THE EFFECTS OF TEMPERATURE ON STREAM ECOSYSTEM STRUCTURE, SECONDARY PRODUCTION, AND FOOD WEB DYNAMICS

by

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DEDICATION

This dissertation is dedicated to my family.

To my parents, Mike and Laura Junker, brother, Adam, and sister, Jackie: Thank you for your support and encouragement.

To my partner, Dr. Juliana D'Andrilli: Thank you for your patience and guidance.

I love you all.

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ABSTRACT

Since 1880, Earth's mean temperature has risen ~0.85 °C, and increases >1.5 °C are likely by the end of the 21st century. Warming temperatures will continue to shuffle and restructure ecological communities and the consequences of these changes for ecosystem processes and services are largely unknown because of the difficulties in measurement and understanding in complex ecological systems. Yet, isolating temperature's influence is crucial to predicting how ecosystems will look and operate in a 'no-analog' future and to begin to integrate warming with the myriad other stressors affecting natural systems. In this dissertation, I leverage a natural stream temperature gradient (~5 – 25 °C) within a geothermal watershed to investigate the effects of temperature on stream ecosystems—with three specific questions: 1) what is the relative influence of temperature and stream flow on whole-ecosystem biomass and element storage? 2) how does temperature shape patterns of animal production across and within streams? and 3) how does temperature modify the seasonal patterns of consumer-resource interactions in stream food webs? I found stream flow to have primacy in driving the 2 orders of magnitude variation in ecosystem biomass and element storage—mediated through flow's effect on plant body size. At higher trophic levels, temperature strongly shaped the patterns of secondary production coinciding with a 45-fold increase in annual secondary production across streams. This positive relationship was mediated through covariation between temperature and basal resource availability, both across and within streams. Consumer interactions with basal resources showed differing seasonality with increasing temperature. At higher temperatures, consumer demand and resource availability were strongly coupled seasonally compared to cooler streams. Tighter coupling between consumers and resources with temperature lead to more consistent, if higher, interaction strengths through the year. My work shows temperature as an important structuring driver of ecosystem structure and process, however, a common thread through each chapter shows the influence of temperature is mediated through its interactions with other ecosystem drivers. Ultimately, as the covariation between temperature and other environmental drivers (e.g., disturbance, nutrient and light availability, etc.) shift globally, recognizing these interactions is increasingly important.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Statement of Problem

Since 1880, global surface air temperatures have increased ~0.85 °C in response to anthropogenic greenhouse gas emissions (IPCC 2013). Regardless of any future reductions in greenhouse gases, further temperature increases are likely to exceed 1.5 to 2.0 °C over the next century (IPCC 2013). Changes in the climate have already led to observable shifts in their structure and function, including changes in species' distribution (Chen et al. 2011), altered timing of life-history events (Menzel et al. 2006, Wolkovich et al. 2012), and reductions in the average body size of organisms (Daufresne et al. 2009). While these changes are undeniable, we are still unable to accurately predict how the effects of warming will manifest across time scales, levels of biological organization, and among different ecosystem types (Yvon-Durocher et al. 2012).

Our basic understanding of how ecosystems respond to warming is hindered by a number of factors, including: (1) a paucity of long-term observations across multiple ecosystem types (e.g., Root et al. 2003, Winder and Schindler 2004, Durance and Ormerod 2007); (2) logistical constraints of large-scale temperature manipulations (Schindler 1998;);(but see Hogg and Williams 1996, Melillo et al. 2011, Canhoto et al. 2013); and (3) the inherent limitations of space-for-time substitution studies (Vitousek 1991). Consequently, much of our current understanding about climate warming is based on small-scale and short-term experiments (e.g., Chapin et al. 1995, Schiel et al. 2004,

Strecker et al. 2004, Yvon-Durocher et al. 2011). Yet, recent work has shown that such experiments may not accurately predict ecosystem responses at large spatial and temporal scales (Dunne et al. 2004). For instance, Chapin and others (1995) found that responses of arctic tundra ecosystems to three years of warming poorly predicted changes that emerged nine years post-warming. These incongruities across time scales must be reconciled if we are to predict the structure and function of ecosystems in a warmer world.

While recognition of the complex drivers involved in the response of ecosystems to warming has advanced in terrestrial ecosystems (Shaver et al. 2000), research has not progressed to a similar extent in aquatic ecosystems. Aquatic environments have experienced measurable increases in temperatures over recent decades (Adrian et al. 2009, Kaushal et al. 2010). Yet, important questions remain with respect to how responses to warming in aquatic systems may mirror or diverge from changes in other ecosystem types (Woodward et al. 2010), as well as how warming-induced changes in ecosystem structure manifest in functional responses (Petchey et al. 1999); herein lies the goal of this dissertation. Closing these knowledge gaps requires identifying study systems that effectively isolate the influences of temperature while minimizing other confounding factors across relevant spatial and temporal scales.

