# Building a Food Web Portfolio:

## Hydrologic Heterogeneity Creates Food Web Diversity on a Glacial Meltwater Landscape

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# Abstract

Meltwater streams fed by glaciers, icefields, and snow frequently have flow, temperature, and biogeochemical regimes distinct from non-meltwater streams. This physicochemical heterogeneity may support a diversity of freshwater food webs in landscapes where meltwater and non-meltwater streams currently co-occur. Additionally, these streams exist along a continuum which may serve as a space-for-time proxy for changes to physicochemical conditions as glacial and snowmelt influence diminishes with climate change. However, there remains a paucity of knowledge about how food webs are assembled on these rapidly changing landscapes. In the following pages, I describe three studies which examine how the structure of food webs supporting Pacific salmon vary between four streams in coastal southeast Alaska: glacier-fed, snow-fed, rain-fed, and one fed by a combination of rain, snow and glacial-melt. I first assess the temporal dynamics and synchrony of abiotic patterns and biomass waves of the trophic base of the food web. I then analyze the community structure and secondary production dynamics of the aquatic invertebrate community at an annual scale. Lastly, I present quantitative flow food web models using trophic-basis-of-production approach to illuminate the pathways of energy flow that support juvenile salmon. Using these approaches, I found that these cryospheric streams vary greatly in the biophysical patterns and community diversity and structuring. These differences, in turn, create distinct trophic pathways that support fish production between stream types with few shared links between and a greater number of resource flows supporting Coho and Dolly Varden in glacial- and snowmelt streams and substantial overlap in rainwater and combined-signature sites. Although glacial meltwater streams may be less productive overall, they support fish via distinct and diverse pathways from non-meltwater streams and contribute to landscape variation and prey community *beta* diversity is theorized to increase food resilience and stability. This may be especially true for mobile consumers like juvenile salmon which may track different growth opportunities and energy flow pathways across spatially structured food webs. As glacial and snowmelt contributions to surface waters decline, these distinct meltwater food webs are at risk of extirpation, which could leave salmon populations vulnerable to disturbance and may simplify the overall community structure on the landscape.

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# Dedication

To my wife, my partner, and my editor-in-chief, Danielle Berardi, I dedicate this dissertation. I could not have gotten through the last five years without you by my side. To our dogs, Django and Salix, who have piled into the back of my pickup and driven back and forth two Alaska a couple of times.

Lastly, to the little one we have on the way:

I hope the work your mom and I do leaves you a better world than it might have been.

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# Statement of Contribution

Chapters 2-4 of this dissertation represent collaborative research that will be submitted as multi-authored articles for peer review. In certain cases, plural is used to reflect the views of multiple co-authors. All chapters were conceived by M.R. Dunkle, J.R. Bellmore, J.B. Fellman and C.C. Caudill. E. W. Hood contributed specific background and glaciological/environmental science support for chapter 2. J.B. Fellman led physico-chemical sampling and analysis. M.R. Dunkle led field sampling, laboratory processing, data analysis, and drafting of all chapters. All authors have provided feedback and revisions on data chapters.

# Chapter 1 - Introduction

*"It is interesting to contemplate a tangled bank… and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us…" Charles Darwin, On the Origin of Species*

A central concept in ecology is that spatial heterogeneity in abiotic conditions can create biological diversity from genes to individual behaviors to populations, species assemblages, and community interactions (Whittaker 1970, 1972, Whittaker et al. 1973, Ricklefs 1987, 2004). Ecological theory predicts that biodiversity at all levels contributes to ecological stability, community resilience, and adaptive capacity to climate change (McCann 2000, Loreau et al. 2003, Hooper et al. 2005, Hendry 2013, Alsterberg et al. 2017, Moore and Schindler 2022, Oliveira et al. 2022). However, landscapes are undergoing unprecedented homogenization in both abiotic and biotic conditions though the movement of organisms (Olden et al. 2005, Olden 2006, Wang et al. 2021), large-scale land use change(Gámez-Virués et al. 2015), and global climate change (Chai et al. 2020). Of those factors, the influence of climate-driven homogenization of the flow dynamics of rivers and streams have received renewed attention – particularly in landscapes influenced by the seasonal or semi-permanent cryosphere (Huss et al. 2017, Elser et al. 2020). Although the fading of glacial and snow meltwater influence on the physical and chemical conditions in downstream ecosystems have been speculated to include changes to food web complexity and ecosystem functioning, these impacts remain empirically elusive (Milner et al. 2017, Fell et al. 2017, Zhang et al. 2017).

The following pages, I describe three related studies of the relationship between hydrologic heterogeneity and the way food webs are constructed on a complex landscape. The first goal of this work is to evaluate specifically how landscapes vary physically and chemically and what the resulting biotic patterns are. Where possible, I emphasize the role of time in creating observed patterns although secondary production and food web structure are presented on an annualized scale. The second goal is to empirically, and, to the extent this field biologist can, conceptually explore the potential implications of climate change on the ways landscapes fuel consumer growth.

To this end, streams in Southeast Alaska represent a compelling system for evaluating these processes. Few areas on the planet contain variation in water source in such proximity as the glacial coastal margin of Southeast Alaska, where alpine to estuarine conditions exist across short distances. In the simplest classification, streams are frequently sorted into three categories: glacial, snowmelt, or rainwater. *Glacial streams* are primarily fed by glaciers, *snowmelt streams* generally drain alpine zones are primarily fed by snowmelt runoff, and *rainwater streams* drain lower elevation forests and wetlands primarily fed by rainwater. In fact, these stream types are so visually distinct that they are often referred to by their color: *glacial, clearwater, and brown-water* (LaPerriere et al. 1989, Hood et al. 2007, Fellman et al. 2009a, Wesener et al. 2011, D'Amore et al. 2015, Orians and Schoen 2017). Climate change is expected to decrease glacial coverage and the physico-chemical signature glaciers provide over the next century (Larsen et al. 2015, O'Neel et al. 2015) coinciding with an increase in wintertime air temperatures and a decrease in winter snowfall. The loss of this signature, along with the ensuing shift from heterogeneous watershed chemistry and hydrology along the coastal margin to more homogenous, rain-dominated conditions, has the potential to alter the ecosystem processes that support economically and culturally important species, such Pacific salmon in the genus *Oncorhynchus* (Pitman et al. 2020, 2021).

This landscape is dramatic and complex, with substantial variation in fundamental physical and chemical conditions over distances that are within the dispersal capacity of many, if not most, organisms present. This is also a landscape that is relatively depauperate due to its evolutionarily recent (and ongoing) deglaciation, meaning the number of players is tractable and the communities are not so complex as to mask overall structure. While much work has focused on climate impacts in arctic ecosystems, high-latitude temperate forests also experience substantial seasonality and complexity to warrant research focus. Lastly, this landscape produces an abundance of juvenile fish in the family *Salmonidae*. These fish are the cultural and economic backbone of the region and examination of implications of climate change for the ways salmon are produced in the wild is timely. Each of the following studies attempts to advance our understanding of how this magical landscape of rain, rock, ice, and forest produces nested, interacting, and exceedingly beautiful webs of life.

## Meltwater Rivers

Climate change is driving shifts in baseline physical conditions in many ecosystems. Some of the most rapid impacts of climate change are occurring in high latitude and/or altitude environments, where diminishing permafrost, glacial ice and seasonal snowpack will lead to rapid changes in downstream ecosystems. Cryospheric rivers and streams exist in both alpine ecosystems at high elevation and in temperate-polar ecosystems at moderate to high latitudes. Traditionally, alpine streams have been classified as kryal (*glacial*), krenal (*groundwater*), and rithral (*snowmelt*) which reflect somewhat predictable differences in physical, chemical, and biological conditions (Ward 1994), but are typically at elevations which lack higher level consumers like fish or well developed riparian zones. Lower elevation cryospheric rivers may share many similar qualities to higher elevation sources. Unlike true alpine streams, low-elevation streams are more likely to have fish and developed riparian zones, providing a fascinating study system to evaluate intermediately complex food webs across strong physiochemical gradients.

Past reviews of cryospheric river loss have identified ongoing homogenization of water sources in these ecosystems, with impacts on physico-chemical dynamics, species composition, and primary resources (Hotaling et al. 2017, Ren et al. 2019a, Brighenti et al. 2019). Others have emphasized the combined and emergent ecological effects may be more complicated and involve "multi-trophic" or "hydro-ecological" responses (Milner et al. 2009, 2017, Fell et al. 2017a). Generally, glacial rivers are harsh due to low temperatures, high flows, and low primary productivity which results in low diversity but specialized communities (Jacobsen and Dangles 2012, Clitherow et al. 2013, Niedrist and Füreder 2018). Snowmelt streams are common throughout mountainous regions globally and have a predictable seasonal "spring-runoff" hydrograph, to which organisms may be adapted (Yarnell et al. 2010, Docherty et al. 2018a, 2018b). Rainfed streams, which are common in coastal ecosystems and rainforests typically derive most of their water from surface runoff after storm events and may be particularly flashy and prone to seasonal drying during low-precipitation periods (Hood et al. 2007, Wesener et al. 2011, Sergeant et al. 2020). Other water inputs, such as those from permafrost, rock glaciers, or groundwater, may also have distinct physical, chemical, and biotic characteristics (Brighenti et al. 2021), but are outside the scope of this study. While cryospheric river systems are important in their own right and warrant research focus, they also represent ideal study systems for evaluating the role of abiotic gradients on community composition and food web dynamics, as streams in cryospheric conditions may vary dramatically in thermal, flow, and chemical conditions in both scale and timing. Further, relatively low species diversity in these harsh ecosystems results in tractable food webs with shared species across the landscape. This results in strong differences in fundamental physico-chemical conditions over short distances and relatively small species pools, resulting in taxa-to-taxa comparisons between habitats.

## Spatial and Temporal Food Web Theory

A central goal of ecology is to understand how spatial heterogeneity in community structures arise and the dynamics among interacting patches at scales relevant to ecological processes (Gilinsky 1984, Pringle 1990, Holt 1997). A landscape perspective is critical in understanding the scales of processes which are important for conserving and maintaining populations (Turner 1989). When using an *organism of interest* approach (Ivlev 1966, Wiens 1989), two important metrics for ecosystem conservation are processes which influence *productivity* and those which influence *stability*. In this context, I consider *productivity* to mean the capacity of a system to produce consumer biomass. Productivity at higher trophic levels will depend not only on the environmental conditions, which constrain things like consumer metabolism, but also the number of resources available, the quality of those food items, the capacity of consumers to access prey, and the temporal context of those resources relative to consumer needs. Many definitions of *stability* exist (Rutledge et al. 1976, Grimm and Wissel 1997, Donohue et al. 2016) and depend on the types of processes being considered. Whole system stability typically refers to the capacity of a system to return to a previous condition after perturbations or the persistence of a system over time. When using an organism-centric approach, I advocate an adaptation of the *variance stability* definition of McCann (2011), which uses the coefficient of variation in the abundance or biomass of a population over time, but could extend to variance in growth rates or production over time. This *resource variance stability* is useful because it allows us to consider how, when, and where organisms in variable landscapes obtain resources. In this framework, high variance in resource and consumer productivity over time is likely to create less resource stability for consumers than systems with low variance.

The apparent stability of ecosystems relies in part on the “tangled bank” of interactions between organisms (McCann 2000). Among the most important of those interactions are the feeding relationships which harness, alter, and transfer energy and nutrients from producers to consumers (Thompson et al. 2012). Food webs are the collective network of trophic interactions among a community occupying a defined area and are essential to our understanding of ecosystem structure and functioning (Paine 1966, 1969). Landscape-scale processes such as meteorological patterns, physical geography, and biogeochemistry can act as filters on community composition and structure and thus potential food web components and as drivers of food web dynamics (Polis and Strong 1996a, 1996b, Polis et al. 1997). Thus, variation in food webs may be high across complex landscapes, which in turn may lead to asynchronies in productivity at different trophic levels (Bellmore et al. 2022). Physico-chemical patterns derived from landscape complexity may add to stability and resilience by 1.) creating distinct waves of resource availability across landscapes, providing opportunities for mobile consumers to integrate and maintain populations (Armstrong et al. 2016) and 2.) by creating a diversity of feeding relationships across the landscape, weakening the reliance of a single consumer taxa on a few potentially unstable prey items (Rooney et al. 2008). Although food webs may be considered finite, closed systems in an abstract sense, they are essentially nested and linked structures across space and time (Holt 2002, McCann et al. 2005).

If landscapes are spatially heterogeneous in their physico-chemical dynamics and communities are comprised of organisms with distinct phenologies, dynamics of primary and secondary resources will likely be asynchronous on spatial and temporal scales relevant to upper trophic level consumers (Armstrong et al. 2016). Given sufficient connectivity, mobile consumers and resources may flow between patches across the landscape, buffering extreme highs and lows of resource availability or consumer growth opportunities. Indeed, all food webs, to varying degrees, should be considered as components of nested, meta-food webs on a shifting mosaic of abiotic and biotic conditions over space and through time. At the landscape scale, this heterogeneity in abiotic conditions creates spatial structuring of food webs via three dominant (and interrelated) mechanisms: 1) *the direct effects of variation in physico-chemical dynamics across landscapes on nutrient availability and metabolic conditions* (Milne 1991), 2) *the environmental filtering of a regional species pool creating distinct local community structures* (Cadotte and Tucker 2017), and 3) *the emergent dynamics of coupled abiotic variation, biotic structuring, and community interactions* (McCann and Rooney 2009).

## Quantitative Food Webs

To understand the role of landscape heterogeneity on consumer production, a quantitative food web approach is necessary. Lindeman (1942) emphasized *trophic dynamics* as a major driver of ecosystem processes. This approach to characterizing energy flow through systems provides a critical understanding of how organisms interact within and among each other and how the entire system functions. Odum (1957) employed this approach to characterize the whole system energy balance of a section of an upwelling spring in Florida with the goal of "complete quantitative determination of the states and flow… as well as the control mechanisms…" of the ecosystem.

The trophic basis of production approach (Benke and Wallace 1980, 1997, Hall Jr et al. 2001) builds off earlier energetic food web studies and seeks to quantify specifically how energy flows to consumers of interest and which flows are converted into secondary consumer biomass. This approach combines consumer production estimates, diet proportions, and bioenergetic efficiencies to create quantitative flow food webs which shows the pathways and magnitudes of energy flow that supports consumers per unit space and time. One major advantage of this quantitative approach is that it can be used to calculate rates of material flux throughout the whole system, allowing for the exploration of top-down versus bottom-up forces and calculations of trophic *interaction strength* (De Ruiter et al. 1995, Berlow et al. 2004, Bellmore et al. 2015).

## Summary

In Chapter 2, I describe the seasonal and annual heterogeneity in physico-chemical patterns across four study streams spanning the abiotic gradient and how that physiochemical variation contributes to biomass dynamic of detritus, periphyton, and invertebrates. I then analyze the synchrony of abiotic and biotic patterns under current conditions and ask how climate change-driven loss of stream physico-chemical diversity might impact overall biological synchrony across the landscape. Chapter 3 digs more specifically into how physicochemical variation influences the aquatic invertebrate communities among my study streams. I assess differences in secondary production and show that communities vary between streams associated with physico-chemical differences related to temperature, discharge, nutrient availability, and water chemistry. In Chapter 4, I synthesize the findings of the first two chapters to create quantitative flow food webs for the four streams across the landscape. To do this, I analyze the trophic basis of secondary production of the fish community among streams by first estimating the trophic basis of the invertebrate community using stable isotope mixing models, then estimate fluxes to fish using diet analysis. This approach resulted in the first quantitative food webs for salmon streams in Southeast Alaska and reflect the dominant trophic interactions and pathways for energy flow in these riverscapes. Further, few if any studies have simultaneously built quantitative food webs across multiple sites reflecting strong abiotic gradients. As this landscape changes and glacial and snowmelt influences fade, the patterns and interactions presented herein are likely to be the first things to be affected.

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# Chapter 2 - Glacial runoff promotes seasonal asynchronies in freshwater resource availability between meltwater and non-meltwater fed streams

## Abstract

Biogeochemical regimes can vary among watersheds over relatively short distances on physically complex landscapes. How seasonal resource dynamics in streams vary over similar scales remains largely uninvestigated. In many mountainous or high-latitude regions, meltwater streams from glaciers, icefields, and seasonal snowpack occur in close proximity to non-meltwater streams. As first order controls on river food web, these distinct physicochemical regimes have the potential to support seasonal resource asynchronies thought to promote ecological stability. Here, we measured seasonal cycles of physicochemical conditions and biomass dynamics of three components of aquatic food webs (detritus, periphyton, and aquatic invertebrates) in streams with predominantly glacial, snowmelt, and rainfed runoff, as well as a stream experiencing a meltwater-rainfed transition. In addition, we conducted a synchrony analysis to quantify the contribution of each stream type to temporal asynchronies in physicochemical conditions and resource availability. We found that streams had distinct temperature, flow, and nutrient regimes, as well as asynchronous cycles of detritus, biofilm, and aquatic invertebrate biomass. The strongest differences were found between the glacial stream and other streams during the meltwater season, when abiotic patterns of temperature, flow, and water chemistry and biotic patterns of detrital, periphyton, and invertebrate biomass diverged. Our findings suggest that the disappearance of the global cryosphere may synchronize the seasonal resource dynamics of meltwater streams. This could have implications for ecological stability, especially for mobile consumers that may have few foraging and growth opportunities as distinct cycles of resource availability are lost.

## Introduction

Climate change is homogenizing landscapes across the globe, potentially destabilizing biotic communities, and threatening ecosystem services. In mountainous and high latitude regions, rapid loss of the cryosphere is dramatically—and often irreversibly—homogenizing the flow, temperature, and biogeochemistry of mountain watersheds (Ren et al. 2019b, Elser et al. 2020), which frequently contain a mosaic of glacial, snowmelt, and rainfed tributaries (Sergeant et al., 2020; Curran and Biles, 2021; Giesbrecht et al., 2022). As glaciers recede and precipitation transitions from snow to rain, the physical and chemical characteristics that make glacial and snowmelt streams distinct from rainfed streams is disappearing. Previous research suggests that this "hydrologic homogenization" will decrease landscape-scale freshwater biodiversity via the loss of cold-water adapted organisms such as bacteria, algae, and invertebrates (Milner et al. 2009, 2017, Giersch et al. 2017). However, an additional possibility that has not been empirically investigated is that hydrologic homogenization could destabilize aquatic communities within and across stream networks by synchronizing the seasonal phenology of river food webs (Bellmore et al. 2022, Moore and Schindler 2022).

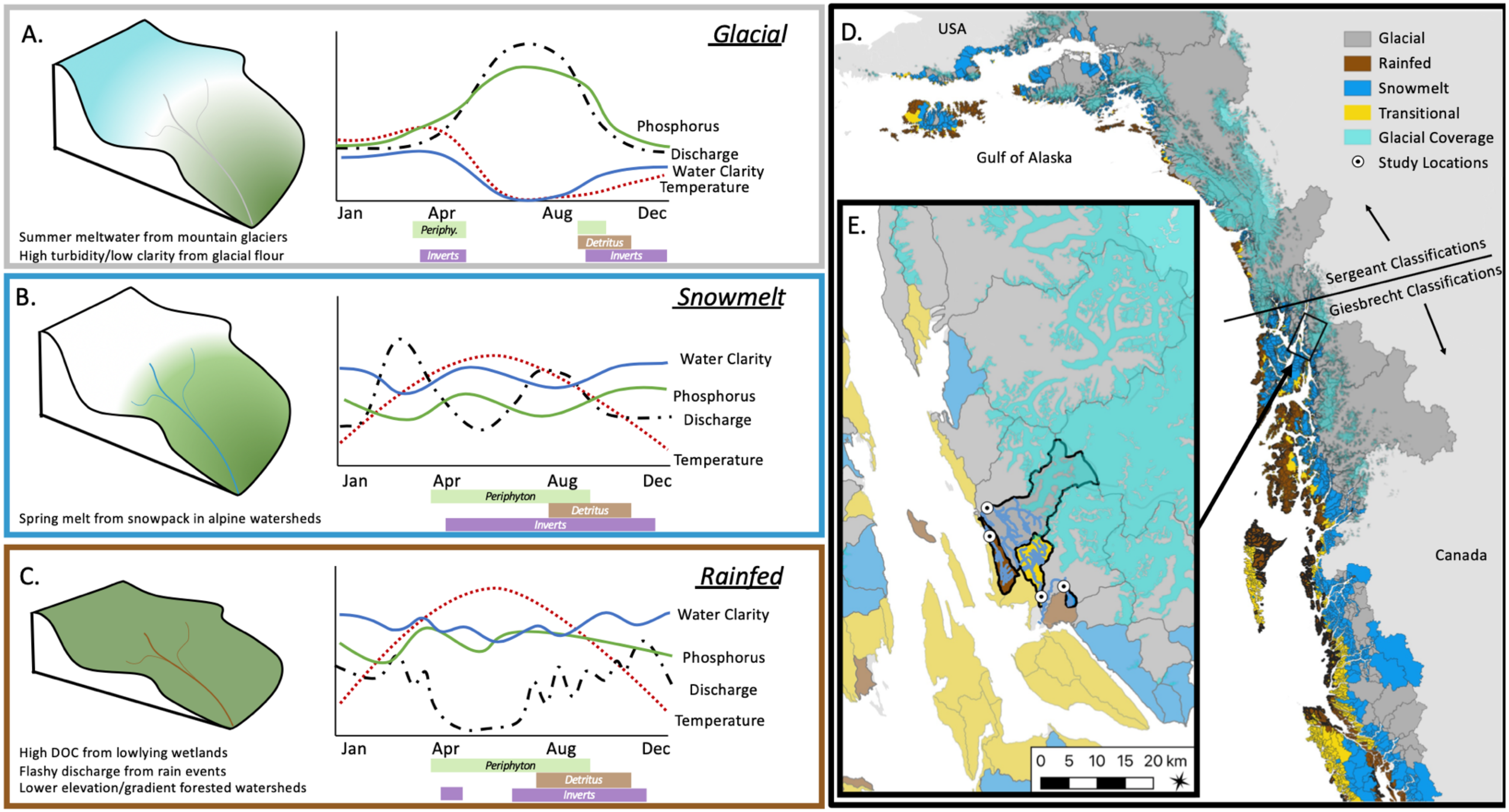
In temperate watersheds, streams derived from glacial melt typically experience high, cold, and turbid flows that limit aquatic productivity during summer months (Figure 2-1A), but may experience higher primary and secondary productivity during shoulder seasons (spring and fall), when flows are relatively low and clear, and nutrient availability is still high (Uehlinger et al. 2010, Siebers et al. 2022). Conversely, streams with significant contributions of snowmelt (Figure 2-1B) typically experience a spring runoff pulse from melting snowpack followed by more stable summer and autumn flows allowing peaks in productivity in midsummer. Streams fed by rainfall (Figure 2-1C) experience spates during storm events followed by low base flows and warm temperatures in midsummer which may allow for high production but decreased biomass at lower trophic levels. Further heterogeneity may be derived from streams fed by other sources (e.g., groundwater springs or subterranean ice; Brown & Hannah, 2008; Brighenti et al., 2021). Thus, watersheds containing a mosaic of stream types may support seasonal asynchronies in the production and biomass of aquatic resources such as biofilm and aquatic insects, which may contribute stability across trophic levels. Mobile consumers, such as fishes, bats, and birds, frequently move and integrate prey production across riverscapes (Baxter et al. 2005, Jackson et al. 2020); if climate-driven changes to landscapes homogenizes abiotic regimes and reduces resource asynchronies, growth opportunities for mobile consumers may be reduced (Armstrong et al. 2016, Bellmore et al. 2022).

In this study we ask two questions: (1) "*how does the seasonal timing of aquatic resources vary over space among glacial, snowmelt, and rainfed streams?"* and (2) *how might the loss of meltwater-fed streams influence asynchrony dynamics and the seasonal availability of food web resources across a landscape*? To answer the first question, we combined high-frequency sampling of temperature, flow, and chemical properties with approximately monthly sampling of benthic periphyton, benthic organic matter, and aquatic invertebrates for 13 months in four neighboring streams with different sources of runoff: *(a)* a stream fed primarily by melting glacial ice ("glacial"), *(b)* a higher elevation stream fed primarily by melting snow ("snowmelt"), *(c)* a low elevation stream fed primarily by rainfall ("rainfed"), and *(d)* a stream experiencing a meltwater-rain transition ("transitional") which contains a mix of sources. We predicted that streams would have distinct flow, temperature, and biogeochemical regimes resulting in seasonal asynchronies in resource dynamics (Figure 2-1) and we made the following specific predictions:

- The glacial stream would peak in primary producer and consumer biomass in early spring prior to the onset of glacial melt (Figure 2-1A)
- The rainfall stream would peak in primary producer and consumer biomass in the summer when water is low and warm and nutrient availability is high (Figure 2-1B)
- The snowmelt stream would exhibit a summer biomass peak, but higher biomass would be maintained into the autumn due to lower and more stable flows (Figure 2-1C)
- The transitional stream would generally exhibit less distinct peaks and troughs in producer and consumer biomass because it integrates the physicochemical differences of the other stream types

To address the second question, we calculated synchrony in measured parameters across stream types and then sequentially removed individual streams to evaluate the effects of losing resource cycles supported by glacial, snowmelt, and transitional streams. We expected biophysical synchrony to be relatively low across the landscape, but that glacial meltwater would contribute the most to abiotic and biotic asynchrony. In turn, we predicted that the loss of glacial signatures would confer the greatest increase in overall synchrony in biotic and abiotic conditions.

Figure 2-1. (A-C) Conceptual diagram of seasonal differences in physicochemical conditions that control aquatic primary producers and consumers in glacial, snowmelt and rainfed streams: water clarity, discharge, nutrient availability (phosphorus), and water temperature. Also marked are the hypothesized “productive” windows (green bars), expected pulses of external detritus (brown bars), and lagged invertebrate pulses (purple bars). (D) Distribution of stream types in the Pacific Coastal Temperate Rainforest as determined by Sergeant et al. (2020) for the Northern Gulf of Alaska region and Giesbrecht et al. (2022) for Southeast Alaska and Coastal British Columbia, Canada. Here we present the primary classifications from both studies and consider Sergeant’s “rain-snow” and Giesbrecht’s “rain mountain” classifications as transitional watersheds which are presumed to be the most affected by shifts from winter snow to winter rain. (E) Our four focal watersheds near Juneau, AK, USA with location of sampling reaches (points). Conceptual diagrams (A-C) adapted from Giesbrecht et al. (2022) and data used to parameterize model simulations by Bellmore et al. (2022). *Figure appears on following page*.


