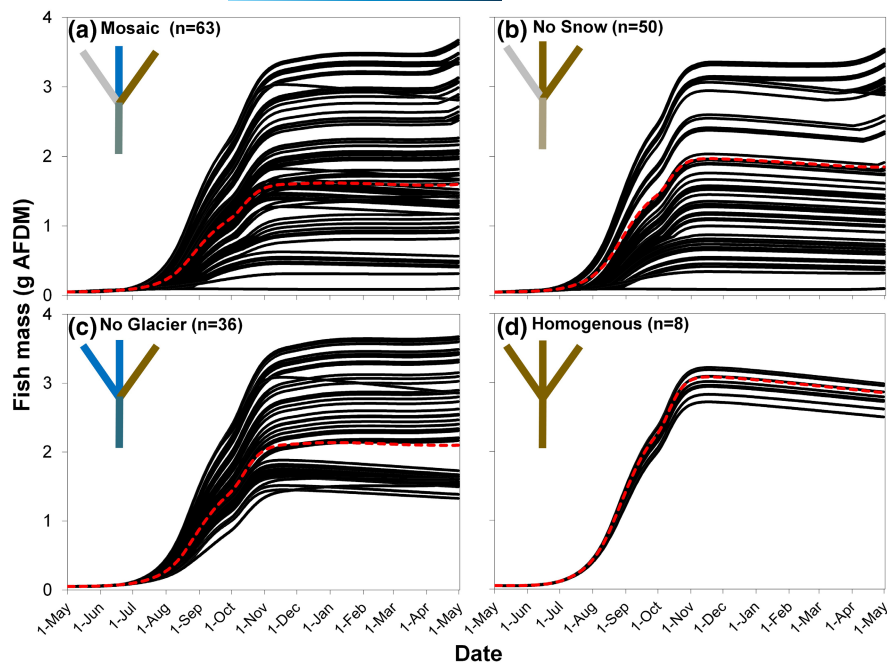


FIGURE 5 Juvenile salmon growth trajectories in modeled river networks: (a) “mosaic,” contained glacier-, snow-, and rain-fed tributaries, (b) “no snow,” snow-fed tributary replaced with rain-fed tributary, (c) “no glacier,” glacier-fed tributary replaced with snow-fed tributary, and (d) “homogeneous,” all tributaries converted to rain-fed. Dotted red line is the average growth trajectory. Simulations conducted with an individual based model initialized with 200 fish. N = the number of unique growth trajectories produced in each scenario, where each unique trajectory represents a different final fish mass. AFDM, ash-free-drymass

4 | DISCUSSION

Previous studies show that the co-occurrence of meltwater and non-meltwater fed streams can promote genetic, species, and community diversity within watersheds and across regions (Fell et al., 2018; Finn et al., 2013; Wesener et al., 2011). Our analysis highlights an additional possibility where this hydrologic heterogeneity may also support distinct food webs with seasonal variations in resource availability (Palmer & Ruhi, 2019). In watersheds with multiple stream types, this phenological variation may provide a more stable food base for mobile consumers, such as fishes, that can move across river networks tracking ephemeral foraging opportunities. As glaciers and snow fade in a warming atmosphere, and the hydrology of watersheds and regions becomes more homogeneous (Barnett et al., 2005; O’Neel et al., 2015), a consequence could be the loss of distinct food webs and a shrinking window of foraging and growth opportunities for mobile species as seasonal patterns of resource availability become more synchronized (Sarremejane et al., 2021). Although our model simulations focused on fish, these findings could also apply to other mobile organisms such as some aquatic insects and amphibians, and terrestrial consumers that forage in and adjacent to rivers. For instance, seasonal asynchronies in aquatic insect emergence could extend foraging windows for insectivorous birds and bats that have been shown to track differences in aquatic insect availability across space and time (Fukui et al., 2006; Uesugi & Murakami, 2007).

Modeled resource asynchronies were a result of distinct flow, temperature, turbidity, and nutrient regimes that exist between glacier-, snow- and rain-fed streams. In turn, these asynchronies allowed juvenile salmon to grow faster, achieve larger sizes, and express a broader range of growth trajectories by tracking energetically favorable foraging and growth opportunities as they shifted through time (Armstrong et al., 2016; McMeans

et al., 2015). These findings assumed that some juvenile salmon could perfectly track growth opportunities between streams with no energetic cost. This assumption could approximate reality in locations where these stream types occur in close proximity, such as at river confluences (Figure 1). Indeed, studies show that freshwater fishes can quickly cycle between adjacent habitats at hourly-to-weekly timescales to minimize energetic costs and maximizing growth (e.g., Wurtsbaugh & Neverman, 1988). Diel vertical migration, for instance, is a behavior common to salmonids that reside in lakes and reservoirs (Eckmann et al., 2018); and in rivers, short-timescale horizontal migrations to track suitable growth conditions have also been observed (Armstrong et al., 2013). Nevertheless, our simulations likely represent the maximum growth benefits juvenile salmon could achieve. The proximity of different tributaries, costs of movement, presence of other fish species, and other factors would likely constrain growth benefits in real river networks.

Our model finding suggest that continued declines in glacier and snow meltwater contributions to stream networks may reduce foraging opportunities for mobile consumers in watersheds along the GOA and in other meltwater-fed rivers across the globe. Shrinking forage and growth windows may be particularly detrimental in cold climates where aquatic ecosystems are unproductive much of the year and opportunities for growth are fleeting, and where organisms—such as many poikilotherms—survive at temperatures below their thermal optima (Armstrong et al., 2021). In our model analysis, glacier- and snow-fed streams provided important foraging and growth opportunities for juvenile salmon during critical windows in the spring, when fish are just emerging from their gravel nests, and again in the autumn and winter—an important period when fish size and body condition influence over-winter survival (Ebersole et al., 2006). For instance, greater spring-time growth in the glacier stream increased the modeled

size of juvenile fish shortly after they emerged from their gravel nests, and these early growth benefits compounded through time even after the fish moved to the rain- and snow-fed streams. As a result, removing the seemingly small growth benefits provided by meltwater streams reduced modeled fish growth between 9% and 26%, which in real river networks would likely have deleterious impacts on fish survival and population abundance (Ebersole et al., 2006; Kennedy et al., 2008).

Diminished glacier meltwater contributions could also result in the loss of a unique energy pathway driven by aged organic carbon released from melting glaciers. Previous food web studies have shown that this ancient glacial organic carbon is incorporated into biofilm, aquatic invertebrates, juvenile salmonids, and terrestrial spiders in proglacial forelands and streams (Fellman et al., 2015; Hågvar & Ohlson, 2013). Although the importance of this aged carbon subsidy to annual aquatic productivity remains to be quantified, it is another pathway by which a melting cryosphere may rewire the energetic pathways that support aquatic food webs.

Hydrologic homogenization could also constrain the range of growth trajectories expressed by mobile organisms (Brennan et al., 2019). In populations where individuals vary in their propensity to move, loss of asynchronous foraging opportunities could leave individuals with fewer pathways to grow and survive (Armstrong et al., 2016). The removal of glacier- and snow-fed streams in our analysis resulted in the loss of both the fastest juvenile salmon growth trajectories—associated with more nomadic fish that tracked resource asynchronies across space and time—and the slowest trajectories, associated with stationary fishes that primarily lived year-around in the colder glacier- and snow-fed streams (Figure 5). Because juvenile salmon growth is known to influence life-history decisions (e.g., when to smolt; Quinn, 2018), this more constricted range of growth opportunities could be associated with reduced life history diversity shown to promote population stability in the face of environmental stochasticity (Moore et al., 2014; Schindler et al., 2010), and destabilize salmon populations by reducing their adaptive capacity.

Reduced life history diversity, however, does not equate to reduced salmon productivity. Modeled salmon growth was on average 80% higher in the homogenous rain-fed river network relative to the mosaic network that contained glacier- and snow-fed tributaries (Figure 5). Rather, diminished life history diversity may reduce a population's ability to buffer against natural perturbations. Such as droughts, scouring floods, and warm summer water temperatures. All of these disturbances are expected to become more frequent and severe in coastal Alaska, especially in rain-fed watersheds that already experience the strongest fluctuations in stream flow and water temperature (Jones et al., 2020; Milner et al., 2013; Sergeant et al., 2020; Winfree, 2017).

The idea that melting glaciers and snowfields may have deleterious effects on mobile organisms such as salmon could be considered counterintuitive. Diminished meltwaters are likely to result in warmer, clearer, and—on average—more biologically productive watersheds that also contain more spawning and rearing habitat (Pitman et al., 2020). For example, studies suggest that glacier rivers

have extremely low levels of primary and secondary productivity during the summer meltwater season (Burgherr & Ward, 2001; Uehlinger et al., 1998), which are likely to improve as glacier influence declines. However, our analysis suggests that perceived “improvements” in the environmental conditions of meltwater streams (e.g., warmer temperatures) overlook the potential loss of seasonally ephemeral—but ecologically important—peaks in productivity that may sustain mobile organisms. To our knowledge, this is the first study to examine year-round resource dynamics of proglacial streams that contain anadromous fishes. This information is critical for understanding how cryospheric heterogeneity in watersheds along the GOA and other mountainous coastal margins influences the dynamics and stability of salmon and other mobile consumer populations in a changing climate. Studies that examine year-around resource dynamics in glacier- snow- and rain-fed streams, as well as the growth benefits these streams provide to mobile consumers are needed. For example, direct observations of salmon habitat use and movement (Armstrong et al., 2013) could be combined with otolith microchemistry analyses (Brennan et al., 2019) to partition growth by stream type.