A.
Glacial
Phosphorus
Discharge
Water Clarity
Temperature
Jan
Apr
Aug
Dec
Periphy.
Inverts
Detritus
Inverts
Summer meltwater from mountain glaciers
High turbidity/low clarity from glacial flour
B.
Snowmelt
Water Clarity
Phosphorus
Discharge
Temperature
Jan
Apr
Aug
Dec
Periphyton
Detritus
Inverts
Spring melt from snowpack in alpine watersheds
C.
Rainfed
Water Clarity
Phosphorus
Discharge
Temperature
Jan
Apr
Aug
Dec
Periphyton
Detritus
Inverts
High DOC from lowlying wetlands
Flashy discharge from rain events
Lower elevation/gradient forested watersheds
D.
USA
Gulf of Alaska
Canada
Glacial
Rainfed
Snowmelt
Transitional
Glacial Coverage
Study Locations
Sergeant Classifications
Giesbrecht Classifications
E.
0 5 10 15 20 km

## Materials and Methods

### *Study area*

Coastal watersheds in the Gulf of Alaska (GOA) drain a heterogeneous landscape. In this region, stream physical and chemical properties are influenced by the dynamics of alpine glaciers and icefields, seasonal melt of snowpack, and forested peatlands (Figure 2-1; Sloat et al. 2017, Sergeant et al. 2020, Pitman et al. 2020, 2021). These watersheds are also important nurseries for juvenile salmonids and other anadromous fish (Johnson et al. 2020) which rely on freshwaters for the first 1-3 years of growth prior to emigration to the marine environment (Quinn 2018). However, the GOA region is experiencing some of the most rapid rates of glacial decline in the Northern Hemisphere (Larsen et al. 2015, Pitman et al. 2020, 2021) and shifts from winter snowfall to winter rain (Young et al. 2021), foreshadowing consequences to stream physicochemical and food web dynamics to similar systems globally.

Study streams are located along the western margin of the Juneau Icefield in the northern region of the Pacific coastal temperate rainforest. The region has a cool maritime climate characterized by mild summers and winters (annual mean 2.17°C) with roughly 4000 mm of precipitation falling annually (1991-2020 Average at Long Lake SNOTEL Site #1001: 58.1833°-133.833°, Elevation 300 m). The Juneau Icefield is the third largest in North America at ~ 4,149 km$^2$ and is experiencing some of the highest rates of mass loss globally (Larsen et al. 2015). We chose one stream each to capture relative endmember conditions characteristic of *glacial-, snowmelt-,* or *rain-fed hydrologic regimes*, which are common around the GOA (Sergeant et al. 2020, Bergstrom et al. 2021, Curran and Biles 2021, Giesbrecht et al. 2022) (Figure 2-1) and in other high-elevation and/or -latitude ecosystems globally (Milner et al. 2010, Li et al. 2018, McPhee et al. 2021).

The *glacial* Herbert River watershed has an area of 152 km$^2$ and is dominated by the Herbert Glacier (~49% glacier coverage), which is a major outflow glacier from the Juneau Icefield (Fellman et al. 2015a). The *rainfed* Peterson Creek drains a lower gradient and elevation forested watershed of 25 km$^2$, and contains a shallow lake and numerous wetlands (34% coverage by area), which contribute high loads of DOC (Fellman et al. 2008). The *snowmelt* Steep Creek drains a hanging valley of 4.9 km$^2$, which is largely unforested alpine terrain that seasonally accumulates large snowpacks. Montana Creek has a watershed area of 39 km$^2$, and although it is primarily rain-fed, it contains a major tributary that is influenced by several hanging glaciers and small alpine snowmelt tributaries above the study reach. All four study reaches have a riparian and terrestrial zone dominated by a mix of Sitka spruce (*Picea sitkaensis)*, Black cottonwood (*Populus trichocarpa),* willows (*Salix spp.), and* alders *(Alnus spp.).* The riparian zones of Montana and Peterson Creeks have well developed conifer coverage, whereas the Herbert River watershed and lower portions of Steep Creek below a large waterfall (including our study reach) are dominated by early seral species due to more recent glacial coverage and/or glacial-melt driven erosion. Within each watershed, we selected a single main-stem study reach (75-125 meters long) and sampled every four weeks from April 2018-November 2018 and again in January and April 2019. During November and January sampling events, samples were collected by breaking through surface ice using a sledgehammer.

### *Discharge*

We measured discharge using techniques tailored to each site: Discharge in the glacial Herbert River was calculated using a five year modeled relationship from historic U.S. Geological Survey gauged discharge measurements in the nearby glacial Mendenhall River (Hood et al. 2020), and was supplemented with additional flow measurements (>15) using a River Ray ADCP. At Peterson Creek, we estimated stage height at 15-minute intervals using a stilling well equipped with a pressure transducer (In-Situ Level TROLL). Point measurements (n>20) using a SonTek FlowTracker ADV across a wide range of flow conditions were used to establish a stage-discharge relationship, which was then used to calculate streamflow. Discharge at Montana Creek and Steep Creek were measured by stream gauges maintained by the National Weather Service in Juneau, AK, and Alaska Hydroscience, respectively. Because ice cover created large errors in discharge measurements during the winter months, we present only measurements from the ice-free period of April-December 2018. All discharge data were converted to daily runoff by dividing total daily discharge by watershed area and are presented in mm day$^{-1}$.

### *Water chemistry*

We used a combination of *in situ* sensors and discrete surface water samples to assess physical and chemical properties across streams from April until December of 2018, which is the approximate period that streams were not covered with ice. Hourly stream temperature was recorded using an automated temperature sensor (YSI Inc. Yellow Springs, OH USA). During each sampling event, stream water turbidity was measured in triplicate using a Hach Turbidity meter and pH was measured using an Orion Star A221 pH meter (ThermoFisher Scientific, Waltham, MA USA). Additionally, total suspended sediment (TSS) was measured by passing a known volume of water through a pre-weighed glass microfiber GF/F filter that was subsequently re-weighed after drying for 24hrs at 60°C.

Monthly water samples were collected for dissolved organic carbon (DOC), pH, total dissolved nitrogen (TDN), total dissolved phosphorous (TDP), and turbidity. Concentrations of DOC and TDN were analyzed using an elemental analyzer (Model TOC/TN-V-CSH, Shimadzu Corp. Kyoto, Japan). A persulfate digestion combined with the ascorbic acid method were used to measure TDP (Valderrama, 1981). Specific conductivity was measured using a hand-held sonde (Model 556, YSI Inc. Yellow Springs, OH USA) during monthly point sampling.

### *Periphyton biomass*

For each sampling event, five composite periphyton samples were taken within each reach. Each composite sample was created by collecting three rocks from riffles from throughout the study reach. These three rocks were scrubbed using a stiff wire bristle brush into 1 L of stream water, and a subsample of this solution was passed onto a pre-ashed (4 hrs. at 450°C) glass microfiber filter (GF/F). Filters were wrapped in pre-combusted (4 hrs. at 450°C) aluminum foil and frozen prior to analysis in the lab. We quantified the upward-facing 2-dimensional surface area of rocks by photographing them with a ruler in view and measured planar area using ImageJ (Schneider et al. 2012). In the lab, filters were divided in half, with one half used for chlorophyl analysis and the other used for ash free dry mass (AFDM). For chlorophyl, one half of the filter was placed in 10 mL of 95% ethanol in a centrifuge tube and macerated vigorously for 60 seconds using a glass rod then placed inside a dark cooler inside a refrigerator for 24 hours. After 24hrs, a small volume (~3 mL) was placed in a 1cm polystyrene or quartz crystal spectrophotometer cell and analyzed for chlorophyll *a* using a spectrophotometer at wavelengths 750, 649, and 650 nm (Beckman-Coulter Model DU-640, Brea, California, USA). For ash-free dry mass, the remaining half of the filter was placed on a labeled aluminum dish, dried to constant weight at 60°C, weighed, and ashed in a muffle furnace at 500°C for 1hr prior to being weighed again using the methods described in Steinman et al. (2017). Per area estimates of periphyton ash-free dry mass (AFDM) were calculated as the difference between the dried weight on the filter and the weight after combustion and was scaled to the planar area of benthic substrata that were sampled.

### *Benthic invertebrate and detritus biomass*

During each sampling event, five composite benthic invertebrate samples were taken within each reach using a 250-micron Surber sampler with a sample area of 0.25 $m^2$. As with periphyton, each invertebrate sample was composed of three net placements from riffles throughout the study reach. For each net placement, the stream bed within the net frame was vigorously disturbed for approximately two minutes and a depth of 10 cm. After collection, we pooled the three-placement composite sample and transferred to a small plastic tub. In the field, we elutriated organic matter from stream gravel and passed the sample over a 250-micron sieve prior to preserving in 70% ethanol. In the laboratory, invertebrates were separated into those > 1.5 cm and those <1.5 cm. All invertebrates from the >1.5 cm class were considered *large and rare* and were removed and identified. We then subsampled using a 120 µm sieve divided into eight equal sections and processed complete subsamples until at least 500 aquatic invertebrates were obtained (Vinson and Hawkins 1996). All invertebrates from subsamples were separated from detritus under a compound microscope, identified to the lowest practical taxon (typically genus for all but *Chironomidae, Oligochaeta,* and terrestrial insects), counted, and a representative subset were measured for standard body length to the nearest 0.5 mm and classified by dominant functional feeding group (Merritt et al., 2019). We estimated biomass from length-weight regressions from the literature (Benke et al. 1999, Sabo et al. 2002). For individuals which were counted, but not measured individually, we estimated mass as the within-sample mean body length. Per meter square biomass estimates for each taxon was calculated by correcting by the subsample volume and dividing by the area of benthic habitat sampled.

Benthic detritus biomass was determined by placing the sorted detritus into pre-ashed and weighed aluminum pans and dried at 60°C for at least 24hrs, weighed, ashed in a muffle furnace at 550°C for 40 min, dried, and weighed again following the protocols described by Benfield, Fritz, and Tiegs (2017). Ash-free dry mass was then calculated as the dry weight corrected by the percent organic matter. Per meter square detritus biomass estimates for each taxon was calculated by correcting by the subsample volume and dividing by the area of benthic habitat sampled.

### *Data Visualization and Analysis*

We constructed time-series graphs for mean physicochemical conditions and resource biomass in our dataset. Loess smoothing function was used to show seasonal trends in water chemistry and turbidity. We compared all data by calculating 95% confidence intervals and coefficients of variation in our time series using the ‘gmodels’ R package (Warnes et al. 2018). Data for synchrony analyses were z-transformed using base R and Pearson Correlations. We plotted standardized values of temperature, discharge, and aquatic biomass to show seasonal asynchronies in anomalies of each variable. We calculated synchrony (S) using the approach described by Vogt et al. (2011) by first z-transforming all abiotic and biotic parameters in our time series then calculating the mean pairwise Pearson correlation coefficients. This results in a value of S between 0 and 100%, with 0% reflecting perfect asynchrony and 100% being perfect synchrony. To explore the implications of losing each stream type from the landscape, we systematically removed individual streams (glacier, snow, rain, transitional) from the dataset and recalculated synchrony to estimate the relative effect of removing each stream on synchrony values for each parameter.

## **Results**

### *Runoff*

The patterns in daily runoff were similar across all sites during the winter months but diverged in the spring through fall (Jun-Oct), as the glacial river experienced high runoff and consistently low temperatures (95% CI: 2.29-2.45°C) during active glacial melt season (May-Sep, ~22-26 mm $d^{-1}$) (Figure 2-2 A-B). The rainfed stream experienced several precipitation-driven spikes (e.g., a 37-fold increase in runoff from a daily average of 0.94 mm $d^{-1}$ in July 2018 to a maximum of 35.7 mm $d^{-1}$ on August 9, 2018) followed by rapid declines to low base-flow conditions (~0.8-2 mm $d^{-1}$) (Figure 2-2b). Episodic rainfall-driven increases in runoff were observed in the snowmelt and transitional creeks, but base flows were generally higher and more stable than in the rainfed creek (July 2018 average base flow: *snowmelt* ~2.1-3.2 mm $d^{-1}$, *transitional* ~2.5-3.2 mm $d^{-1}$).

### *Physical and chemical properties*

The rainfed, snowmelt, and transitional streams experienced highest temperatures in the summer months of June-August (12-15°C) and lowest measured temperatures in April (2-3°C), though the snowmelt stream had its lowest temperature in November prior to freezing. We anecdotally observed complete ice-over in all streams except the glacial system, where the margins froze and only the middle of the channel remained largely open. Because of ice-formation, we were unable to record water temperatures from November 2018– April 2019. The turbidity and chemical regimes varied seasonally between stream types (Figure 2-3). The glacial stream peaked in turbidity and TDP and troughed in DOC and TDN during active glacial melt. In the rainfed stream, both turbidity and nutrient concentrations all peaked during late summer, whereas water chemistry was moderate and the most stable in the snowmelt stream. The transitional stream was somewhat intermediate in water chemistry in both constituent concentrations and timing relative to the patterns observed in the other stream types.

### *Detritus*

Streams had asynchronous seasonal and annual mean detritus biomass (Figure 2-4A). The glacial stream exhibited high detritus biomass in late winter (April 2018), followed by a rapid decrease during a spring snowmelt pulse, an uptick during late spring, and consistently low biomass during the glacial melt season. In the transitional stream, a moderately high load in the spring was followed by low levels during summer and a large detrital pulse in the late fall. Both the rainfed and snowmelt stream had variable detrital biomass pulses which seemingly corresponded with high flow events (Figure 2-6).

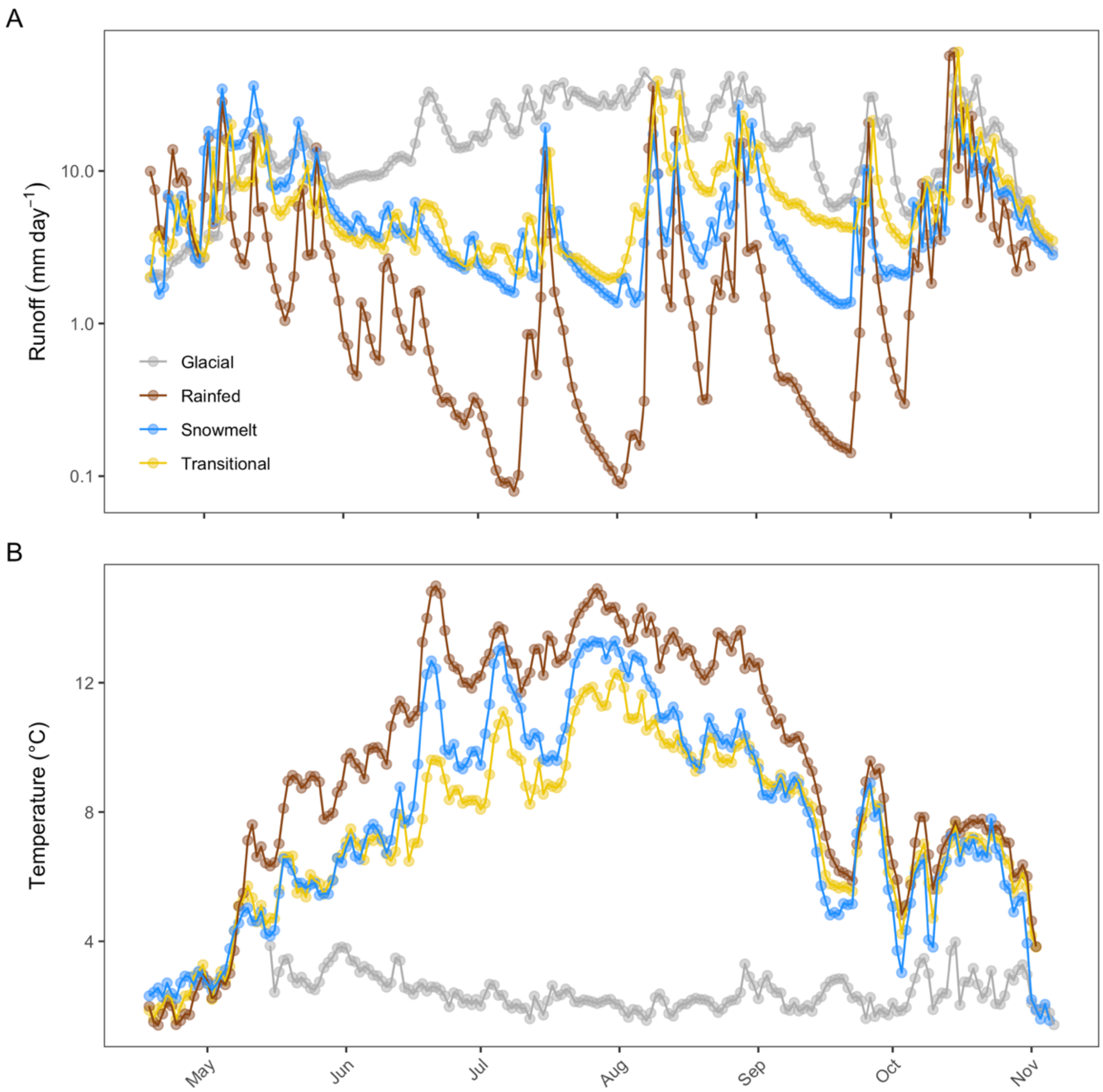


Figure 2-2 Mean daily runoff (A) and temperature (B) for the four study streams from April to November 2018. *Note the log scale for runoff to emphasize mid-summer divergence between glacial and rainfed streams.

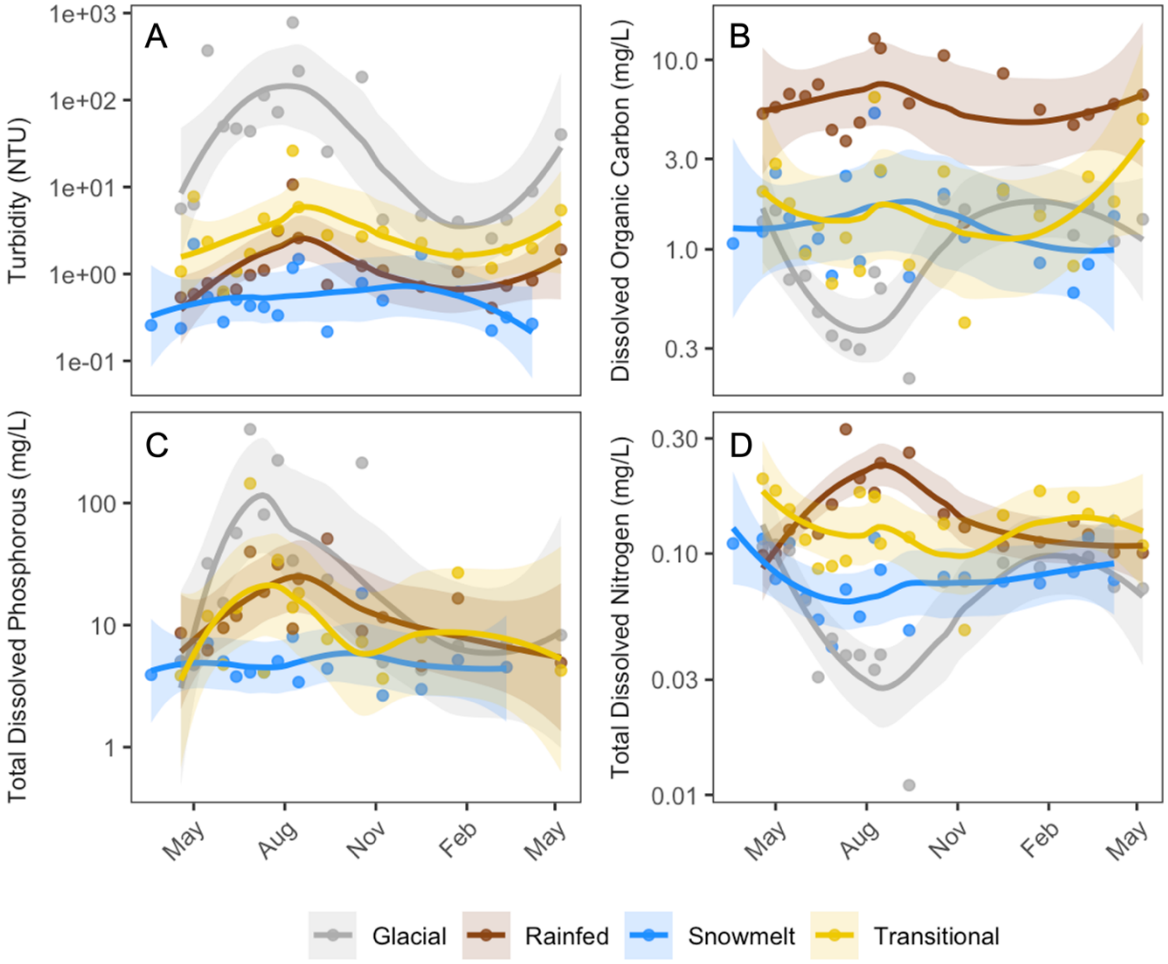


Figure 2-3 Measured monthly values and smoothed time series of turbidity (A), dissolved organic carbon (B), total dissolved phosphorous (C), and total dissolved nitrogen (D) from early April 2018 to late April 2019.

### *Periphyton*

Periphyton biomass concentrations (assessed through AFDM per planar area of streambed) varied by more than an order of magnitude within streams throughout the measurement period and as much two orders of magnitude across streams, yet peak values were similar among the four streams. Periphyton biomass exhibited asynchronous seasonal waves between stream types (Figure 4b). In the glacial stream, periphyton AFDM was highest during the spring and winter seasons (January-April) and was lowest during the summer and autumn (June-November) when high flow and turbidity and low temperatures likely limited periphyton growth. In contrast, both the snowmelt and rainfed systems exhibited summer peaks in periphyton biomass, when flows were lower, and temperatures were higher. The transitional stream exhibited no clear seasonal dynamic but remained somewhat stable throughout the year. Average annual periphyton biomass was highest in the rainfed stream at 364 mg m-2 (273-455 mg m-2), lowest in the glacial stream at 108 mg m-2 (38-177 mg m-2), and similar in the snowmelt and transitional streams at 275 mg m-2 (229-322 mg m-2) and 276 mg m-2 (240-313 mg m-2).

### *Benthic Macroinvertebrates*

Spatial and seasonal differences in aquatic invertebrate biomass were observed throughout the year. In July, there was more than 1000-fold greater average insect biomass observed in the rainfed stream than the adjacent glacial system. Differences in biomass were driven by asynchronous patterns in common taxa and varied by functional feeding groups (Figure 2-5). This resulted in asynchronous timing of within-stream peaks of relative invertebrate biomass, with the glacial system peaking in late winter/early spring, the rainfed system peaking in early summer, and the transitional and snowmelt streams peaking in late summer (Figure 2-6). Biomass and abundance were lowest in the glacial stream (95% CI, 24.6-47.1 g m-2; 95% CI, 64-128 individuals m-2) and were significantly different than adjacent streams (Figure 2-4C).

### *Synchrony*

We evaluated potential implications of climate-driven loss of hydrologic heterogeneity on streams by systematically removing streams prone to loss from the dataset and assessed changes to synchrony estimates (Figure 2-7). Overall, we found moderate average synchrony across the landscape (45.2% for abiotic factors and 38.9% for biotic factors) which was driven by high synchrony in temperature and flow in the three non-glacial streams and a general convergence of all conditions in winter. We found that removing the glacial stream from the dataset resulted in the greatest increase in mean landscape synchrony of both abiotic and biotic factors. Invertebrate abundance and biomass had the greatest relative increases in biotic synchrony (~30%) when we removed the glacial stream – presumably due to the loss of meltwater periods of low temperature and invertebrate standing stocks. These coincided with abiotic increases in the synchrony of water temperature and DOC. The loss of the transitional stream increased biotic synchrony at a greater rate than loss of the snowmelt stream. Conversely, removing the transitional and snowmelt streams had opposite effects on abiotic synchrony: the loss of snowmelt increased landscape synchrony and loss of transitional decreased landscape synchrony.

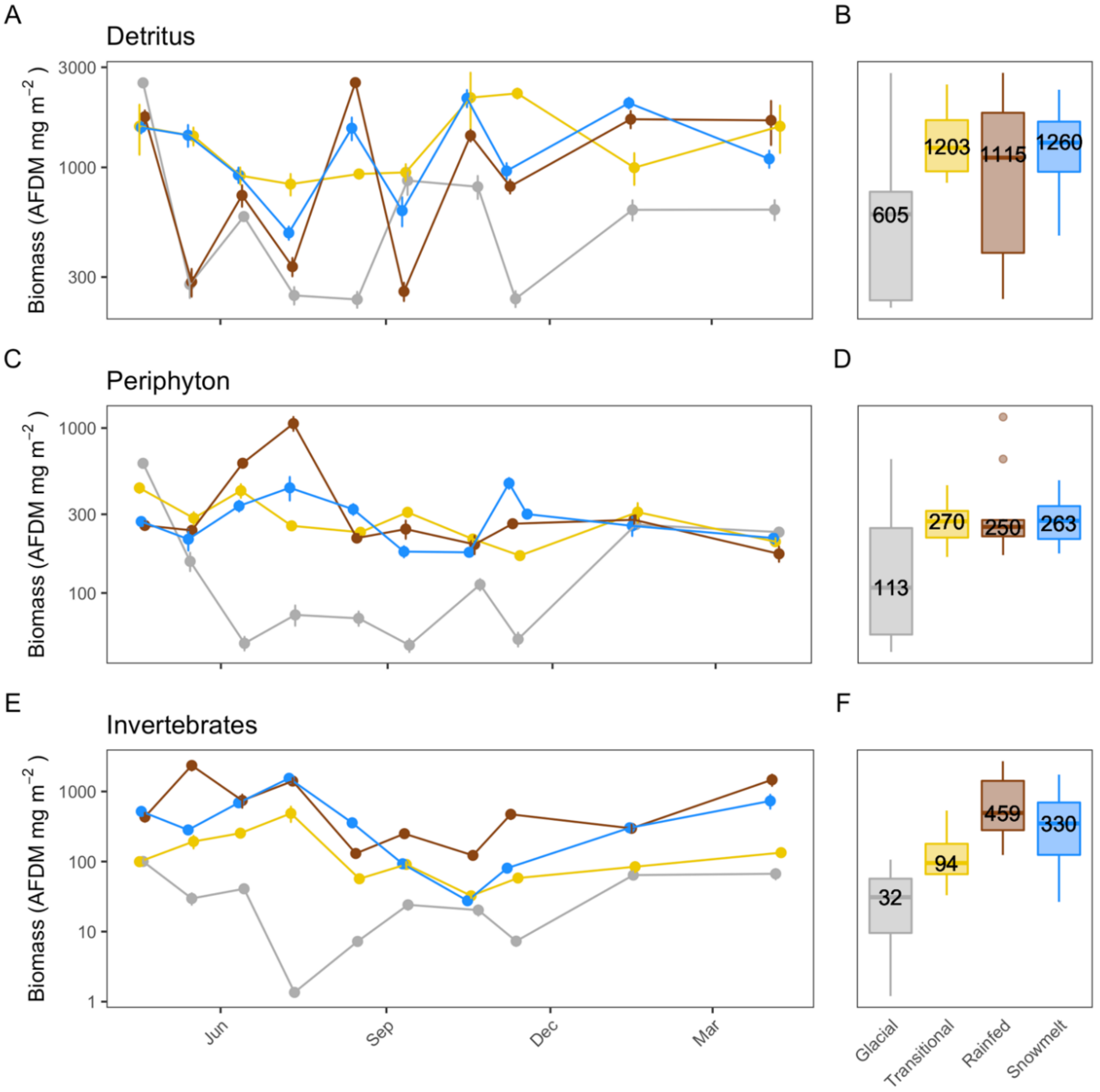


Figure 2-4 Mean concentrations (±1 SE) of invertebrate (A), periphyton (C), and detritus (E) standing biomass from April 2018 – April 2019. Boxplots for time series (B, D, F) where the line within each box is the median outcome, box boundaries are 25th and 75th percentiles, whiskers are 5th and 95th percentiles, and numbers within the box report the median value. Note the logarithmic scale shared between time series and boxplots.

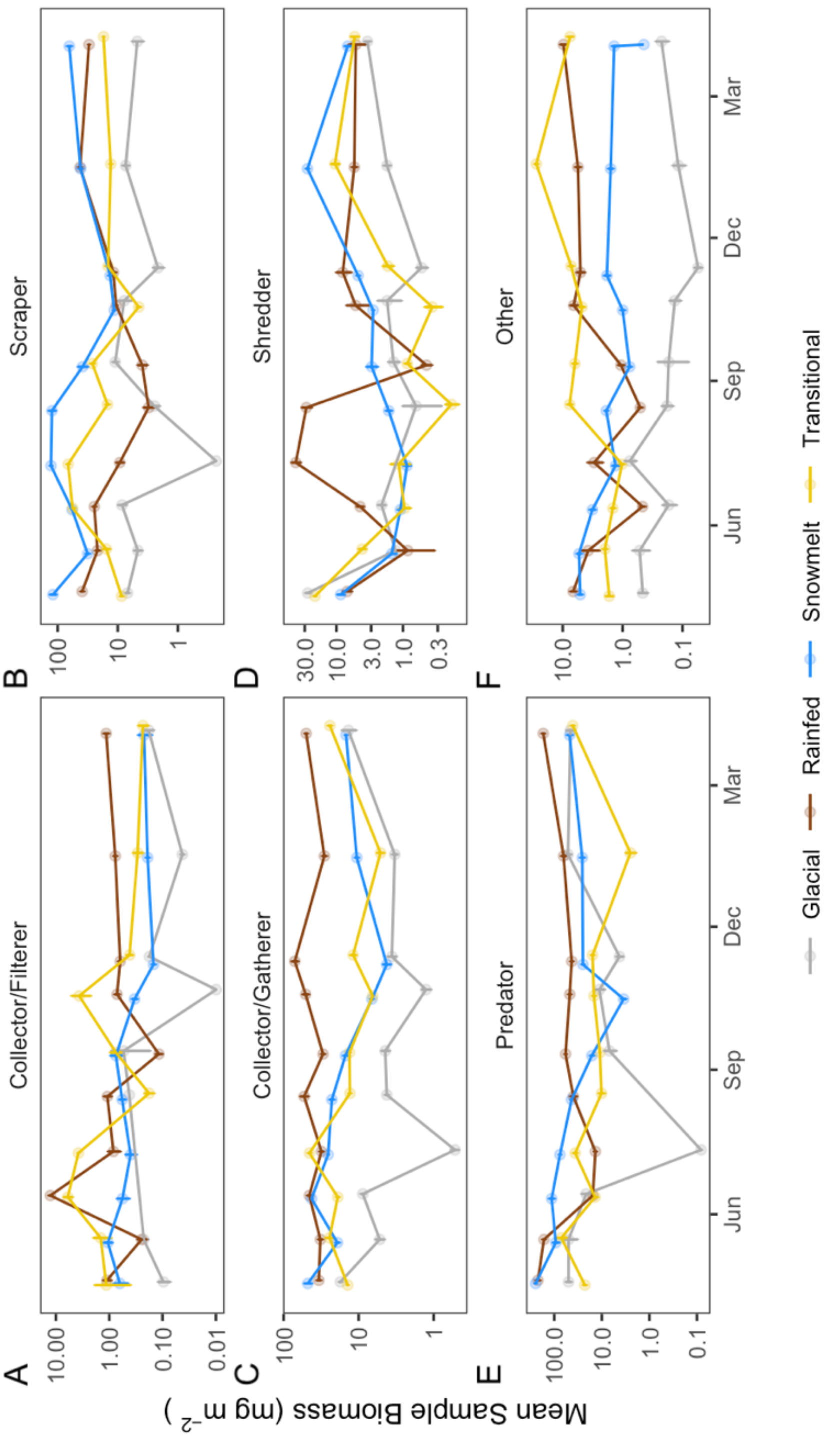


Figure 2-5 Seasonal variation in invertebrate biomass (mean ± 1 se) by primary functional feeding group classification (Merritt et al. 2019): collector/filterer (A), scraper (B), collector/gatherer (C), shredder (D), predator (E), and 'other' uncategorized taxa (F).

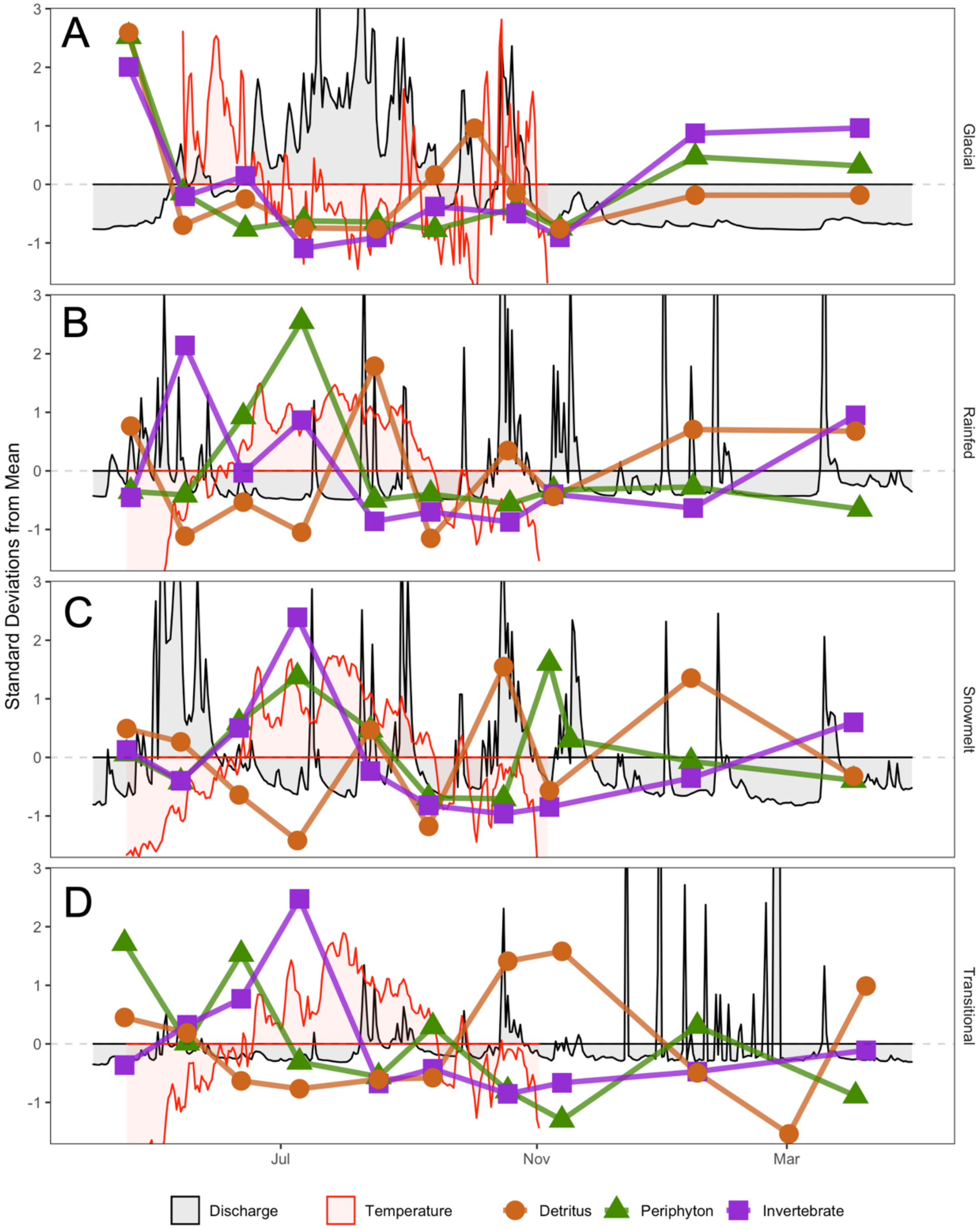


Figure 2-6 Standardized anomalies of detritus, periphyton, and invertebrate biomass in relation to stream temperature and discharge reflects uneven physical forcing on stream food webs in glacial (A), rainfed (B), snowmelt (C), and transitional (D) streams.

## Discussion

Climate change is driving the decline of the global cryosphere in high latitude and mountainous areas (Hock et al. 2019, Elser et al. 2020) and some of the most dramatic changes are occurring in places influenced by glaciers and in areas experiencing snow-rain transitions (Gardner et al. 2013, Radic et al. 2013). Here, we demonstrate that physicochemical differences among streams are associated with both spatial and temporal heterogeneity in the biomass of key food web compartments suggesting that the loss of glacial and snow meltwaters may simplify the trophic landscape by spatially *homogenizing* the physicochemical conditions and temporally *synchronizing* the patterns of primary and secondary biomass in stream food webs. In turn, changes to food web components could affect the timing and capacity of streams to support higher-level consumers (e.g., invertebrate predators, riparian birds, and Pacific salmon *Oncorhynchus spp.*) and associated ecosystem services of food production, traditional uses, and tourism.

As anticipated, our sites experienced marked differences in total dissolved nitrogen and phosphorous, critical nutrients in oligotrophic streams (Dodds et al. 1998). Dissolved organic carbon was consistently high in the rainfed stream, contributing to its common regional classification as "brown-water stream" (Hood et al. 2007). Wetland-derived DOC in rainwater streams on this landscape is fractionally less labile than DOC in non-rainfed streams but found at much higher concentrations leading to greater overall bioavailable DOC (Fellman et al. 2009b). DOC may alter light penetration to the benthos even at shallow depths (Morris et al. 1995) and has bene shown to inhibit chlorophyll A, but not biomass of periphyton (Bechtold et al. 2012), due to a shift from autotrophic to heterotrophic biofilms. Streams also varied in their thermal and flow regimes, with the glacial system experiencing invariably low temperatures throughout the year and high, turbid flows in summer. All other streams shared generally similar patterns of seasonal changes in temperature, though the scale varied with the rainfed stream being the warmest, followed by the snowmelt and transitional streams. Temperature directly influences metabolic rates of primary (Padfield et al. 2017) and secondary trophic (Vannote and Sweeney 1980) levels as well as decomposition rates of biofilms and terrestrial detritus. In non-meltwater streams, water temperature tracks ambient air temperature (Bogan et al. 2003, Letcher et al. 2016). In meltwater streams, however, water temperature and air temperature often do not track due to cold water inputs during periods of high air temperature and albedo (Slemmons et al. 2013, Fellman et al. 2014b). As predicted, the rainfed stream was flashy during all seasons – particularly during low flow periods in the summer where spates led to rapid increases then decreases in flow. All four systems were influenced by heavy fall rains during Sept-

Oct 2018. Flow and related sediment dynamics potentially limit all trophic levels through bed instability, turbidity-mediated light limitation, and shear stresses on biota. This is particularly strong in glacial meltwater streams, where low bed stability and light-limiting glacial silt constrain periphyton and aquatic invertebrate biomass (Milner et al. 2009, 2017, Slemmons et al. 2013). If physically harsh and low productivity streams are indeed structured by bottom-up controls (Niedrist et al. 2018), these differences in the abiotic environment and the trophic base of the food web should underpin the dynamics of higher trophic levels, such as secondary invertebrate consumers and suggest these systems are highly vulnerable to climate change due to dramatic changes in temperature, shifts in precipitation, and the transient increases in meltwater during accelerated glacial recession. These differences in the physical and chemical dynamics of sites created substantial variation in biomass of the trophic base of the aquatic food web.

Our observed patterns in abiotic conditions and biomass among streams and across seasons imply strong physiochemical controls which were generally consistent with our conceptual model (Figure 2-1; Figure 2-4). Peak periphyton and detritus biomass was similar across sites though the timing of those peaks varied. Mean annual periphyton and detritus biomass, however, was reduced by more than half in the glacial stream due to extreme lows during the active melt season. The patterns of periphyton biomass in the glacial stream were consistent with our prediction of a peak in early spring prior to the onset of glacial runoff, when high, cold, and turbid flows would cause scouring flows and low production. Both the rainfed and snowmelt streams had predicted peaks in periphyton biomass in midsummer, but we did not predict that these streams would experience several increases and decreases in detritus over the year. Rather, we expected detritus to peak in the fall in both the glacial and non-glacial systems, though the timing would vary by location. However, this may be an artifact of monthly sampling and higher-frequency sampling may highlight the influence of storm flows on stream detritus pulses (Delbecq and Fitzgerald, *in prep*.). The variation in detrital pools supports the idea that terrestrial inputs and breakdown in streams reflects an interplay of leaf-fall and transfer processes (Marcarelli et al. 2011), but both the rainfed and snowmelt stream had variable detrital biomass pulses which seemingly corresponded with high flow events (Fellman et al., 2022).

We expected that invertebrate biomass would track the seasonal dynamics of basal resources, but the patterns were much less clear. Annual mean invertebrate biomass differed among streams by more than an order of magnitude. Invertebrates saw a similar drop in biomass during the glacial melt season, though from our data we cannot discern whether this is a matter of hydraulic flushing of the community, adaptation of life history to avoid vulnerability during high flows, or vertical or lateral movement to more stable areas of the streambed and/or top-down pressure from predation. We instead observed highly variable biomass dynamics in the benthic invertebrate community, which was likely driven by both life history differences (e.g., emergence, Füreder et al., 2005) and pressures on traits, such as feeding behavior (Ledger et al. 2011). Past studies predicted that glacial streams would have spring and fall shoulder seasons of high periphyton biomass and a fall pulse of detritus when meltwaters declined (Uehlinger et al., 2010). Instead, we found evidence for only a spring pulse in periphyton (though a pulse may have occurred between our four-week sampling windows). The lack of an observed fall pulse may be caused active melt in lower elevation glaciers continuing longer into the fall until light availability becomes limiting and/or that the fall wet season often results in prolonged periods of scouring high flows. The relative harshness of flow and low food availability during peak ice melt contributes to the extremely low invertebrate biomass in that stream in midsummer. Even lightly glacierized streams in this region may contain and transport substantial amounts of terrestrial detritus (Milner et al. 2000a, 2009), including at the confluence of a lightly glacial tributary and the headwaters of the transitional stream from this study (Fellman et al. 2022). Periphyton biomass also seemingly drops after high flow events in the rainfed stream, suggesting that bed turnover at this location limited periphyton biomass, though water clarity remained higher throughout the year.

Our data also suggest some internal biotic associations on invertebrate community dynamics via functional feeding traits tracking apparent resources. Invertebrate feeding traits were unevenly distributed in meltwater and non-meltwater streams. For instance, glacial streams were dominated by functional shredders and collector/filterers during peak melt. Further, high glacial runoff during the summer melt season was associated with low biomass of several invertebrate functional feeding groups: particularly those which employ movement and foraging for growth (i.e., predators and collector/gatherers) and that rely on autochthonous production (i.e., scrapers) during the melt season. As a result, glacial streams were dominated by functional shredders and collector/filterers during peak melt. Conversely, the rainfed system had highest collector/filterers and shredders in late spring and midsummer, respectively – likely related to the high average DOC and detritus biomass. In the snowmelt stream, scrapers peaked in midsummer, coinciding with relatively clear water, stable flows, and high nutrient concentrations that likely resulted in both high benthic periphyton and chlorophyll *a* concentration (SI). Surprisingly, the transitional stream had relatively high and stable biomass dynamics for all but shredders, indicating that the combined influence of many water sources could create more diversity in feeding modes. While we recognize inherent flaws in feeding group-based interpretations (Tierno de Figueroa et al. 2019), these relationships among physico-chemistry, habitat heterogeneity, and functional group diversity has been observed for invertebrate assemblages in small lakes in Finland (Heino 2000), in Arctic spring-streams (Huryn et al. 2005) and in agricultural streams in New Zealand (Burdon et al. 2020). Functional traits, such as feeding mode, are likely a major form of ecosystem functionality that will be altered as the cryosphere is lost and the landscape homogenizes (Alsterberg et al. 2017).

Together, the seasonal dynamics in periphyton and invertebrate biomass and functional groups supports the overarching influence of abiotic controls in this ecosystem. Recent analyses have emphasized the overarching effect of light and flow on productivity of rivers and streams (Bernhardt et al. 2018, 2022, Junker et al. 2021). This may be particularly strong in watersheds with glaciers, where meltwater influences flow and light penetration dynamics, and where relatively high gradients and flow regimes influence bed stability. Our study generally supports that the overarching effects of flow, but also suggests temperature and nutrient dynamics may influence asynchronous seasonal patterns in primary producer, detritus, and secondary consumer biomass in glacial, snowmelt, and rainfed streams.

### *Implications of meltwater loss*

The loss of glacier ice from high elevation and high latitude watersheds will decrease meltwater inputs to streams thereby increasing hydrologic homogeneity and synchronization of streams around the globe (Figure 2-7). The impacts of the loss of cryospheric streams will vary depending on the context of these features on the landscape. In temperate latitudes, such as Southeast Alaska, melting mountain glaciers and icefields will result in short-term increases in meltwater (Huss et al. 2017) and may open new habitat for mobile consumers, such as Pacific salmon (Milner et al. 2017, Pitman et al. 2020, 2021). However, the loss of glacial meltwaters will also remove a key contributor to heterogeneity on landscapes.

Many mountain watersheds contain a mosaic of tributaries with gradients of water sources. The fading cryosphere is pushing many streams from endmember conditions (e.g., main water source is glacial melt) to more transitional stream types (Sergeant et al., 2021). While glacial streams may have relatively lower annual production, they can be refugia during drought conditions (Van Tiel et al. 2018) and may be the most productive places on the landscape during some periods of time. For example, Bellmore et al (2022) used a mechanistic meta food web model to show that distinct waves of stream biofilms and invertebrates create unexpected growth opportunities for juvenile fish in streams networks containing glacial, snowmelt, and rainfed streams. Our findings generally support

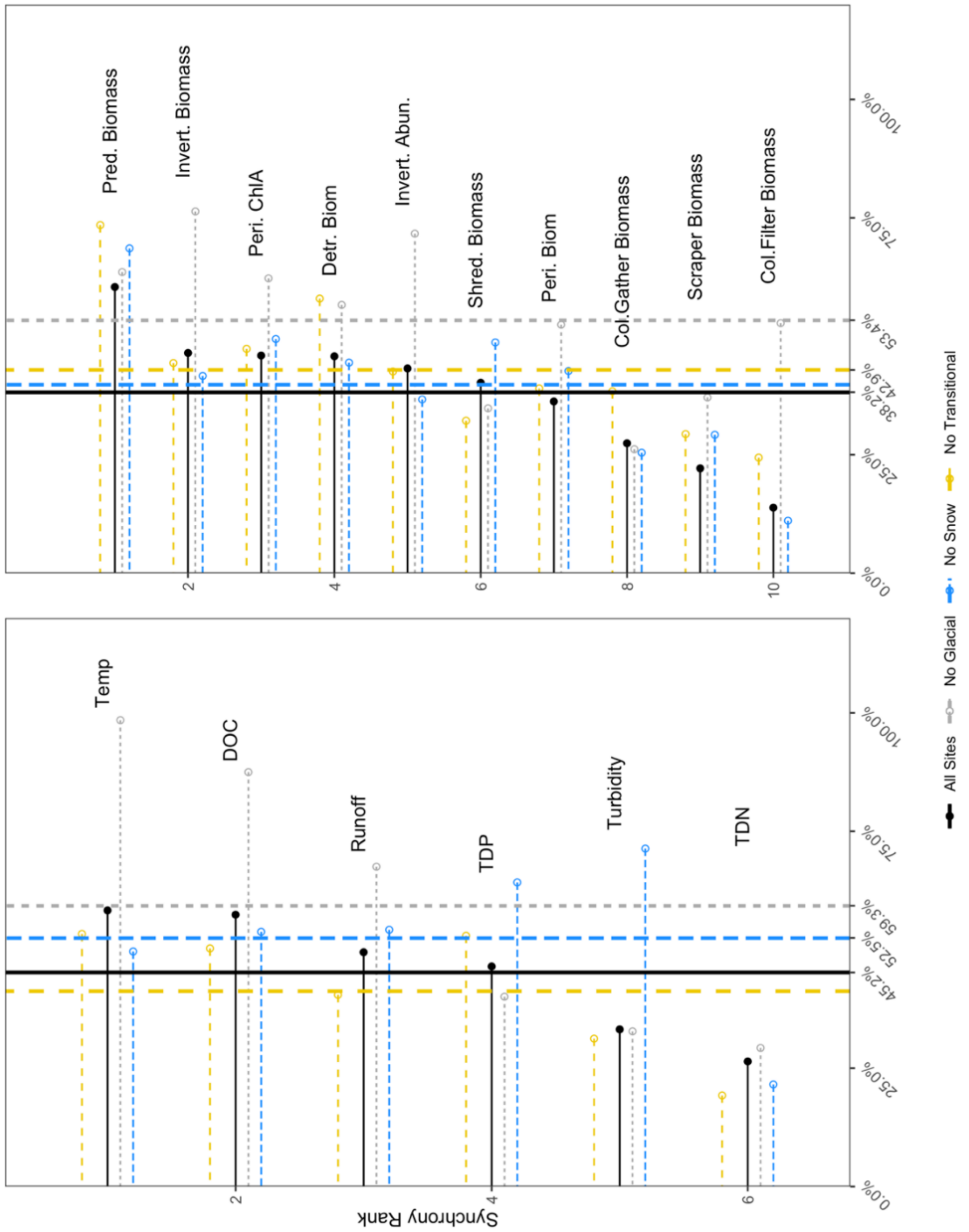


Figure 2-7 Ranked synchrony (S) of landscape elements in the time series including all sites (solid horizontal lines) versus conditions when individual streams are removed (dashed horizontal lines) ranging from perfect synchrony (100%) to perfect asynchrony (0%). Mean landscape synchrony (vertical lines) reflects the greatest increase when glacial stream values are removed relative to losing snowmelt or transitional streams.

the seasonal dynamics of stream biofilms predicted by the model in that periphyton biomass peaked in the glacial system in winter and in spring-summer in the non-glacial streams (Figure 2-6). However, unlike the model predictions, we found invertebrate biomass waves did not consistently track periphyton biomass. Instead, our findings suggest invertebrate biomass is strongly influenced by taxon-specific variation. Our data show that if glacial streams transition to more snowmelt hydrology, they will generally shift from winter to summer peaks in periphyton and aquatic invertebrate biomass coinciding with additional hydrogeomorphic changes to channel structure and stability.

Additionally, its projected that as winter snowfall transitions to rain (Littell et al. 2018, Sergeant et al. 2020), all watersheds will become more influenced by surface runoff during the winter. This may lead to common storm-driven spates across the landscape which may result in flashy biomass waves across trophic levels. Currently, low elevation glacial ice buffers glacial ecosystems from extreme flashy runoff events in winter. Our data also shows that the loss of meltwater signatures will synchronize many conditions, such as temperature, primary producer quality in terms of chlorophyll concentration, and the abundance of aquatic invertebrate prey species. Climate change is predicted to increase extreme rainfall events in this region (Robertson et al. 2015), particularly those driven by large atmospheric river events (Payne et al. 2020). Associated spates may alter resource dynamics as flashy events scour periphyton, flush detrital pools, and alter conditions for aquatic invertebrates (Delbecq et al., *in prep*; Fitzgerald et al., *in prep*). Further, the buffering capacity of ice on the landscape is fading and will decrease glacial refugia during these spates. Asynchrony in resource availability of primary sources within and among watersheds may alter the dominant pathways energy takes from basal resources, like biofilms and detritus, to higher-level consumers like predatory invertebrates, fishes, and birds. Future work should quantify the energy flow pathways in these ecosystems to elucidate potential changes that will occur with climate-change driven homogenization.

Our findings are some of the first to empirically demonstrate that meltwater streams create peaks in resource abundance among several trophic levels relative to different stream types. Future work should quantify the role of hydrologic source on both the secondary production of aquatic invertebrates in these systems and the flows of energy through food webs to support the growth of mobile consumers, such as juvenile salmon which may integrate production across the landscape within their lifetime. In the past, glacial rivers have been thought to contribute little to landscape productivity due to cold and harsh conditions and/or seasonal drying (Clitherow et al. 2013, Robinson et al. 2016, Siebers et al. 2022), but this view could be biased by sampling during the summer melt season. Further, most glacial river research focuses on mountain glaciers in alpine areas with less riparian community development (Pepin et al. 2022) or anadromous fish with complex life cycles. Our data show that in southeast Alaska, low elevation glacial rivers can contribute to distinct resource dynamics across landscapes and can support productivity when other areas on the landscape are less productive (O'Neel et al. 2015).

This study emphasizes the growing body of evidence that the cryosphere contributes to environmental heterogeneity can create spatial asynchronies in ecological communities across landscapes. However, climate change will continue to diminish the cryosphere globally via the fading of mountain glaciers and shifts from winter snow to winter rain (Shanley et al. 2015, Buma et al. 2017, Lader et al. 2020, Newman et al. 2021) – potentially simplifying and homogenizing downstream landscapes. While much attention has been paid to the direct consequences of glacial and snowmelt declines on diversity and distribution of species and populations, a potential further consequence will be the simplification of resource phenology in these places. It is entirely plausible, if not probable, that we will see an increase in annual productivity in cold and harsh areas, but this may coincide with a reduction in the seasonal variation in resources, which could render these landscapes less stable and more susceptible to future climate impacts assuming the variation we document among watersheds is tractable to mobile consumers within and among watersheds.

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# Chapter 3 - Contrasting diversity and secondary production of benthic stream macroinvertebrates across a rapidly changing glacial meltwater landscape

## Abstract

The mountain cryosphere contributes to the variation in physical and chemical dynamics of nearby rivers and streams. In turn, this heterogeneity can influence species distributions and organic matter processing. Much work has focused on the implications of climate change on the diversity of aquatic communities in meltwater streams, but few have quantified the rates of secondary production of consumer biomass in streams with differing hydrologic sources. Here, we simultaneously measure the invertebrate community in streams representing *glacial melt, snowmelt, rainfed,* and *transitional* sources near the Juneau Icefield, Alaska, USA and measure invertebrate taxonomic and functional community traits, biomass waves, and secondary production over a year. We show substantial variation in *alpha* diversity within and *beta* diversity across glacial, snowmelt, rainfed, and transitional streams resulting in invertebrate communities with distinct taxonomic and functional traits. Our data support the view that glacial rivers are physically harsh, relatively low productivity environments but also find that they contribute the most to *beta* diversity on the landscape. The snowmelt stream was both the most diverse and the most productive stream on the landscape. As glaciers recede and the region experiences climate change-driven snow-to-rain shifts, the distinct communities, functional assemblages, and productive capacity of watersheds may homogenize in both space and time, trending toward general increases in invertebrate alpha diversity and secondary production but lower regional heterogeneity in community structure.

## Introduction

Loss of the cryosphere is driving global changes to the patterns of ecosystem structure and function by reshaping physical and chemical regimes to which species and communities have adapted (Elser et al. 2020). In high-latitude or mountainous freshwater ecosystems, melting glaciers and seasonal snowpack can be a major influence on stream properties, such as stream flow, water temperature, and nutrient availability (Milner et al. 2017). Proglacial aquatic environments are also among the most rapidly changing as global climate change increases ambient air temperatures, alters seasonal precipitation patterns and forms, and increases short-term glacial meltwater contributions prior to complete glacial loss. Past studies suggest the loss of glacial and snowmelt signatures will alter the *diversity* of downstream ecosystems as they become warmer, increase in clarity and bed stability, and decrease in turbidity, overall, becoming less harsh (Jacobsen and Dangles 2012, Pitman et al. 2020, Bellmore et al. 2022). However, few studies have examined the accompanying changes in biological *productivity* of downstream ecosystems and their capacity to produce secondary consumer biomass.