Our analysis included several assumptions meant to maintain the heuristic value of the model, but which also limit its inference. First, the loss of meltwater fed streams would not create identical physical and chemical conditions throughout the watershed as we assumed in our river network simulation. However, we do expect that the strength of these physicochemical contrasts will be significantly weakened by diminished glacial and snowmelt contributions (Fellman et al., 2015; Littell et al., 2018). Second, the diverse communities of organisms found in glacier-, snow-, and rain-fed rivers (Brown et al., 2007; Clitherow et al., 2013; Hotaling et al., 2019; Wesener et al., 2011) were not included in our food web model. Glacier-fed streams in particular have been shown to contain specialized taxa and distinct food web pathways that could be accounted for in future analyses (e.g., assimilation of aged organic-carbon, consumption of fine sediment by invertebrates; Clitherow et al., 2013; Fellman et al., 2015). Third, for the purpose of creating a controlled model experiment, we assumed each stream type had the same channel morphology, riparian vegetation structure, and timing of terrestrial and marine subsidies. Not accounting for differences in these conditions likely resulted in conservative estimates of resource asynchronies. Fourth, our model analysis was conducted using average flow, temperature, turbidity, and nutrient regimes that represent generalizable *intra*-annual patterns for each stream. However, *inter*-annual variability in climate would alter these physicochemical conditions, weakening or strengthening resource asynchronies from year-to-year (Figures S3 and S4). Finally, most watersheds are not composed of equal parts glacier-, snow-, and rain-fed streams, as we assumed in our river network analysis. The proportion and spatial juxtaposition of each stream type should be considered when examining these dynamics in specific locations.

Despite these simplifying assumptions, our novel model analysis provides a foundation for more complex and location-specific

exploration, as well as a guide for future field studies. Specifically, our analysis generated three ecologically important and empirically testable hypotheses (H) that extend broadly to landscapes where meltwater and non-meltwater fed streams cooccur:

- (H1) The distinct physicochemical conditions of glacier-, snow-, and rain-fed streams support unique seasonal cycles of primary producers and consumers (biofilm and aquatic invertebrates).
- (H2) These seasonal resource asynchronies support the growth of mobile consumers that can move between stream types.
- (H3) Loss of glacier- and snow-fed streams with climate change will constrain growth opportunities for mobile species.

Although there is some empirical support for the first hypothesis (Heiber et al., 2001; Robinson et al., 2002; Uehlinger et al., 1998), we are unaware of any studies that have examined the growth benefits of meltwater and non-meltwater fed streams (nor the loss of these benefits) for mobile consumers (H2 & H3). The need is urgent for studies that elucidate how the rapid loss of glacier and snowmelt contributions to surface waters will rewire the food webs that support mobile organisms, which include not only fishes but numerous other aquatic and terrestrial species such as amphibians, river otters, bats, and songbirds (Fukui et al., 2006; Uesugi & Murakami, 2007).

5 | CONCLUSIONS

Alteration to catchment hydrology due to a melting cryosphere is a global phenomena. Many watersheds will undergo hydrologic homogenization as glacial and snowmelt contributions to streamflow diminish (Barnett et al., 2005; Sergeant et al., 2020). Our findings suggest that threats to biodiversity as these meltwaters disappear may be broader than currently understood. To date, research has shown that the presence of glacier- and snow-fed streams—despite having lower biodiversity relative to non-meltwater systems (alpha-diversity)—can enhance species and community diversity at watershed and regional scales (gamma-diversity) due to the presence of endemic taxa and communities not found at other locations in river networks (Brown et al., 2007; Finn et al., 2013). Our model analysis suggests an analogous finding. The presence of glacier- and snow-fed streams—despite being colder and having lower productivity relative to rain-fed streams—may contribute to a diverse portfolio of foraging and growth conditions at the watershed scale by hosting unique seasonal cycles of resource availability that provide extended foraging opportunities for mobile organisms. Thus, threats to biodiversity may not only include the loss of specialized meltwater species, but also the loss of unique cycles of resource availability that provide spatially and temporally distinct foraging compartments. An important avenue for future research will be investigating the consequences of a melting cryosphere on the spatially linked food webs that contribute to ecological stability and resilience (Palmer & Ruhi, 2019).

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in “figshare” at <https://doi.org/10.6084/m9.figshare.4287692.v1>.

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SUPPORTING INFORMATION

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