As meltwater signatures fade from river networks, biodiversity is expected to change at several ecological and spatial scales. Local *alpha* diversity (i.e. diversity within an individual stream) in cold or harsh glacial or intermittent meltwater streams is predicted to increase as they become warmer and more stable, and likely more suitable to a broader range of organisms (Milner et al. 2009, 2017), whereas *beta* diversity (i.e. dissimilarity of species assemblages between different streams) between sites is predicted to decrease as communities homogenize and the unique assemblages adapted to meltwater streams are lost (Brown et al. 2006, 2007a). A decrease in beta diversity corresponds with biotic homogenization (Gámez-Virués et al. 2015), as specialist taxa are supplanted by more generalist taxa which may become dominant across the landscape. These changes to biodiversity will have knock-on effects on both the pathways and the rates of secondary production of animal biomass (Benke 2018). While it is generally predicted that loss of harsh habitats should increase diversity and production (Dolbeth et al. 2012, 2015), how this will occur has not been explicitly measured. It is possible that productivity may increase as specialist taxa are replaced with higher production cosmopolitan taxa. Alternatively, productivity of existing communities may increase due to more favorable conditions for primary production and consumer metabolism.

On physically complex landscapes, a mosaic of distinct physicochemical conditions may occur over relatively short distances. In high elevation or high latitude areas, freshwaters sourced by melting ice or seasonal snowpack co-occur with streams draining other water sources (e.g., rainfall/surface runoff, groundwater upwelling, or subterranean ice melt) within and among watersheds (Brown et al. 2003, Brown and Hannah 2008, Milner et al. 2010). This hydrologic heterogeneity creates spatial and temporal environmental gradients in runoff, water temperature, and water chemistry (Chapter 2). Glacial systems are typically characterized by seasonally high, turbid, and cold flows during active glacial melt. Snowmelt streams have a pronounced snowmelt pulse in early summer, followed by declining flows and increasing temperatures into autumn. Rainfed streams, which are predominantly found in lower elevation/gradient watersheds are fed by recent precipitation and may be flashy during storm events followed by low base flows during dry spells. Commonly, these endmember conditions are found in tributaries which combine to form a watershed mosaic of physicochemical conditions – particularly in watersheds undergoing transitions from glacial- to snowmelt signatures or those moderate elevation systems transitioning from snowmelt-to-rainfed signatures. To date, no studies have concurrently examined both biodiversity and secondary production in stream food webs across this hydrologic gradient. Understanding how climate change will impact diversity and production capacity of watersheds fed by meltwater requires a knowledge of the current variation in taxonomic and functional assemblages of aquatic organisms as well as the rates of secondary production across a natural landscape gradient.

Here, we ask the following motivating questions:

(1) Does hydrologic heterogeneity create different aquatic insect communities with distinct functional and temporal dynamics?

(2) Does hydrologic heterogeneity create spatial or temporal differences in the rate by which streams produce secondary consumer biomass? And

(3) Is secondary production controlled by differences in *community composition* (i.e. species turnover) or are differences driven by variation in production rates of generalist taxa found across stream types?

To answer these questions, we collected physico-chemical and aquatic invertebrate community production samples from four streams reflecting relative end members of glacial, snowmelt, rainfed, and transitional signatures near the Juneau Icefield, AK USA (Sergeant et al. 2020; Giesbrecht et al 2022). We predicted these streams would have substantial differences in abiotic conditions, nutrients, and primary/detrital pools (see Chapter 2). Specifically, we expected the glacial stream would have the lowest macroinvertebrate diversity, the most distinct community, and the lowest secondary production of all the sites due to low temperatures and high flow during summer months. The rainfed stream was predicted to have the highest macroinvertebrate diversity, production, and biomass due to warm temperatures. Snowmelt and transitional streams were predicted have intermediate values of diversity and productivity due to moderate temperature- and flow-limitations. Additionally, we expected that streams would be temporally asynchronous in their composition, diversity, standing stock biomass, and rates of secondary production – specifically that the glacial system would have "shoulder seasons" of higher diversity and production when glacial melt is absent and that the rainfed stream communities will be impacted by extreme low flows during periods without rain. This should lead to greater diversity and secondary production in the warmer and more stable streams and distinct invertebrate communities driven by filtering of the landscape species pool.

## Materials and Methods

### *Study Area*

The coastal streams on the western edge of the coastal Juneau Icefield, Alaska (~3800 km$^2$) express a diversity of water sources and support large populations of Pacific salmon (*Oncorhynchus spp.*), Dolly Varden char (*Salvelinus malma*), and sculpin (*Cottus aleuticus*) which rely on production of aquatic invertebrates for primary growth during early freshwater rearing. The Juneau region has a cool maritime climate (mean annual temperature = 2.17°C) with a 30-year precipitation average of ~4,068 mm (Long Lake SNOTEL Site #1001: 58.1833°- 133.833°, Elevation 300 m)). The landscape is characterized by dense forests, high mountain peaks, a mix of large and small glaciers and snow- and icefields, and numerous low-lying peat wetlands, contributing to heterogeneity in the physico-chemical regimes of rivers and streams (D'Amore et al. 2015, Shanley et al. 2015). This region is also undergoing some of the fastest rates of glacial decline globally (O'Neel et al. 2015, Bergstrom et al. 2021) as well as experiencing winter snow-to-rain shifts in precipitation (Shanley et al. 2015).These watersheds are also a critical nursery habitat for Pacific salmonids (Johnson et al. 2019), which return to spawn and rear in coastal streams in large numbers.

Our study sites included (1) the glacier-fed Herbert River (hereafter "glacial"), (2) the rainfed Peterson Creek (hereafter "rainfed"), (3) the snow-fed Steep Creek (hereafter "snowmelt"), and 3) Montana Creek, which is a snow-rain transitional stream with tributaries reflecting each of the above classifications (hereafter "transitional") (Figure 3-1). Herbert River is a moderately sized glacial river near the Juneau Icefield in the Tongass National Forest in southeast Alaska with a watershed area of 152 km$^2$ and relative glacial coverage of 40.3%, 25% forest coverage, and wetland coverage of 4.8% (Fellman et al. 2014a). Our study reach consisted of ~100m riffle/run with large debris dams from high flow events near the upper part of a gravel bar. At moderate to high water during May-October, a connected side channel was also present. Peterson Creek is a predominantly rainfed stream nearby with a watershed area of 24 km$^2$, 92% forest coverage, and 31.9% wetland coverage. The Peterson Creek study reach consisted of a slightly undercut bank with ~1m deep pools on one side and a low gradient vegetated bar on the opposite side, generally alternating from shallow riffles to shallow runs during standard summer flows. Steep Creek is a tributary of the Mendenhall River with a watershed area of 4.9 km$^2$ which largely drains a hanging valley. Our study reach consisted of a braided channel below an impassible waterfall that contained a mix of riffle, run, and off-channel pool habitats above its confluence with the glacial Mendenhall Lake. The watershed has a relative forest coverage of 44% and a wetland coverage of 8%. Montana Creek is a tributary of the glacial Mendenhall River with a watershed area of 37 km$^2$ with 66% forest and 7.7% wetland coverage. A major tributary, McGinnis Creek, contributes a small glacial influence (2.5% by total Montana Creek watershed area). Our study reach was below the meltwater-rainfed confluence in the lower valley where the gradient was like other study locations and consisted of a wide channel transitioning from riffle to braided debris dams and back to riffles. Watersheds were selected to represent relative endmember conditions on the Juneau Road System based on previous studies (Fellman et al. 2014a, 2015b) and reaches were selected for similar gradient, distance from ocean entry, and access to Pacific salmon. Additionally, wetted widths were similar (~8 m) during winter months, though much wider in the glacial stream during peak summer melt (~20m) and narrower in the rainfed stream during dry periods (~2m).

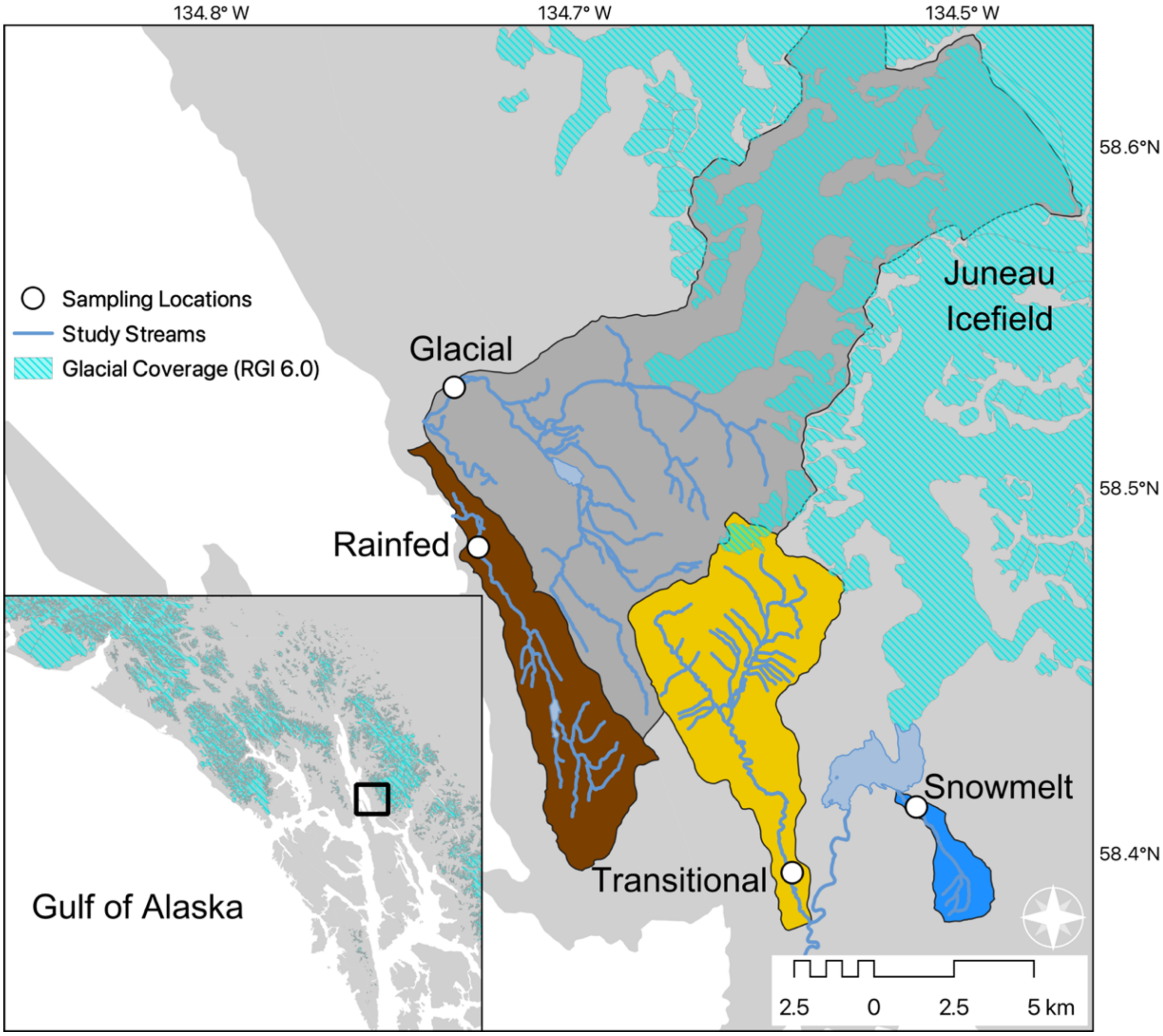

Figure 3-1 Map of study location near the Juneau Icefield in Southeast Alaska and regional ice coverage from the Randolph Glacier Inventory version 6.0 (RGI Consortium 2017).

### *Stream Physico-chemistry*

In each stream, we used an automated sonde (YSI Inc. Yellow Springs, OH USA) to take hourly measurements of water temperature. Runoff measurements were tailored to each site. We measured runoff using a pressure transducer in the rainfed stream. In the glacial river, we used a modeled relationship with a nearby gauged glacial river (CITE Eran) and supplemented with >20 measurements using an acoustic doppler current profiler (RiverRay, Teledyne RD Instruments Inc.) at different flow levels. The snowmelt and transitional streams were gauged and managed by Alaska Hydroscience and the National Weather Service, Juneau Office, respectively. We collected point samples for water chemistry once per month. We measured dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) using an elemental analyzer (Shimadzu Model TOC/TN-V-CSH) and we measured total dissolved phosphorus (TDP) using the ascorbic acid method (Valderrama, 1981). Turbidity was measured in triplicate in the field using a Hach Turbidity Meter (add model #, etc.). During point sampling events, we measured pH using a handheld pH Meter (Orion Star A221, ThermoFisher Scientific, Waltham, MA) and conductivity using a handheld sensor (YSI Model 556, YSI Inc., Yellow Springs, OH, USA). We assessed significant differences in mean physico-chemical values using pairwise Wilcox tests using the R package “ggpubr” (Kassambara, 2020).

### *Benthic Invertebrate Sampling*

We sampled benthic invertebrates every four weeks (Apr 2018 - Nov 2018) and every eight weeks (Dec 2018 - Apr 2019) resulting in 10 sampling events per site over 13 months. During each sampling event, we collected five replicate samples of benthic invertebrates using a standard Surber sampler (0.25 $m^2$, 250-µm mesh, Aquatic Research Instruments, Hope, ID, USA). Each sample was a composite of three subsamples collected from riffle habitats at the bottom, middle, and top of each reach. We elutriated samples in the field to separate organic material from stream gravel and preserved the former in 95% ethanol. In the lab, we transferred the sample to a 120 µm sieve and first removed large and rare organisms (body length ≥ ~15 mm). We then extracted 1/8th subsections until a minimum of 500 individuals were present in the subsample fraction. We removed macroinvertebrates from detritus under 10x magnification using a dissecting microscope, identified to the lowest practical taxonomic level (generally genus or lower for all taxa except *Chironomidae*, *Oligochaeta, Gastropoda, and Mollusca*) and measured body length to the nearest 0.5mm using either an ocular micrometer or grid paper.

### *Diversity and Community Traits*

The density (individuals $m^{-2}$) and richness (distinct taxa $m^{-2}$) of benthic invertebrates from each sample were used to calculate invertebrate *alpha* diversity (Shannon-Weaver S') and evenness (Pielou's J) and between stream *beta* diversity (Sorensen's index). We conducted pairwise comparisons of mean values for each diversity metric using a Wilcoxon test using the R package "ggpubr" (Kassambara, 2020). We estimated community trait values by calculating a community-weighted mean (CWM) trait set for each sample (Shipley et al. 2011). CWMs were calculated by taking the within-sample mean values for the continuous variables of total invertebrate density, body length, individual mass, size-at maturity, voltinism, and thermal preference and assigned values for categorical variables of feeding guild and habit as the relative within-sample proportion of those classifications (further described in *SI*). All values were weighted by the relative density of each taxon in each sample. Continuous variables of size-at-maturity, voltinism, and thermal preference were provided by a trait dataset established for the Pacific Northwestern US (Wisseman *unpublished data*). We used non-metric dimensional scaling (NMDS) to visualize variation in community structure by family-level abundance and CWM trait values. We then used canonical correspondence analysis (CCA) to evaluate the role of eight stream properties (temperature, discharge, TDP, TDN, DOC, turbidity, pH and conductivity) on community functional separation. All analyses were done in R using the package 'vegan' (Oksanen et al., 2013). Plots and standard ellipses were created using the package 'ggplot2' (Wickham et al. 2016).

### *Biomass and Secondary Production*

Individual macroinvertebrates biomass was calculated using literature-based length-mass relationships (Benke et al., 1999; Sabo et al., 2002; R. Wisseman, *unpublished data*) and scaled by abundance to estimate population-level biomass for each taxon. We estimated production for most taxa at the family-level using the size frequency method corrected for cohort production interval (Benke and Huryn 2017). For rare or unevenly sampled taxa, we converted biomass to production using either the mean landscape P:B values from all sites or literature-based P:B values (e.g. *Oligochaeta* (1.4-5.5; Rîşnoveanu & Vãdineanu, 2003)*, Chironomidae* (2.01-2.6; Niedrist et al., 2018)*, Gastropoda & Mollusca* (~5; Benke et al., 1984)). We calculated confidence intervals on production estimates by bootstrapping field data, whereby we randomly sampled with replacement five samples from each site by date to create an array of 50 samples per site-year. We repeated this 10,000 times and calculated the mean annual biomass for each taxon, then calculated the mean and variance of the annual biomass estimates. We then calculated total annual production as the sum of the mean annual production estimate of each taxon.

## Results

### *Stream physico-chemistry*

Mean daily runoff and physico-chemistry varied strongly between streams on an annual scale (Figure 3-2). Mean daily temperature (2.3°C) was lowest ($p < 0.001$) in the glacial river, but similar at other sites (5-7°C). Although discharge was substantially higher in the glacial river than other sites, when scaled to watershed area, mean daily runoff was only significantly higher in the glacial and transitional systems than in the rainfed stream. All other comparisons of runoff were not significant (glacial-snow, glacial-transitional, transitional-snow, snow-rain). All streams differed in turbidity with the glacial stream being the highest and the snowmelt stream being the lowest ($p < 0.01$). Water chemistry also varied between streams, with DOC concentrations significantly higher in the rainfed stream compared to all other sites ($p < 0.0001$). Concentrations of TDN were significantly higher in the rainfed and transitional streams compared to the glacial and snowmelt streams. Concentrations of TDP were lower in the snowmelt stream than all other sites ($p < 0.05$). Additionally, both pH and conductivity were highest on average in the snowmelt and lowest in the rainfed streams, though all streams were in the 6-8 pH range and conductivity was 16.6 - 64.29 (µS/cm) (Supplementary Information).

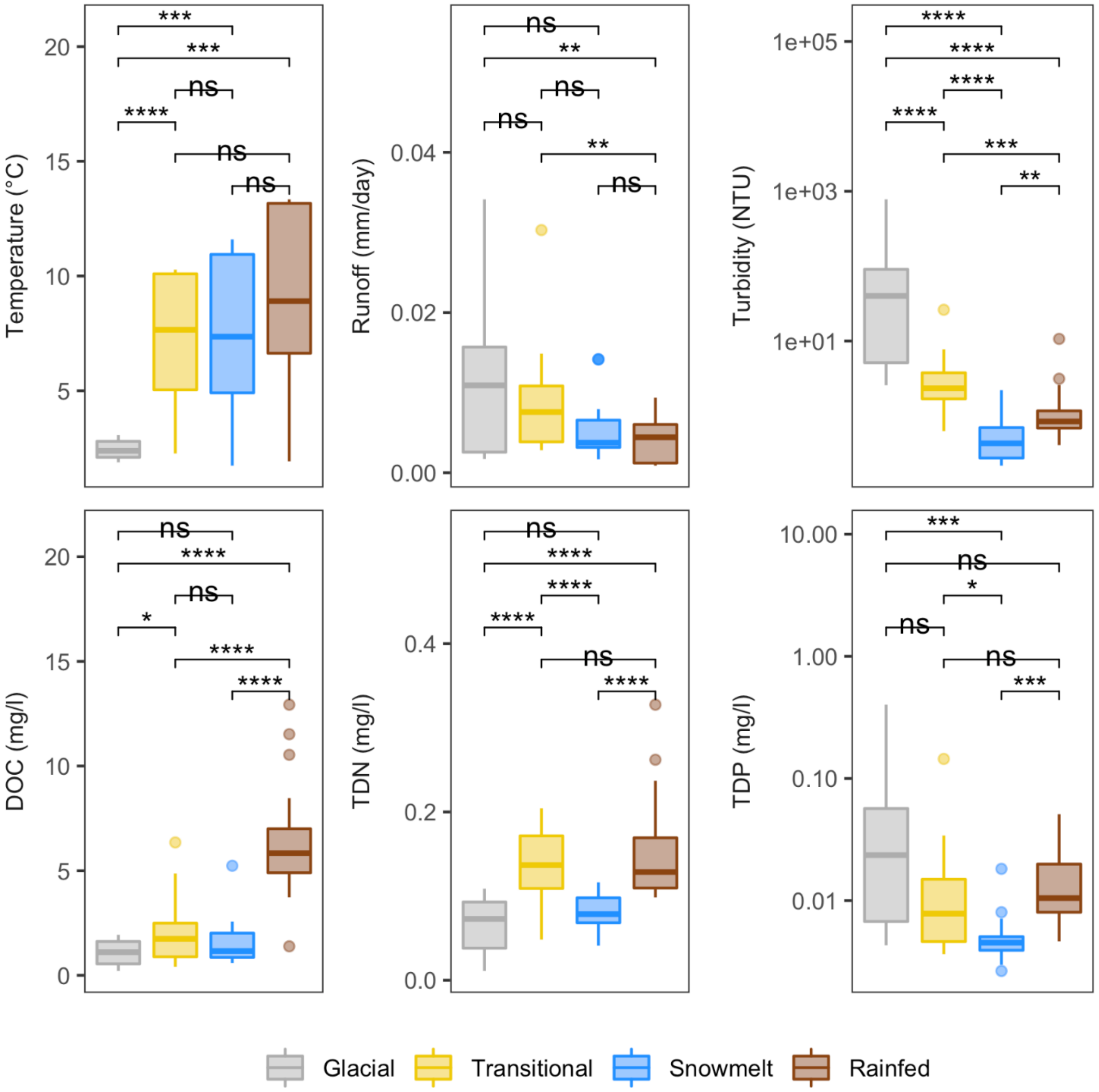

Figure 3-2 Box and whisker plots and points of monthly mean values of water temperature, runoff, dissolved organic carbon (DOC), total dissolved nitrogen (TDN), turbidity, and total dissolved phosphorus (TDP) reveal substantial variation in the abiotic conditions

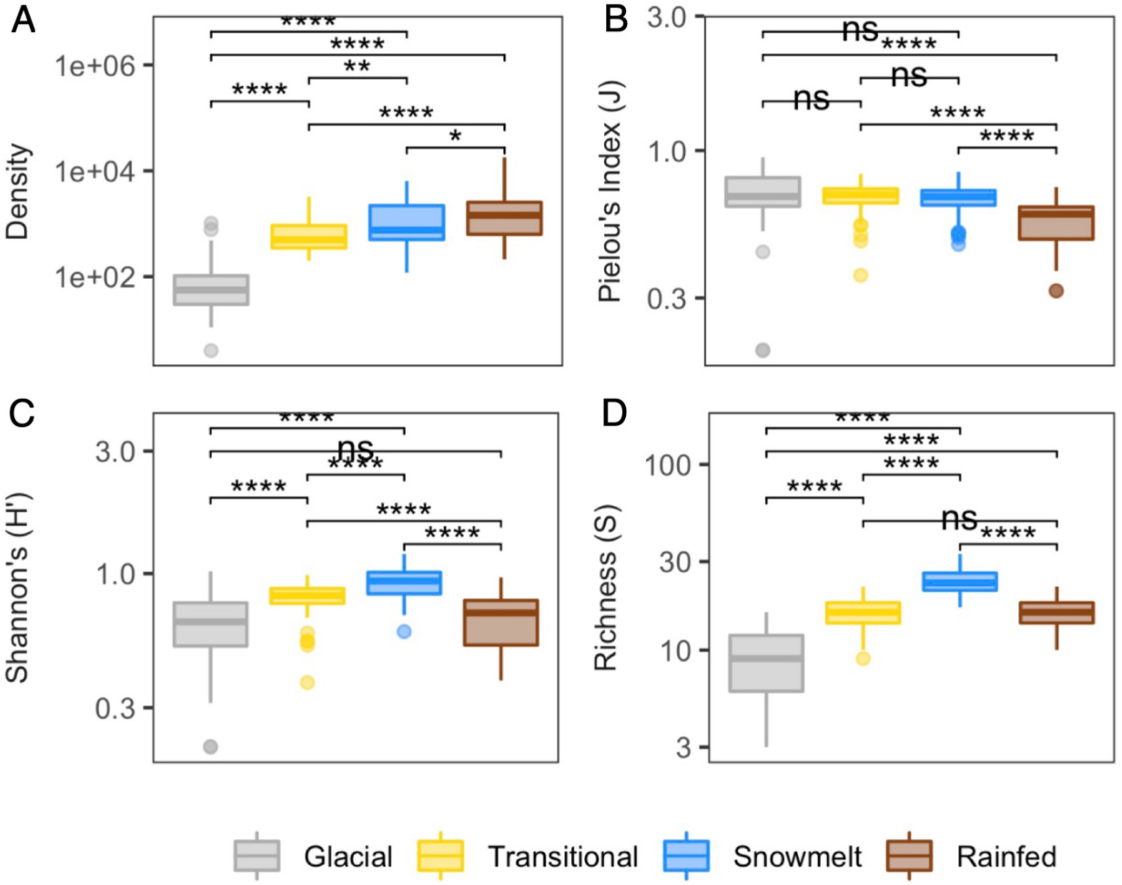

Figure 3-3 Box and whisker plots of (A) density (individuals m-2), (B) Pielou's evenness index (J), (C) Shannon's diversity index (H'), and (D) sample richness (S) for individual invertebrate samples. Mean comparisons conducted using Wilcox tests and statistical symbols: ns: p > 0.05, *: p <= 0.05, **: p <= 0.01, ***: p <= 0.001, ****: p <= 0.0001.

### *Macroinvertebrate community structure, and diversity*

We observed substantial differences in mean diversity metrics among streams (Figure 3-3). Mean richness and Shannon (*alpha*) diversity were both highest in the snowmelt stream ($p < 0.0001$) yet densities were greatest in the rainfed stream ($p < 0.0001$). Shannon diversity was higher in the transitional stream than the rainfed stream ($p < 0.0001$) despite 3.6-fold lower density between these sites. Pielou's evenness was highest in the glacial ($p = 0.018$) and lowest in the rainfed stream ($p < 0.0001$), though similar between the glacial, snowmelt and transitional streams. The transitional stream was not significantly different with respect all other sites together, though had pairwise differences between the rainfed and snowmelt streams in density, and Shannon diversity ($p < 0.04$) and with the rainfed stream in Pielou's index ($p << 0.0001$). The glacial stream was not different than the rainfed stream in Shannon diversity ($p = 0.26$), despite significantly lower richness ($p <<< 0.0001$). (All other significance tests may be found in Supplementary Table xx).

We calculated the inverse of *beta* diversity using Sorensen's similarity index. We found the most similarity on average between rainfed and transitional streams followed by rainfed-snowmelt streams and the least similarity between the glacial stream and either the rainfed or snowmelt systems. *Beta*-diversity was highly seasonal, with consistent similarity between the transitional, snowmelt, and rainfed streams over time, but seasonally low similarity between glacial stream and all others during midsummer (Figure 3-4). This pattern faded outside the glacial melt season, as all sites becoming more similar (i.e., lower *beta* diversity) in fall, winter, and spring.

NMDS revealed distinct communities both by taxonomic groupings (Figure 3-5A) and by functional traits (Figure 3-5B). NMDS differences were associated with stoneflies in the *Nemouridae* and *Perlodidae* (glacial), segmented worms and *Limnephilidae* caddisflies (rainfed), and mayflies in the *Baetidae, Heptageniidae*, and *Ephemerellidae* (snowmelt). The transitional stream occupied a central position between snowmelt and rainfed communities. Because both approaches yielded distinct communities, we chose to further analyze the community-weighted mean trait values, as those contained more information than abundances alone. The least overlap in our ordinations were between glacial, rainfed, and snowmelt streams, which were chosen to reflect relative endmembers of these stream types. As we expected, the transitional stream was intermediate in both taxonomic and functional indices. This revealed greater functional overlap between snowmelt and rainfed streams (Figure 3-5B) than taxonomic metrics alone (Figure 3-5A). Additionally, the glacial stream taxa and traits were spread over greater ordination space, suggesting higher variation in community composition and traits relative to other locations. We used canonical correspondence analysis to evaluate physico-chemical and temporal drivers of community trait separation among the stream types. The strongest abiotic correlates differed between streams (Figure 3-5C). In our CCA analysis, axis one was associated primarily with favorable production conditions (TDN, DOC, and temperature) whereas axis 2 was primarily associated with factors that influence harshness (flow, pH, and turbidity). The strongest associations were in the glacial stream separated positively by turbidity, flow, and total dissolved and soluble reactive phosphorous in mid-to-late summer (Figures 3-5 C-D). CWM in the snowmelt stream was primarily associated with pH and conductivity, which co-varied in our dataset, though possibly also by this site's opposite position from DOC and TDN axes. As with our NMDS ordinations, the transitional stream occupied a middle ground due to intermediate values of explanatory variables. We also observed substantial temporal variation in the community, with the greatest differences among sites in the late summer, when the glacial stream moved further from the mean traits across the landscape (i.e., the center of the ordination), and the fall, when the snowmelt stream moved further from the center (Figure 3-5D).

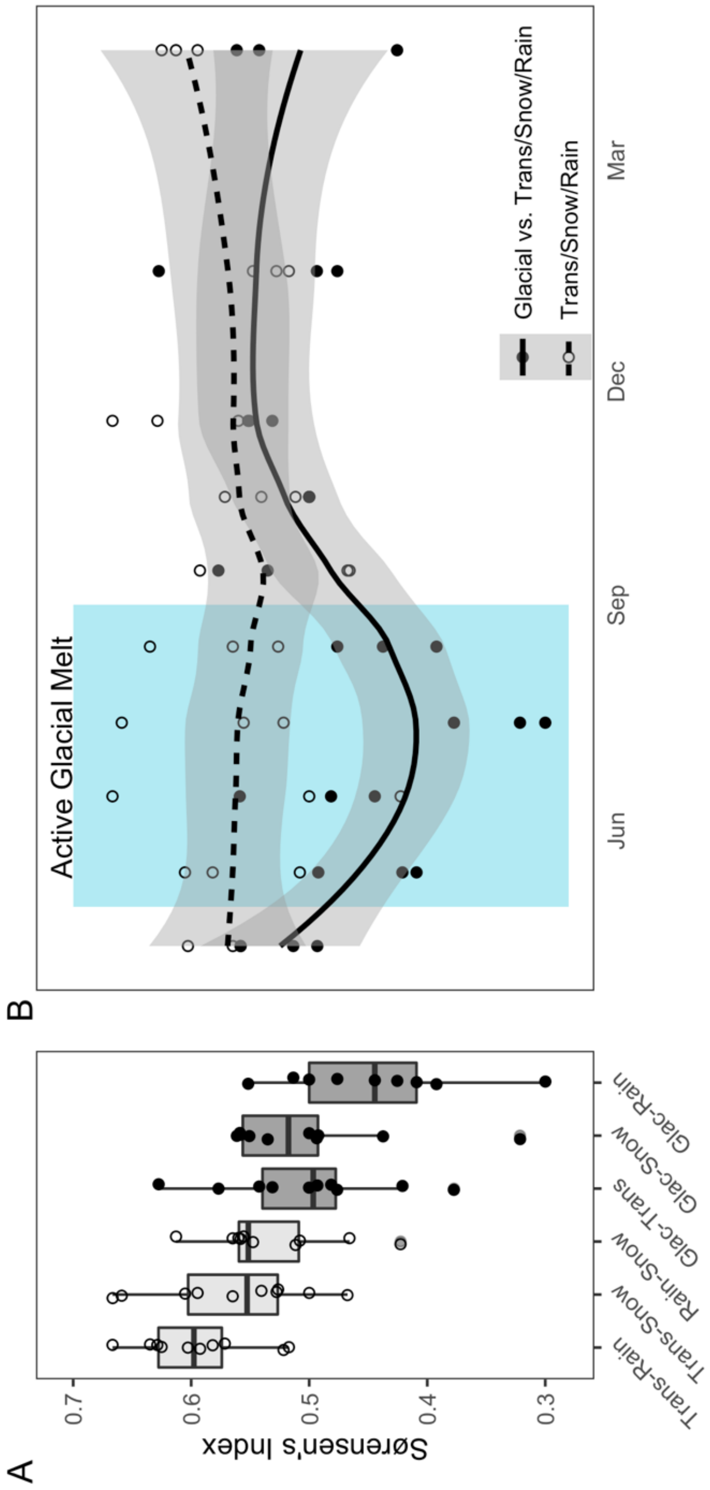

Figure 3-4 Beta diversity between glacial and non-glacial streams calculated using Sorensen's index for each sampling window (A) and temporal patterns of beta diversity across the landscape (B) between the glacial stream and transitional, snowmelt, or rainfed. Season of active glacial melt (May-September) shaded in light blue. Values closer to 1 are more similar; values closer to 0 are less similar.

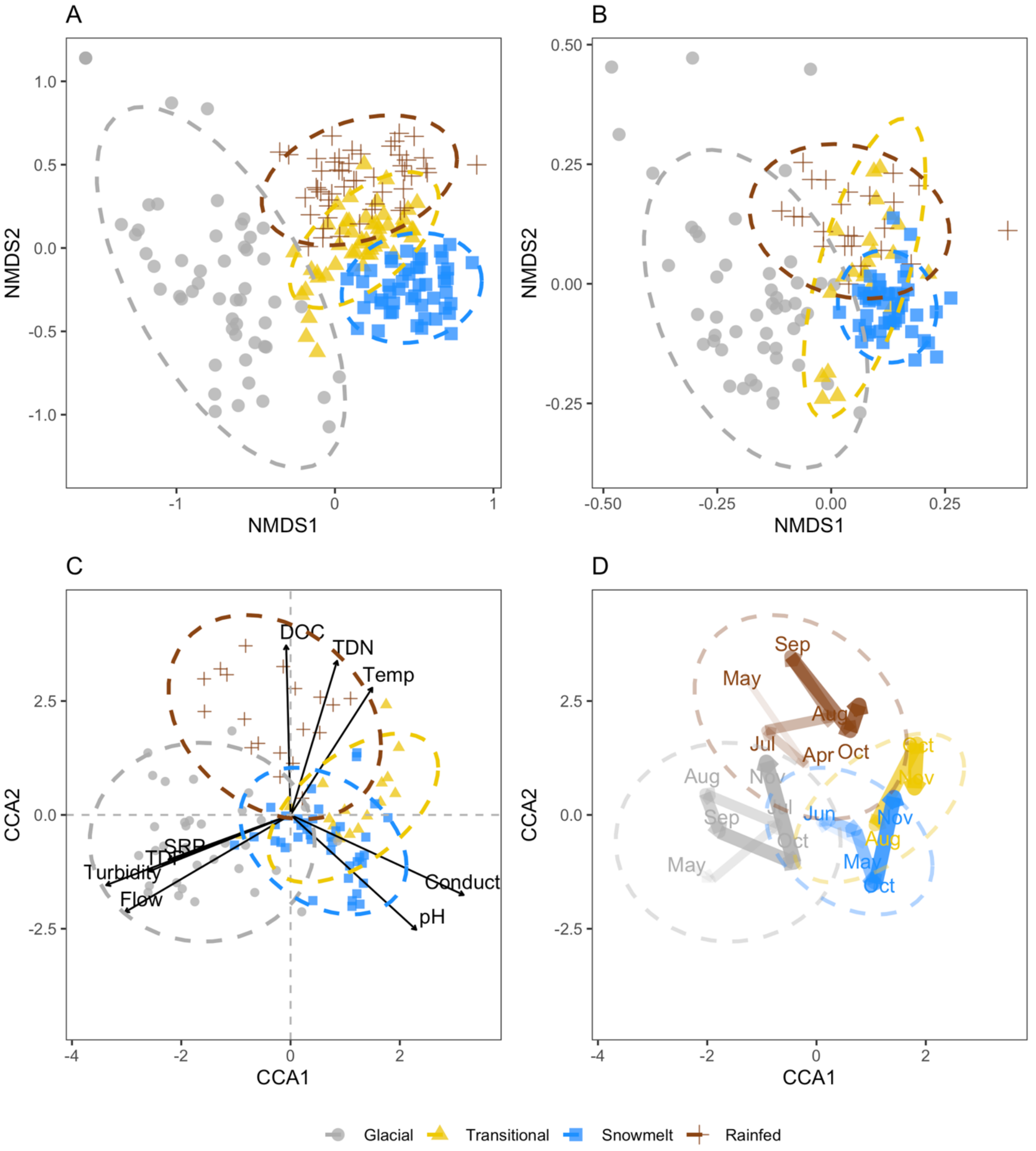

Figure 3-5 NMDS plots of invertebrate community (A) taxonomic-only and (B) community-weighted mean (CWM) functional structure. CCA plots of (C) physico-chemical and (D) temporal drivers of CWM functional structure. Each point in (A-C) represents one of five Surber samples collected on each date. Each point in panel (D) is the mean trait value for each site*sample date. Note: one outlier from the snowmelt stream is not shown on panel B.

### *Biomass and Secondary production*

We observed strong seasonal differences in the biomass waves of invertebrates on the landscape (Figure 3-6). In the glacial stream, biomass peaked in winter -- dominated mainly by stoneflies in the family *Perlodidae* (particularly *Isoperla sordida*). The rainfed stream peaked in spring and was driven mostly by stoneflies in the family *Chloroperlidae* but also had seasonally high biomasses of segmented worms (*Oligocaheta*) and, to a lesser extent, midges (*Chironomidae*) and caddisflies (*Limnephilidae*). The snowmelt stream had peak biomass in early spring and was dominated by both stoneflies in the families *Perlodidae* and *Chloroperlidae,* as well as mayflies in the family *Heptageniidae* (generally *Cinygmula sp.* > *Epeorus* sp. > *Rithrogena* sp.). The transitional stream peaked later in summer and contained mostly *Heptageniidae* mayflies and *Chloroperlidae* stoneflies. On an annual scale, biomass was similar and highest in the rainfed and snowmelt streams. However, there were pronounced seasonal peaks in biomass the glacial stream in winter and in the transitional stream in late summer

As predicted, the glacial stream had the lowest annual production at 0.55 g $m^{-2}$ $y^{-1}$. We calculated over 4-fold greater secondary production in the snowmelt and rainfed streams than the glacial stream. The transitional stream had twice the annual production of the glacial stream, yet less than half that of the snowmelt and rainfed systems. To estimate the drivers of increased production, we looked at production in taxa found across all streams (aka “Shared Taxa”) and the production of taxa not found in the glacial stream (aka “New Taxa”) (Figure 3-7A). This revealed a greater increase in the production of glacial taxa in the snowmelt than rainfed stream and that ~21-36% of increased production was from species which were not in the glacial system at all. The most productive taxa varied considerably between streams (Figure 3-7B). Production in the glacial stream was dominated by large, bodied stoneflies in the predatory family *Perlodidae*, whereas the snowmelt stream experienced high production in mayflies (e.g., *Heptageniidae, Baetidae*). Both the rainfed and transitional streams had substantial production of functional shredders or collector-gatherers (e.g., *Chloroperlidae, Oligochaeta)*. Generally, most productive taxa were also high in biomass across the landscape, except for *Baetidae* in the glacial stream, which had high production but low biomass presumably due to rapid growth an emergence, mortality, or ability to avoid collection at this site.

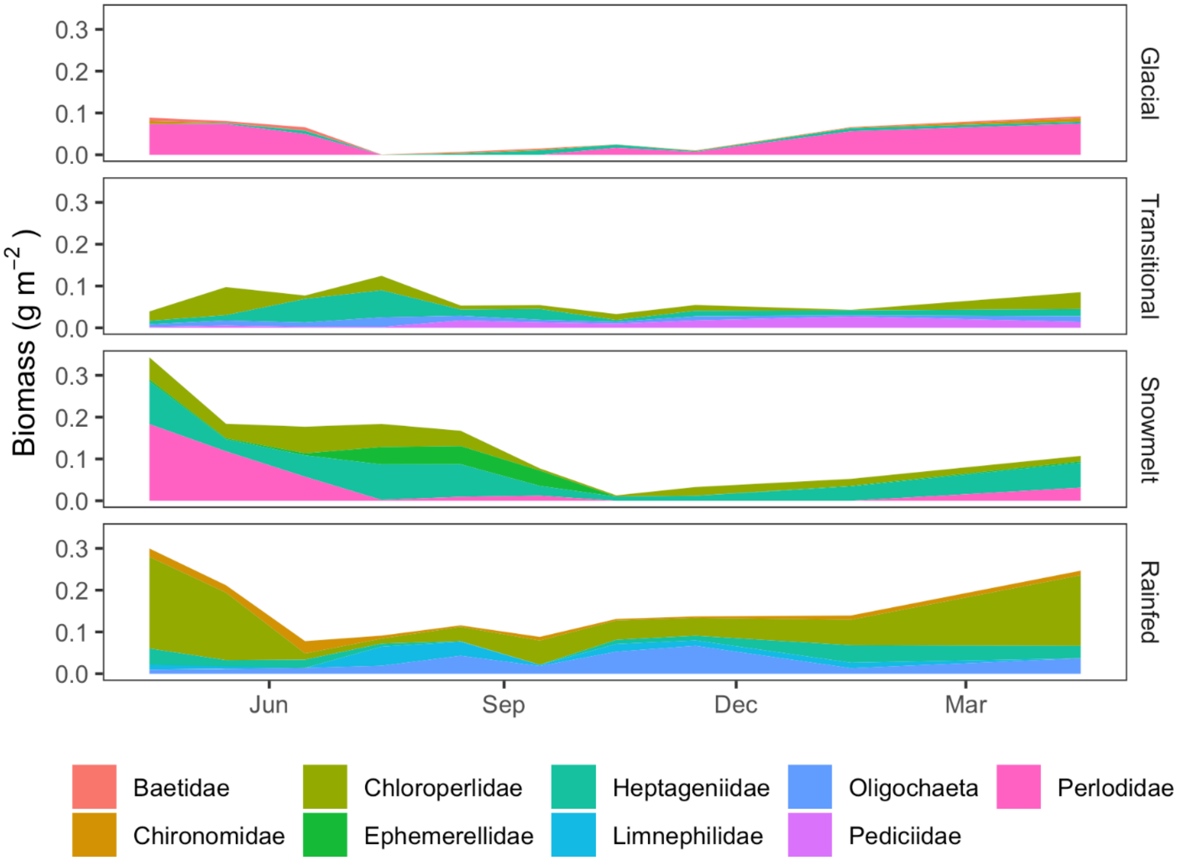

Figure 3-6 Biomass waves of top 4 taxa for each stream (~72%) of mean annual biomass) in each stream.

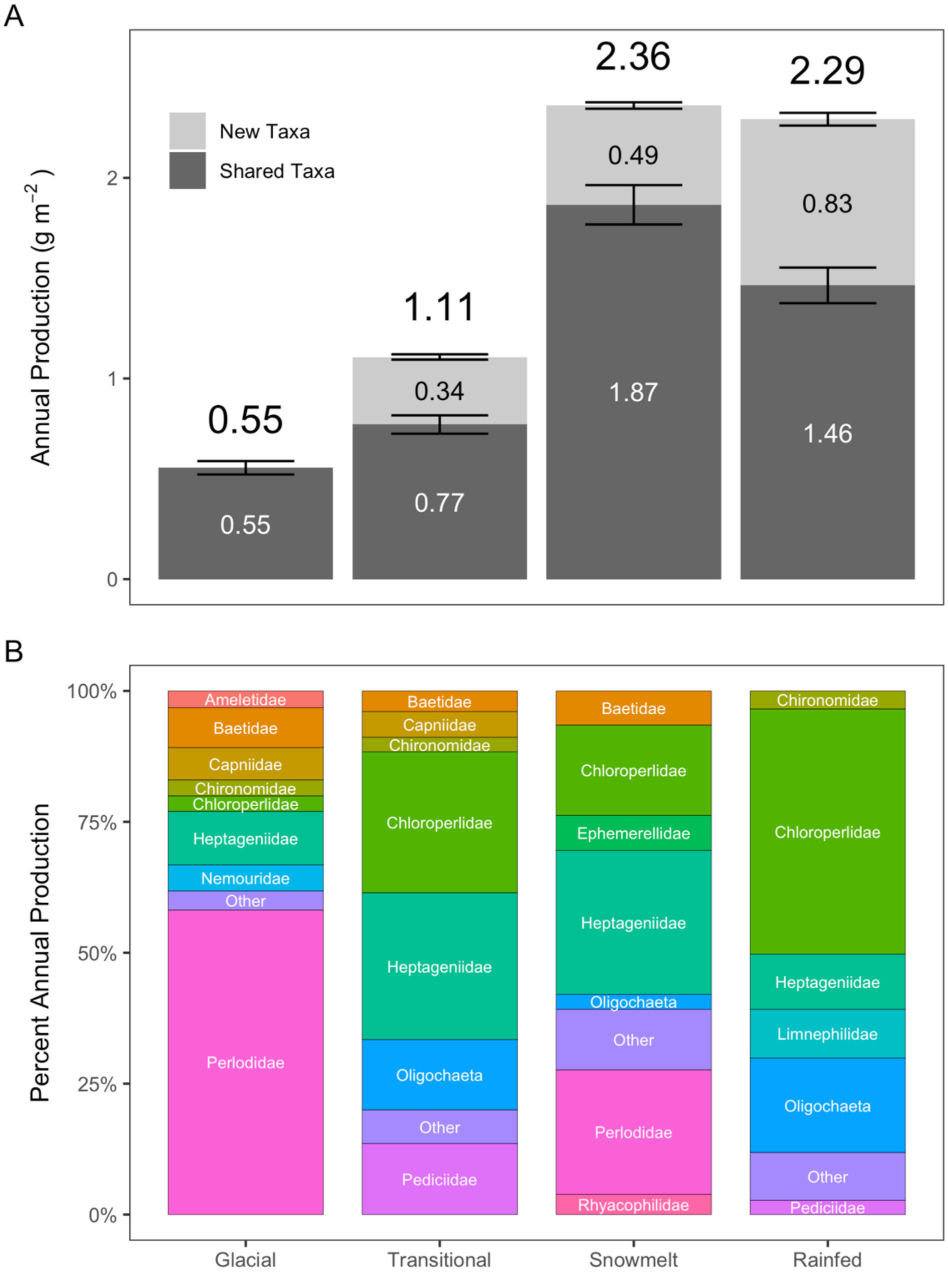

Figure 3-7 (A) Mean ± 1SD of bootstrapped annual secondary production of taxa found in the glacial river "shared taxa" and taxa not found in the glacial river "new taxa" with total mean annual production above. (B) Proportional production of taxa comprising at least 2.5% of annual production, all less than 2.5% combined as "Other".

## Discussion

Climate change is poised to diminish the global cryosphere with implications for the diversity, functional traits, and productive capacity of downstream freshwaters (Milner et al. 2017, Elser et al. 2020). Many investigators have recognized that water source in high elevation or cryospheric streams can create distinct physical and chemical properties (Brown et al. 2003, Milner et al. 2010, Hotaling et al. 2019a). To date, most studies of have focused on implications for community diversity (Brighenti et al., 2021; L. E. Brown et al., 2006, 2007; Füreder et al., 2001) or species persistence (Birrell et al., 2020; Giersch et al., 2017; Hotaling et al., 2020; Niedrist & Füreder, 2018), but few have explored how this variation affects the functional traits of stream communities – namely the rates and forms of secondary production of consumer biomass (Benke 2018). In this study, we show that hydrologic heterogeneity in mountain streams can indeed create different aquatic insect taxonomic and functional communities. These communities vary widely in their rates and forms of secondary production of invertebrate biomass, with snowmelt and rainfed streams having over 4-fold greater annual production than a nearby glacial meltwater stream. Additionally, a snow-rain transitional stream, with a rapidly diminishing small glacier in its watershed expressed intermediate community structure and secondary production, potentially reflecting the expected conditions in many watersheds as small glaciers are lost and winter snow is replaced by winter rain. As the cryosphere fades, the diversity and functional qualities of downstream freshwaters will inevitably change and this will alter how these landscapes support higher level consumers, such as fish and riparian birds (Elser et al. 2020).

While we expected streams would differ in their physical and chemical properties (Bellmore et al. 2022), we had only general expectations for different rates of production largely based on thermal and physical constraints. We predicted low secondary production in the glacial stream due to turbid, cold, and high flow conditions during the summer months and high secondary production in the rainfed stream, due to warmer conditions. Unsurprisingly, the glacial community had very low annual secondary production. However, we found similar production in the snowmelt and rainfed streams despite marginally warmer conditions and substantially greater DOC, TDN, and TDP concentrations in the rainfed stream. The transitional stream had twice the production of the glacial stream, but only half that of the rainfed and snowmelt streams, suggesting that as glacial systems transition to less physically harsh conditions, secondary production rates might increase. The increase in secondary production was largely driven by higher production of common taxa in all locations with only a quarter to a third of increased production coming from new species that were not present in the glacial stream. The production and biomass in the glacial stream were dominated by stoneflies – namely large-bodied predators in the family *Perlodidae*. Contrary to past studies conducted closer to glacial termini (Lods-Crozet et al. 2001, Robinson et al. 2007, Niedrist et al. 2018), we observed only marginal biomass and production in the family *Chironomidae* (though we anecdotally observed dense populations several km above our study reach near the glacial snout). Other sites had substantial stonefly production in the family *Chloroperlidae* as well as mayflies in *Heptageniidae* and *Baetidae.* Notably, segmented worms in *Oligochaeta,* which were uncommon in the glacial river, contributed substantially to production in the transitional and rainfed streams. It seems probable that the glacial river community will become more similar to other streams lower in the watershed as physical constraints are lessened.

Our estimates of secondary production are very low, particularly in the glacier-fed and transitional streams, but similar to those reported by Entrekin and colleagues (2007, 2009) who used similar methods in northern Michigan and proposed temperature, flow intermittency, and substrate mobility can limit secondary production. These findings support the assertion that production may be constrained by flow and temperature stability (Chadwick and Huryn 2007, Ledger et al. 2011, Mehler et al. 2015). Most aquatic invertebrate secondary production studies have occurred in much warmer or lower latitude ecosystems (Washington State: (Bellmore et al., 2013), Minnesota: (Krueger and Waters 1983), Illinois (Walther and Whiles 2011)) and report as much as an order of magnitude greater production and twice the richness (Appalachia: (Johnson et al. 2013)). We found similar abiotic conditions and community dynamics as a previous study of benthic and hyporheic invertebrate community dynamics among streams representing glacial, snowmelt (*"clearwater"*), and rainfed (*"brownwater"*) conditions in this region (Wesener et al. 2011). I'm aware of only one study of secondary production conducted in this region, which focused on the role of marine-derived nutrient subsidies in non-meltwater streams near the Juneau Icefield (Lessard et al. 2009) and reported much higher production estimates response to marine-derived nutrient subsidies, but we caution interpretation of these results as *annual* production estimates were based on sampling during May-September and may overestimate true annual production in these streams.

This study represents one of the most comprehensive comparative analyses of invertebrate community dynamics amongst streams reflecting different hydrochemical regimes. However, this level of detail on four streams monitored over a year reflects a trade off in site-level detail over spatial replication. It is likely that interannual variation in secondary production may be high – particularly in response to variation in stream flow, ambient temperatures, or marine-derived nutrient subsidies from spawning salmon. Additionally, because we focused our sampling on riffles, the sites of the highest production within streams (Brown and Brussock 1991, Buffagni and Comin 2000) we were unable to represent variation in community structure or production between channel units. Secondary production measurements remain a challenging and underutilized tool to understand aquatic ecosystems (Dolbeth et al. 2012, Layman and Rypel 2020), but may provide a powerful approach to understanding how climate change will restructure food webs. The capacity of landscapes to produce secondary invertebrate biomass will influence the ability to support the growth of higher-level consumers. It is critical to link robust secondary production estimates with dietary and energetic demands of consumers to elucidate the trophic basis of fish growth and the potential implications of climate change-driven homogenization on the functional capacity and diversity of stream invertebrate communities (Fell et al. 2017a).

These findings align with past alpine and cryospheric stream research that has shown snow and/or glacial fed streams have distinct hydrologic sources host distinct communities and contribute to landscape biodiversity (Brown et al. 2006, Milner et al. 2010, Hotaling et al. 2019a). We found that the current landscape heterogeneity from glacial meltwaters does contribute to landscape *beta* diversity relative to streams sourced by seasonal snowmelt, and flashy rain-fed watersheds despite relatively low invertebrate densities, species richness, and *alpha* diversity in glacial streams. The greatest *beta* diversity on the landscape was between glacial and non-glacial streams during peak glacial melt, with streams becoming more similar during winter months. Our assessment of *alpha* diversity also supports past work suggesting diversity will increase in glacial streams as conditions become less harsh with respect to flow, temperature, bed stability, and/or light (Milner et al. 2009, Slemmons et al. 2013), but communities across the landscape will become dominated by generalist taxa, reducing *beta* and *gamma* diversity (Brown et al. 2007a, Jacobsen and Dangles 2012, Niedrist and Füreder 2018, Füreder and Niedrist 2020). Unlike prior cryospheric stream invertebrate research, we show that snowmelt streams may be particularly diverse relative to other stream types. This may be due to the more predictable and less intermittent annual hydrographs in snowmelt streams relative to rainfed streams, which are prone to both periodic drought and rain-driven freshets. If widespread summer drought continues in this region and in other mountainous regions, snowmelt streams may be refuges of diversity and production in mountain streams**.** However, the stability benefits of snowmelt streams may be diminishing, with implications for the diversity and production of invertebrates in these streams (Docherty et al. 2018a, 2018b). More broadly, these patterns point to a need to understand the role of *alpha* vs. *beta* diversity in shaping patterns of secondary production in space and time.

Community diversity metrics alone may not capture how cryospheric streams are changing. When invertebrate assemblages were assessed using CWM traits of abundance, feeding mode, habit, tolerance, body size, size at maturity, individual mass, and voltinism, we saw substantial variation between stream types. The proximate drivers of community trait variation show that physical forces and nutrient availability pull communities in different ways. We found that the glacial river community separation was driven by temperature, discharge, and turbidity, supporting the view that physical harshness may control this system. Conversely, other streams were separated more by water chemistry (e.g., DOC) nutrient availability (e.g., TDN), and temperature. Again, this functional approach revealed that the transitional stream occupied an intermediate trait space relative to other streams, supporting that these differences on the landscape fall along a continuum of water sources that are changing. Together, these analyses support the landscape filtering hypothesis (Poff 1997), whereby differing environmental conditions act as filters through which potential organisms must pass to be present in a location, as all sampling locations were within the assumed distribution and colonization range of emergent invertebrate taxa. Again, as abiotically harsh parts of the landscape become more benign, community structure and traits will likely homogenize.

Climate change is poised to restructure and potentially homogenize stream networks where energy flow dynamics are influenced by seasonal inputs of snow and ice melt (Hock et al. 2019, Elser et al. 2020). Yet, there remains a paucity of knowledge on higher-level and/or "multitrophic" implications of melting ice reserves on downstream ecosystems (Fell et al. 2017b). Climate change will likely alter the diversity and production of macroinvertebrate communities in meltwater and non-meltwater streams in different ways. As these meltwater streams fade, we may see an overall increase in the capacity of the landscape to produce higher-level consumers (Pitman et al. 2020, 2021), but this may come at the cost of the biodiversity and heterogeneity on these landscapes. Here, we've shown that variation in the dominant contributing water source creates both distinct taxonomic and functional communities with uneven productive capacity. As the cryosphere fades, communities may become more similar and the energetic pathways that support higher level consumers may be simplified. Future studies should place invertebrate production in the context of consumption by higher consumers, such as riparian songbirds or juvenile fish. Additionally, modeling efforts could reveal the emergent implications of simplification on interacting meta-food webs in meltwater landscapes (Bellmore et al. 2022). Lastly, we need comparative studies not only among streams on cryospheric landscapes as we have shown here, but also between landscapes experiencing different rates of change. Climate change is impacting the diversity and functioning of stream ecosystems across the globe (Sabater et al. 2018, Tiegs et al. 2019). This is particularly true in areas influenced by the melting cryosphere, where losses to glacial and snowmelt streams may alter community structure and capacity to produce secondary biomass. Despite glacial streams being cold, harsh, and having relatively low annual production, they contain communities with distinct functional traits and contribute greatly to landscape *beta* diversity. As climate change decreases the heterogeneity on the landscape, we may see an increase in secondary production, but a decrease in *beta* diversity and a synchronization of the timing of growth opportunities for mobile consumers, such as juvenile salmonids.

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# Chapter 4 – Physical and chemical variation creates a portfolio of food webs on a glacial landscape: implications for juvenile salmon and climate-driven loss of the cryosphere

## Abstract

Climate change is poised to restructure food webs across landscapes by altering the physical and chemical regimes that control energetic pathways from lower trophic levels to high-level consumers. Climate change has the potential to drive a loss of distinct structures and flows of energy through aquatic food webs, resulting in the narrowing of the trophic portfolio supporting higher trophic levels like fish at the landscape scale. Streams in glaciated high latitude and/or elevation landscapes are experiencing some of the most rapid biogeochemical changes globally and represent an ideal study system for evaluating how abiotic conditions influence food web architecture. We quantified the food webs that support the production of fish and aquatic invertebrates using the trophic basis of production approach using stable isotope- and diet-based inferences. We then constructed annual flow webs of the aquatic food web in four adjacent streams on the margin of the Juneau Icefield, Alaska, USA, reflecting relative endmember conditions of glacial-, snow-rain transitional, snowmelt-, and rainfed signatures. We found that communities contained many shared species, yet the food web structures, and timing of productivity varied between streams, resulting in different food webs and, in turn, distinct energetic pathways supporting juvenile salmonid growth across the landscape. Secondary production of fish and invertebrates was highest and similar in the snowmelt and rainfed streams and lowest in the glacial stream. Food web complexity was lowest in the glacial stream with relatively weak linkages between consumers and resources; the transitional stream had higher network complexity and more even linkages and flows from basal sources to invertebrates and fish; the snowmelt stream had the most diverse invertebrate community with many linkages from basal sources, but flows to fish were seasonally dominated by salmon egg subsidies that subsequently also dominated annual estimates; the rainfed stream had fewer basal to invertebrate linkages than the snowmelt stream but a greater diversity of flows from invertebrate prey to fish. This work represents some of the first quantitative energy flow food web work in rapidly changing periglacial landscapes and suggests that management should seek to maintain heterogeneity and diversity on the landscape rather than productive capacity alone as heterogeneity creates variation in energetic pathways supporting consumers which may increase stability and resilience to climate change.

## Introduction

Climate change is restructuring ecological communities and altering biotic interactions in myriad and often indirect ways (Walther 2010). Food webs provide a powerful, integrative approach to analyzing community responses to the abiotic environment by incorporating both structural and interactive dynamics of organisms and by representing how energy flows from primary sources to support higher-level consumers (Dolbeth et al. 2012, Benke 2018, Layman and Rypel 2020). On complex landscapes, heterogeneity in physical and chemical regimes can occur over relatively short distances, potentially creating distinct food web structures across landscapes (Milne 1991, Palmer and Poff 1997, Loreau et al. 2003). Although it has been suggested that climate change could create additional heterogeneity by rewiring food webs (Bartley, McCann et al 2019), a perhaps unforeseen consequence may be the homogenization of food webs across space as abiotic regimes synchronize (Wang et al. 2021, Seybold et al. 2021) and specialist taxa or trophic structures are lost (Gámez-Virués et al. 2015).

However, few studies have empirically evaluated how food webs vary across rapidly changing landscapes, limiting our ability to develop a unified theory for ecological responses to changes (Thompson et al. 2012). This is in part due to logistical challenges in quantifying food web linkages which often requires moderate-to-high frequency sampling over time to capture the change in the abundance of consumers and resource use (Banašek-Richter et al. 2009, Benke and Huryn 2017). One approach is to scale the rates of consumption of individual prey types to the overall production of consumers, thereby representing not only the linkages between organisms but also the flows of energy or material within the food web (Benke and Wallace 1980, 1997). Quantitative flow food webs have been created using several approaches, but most involve leveraging proportional diet information with the estimated efficiency of consumers to convert consumption into secondary biomass (Dunne 2006, 2009, Moore and de Ruiter 2012). When conducted for most common consumer taxa in a community, flow webs visualize the energetic structure of food web networks and highlight the pathways energy and material take through the system from basal resources to higher trophic levels.

All components of food webs, both biotic and abiotic, are susceptible to environmental change and may have unexpected effects on material flow through food web network (Watkins and Freeman 2008). A critical step to understanding how climate change will affect landscapes is to address if current landscape heterogeneity creates distinct structures and energy flow patterns between nearby food webs. Food web ecology exists at the intersection of community and ecosystem ecology, as it integrates processes that govern community assemblage as well as the abiotic conditions and flows of materials, including nutrients, between biotic and abiotic compartments (Thompson et al. 2012, Benke 2018). Food web composition is likely driven by an interplay between abiotic filtering (Poff 1997)and by biotic interactions such as competition from functionally similar taxa (Cadotte and Tucker 2017). Abiotic filtering may strongly determine which organisms are found in food webs on complex or harsh landscapes where abiotic regimes vary greatly over small spatial scales (Niedrist and Füreder 2018).

Such ecosystems are often found in high latitude and/or altitude regions where meltwaters from glaciers and seasonal snowpack can be important sources of water and chemicals to downstream ecosystems (Milner et al. 2017, Elser et al. 2020). These landscapes are also among the most rapidly changing as global climate change increases ambient air temperatures, alters seasonal precipitation patterns and forms, and increases glacial melt (Huss et al. 2017, Hock et al. 2019). Loss of meltwater signatures may result in the loss of distinct food webs relative to nearby streams draining other sources (e.g., subterranean ice, groundwater, or rainfall; Bellmore et al. 2022). Many of these ecosystems along the coastal margin of the North Pacific Ocean also support the production of culturally, economically, and ecologically important fish taxa, such as juvenile Pacific salmon (*Oncorhynchus spp.*) and char (*Salvelinus* spp.) (Johnson et al. 2019, Pitman et al. 2020). In freshwaters, juvenile salmon production is fueled by the consumption of invertebrate prey, particularly in the first year of growth. Ironically, the climate-driven loss of meltwater streams may result in an increase in secondary production of juvenile salmon (Milner et al. 2000b, 2009, Pitman et al. 2021) if streams become more productive and closer to the metabolic optima for fish growth. However, this increase in overall productivity may coincide with a homogenization of abiotic dynamics and community structure community structure leading to loss of meta-food web diversity. Here we ask:

*How do the pathways of energy flow that support fish and invertebrate consumers vary amongst glacier, snowmelt and rainfed streams?*

We predict that different food web structures should emerge between habitats with asynchronous patterns of abiotic conditions, such as temperature, physical stress, and nutrient availability. To address this, we calculated the annual trophic-basis of invertebrate and fish production (Benke and Huryn 2017, Benke 2018) among streams representing relative endmember conditions of *glacial melt*, *snow-rain transitional*, *snowmelt*, and *rainfed* hydrologic sources in the Pacific coastal temperate rainforest of Southeast Alaska USA. We used a combination of fish diet sampling and whole community stable isotope analysis to estimate proportional resource use by fish and invertebrates respectively. We expected to find broadly similar fish and invertebrate communities in all food webs across sites due to relatively depauperate communities and proximity but that a.) glacial food webs would have much lower energy flow through the food web due to harsh conditions that limit consumer production, that b.) transitional streams would share qualities of the other systems due to intermediate community structure and abiotic conditions, that c.) snowmelt streams would have the most complex food webs due to higher invertebrate alpha diversity, and that d.) rain-fed food webs would have the greatest fish production, but be dominated by relatively few strong pathways due to warm conditions.

## Methods

### *Study site and design*

We sampled the physico-chemistry and aquatic food webs in four streams representing distinct hydrologic sources and consequent physico-chemistry on the Western slope of the Juneau Icefield, Alaska USA (Figure 4-1). We chose sites with similar distances to ocean entry (~3km), and which represented relative endmember conditions of common stream types found in the Pacific coastal region: glacial, snowmelt, rainfed, or snow-rain transitional *(Sergeant et al. 2020, Giesbrecht et al. 2022)*. Past work has shown that these sites vary widely in temperature, discharge, water chemistry and nutrient availability. Concurrent studies also evaluated the abiotic and biotic seasonality (*Chapter 1*) and invertebrate community structure and secondary production *(Chapter 2*) at these sites. Generally, glacial streams are characterized by high, cold, and turbid summer flows during active glacial melt; snowmelt streams are generally clear, experience a spring runoff pulse from melting snowpack, and have stable base flows during summer; rainfed streams have flashy hydrographs during heavy precipitation events, are generally warmer, and have high levels of DOC and TDN; and snow-rain transitional streams reflect a mixture of water sources and may be intermediate for most conditions (Brown et al. 2003, Wesener et al. 2011, Sergeant et al. 2020, Giesbrecht et al. 2022).

We measured discharge using a combination of modeled relationships with gauged rivers (*glacial*), a pressure transducer in a stilling well combined with point measurements using an acoustic doppler velocimeter (*rainfed*), or publicly managed stream gauges (*transitional* and *snowmelt*). Water chemistry was measured using both *in situ* sensors and discrete surface water samples for temperature, turbidity, pH, total suspended sediments, dissolved organic carbon, and total dissolved nitrogen and phosphorous. (*Detailed description of water chemistry analysis may be found in Chapter 1*).

Table 4-1 Description of study reaches from Netmap database (Benda et al. 2007) reflecting location, watershed area, relative gradient, bankfull width, depth, velocity, and flow rate.

| **Stream Name** | **Stream Type** | **Lat** | **Long** | **Area ($m^2$)** | **Gradient** | **Width (m)** | **Depth (m)** | **BFV ($m\ s^{-1}$)** | **BFQ ($m^3s^{-1}$)** |
|---|---|---|---|---|---|---|---|---|---|
| Herbert River | Glacial | 58.53199 | -134.783765 | 1286 | 0.02 | 28.44 | 0.729 | 3.74 | 77.50 |
| Montana Creek | Transitional | 58.39473 | -134.607779 | 954 | 0.02 | 18.92 | 0.633 | 3.19 | 38.22 |
| Steep Creek | Snowmelt | 58.41306 | -134.542699 | 485 | 0.05 | 10.89 | 0.522 | 4.02 | 22.78 |
| Peterson Creek | Rainfed | 58.48347 | -134.774810 | 600 | 0.03 | 16.76 | 0.606 | 3.88 | 39.45 |

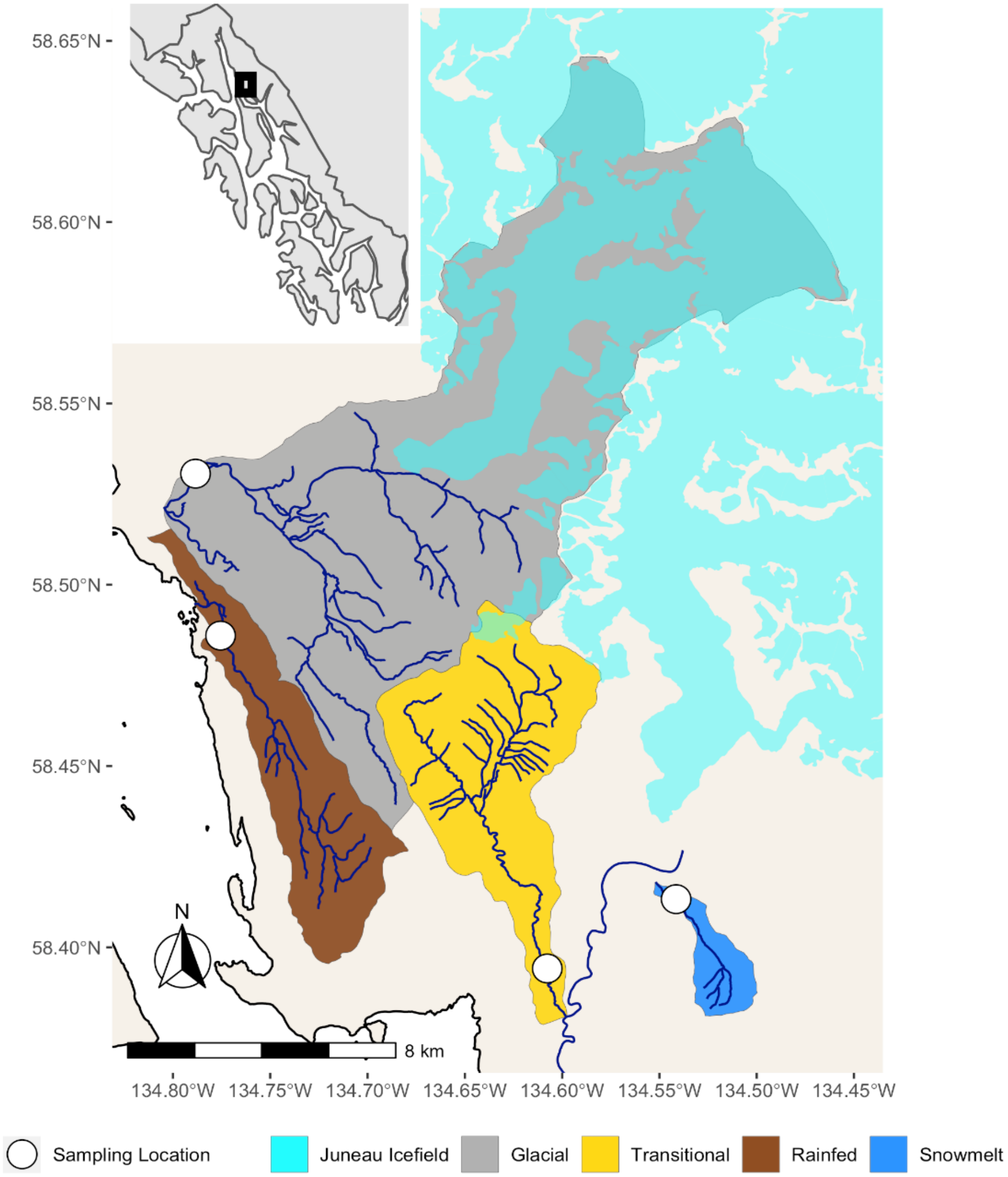


Figure 4-1 Map of study locations and ice coverage from the Randolph Glacial Inventory (RGI 6.0).

### *Invertebrate production*

We sampled benthic invertebrates every four weeks from April - November 2018 and every eight weeks from January - April 2019 using a standard Surber sampler (250um mesh size, 0.25m$^2$). Each sample comprised three net placements from throughout the reach, resulting in 0.75 m$^2$ area measured per sample. We elutriated samples in the field to remove inorganic material and preserved in 70% ethanol. In the laboratory, we removed large and rare individuals (> ~15mm) under a lighted lens and then transferred the sample to a 120um sieve with 8 equal divisions. We removed a 1/8th subsample and separated all invertebrates from detritus until the subsample contained at least 500 individuals or the entire sample was processed, whichever came first (Vinson and Hawkins 1996). We then identified invertebrates to the lowest practical taxonomic level (generally genus for all except *Chironomidae, Gastropoda, Mollusca,* and *Oligochaeta*) and measured body length to the nearest 0.5mm using either an ocular micrometer or gridded paper and converted to dry mass using published length-weight regressions. We estimated invertebrate secondary production using the size frequency method (Hynes 1961, Hynes and Coleman 1968, Benke 1979, Benke and Huryn 2017) on field data to calculate site-specific and landscape-level production to biomass (*P:B*) ratios and multiplied by biomass estimates obtained by bootstrapping our field data 10,000 times and calculating a mean annual biomass. (*These methods are described in greater detail in Chapter 2.*)

### *Stable Isotope Sampling, Laboratory Methods, and Mixing Models*

A periphyton sample for stable isotope analysis was collected from the pooled remaining periphyton from per-area sampling and passed onto a pre-ashed glass fiber filter with the goal of obtaining a large amount of biomass. Aquatic invertebrates were collected with a 250-um kick net from the study reach after quantitative insect sampling was complete and sorted in the field. Individual insect taxa were placed into vials containing stream water and allowed to clear their guts in a laboratory refrigerator for 24-72 hours. Insects were then identified under a dissecting microscope, placed into a small plastic Eppendorf tube, and frozen until analysis. To achieve a signature for the fish community, small portion of caudal fin was clipped from a random subset of fish and pooled by size class (< 75mm (~age-0), 75-125mm (age-1-2), and 125+ (age 3+). All samples were kept frozen until laboratory processing at the Washington State University Stable Isotope Core Lab (Pullman, WA, USA), where samples were freeze dried, homogenized, and weighed prior to analysis. All samples were then analyzed for $\delta^{13}$C and $\delta^{15}$N using a pass-through flow spectrometer. Isotopes are expressed in permil ratios relative to a standard ($^{13}$C/$^{12}$C: PeeDee Belemnite (PDB); $^{15}$N/$^{14}$N: Air). All samples were analyzed as bulk tissue and no lipid extractions were conducted prior to analysis.

Data were analyzed using MixSIAR (Stock et al. 2018) on a monthly timestep with a one-month lag between sources and consumers to allow for incorporation into tissue. We ran models for invertebrates with uninformed priors due to high diet flexibility in harsh environments. We grouped invertebrate taxa by family and compared with sources comprising a mean landscape marine derived nutrient signature (i.e., eggs, salmon carcass tissue) and local site periphyton, aquatic detritus, riparian vegetation. Additionally, because many invertebrate taxa in the Herbert River in winter were observed to be extremely depleted in $\delta^{13}$C, we simulated a methanogenic proxy source using the upwelling methane $\delta^{13}$C value reported in a Japanese headwater stream at a similar latitude 65.9 ± 2.4 ‰ (Kohzu et al. 2004) (Kohzu et al., 2004). Our proxy was given a $\delta^{15}$N value of 0 ± 2 ‰. We used standard trophic enrichment factors for all taxa and sources ($\delta^{13}$C :1.3 ± 0.4 ‰; $\delta^{15}$N: 3.4 ± 1‰). Annual proportional consumption was calculated by taking the average of the monthly time-step estimates for each family at each site.

### *Fish abundance, biomass, diet, and production*

We sampled juvenile fish rearing in study reaches using minnow traps baited with cured salmon eggs in a perforated Whirlpak. Traps were operated either overnight (in cold conditions and in the glacial *Herbert River*) or during 2 or 3 subsequent sets during the day without replacement (30 min – 1hr per set during warm conditions outside in limited-to-no glacial influence streams). Minnow trap-based depletion has been shown to be effective for juvenile salmonids in the region (Bryant 2000)and we estimated abundance using the Seber multi-pass method in the R package FSA (Ogle 2013, 2018). Fish were anesthetized using Aqui-S, identified to species, and measured to fork length (FL), weighed (± 0.1 g wet mass: WM). A subset of individuals was implanted with a passive integrated transponder (PIT) tag for individual growth estimates upon recapture. Growth rates were estimated primarily from size-frequency analyses and supplemented with specific growth of recaptured tagged individuals. We converted wet mass to dry mass using the coefficient of 0.2 for salmonids and 0.25 for sculpin (Bellmore et al. 2013). Population biomass was estimated as the product of the average species-specific mass and the abundance estimate from our two-pass depletion estimate. For taxa on sampling events where two-pass depletions were inconclusive, we estimated abundance from either the seasonal average capture probability or, if that was unavailable, we used the annual average capture probability of all species at that site. Abundance in the glacial river was estimated using capture probabilities from two-pass sampling during declining glacial melt in September of 2018 (est. $p = 0.836 \pm 0.194$) and again at peak glacial melt after our study ended in August of 2019 (est. $p = 0.216 \pm 0.048$), which we applied to the non-glacial and glacial-melt sampling periods respectively.

Fish secondary production was estimated using the instantaneous growth method (Hayes et al., 2007; Myers et al., 2018) for all taxa at all sites using the equation:

$$P = [\log(\overline{W_{\imath+1}}) - \log(\overline{W_\imath})] * \bar{B}$$

where $P$ is the annual production per square meter (m$^2$), $W_i$ is the mean individual weight in size class $i$ and $\bar{B}$ is the average biomass between size classes. Size classes for salmonids were assumed to be <75mm = age0, 75-125: age1, 125+ = age2+ as determined using size-frequency distributions of fish. As with invertebrates, $P{:}B$ ratios were estimated on the annual scale. Production estimates obtained from this approach were similar to those calculated using the size-frequency method (Hayes et al., 2007), and from production estimates calculated using growth rates of recaptured individuals.

We collected gut content samples from a randomly sampled subset of fish across the size spectrum using gastric lavage Table 2**.** During each sampling event, we attempted to collect at least 10 diet samples from each taxon across the size spectrum above a minimum size threshold (generally > 65mm for juvenile salmonids; > 50mm for sculpin). As with our macroinvertebrate analyses, diet components were identified, measured under magnification, and dry mass was estimated using length-mass relationships. We estimated the proportional diet contribution by ash-free-dry-mass for each individual diet sample then averaged these proportions across taxa within a given stream and sampling event. All fish handling was approved by USFS Institutional Animal Care and Use authorization #IACUC 2018-006 and University of Idaho #IACUC-2018-15. Fish sampling was conducted under Alaska Department of Fish and Game permits SF2017-194d, SF2018-054d, SF2019-214, and SF2019-040.

### *Trophic basis of fish production and flow food webs*

We constructed organic matter flow food webs using a hybrid approach, whereby fluxes to fish were calculated using direct observations of consumption via diet samples and fluxes to invertebrates were calculated using stable isotope mixing models. For both trophic levels, we used the trophic basis of production approach (Bellmore et al. 2013, Cross et al. 2013) to estimate the relative contributions of each individual food type to the production of consumers. To do this, we first calculated the proportional consumption of each food type by predator groups (invertebrate families, fish by species and size class) using the following equation:

$$F_i = G_i \times AE_i \times NPE$$

where $F_i$ is the fraction of production attributed to each prey type $i$, $G_i$ is proportion prey $i$ in the diet, and $AE_i$ and $NPE$ reflect assimilation and net production efficiencies of each prey type, respectively. We then calculated the proportional contribution of each resource to consumer production:

$$PF_{ij} = \frac{F_i}{\sum_{i=1}^{n} F_i}$$

then estimated flux by multiplying the proportional flux $PF_{ij}$ from each food group $i$ to each fish morphospecies $j$ by the annual production of that consumer ($PF_j$) to calculate the annual flux from resource to consumer ($FC_{ij}$):

$$FC_{ij} = \frac{PF_{ij} \times P_j}{AE_i \times NPE}$$

## Results

### *Invertebrate production, fish production, and consumption of invertebrates by fish*

Invertebrate biomass and production were highest and similar in the snowmelt and rainfed streams (~ (2.3 g $m^{-2}$ $y^{-1}$) though the most productive taxa in the snowmelt stream were stoneflies in the families *Perlodidae* and *Chloroperlidae* and mayflies in the family *Heptageniidae* whereas the most productive taxa in the rainfed stream were stoneflies in the *Chloroperlidae* and segmented worms. Production was lowest in the glacial stream (~0.55 g $m^{-2}$ $y^{-1}$) and dominated by the large-bodied stoneflies in the family *Perlodidae* (~58%), but with substantial production in *Nemouridae*, *Capniidae*, and *Baetidae*. The transitional stream shared traits with the other sites, with intermediate production (1.11 g $m^{-2}$ $y^{-1}$) mainly in *Chloroperlidae*, *Heptageniidae*, Oligochaeta, and *Pediciidae*. Fish secondary production was highest in the snowmelt stream at 631.12 mg $m^{-2}yr^{-1}$ followed by the rainfed stream 524.66 mg $m^{-2}yr^{-1}$, and the transitional stream 411.92 mg $m^{-2}yr^{-1}$ (Figure 4-2; Table 4-2). The lowest total fish production was in the glacial stream at 359.48 mg $m^{-2}yr^{-1}$. However, the glacial stream supported the second highest rates of Dolly Varden production as with the snowmelt and transitional stream despite much lower temperatures and very low levels of invertebrate prey production (Figure 4-2; Table 4-4). Prey consumption by fish consumption was estimated from a total of 973 diet samples (Table 4-2). Fish had an average of 4 items in their diets (95% CI: 3.98-4.82) equating to a mean 35.2 mg AFDM of biomass (95% CI: 25.7 - 44.7 mg) and were predominantly aquatic invertebrate (72%) and terrestrial invertebrate (12%). Piscivory and egg consumption comprised 6% and 9% of diet items across the landscape respectively (Table 4-3).

### *Stable isotope mixing models of invertebrate resources*

We estimated the trophic basis of invertebrate secondary production using stable isotope mixing models at the family level for tissue collected ~monthly over the course of the study period (Figure 4-3). We found that the invertebrate communities in all, but the transitional stream, were predominantly fueled by conditioned stream detritus, whereas the rainfed stream was disproportionately supported by benthic periphyton signatures. Unconditioned terrestrial vegetation was found to contribute to production in all streams but was greatest in the glacial stream. Marine-derived nutrients were a substantial contributor to the production in the rainfed stream and, to a lesser extent, in the snowmelt stream. Additionally, we observed extremely depleted carbon signatures in the glacial and transitional streams – particularly in winter.

### *Trophic basis of production*

We calculated the trophic basis of production for both the invertebrates and fish. Total annual flux to invertebrate production was highest in the snowmelt stream (28,393 mg $m^{-2}y^{-1}$) and dominated by flows from riparian vegetation (46%) and conditioned detritus (46%). Fluxes in the rainfed stream were roughly half (15,037 mg $m^{-2}y^{-1}$) and dominated by consistently high flows from periphyton (43%) and seasonally high flows from MDN (16%). The transitional stream invertebrate community had a total annual flux of (9,009 mg $m^{-2}y^{-1}$) with shifting but equitable fluxes from riparian vegetation (44%) and conditioned detritus (35%), periphyton (13%), and marine-derived nutrients (6%), though we also found evidence suggesting small fluxes from extremely depleted carbon sources to certain taxa during winter ("proxy", ~ 3%). These depleted carbon sources likely played a more substantial role in the annual support of the glacial stream invertebrate community (13%) and seasonally dominant in the winter months. The glacial stream was otherwise driven by fluxes from riparian vegetation (56%) and conditioned detritus (27%) and a total annual flux of (8,519 mg $m^{-2}y^{-1}$). We found minimal evidence of marine-derived nutrient incorporation in the invertebrate community at this site.

Total invertebrate biomass consumption by the fish community was greatest in the snowmelt (6840 mg $m^{-2}y^{-1}$) and rainfed (5173 mg $m^{-2}y^{-1}$) streams, which had the highest invertebrate and fish secondary production and were the warmest streams (Table 4-4). Consumption was lowest and similar in the glacial (3371 mg $m^{-2}y^{-1}$) and transitional streams (3818 mg $m^{-2}y^{-1}$). The top invertebrate fluxes at each site differed among streams. The glacial stream had top fluxes from *Mysidae** and *Perlodidae* to Dolly Varden; the transitional stream had top fluxes from terrestrial *Hymenoptera* to Coho and *Lepidoptera* to Dolly Varden; the snowmelt stream had top fluxes from *Pediciidae* to Dolly Varden and *Lepidoptera* to Coho; the rainfed stream had top fluxes from *Chloroperlidae* and *Limnephilidae* to Coho. These fluxes also varied seasonally between streams (Figure 4-5) reflecting substantial differences in the prey base supporting fish production. (**Mysidae* production almost certainly was from off-channel wetlands or outflow from a lake in a tributary highlighting the open nature of these food webs.)

Table 4-2 Summary of mean annual density, dry biomass, and secondary production of fish.

| | **Glacial** | | | **Transitional** | | | **Snowmelt** | | | **Rainfed** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Density (No. m$^{-2}$)** | **Biomass (mg m$^{-2}$)** | **Production (mg m$^{-2}$ yr$^{-1}$)** | **Density (No. m$^{-2}$)** | **Biomass (mg m$^{-2}$)** | **Production (mg m$^{-2}$ yr$^{-1}$)** | **Density (No. m$^{-2}$)** | **Biomass (mg m$^{-2}$)** | **Production (mg m$^{-2}$ yr$^{-1}$)** | **Density (No. m$^{-2}$)** | **Biomass (mg m$^{-2}$)** | **Production (mg m$^{-2}$ yr$^{-1}$)** |
| Coho | 0.0080 | 11.543 | 13.065 | 0.4704 | 147.479 | **152.809** | 1.6491 | 331.359 | **309.493** | 1.3471 | 305.553 | **278.185** |
| Cut-throat | 0.0009 | 4.353 | 5.183 | 0.0024 | 10.021 | 14.742 | 0.0150 | 18.420 | 16.765 | | | |
| Dolly Varden | 0.0747 | 234.206 | **283.939** | 0.0573 | 122.247 | **184.079** | 0.3973 | 237.026 | **304.861** | 0.0217 | 51.673 | 75.200 |
| Sculpin | 0.0012 | 2.893 | 4.650 | 0.0568 | 82.741 | 54.506 | | | | 0.0147 | 32.189 | 24.233 |
| Steel-head | 0.0019 | 4.807 | 5.995 | 0.0028 | 4.387 | 5.786 | | | | 0.1367 | 125.126 | **147.041** |

Table 4-3 Proportional abundance and biomass of fish diet items collected.

| | | | Biomass | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Species** | **No. Diets** | **Eggs** | **Fish** | **Aquatic Invert.** | **Terrestrial Invert.** | **Eggs** | **Fish** | **Aquatic Invert.** | **Terrestrial Invert.** |
| Glacial | Coho | 51 | 4% | 0% | 81% | 15% | 2% | 0% | 86% | 12% |
| | Dolly Varden | 159 | 7% | 1% | 72% | 20% | 4% | 1% | 80% | 15% |
| | Sculpin | 4 | 0% | 0% | 100% | 0% | 0% | 0% | 100% | 0% |
| Transitional | Coho | 98 | 4% | 1% | 66% | 28% | 1% | 1% | 75% | 23% |
| | Cutthroat | 8 | 0% | 62% | 28% | 9% | 0% | 67% | 26% | 7% |
| | Dolly Varden | 120 | 22% | 6% | 52% | 20% | 14% | 6% | 62% | 17% |
| | Sculpin | 99 | 3% | 3% | 88% | 6% | 2% | 4% | 90% | 5% |
| | Steelhead | 7 | 14% | 0% | 79% | 7% | 12% | 0% | 86% | 1% |
| Rainfed | Coho | 121 | 10% | 3% | 60% | 27% | 4% | 3% | 69% | 25% |
| | Cutthroat | 12 | 0% | 0% | 99% | 1% | 0% | 0% | 91% | 9% |
| | Dolly Varden | 60 | 8% | 9% | 71% | 12% | 8% | 13% | 69% | 10% |
| | Sculpin | 24 | 0% | 10% | 90% | 0% | 0% | 13% | 86% | 1% |
| | Steelhead | 73 | 10% | 13% | 64% | 12% | 6% | 13% | 72% | 8% |
| Snowmelt | Coho | 29 | 54% | 0% | 26% | 19% | 23% | 1% | 51% | 26% |
| | Cutthroat | 18 | 7% | 14% | 54% | 25% | 2% | 14% | 55% | 29% |
| | Dolly Varden | 90 | 34% | 4% | 47% | 14% | 25% | 6% | 56% | 13% |

Table 4-4 Top five invertebrate prey taxa contributing to common salmonid production across sites. Parentheticals show percent invertebrate flux.

| | **Glacial** | | **Transitional** | | **Snowmelt** | | **Rainfed** | |
|---|---|---|---|---|---|---|---|---|
| | **Taxon** | **Flux (mg m$^{-2}$yr$^{-1}$)** | **Taxon** | **Flux (mg m$^{-2}$yr$^{-1}$)** | **Taxon** | **Flux (mg m$^{-2}$yr$^{-1}$)** | **Taxon** | **Flux (mg m$^{-2}$yr$^{-1}$)** |
| Coho | *Nemouridae* | 102.17 (76.25%) | *Hymenoptera* | 444.66 (26.54%) | *Lepidoptera* | 578.61 (17.08%) | *Chloroperlidae* | 776.87 (28.64%) |
| | *Coleoptera* | 4.86 (3.62%) | *Gastropoda* | 261.35 (15.60%) | *Oligochaeta* | 536.17 (15.83%) | *Limnephilidae* | 511.96 (18.87%) |
| | *Capniidae* | 4.78 (3.57%) | *Lepidoptera* | 220.41 (13.16%) | *Brachycera* | 533.56 (15.75%) | *Gastropoda* | 259.84 (9.58%) |
| | *Gammaridae* | 3.93 (2.93%) | *Chilopoda* | 200.97 (12.00%) | *Perlodidae* | 532.34 (15.71%) | *Coleoptera* | 244.71 (9.02%) |
| | *Dytiscidae* | 3.66 (2.73%) | *Pediciidae* | 116.34 (6.94%) | *Heptageniidae* | 266.4 (7.86%) | *Pediciidae* | 170.16 (6.27%) |
| | Total Percent | 89% | Total Percent | 74% | Total Percent | 72% | Total Percent | 72% |
| Dolly Varden | *Mysidae* | 619.81 (19.15%) | *Lepidoptera* | 429.64 (20.66%) | *Pediciidae* | 1506.42 (43.63%) | *Lepidoptera* | 246.45 (29.12%) |
| | *Perlodidae* | 555.11 (17.15%) | *Oligochaeta* | 305.35 (14.68%) | *Lepidoptera* | 434.14 (12.57%) | *Pediciidae* | 163.62 (19.33%) |
| | *Nemouridae* | 346.09 (10.69%) | *Limnephilidae* | 291.47 (14.01%) | *Heptageniidae* | 257.84 (7.47%) | *Chironomidae* | 122.29 (14.45%) |
| | *Lepidoptera* | 310.12 (9.58%) | *Gastropoda* | 272.14 (13.08%) | *Perlodidae* | 237.64 (6.88%) | *Limnephilidae* | 92.53 (10.93%) |
| | *Chironomidae* | 286.55 (8.85%) | *Chloroperlidae* | 137.07 (6.59%) | *Hymenoptera* | 191.77 (5.55%) | *Chloroperlidae* | 86.87 (10.26%) |
| | Total Percent | 65% | Total Percent | 69% | Total Percent | 76% | Total Percent | 84% |
| Steel-head | | | *Chironomidae* | 16.89 (26.75%) | | | *Lepidoptera* | 312.86 (19.38%) |
| | | | *Hymenoptera* | 15.38 (24.36%) | | | *Chloroperlidae* | 275.45 (17.06%) |
| | | | *Coleoptera* | 6.01 (9.51%) | | | *Limnephilidae* | 241.33 (14.95%) |
| | | | *Pediciidae* | 4.74 (7.51%) | | | *Hymenoptera* | 213.55 (13.23%) |
| | | | *Heptageniidae* | 4.23 (6.70%) | | | *Pediciidae* | 118.19 (7.32%) |
| | | | Total Percent | 75% | | | Total Percent | 72% |

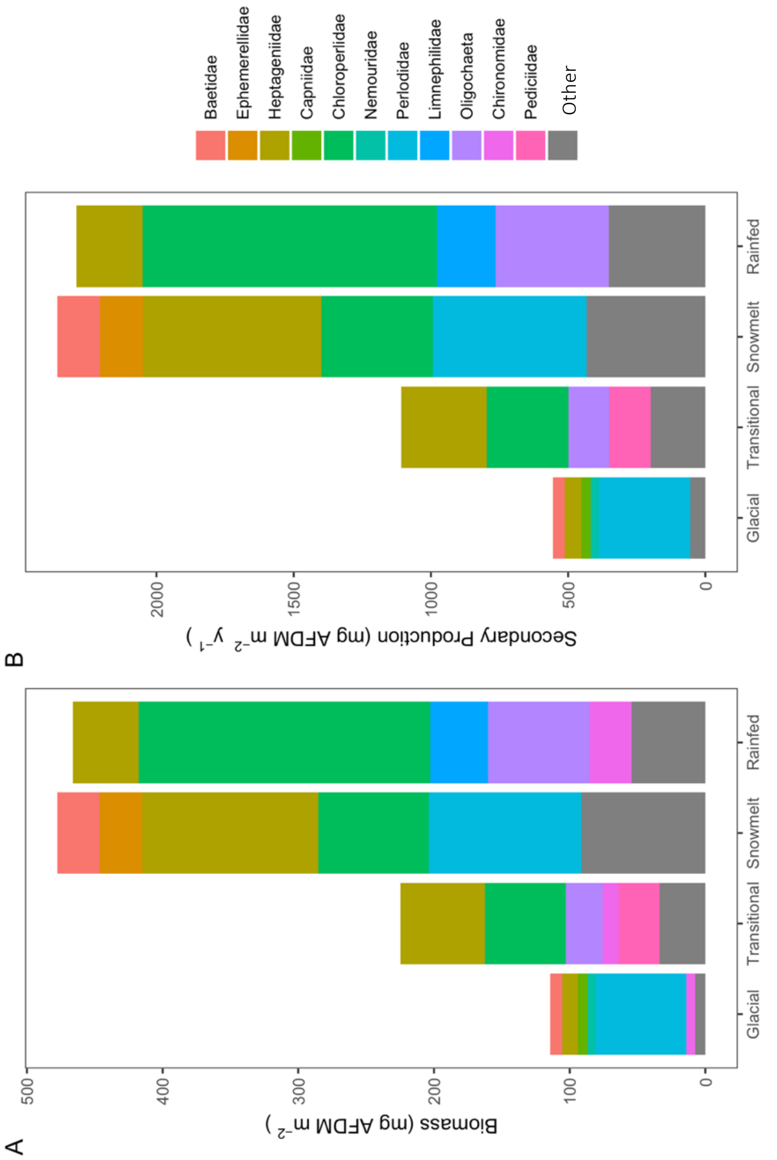


Figure 4-2 (A) Invertebrate mean annual biomass and (B) annual secondary production of all taxa representing at least 5% of biomass or production, respectively, at each site. All other biomass and production grouped as “other”.

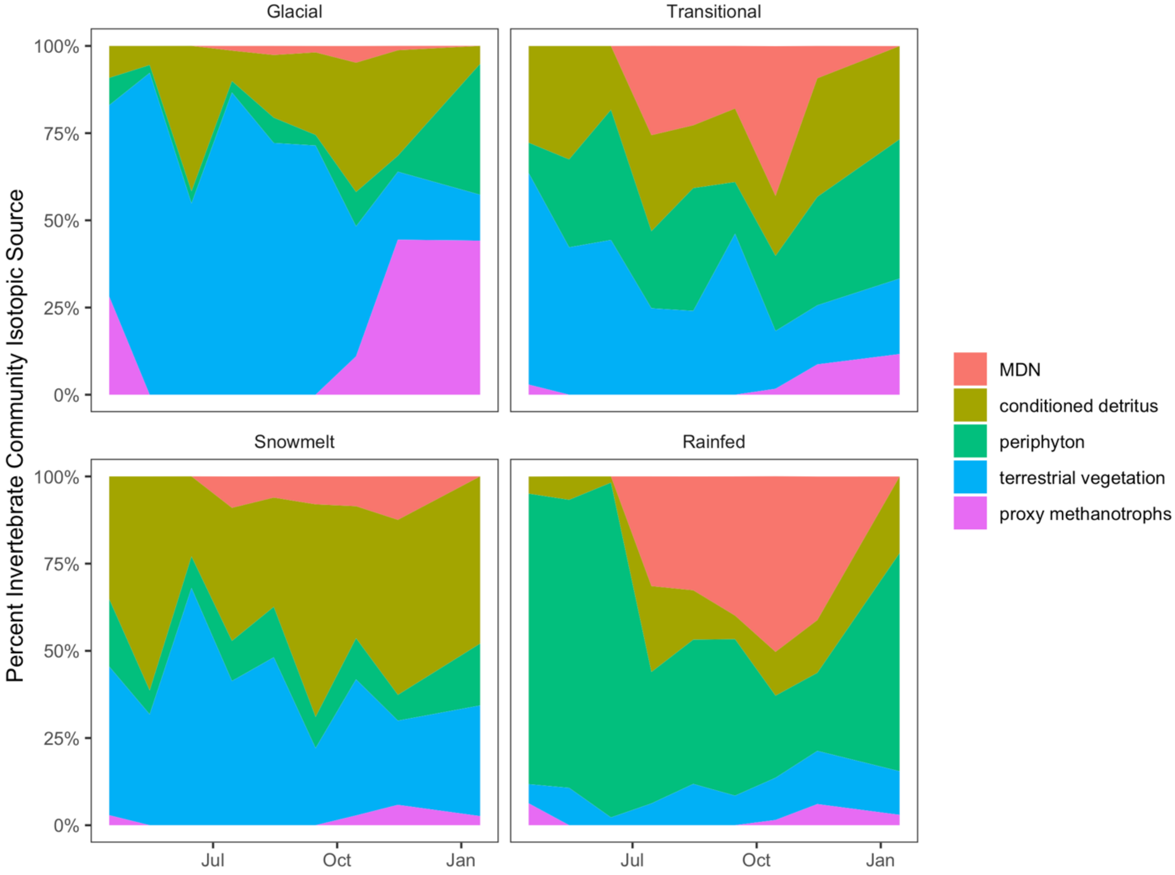


Figure 4-3 Proportional assimilation of resources of invertebrate community from stable isotope mixing models. Proxy methanotrophs represent a possible extremely low d13C source for invertebrates observed in winter months.

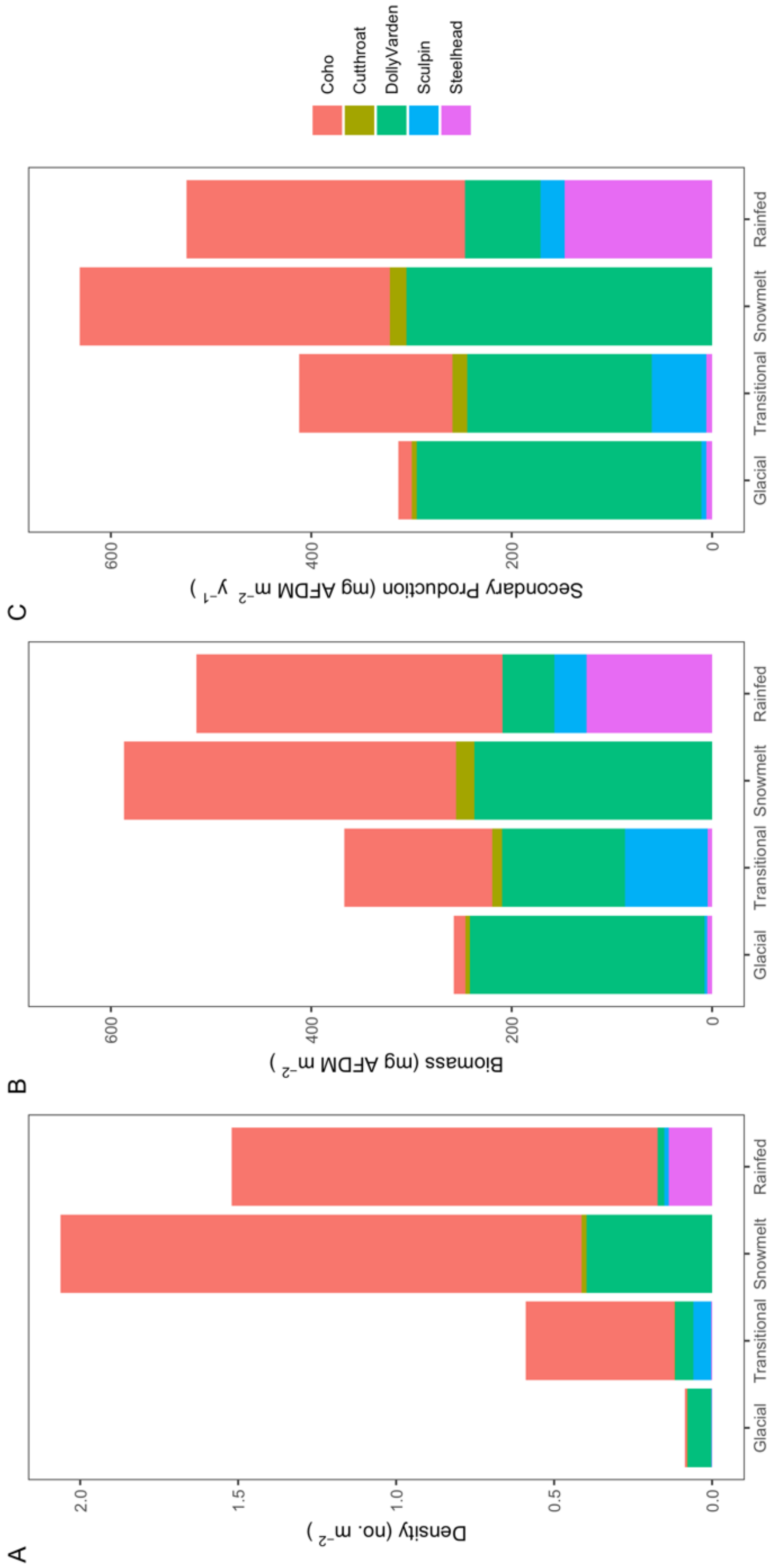


Figure 4-4 Annual mean density, mean biomass, and estimated secondary production of fish in study streams.

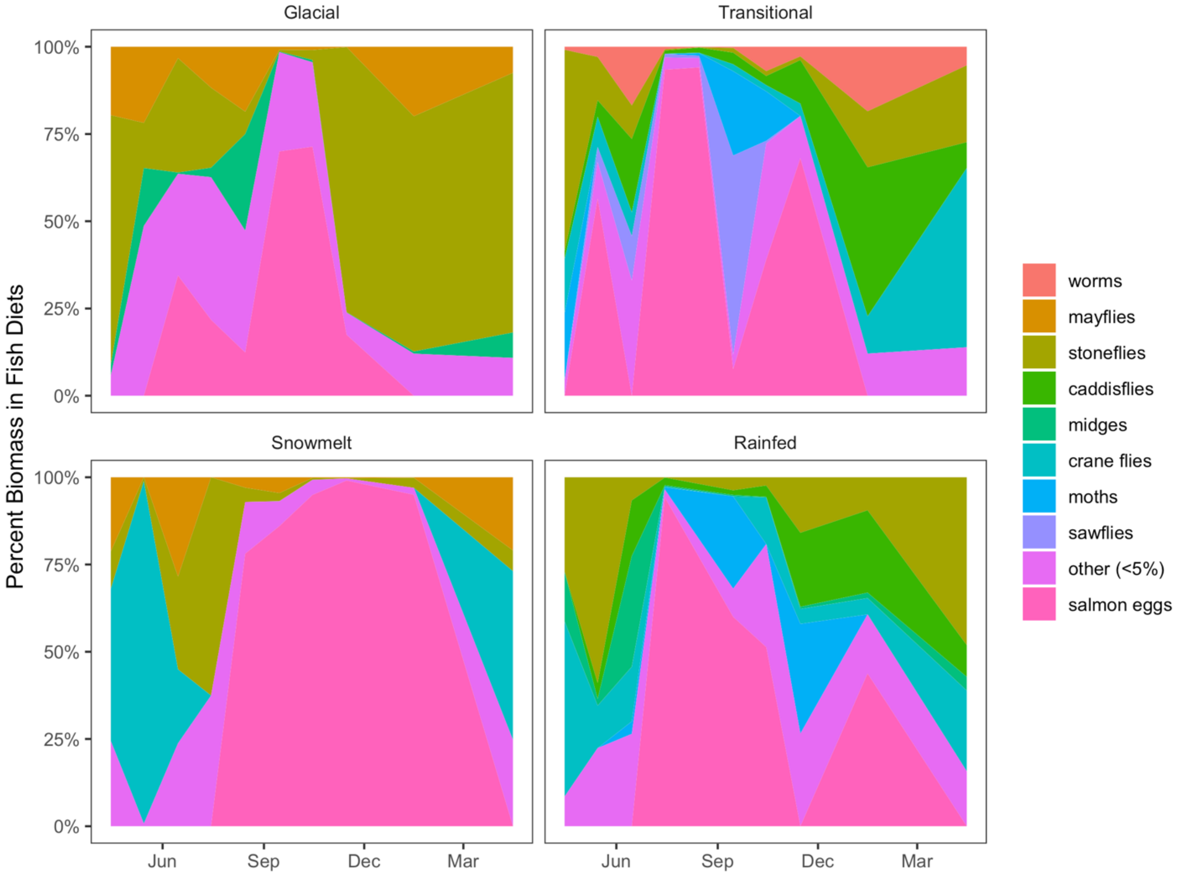
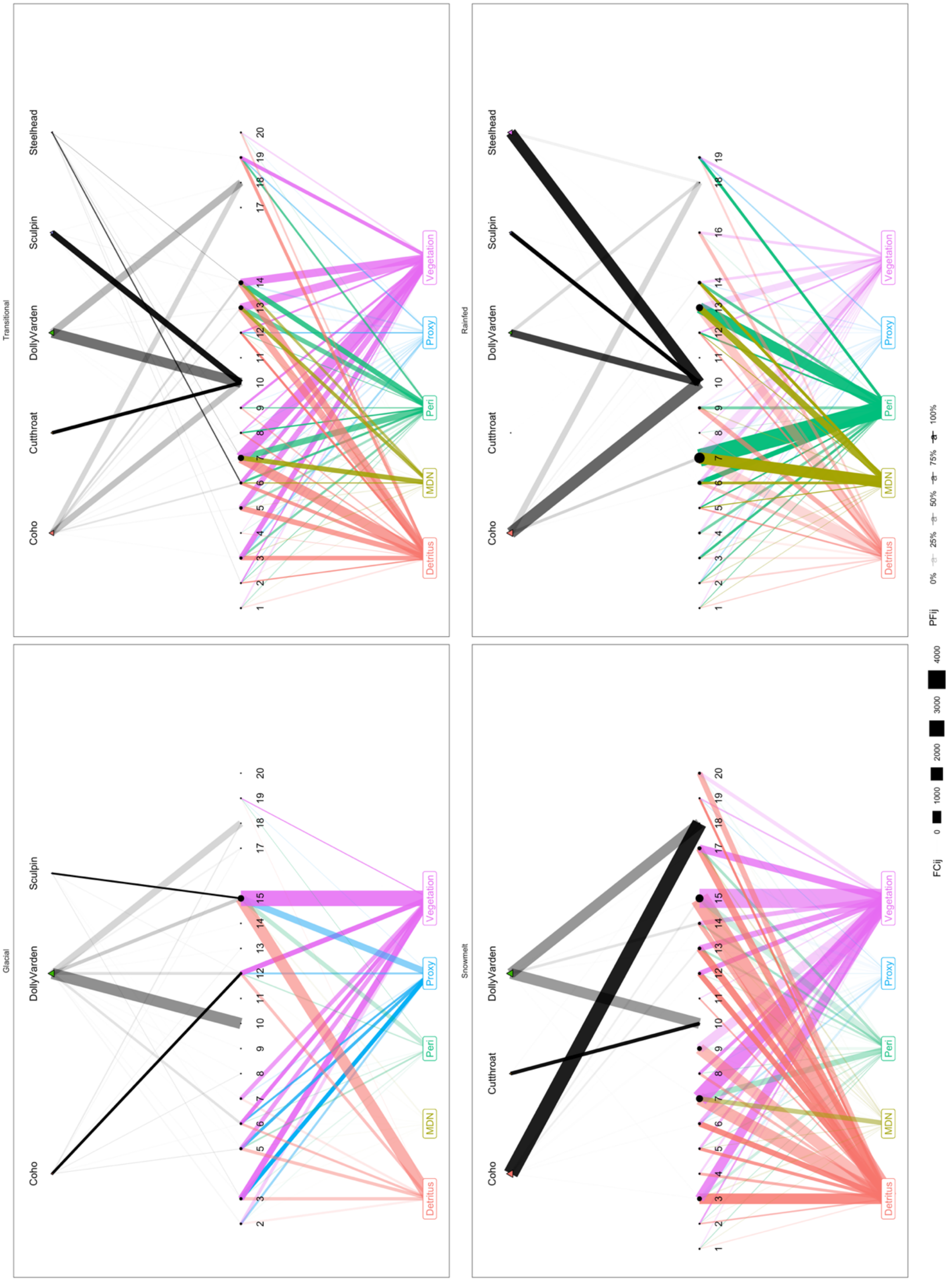


Figure 4-5 Proportional fish community consumption by higher-order common name groupings reflects timing of salmon egg subsidies to streams. Diet items with an annual average relative biomass of < 5% are grouped as “other (< 5%)”.

### *Annual flow food webs*

We observed strongly different annual flow webs across the landscape due to distinct secondary production dynamics of invertebrates and relative consumption by fish (Figure 4-6). The glacial system was the simplest food web and had highest production in Dolly Varden char attributed to fluxes from *Perlodid* and *Nemourid* stoneflies as well as smaller fluxes from *Chironomid* midges. The invertebrate community was largely fueled by fluxes from riparian vegetation, conditioned detritus, and seasonally, from a potential depleted carbon methanotrophic source. The transitional stream was more complex with large fluxes from detritus, vegetation, and marine-derived nutrients to *Oligochaeta* and fluxes of detritus, vegetation, and periphyton to *Chloroperlid* stoneflies, which in turn flowed to Dolly Varden and Sculpin. Coho were supported by weaker fluxes from aquatic invertebrates. The snowmelt stream was driven by fluxes from riparian vegetation and detritus to a diversity of productive invertebrate taxa including *Oligochaeta*, *Rhyacophilidae*, *Chloroperlidae, Perlodidae*, *Baetidae,* and *Simuliidae*. Fish in the snowmelt stream were supported by large fluxes from *Perlodid* stoneflies and *Oligochaetes* to Coho and more even fluxes from *Perlodid* and *Chloroperlid* stoneflies, *Oligochaetes,* and *Rhyacophilid* caddisflies to Dolly Varden. The snowmelt stream also had more fluxes to invertebrates which did not lead to fish – namely in the *Empididae, Tipulidae, Brachycentridae*, and *Taeniopterygidae*. Lastly, the rainfed stream was the only system largely fueled by fluxes from MDN and periphyton to invertebrates. Production of *Oligochaetes* and *Chloroperlids* were the largest and, in turn, supported the greatest fluxes to fish. The largest invertebrate to fish fluxes were from *Chloroperlidae* to Coho and Steelhead. As with the snowmelt stream, we observed several flows to taxa which did not lead to fish including those to *Brachycentridae*, *Ameletidae*, *Phryganedae,* and *Capniidae*.

Figure 4-6 Fish and invertebrate flow webs for four study streams reflecting differences in basal sources, and relative proportion of MDN support. Point sizes represent secondary production of fish and invertebrates. Those marked with “x” do not have production estimates yet were found in diets. Prey codes: *Acari (1), Ameletidae (2), Baetidae, (3), Brachycentridae (4), Capniidae (5), Chironomidae (6), Chloroperlidae (7), Empididae (8), Ephemerellidae (9), Fish (10), Leuctridae (11), Nemouridae (12), Oligochaeta (13), Pediciidae (14), Perlodidae (15), Phryganeidae (16), Rhyacophilidae (17), Salmonid eggs (18), Simuliidae (19), Taeniopterygidae (20). Figure appears on following page.*


Glacial
Coho
DollyVarden
Sculpin
2
3
4
5
6
7
8
9
10
11
12
13
14
15
17
18
19
20
Detritus
MDN
Peri
Proxy
Vegetation
Transitional
Coho
Cutthroat
DollyVarden
Sculpin
Steelhead
1
2
3
4
5
6
7
8
9
10
11
12
13
14
17
18
19
20
Detritus
MDN
Peri
Proxy
Vegetation
Snowmelt
Coho
Cutthroat
DollyVarden
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
17
18
19
20
Detritus
MDN
Peri
Proxy
Vegetation
Rainfed
Coho
Cutthroat
DollyVarden
Sculpin
Steelhead
1
2
3
4
5
6
7
8
9
10
11
12
13
14
16
18
19
Detritus
MDN
Peri
Proxy
Vegetation
FCij
0
1000
2000
3000
4000
PFij
0%
25%
50%
75%
100%

## Discussion

Climate change is poised to reorganize communities and alter the pathways and magnitudes of energy flow through food webs (Bartley et al. 2018, Barbour and Gibert 2021). However, few empirical analyses have quantitatively evaluated energy flows through multiple food webs on a heterogeneous, but rapidly changing landscape (Zhang et al. 2017, Bellmore et al. 2022). Here, we used an isotopic and diet-based food web approach to quantify the material flow webs from basal resources to juvenile fish in streams with distinct water sources near the Juneau Icefield, Alaska. This complex landscape contains some of the most rapidly declining glaciers in the world (O'Neel et al. 2015) as well as a predicted transition from winter snowfall to winter rain (Buma et al. 2017) with implications for downstream ecosystems that support the production of juvenile Pacific salmon (Milner et al. 2017, Pitman et al. 2020). Using a quantitative flow food web approach, we found substantial variation in the pathways and magnitudes of energy flow that supported invertebrate and fish production amongst streams fed primarily by glaciers, snowmelt, and rainfall. This work also shows strong seasonality in resource use, variation in production rates, and heterogeneity in food web dynamics among streams influenced by glacial melt, snowmelt, rainfed and snow-rain transitional water sources and provides an empirical test of the role of community structure and the abiotic environment on ecosystem productivity.

We observed similar community assemblages in streams but vastly different food web structures in terms of biomass and material flux. The total number of linkages were lowest in glacial and highest in snowmelt stream. The transitional stream had the most even distribution of primary linkages from basal resources to invertebrates and a relatively high number of linkages from invertebrates to fish. Similar community structure is likely due to a small regional species pool and proximity. In general, most of the invertebrate community on the landscape was supported by conditioned detritus and terrestrial vegetation sources. Contrary to our expectations, however, the relatively shaded rainfed stream had substantial fluxes from periphyton to the invertebrate community. All sites had large fluxes from salmon eggs to juvenile fish, but invertebrate fluxes varied widely by stream type, fish species, and size. Further, we wondered whether abiotic dynamics or biotic community structures control these food web dynamics, though our study is insufficient to fully disentangle abiotic versus biotic controls. We expected to find common food web motifs (Rooney and McCann 2012) driven by a few common flows from basal resources to high-production prey items to top consumers, but we hypothesized that the scale of those fluxes would be sensitive to strong abiotic controls, such as temperature, discharge, light penetration, and nutrient availability.

We predicted that glacial food webs would be relatively simple and populated by weak fluxes due to harsh conditions requiring generalist feeding behaviors in both invertebrate and fish communities (Clitherow et al. 2013, Niedrist and Füreder 2018). This was supported to a degree and particularly for Dolly Varden char, which were year-round residents in the glacial mainstem. There were indeed fewer interactions due to lower species diversity. We were surprised to find similar secondary production of Dolly Varden char in glacial and non-glacial streams despite the low prey production and seemingly unfavorable metabolic conditions in cold glacial meltwaters. Additionally, fish in the glacial river relied to a greater extent on small-bodied stoneflies in the family *Nemourid*, mayflies in the families *Baetidae* and *Heptageniidae*, and *Chironomid* midges. Conversely, Coho salmon were supported by a few strong interactions supporting growth likely due to their seasonal presence. We hypothesized the mixed-signature stream would share qualities of the other streams due to intermediate community structure and intermediate disturbance conditions from a diversity of water sources. This was generally supported, as no single fish or invertebrate taxa dominated material fluxes. Additionally, the invertebrate community was supported by stable fluxes from the base of the food web, with proportional incorporation into invertebrate tissue fluctuating seasonally much less than at other sites. We predicted the snowmelt stream to have the most complex food webs due to due greater aquatic invertebrate species richness (Chapter 2) (Brown et al. 2007b). This was only supported for invertebrates, which were indeed diverse and supported by myriad basal resources resulting in an overall greater number of fluxes. However, fish in this stream were supported by large fluxes from salmon eggs, swamping all other fluxes at the annual scale. We expected the rainfed food web would be dominated by a few strong pathways due to warm conditions and large basal resource pools. This too was supported as we found major fluxes from MDN and periphyton to a few highly productive invertebrate taxa (*Chloroperlids* and *Oligochaetes*), which then support fish growth.

While flows through the aquatic invertebrate community support substantial portions of fish production and varied between streams, patterns were somewhat obscured by marine-derived nutrient subsidies from spawning salmon. Past work has shown strong, but highly variable impacts of MDN subsidies on food webs depending on resource form (e.g., excretion (Samways and Cunjak 2015), post-spawn carcasses (Bilby et al. 1998, Cederholm et al. 1999), or eggs (Armstrong et al. 2010)) and on direct versus indirect flows to top consumers (Collins et al. 2016). Direct consumption of eggs and carcass material may increase juvenile fish growth (Wipfli et al. 2003, Guyette et al. 2013) or alter juvenile fish density and movement behaviors (Dunkle et al. 2021). We observed variable seasonal incorporation of marine-derived carbon and nitrogen (< ~ 50%) by the aquatic invertebrate community among our study streams during peak spawning. We found greater evidence of direct consumption of MDN in the form of salmonid eggs by juvenile fish, which supported a substantial portion of annual fish production in the snowmelt and rainfed streams. However, high biomass and readily digestible salmon eggs are only found in some diets and only available during a portion of the year, which may be overemphasized in annual food web quantification.

Annualized food webs may be an inappropriate representation of dominant energetic structures in highly seasonal and ephemerally subsidized ecosystems. We expected direct marine-derived resources in the form of fish eggs, carcass tissue, and emergent fry would be incorporated into fish diets. Further, we predicted that marine-derived nutrients would be indirectly incorporated through primary and secondary production. Our analyses revealed greater direct consumption of marine resources by fish than indirect pathways through invertebrates, but future analyses should model food webs on a seasonal basis. For example, the biotic and abiotic conditions during late summer and fall represent an ecologically distinct season relative to the winter and spring due to warmer conditions and the presence of marine subsidies.

Many studies have focused on the diversity and future trends of specialist taxa in glacial and other alpine river systems (Giersch et al. 2017, Birrell et al. 2020, Hotaling et al. 2020) and these ecosystems are thought to be highly sensitive to climate change (Fell et al. 2017a, Elser et al. 2020). Differing water sources have distinct physico-chemistry (Brown et al. 2003) with predicted effects on microbes (Hotaling et al. 2019b), periphyton (Uehlinger et al. 2010, Niedrist et al. 2018), invertebrates (Füreder et al. 2001, Brown et al. 2006, Ren et al. 2017), and the role of external versus internal primary production (Clitherow et al. 2013, Kohler et al. 2022). Harsh conditions should mediate which organisms are present (Jacobsen and Dangles 2012, Niedrist and Füreder 2018, Niedrist et al. 2018). Climate change is leading to warmer but more extreme conditions, which result in a short-term increase in glacial melt but a long-term loss of meltwater influence on proglacial landscapes (Huss et al. 2017, Hock et al. 2019). This loss of glaciers may open new habitat for salmon spawning and rearing (Milner et al. 2017, Pitman et al. 2020, 2021) and may increase primary and secondary production but coincide with the homogenization of food web structures and flows thereby constraining the seasonal prey base for fish (Bellmore et al. 2022). These changes, along with ongoing shifts from winter snow to winter rain may render landscapes such as Southeast Alaska vulnerable to disturbances including landslides, rain-on-snow driven winter flooding, and prolonged summer drought conditions.

Energy and material flow food webs provide a powerful, but underutilized approach to understanding the structure and dynamics of food webs cross landscapes (Dolbeth et al. 2012, Benke 2018, Layman and Rypel 2020). Past work in river ecosystems has found that flow food webs may vary longitudinally downstream from a barrier (Cross et al. 2013) and laterally across floodplains (Bellmore et al. 2013). Although heterogeneity in stream hydrologic sources and physico-chemical dynamics exists on many landscapes, few studies have constructed food webs among nearby streams with distinct hydrologic conditions. Although we were only able to sample one stream within each hydrologic category (glacier, snow, rain, transitional) due to the complexity of our sampling, our systems were carefully selected—using empirical physicochemical data—to best represent each stream type category. This study represents one of the first comparative flow food web work on salmon streams in coastal North America. We empirically measured the entire food web of multiple streams roughly monthly over an entire year. Despite this effort, we were limited to estimating production at the taxonomic family level for invertebrate analysis. Further, organisms are differently influenced by water temperature and prey items in fish diets are evacuated at differing rates, potentially biasing our interpretations of important fluxes. The approach used here assumed similar and quite simple bioenergetic rate functions for fish consumers. This may artificially elevate the estimated flux to Dolly Varden in the cold glacial river, where diets contained relatively large prey biomasses but likely reflected longer digestion times rather than higher consumption rates alone. However, the differences in calculated production and material flux reflect the measured variation in biomass among streams. Leveraging bulk tissue isotopic analysis allowed us to quantify the incorporation of source material in the invertebrate community, which likely better reflects fluxes than diet analysis alone. Future analyses should re-analyze invertebrate diets using a constrained dietary source pool which does not include detritus, which, by definition, comprises both vegetation and microbial decomposers. For fish, we used diet analysis to provide refined linkages at the scale of invertebrate production. Future work should quantify food webs over multiple years to evaluate if these patterns are stable of snapshots of constantly moving dynamics – particularly comparing high versus low salmon subsidy years or during drought or high-water conditions. Addressing the long-term implications of climate change will require repeated analysis over time.

Spatial heterogeneity in abiotic conditions is a ubiquitous feature of many landscapes but landscapes are also changing. Climate change is predicted to rewire food webs by altering the interactions among organisms and how energy flows from basal resources to higher level consumers (Bartley et al. 2018) with implications for stability and resilience of culturally, ecologically, and economically important species like Pacific salmon. We found that hydrologic heterogeneity creates diverse pathways of energy contributing to salmon growth. Ecological theory would suggest that this complementation of distinct but spatially connected “meta-food webs” may contribute to ecological stability. For instance, an interacting and asynchronous meta-food web may increase growth capacity for mobile consumers if they are able to exploit windows of high prey production (Bellmore et al. 2022) providing stabilizing pressure on interacting food webs (McCann and Rooney 2009). The interactions and material flows within and among food webs will likely change well before community assemblages change and representing harbingers of climate impacts on streams and other ecosystems. This is particularly true in landscapes where diversity and heterogeneity are influenced by the diminishing cryosphere. Climate change may drive not only homogenization of communities and abiotic regimes across landscapes, but also simplify the complexity of interacting meta-food webs. How we manage these ecosystems considering climate change remains a challenge, as climate change itself cannot be managed at the landscape scale. Instead, we should manage for heterogeneity of conditions, diversity of organisms, and connective capacity on rapidly changing landscapes (Moore and Schindler 2022).

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# Chapter 5 Conclusion

## Executive Summary

1. Streams along the Pacific coast of North America reflect a gradient of water sources from glacial to entirely rainfed endmembers, with snowmelt and snow-rain transitional streams occupying middle conditions. These streams have relatively predictable patterns in physico-chemical dynamics which confer differences in biomass pools at primary and secondary trophic levels *(Chapter 2).*
2. Across the landscape, these abiotic and biotic patterns are relatively asynchronous, but the fading of glacial and snowmelt influence will likely lead to an increase in overall synchrony with implications for the stability of consumer populations *(Chapter 2).*
3. Distinct abiotic regimes filter the aquatic invertebrate food web, creating different taxonomic and functional communities despite depauperate regional species pool and close proximity of study sites *(Chapter 3).*
4. Differences in secondary production of invertebrates relates to abiotic physical and chemical differences, but also reflects divergent biotic community functional composition and diversity *(Chapter 3).*
5. Variation in the abiotic controls and biotic base of stream food webs scales up to create a portfolio of distinct quantitative flow of food webs across the landscape and shows marked differences in the annual rate and predominant fluxes that support the production of juvenile salmon and other fish *(Chapter 4).*
6. Each of these streams have significant subsidies from salmonid egg inputs, but these are inconsistent and local production may provide a backbone during low-egg years *(Chapter 4).*
7. The highest fish secondary production (insert production # here) was observed in the snowmelt stream which also had the most diverse invertebrate secondary production and linkage density from basal sources to invertebrates. Despite low primary and invertebrate secondary production annually, we observed surprisingly high secondary production of Dolly Varden char in the glacial stream and several fish were recaptured residing and growing in these seemingly harsh conditions year-round (*Chapter 4*).
8. Flows to fish in the snowmelt stream relied disproportionately on salmon eggs compared to other sites despite high prey production *(Chapter 4).*

9. To conserve food web diversity, stability, and resilience to climate change, management should seek to maintain heterogeneity and connectivity across landscapes, rather than managing for high productivity alone.

## Final Thoughts and Future Directions

Nothing in nature exists alone. Rather, the world is comprised of tangled banks of co-dependent components and nested interactions (Watkins and Freeman 2008). This complexity has been recognized for millennia, yet we still have so much to learn about the how this bank is structured, and which dynamics drive the creation of all the biomass we see and depend on (Polis and Strong 1996a). Despite the apparent messiness, the emergent qualities of these interactions are relative stable and reliable providing ecosystem services that society relies on. However, climate change is directly impacting every part of the Earth through myriad alterations to biotic and abiotic processes that underpin the functioning of ecosystems. Understanding how the structure and dynamics of community interactions varies over rapidly changing landscapes – whether from global climate change, land use alterations, or species extinctions or introductions – is critical to effectively prioritize, conserve, and manage these ecosystems if we seek to maintain the ecosystem services they provide (Holt 1997).

Food web analyses represent an intuitive approach to distilling the complexity that underpins ecosystem structure (Dolbeth et al. 2012, Thompson et al. 2012, Donohue et al. 2016). Food webs may be constructed in many ways with the simplest food webs showing single chains from resource to first-order consumer to single second order consumer and so on. These food chains represent individual flows of energy and resources that fuel the growth of organisms. When all simple chains in a location are added together, they reflect a connectance web, which draws links between organisms which feed on one another (Martinez 1992). A drawback of these types of food webs are that major diet sources and minor diet sources are represented by the same size line, obscuring the true structure of the network and failing to quantify energy or material flows through the system. To remedy this, webs may be further elaborated by showing the relative or raw flux between components – typically as ash-free dry biomass or calories – to create quantitative flow food webs. Flows from resources to consumers can be scaled by the availability or production of those resources, representing the *interaction strength* within the network (Berlow et al. 2004, Novak 2010, Tang et al. 2014). Quantitative flow and interaction webs provide a powerful way to evaluate the organization of ecological communities and emphasize the interactions which may be the first harbingers of reorganization with environmental change (Dolbeth et al. 2012, Benke and Huryn 2017, Layman and Rypel 2020).

In this text, I have described a study of how a single reach in four streams on a single landscape creates a portfolio of invertebrate and fish communities, food web structures, dynamics, and productivity patterns. While I have attempted to address and quantify both the patterns and the likely drivers in hopes that a deeper knowledge of variation on one locale can teach us about complexity on different scales, I have not quantified the true diversity of food webs on this landscape. The true diversity is undoubtedly greater, and likely varies longitudinally in streams (Vannote and Cummins 1980), laterally across floodplains (Junk et al. 1989, Malard et al. 2006, Bellmore et al. 2013), or between mainstems and tributaries or above and below confluence complexes (Rhoads and Kenworthy 1995, Benda et al. 2004). Further, I resolved these food webs on an annual average scale, not the fine scale that many trophic interactions occur or over many seasons that variation in weather conditions or salmon subsidies, but one that is relevant to the univoltine life cycle of many invertebrates, annual duration of many fish life history stages, and the multi-year life cycle of fishes present. These streams, while relative end members, may not fully capture the variation in structures found in other *glacial, transitional, snowmelt,* or *rainfed* streams on the landscape.

Despite these drawbacks, this work represents some of the first analyses of secondary production and food web structure and dynamics in salmon bearing streams in the region and a robust quantitative and temporal food web dataset to compare with work in other regions (Camacho et al. 2007, Banašek-Richter et al. 2009). This work is also notable in that, along with my co-investigators, I have connected the annual abiotic dynamics with biomass pools, community functional composition and diversity and overall food web structure to estimate the trophic-basis of invertebrate and fish production. These data show how physical and chemical patterns at watershed scales can contribute to asynchronous waves in resource pools at lower trophic levels in streams, diverging food webs, and differing capacities for consumer growth. As glaciers fade from this landscape and winter snowfall transitions increasingly to winter rain, the differences between these streams may diminish, with knock-on effects for food web structure and fish growth in this region. Very few quantitative glacial river food web analyses have been published – particularly over an entire year and in an explicit comparative design with nearby streams with little or no glacial influence.

There are many potentially fruitful areas of further research that this work has inspired. Firstly, the things I have left on the table: I collected drift samples, albeit with less intense focus and replication that drift analysis requires. It is probable that the prey items in the drift better reflect the resources available to fish than benthic sampling alone. Future work should assess the variation in drifting prey densities over different flow events at a finer scale than our monthly sampling as the relationship between benthic invertebrate densities and drifting prey availability are non-linear due to differences in hydrogeomorphology, discharge, and drift propensity of the invertebrate community. I hope to collaborate with a student in the future to analyze the drift samples to explore the variation in resource flux over time and space in this study system. I also collected fish to use for otolith-based growth and movement reconstructions and tissue for further stable isotope analysis. Again, I hope to collaborate with others to process these samples and learn what we can from them.

I mention the implications of mobile consumers throughout this text yet provide no consumer movement data, which were logistically beyond the scope of the projects. Future analyses would benefit from tracking fish movement, residency times, and foraging areas across these study systems. I am curious how variable upstream and lateral movements are for juvenile Coho and Dolly Varden of all age classes. Further, Dolly Varden appear to be major integrators on this landscape – juveniles spend several years foraging in their natal streams before beginning an extremely mobile consuming phase where they ply the estuary mouths and nearshore environment seasonally, forage for and anecdotally dig up salmon eggs during spawning events, then spawn themselves (Armstrong 1970, 1974; M.R. Dunkle, *personal observation*). I am unaware of any research evaluating how these fish integrate the variation in resource waves across the landscape or the growth/fecundity benefits of efficient subsidy tracking. Further, I observed PIT-tagged Dolly Varden residing in seemingly harsh and low-productivity mainstem glacial rivers for several months at a time with little movement. Fruitful behavioral research could evaluate how sight-feeding predators find prey during seasons of extremely low visibility.

Further research is necessary to determine to what extent the food web patterns we observed at these four sites are applicable across the landscape. Spatial variation in food web dynamics should occur differently depending on the scale. Improving understanding of how stream food webs vary longitudinally in rivers with distinct hydrologic sources would greatly benefit this body of literature. For example, a glacial river food web likely simplifies greatly as you approach the glacier terminus due to extremely low temperature and high discharge conditions, limited terrestrial inputs, and low local production whereas a rainfed stream may have similar food webs from headwaters to estuary due to similar conditions throughout the basin. Findings from this project reduce the research activities required and increase the feasibility of future projects to quantify food web patterns in watersheds across the region. This approach would be to conduct a relatively low-intensity survey of the physico-chemical patterns and fish and invertebrate community composition and biomass pools across several watersheds. The production to biomass ratio data presented herein could be applied to mean biomass measurements of invertebrates elsewhere on the landscape to estimate secondary invertebrate production and fish demand. Additionally, fish production and growth capacity need to be adjusted for water temperature and metabolic efficiencies to truly quantify resource use and interaction strengths. If fish diet samples are collected on a representative subset of fish seasonally, moderately resolved quantitative food webs may be constructed with less effort involved in this work.

Future work should explore food web variation over several seasons and interannual cycles of high and low salmon returns to be able to predict long-term trends in food web responses to ongoing hydrologic change. This study was conducted during an off-year for pink salmon returns year but was a moderately strong chum salmon year (Ricker 1962), but it seems likely that food web structure and energy flows should respond differently to cyclical subsidy regimes. In low salmon subsidy years, support for fish growth should switch to greater reliance on local benthic and terrestrial invertebrate production. My data suggests there is capacity for prey switching particularly in the snowmelt stream which has high egg consumption, but also high invertebrate prey biomass and production. Additionally, future work should address the direct versus indirect pathways marine-derived nutrients play in this system. Much work has been done on this front, but I found evidence of potential delayed subsidies routed from salmon through *Chloroperlid* stoneflies which have high rates of winter production then emerge from the subsurface benthos/hyporheic zone in late winter or early spring in extremely high densities. This timing corresponds with a growth bottleneck for many juvenile salmonids in the early spring after meager winter months for 1–2-year-old fish or post emergence when densities are high for sub yearlings. I would hypothesize that equal biomass or energy in the form of early spring *Chloroperlids* should elicit a greater growth and/or density effect size than the same quantity of biomass or energy in late summer/early fall.

While this work sheds light on the value of asynchronous patterns in a complex landscape, it also has highlighted knowledge gaps and needs for future research and there remains several potentially fruitful uses for these data. Notable, I plan to quantify the interaction strengths and network structure and topology of these food webs. I will do this by first correcting fish consumptive fluxes by temperature-specific metabolic/digestive efficiencies then calculate the proportion of prey production is consumed by the fish community as a whole and for individual tropho-species (Yodzis and Winemiller 1999). Food web theory predicts that networks populated by more but weaker interactions should be more stable and resilient to change than networks dominated by a few very high-strength interactions (Huxel and McCann 1998, Rooney and McCann 2012, Bartley et al. 2018). My data has the potential to quantify the average number of interactions, strength distribution, and connectance in these four food webs and may allow us to make predictions about how communities will respond to hydrologic change. One other theoretical issue I would like to address with these data and future studies is how diversity relates to production rates versus diversity in relation to predictability of conditions. Despite much research on the relationship between biodiversity and ecosystem functioning, the relative drivers of the function of secondary production of stream biomass remain unclear. If diversity is solely driven by primary production at a site, the rainfed stream in our study should have also been the most diverse. However, diversity was highest in the snowmelt stream which seemingly has a somewhat predictable disturbance regime dominated by spring snowmelt and relatively stable flows during the summer. Alternatively, production in the rainfed stream could be limited by high DOC (Seekell et al. 2015a, 2015b) loads and low pH (Griffith et al. 1994, Kobuszewski and Perry 1994, Kocovsky and Carline 2005). Lastly, the invertebrates collected during this study may be used in future studies of cryptic diversity in a depauperate landscape. Because of small body sizes and similar superficial morphologies, many taxa were only identified to genus. Using genetic and genomic techniques will likely reveal more diversity than superficial identification alone. If a proper genomic library is constructed using samples collected for this study, future work could leverage both genomic-based whole diet sample analysis paired with next-generation compound-specific stable isotope analysis to further refine stream food webs. These approaches are gaining traction and this study system is an ideal testing ground for new food web techniques.

To conclude, the three studies that comprise this dissertation are built upon hundreds of hours of field sampling, laboratory processing, and data analysis to come to a fairly simple finding: abiotic heterogeneity on complex landscapes creates distinct food webs through direct effects on community composition and the productive capacity of individual taxa as well as indirect effects on the pathways materials take from primary sources to higher level consumers. This pattern likely holds to varying degrees across all landscapes but may be pronounced when physico-chemical patterns are very different. Humans are particularly good at homogenizing and simplifying landscapes whether by land use, species movements, or global climate change. In the watersheds surrounding the Gulf of Alaska, complexity in salmon-bearing stream food webs is derived from the melting of glaciers, seasonal snowpack, outflows from muskeg wetlands and lakes, and seemingly endless rainfall. With the fading of glaciers and shifts from winter snow to winter rain, the landscape may become more productive, but this increase may coincide with a decrease in food web diversity, asynchrony, and complexity rendering the landscape less stable and resilient. The best way to stay ahead of these changes is to recognize where they might occur, monitor them, and conserve diversity and connection on changing landscapes.

> *"I will tell you something. It is to the thought of the river's banks that I most frequently return, their wordless emergence at a headwaters, the control they urge on the direction of the river, mile after mile, and their disappearance here on the beach as the river enters the ocean. It occurs to me that at the very end the river is suddenly abandoned, that just before it's finished the edges disappear completely, that in this moment a whole life is revealed. It is possible I am wrong. It is impossible to speak with certainty about very much."*
>
> *Barry Holstun Lopez, River Notes*

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