Study design

Geothermal systems provide unique natural laboratories for examining the role of temperature in the absence of many confounding factors (e.g., species pool/biogeography, elevation, nutrient supply) because they often exhibit wide thermal gradients within a

relatively small biogeographic area (O'Gorman et al. 2014). My dissertation was conducted in one such watershed located in the Hengill geothermal area outside of Reykjavik, Iceland. This area is characterized by extreme geothermal activity with large variation in the extent of soil and bedrock heating (Árnason et al. 1969). Spatial variability in geothermal heating leads to wide variation in water temperature (5 – 55°C mean annual temperature) of the mostly groundwater-fed streams. Importantly, the heating is indirect, resulting in streams of differing temperature but similar solute composition (Friberg et al. 2009), allowing me, for the most part (as will be evident in Chapter 2), to isolate the role of temperature on ecosystems that have been 'acclimated' to different temperatures for multi-decadal time scales.

Dissertation Outline

The first manuscript (Chapter 2) examined how steep environmental gradients (i.e., temperature and flow) influence the storage and stoichiometry of biomass in streams. This chapter focused on a suite of streams in Hengill that range from 5 – 28 °C mean annual temperature. Along this temperature gradient, the topography of the landscape produces variation in the degree of flow disturbance among streams, ranging from fully spring-fed streams with little flow variation, to relatively flashy systems that respond rapidly to precipitation or snowmelt events in the proximate watershed. These overlapping gradients generated a series of warm and cool streams with orthogonal variation in flow disturbance. Here, I disentangle how these environmental factors influenced the storage and distribution of energy and nutrients (e.g., nitrogen and phosphorus) in the biomass of living and detrital ecosystem compartments. Surprisingly,

very little is known about how changes in temperature and flow regime influence quantities and stoichiometry of biomass, but this is of fundamental importance for predicting how global change is likely to influence stream ecosystem function. This research is among the first to comprehensively examine changes in stream biomass and stoichiometry in response to global changes drivers.

Chapter 3 moves up trophic levels to quantify how production of the macroinvertebrate community responds to temperature. This chapter set out to test an oft-overlooked prediction of the Metabolic Theory of Ecology (Brown et al. 2004), i.e., that secondary production and energy flux should be temperature-invariant. Here, I traded spatial resolution (and statistical power) for increased temporal resolution and a more parsimonious test of temperature-invariance by focusing on a subset of streams from Chapter 2. These streams maximized the temperature gradient while minimizing any confounding differences in disturbance regime (outlined in Chapter 2) and basal resource community (i.e., study streams were dominated by epilithic primary producers vs. macrophytes). Again, I scaled across biological levels of organization (individuals to whole assemblages) and timescales (daily to annual) to interrogate the basic prediction of temperature-invariance of secondary production. My approach was to deconstruct secondary production into its constituent components, standing biomass and biomass turnover, and to confront their predicted thermal relationships with data. My results provide a unique empirical assessment of secondary production in the context of temperature and Metabolic Theory.

The fourth, and final research chapter, connected the dots by quantifying the influence of temperature on food webs structure, organic matter fluxes, and species interaction strengths. Daily consumption estimates were combined with basal resource biomass to estimate flux-based interaction strengths at annual and seasonal timescales across a range of stream temperatures. Here, the patterning of interaction strengths, as well as the variation in the consumer:resource biomass ratios, were quantified to discern the fates of energy in food webs and the mechanisms by which stream food webs respond to warming. My results provide a comprehensive assessment of the influence of temperature on energy fluxes through food webs—including the explicit inclusion of seasonality and its influence on interactions.

Together, the chapters of this dissertation fill important knowledge gaps with respect to how temperature governs the structure and function of stream ecosystems. These empirical results will be critical for informing predictions about environmental warming, as well as the continued development of ecological theory.

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CHAPTER TWO

PATTERNS AND DRIVERS OF ECOSYSTEM-LEVEL BIOMASS AND STOICHIOMETRY IN STREAMS

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

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Abstract

Understanding connections between biological communities and elemental cycles is increasingly important given alterations to both on a global scale. Biological control of elemental cycles is tied to the patterns of biomass and elemental stoichiometry of organisms that make up ecosystems, which are shaped by environmental, physiological, and ecological variables. In light of ongoing global warming, focus on temperature has been heightened because of its potential to influence the physiological rates, composition, and traits of biological communities. However, changes in temperature occur within gradients of other environmental variables (e.g., disturbance, nutrient availability) that also modify community composition and traits. Here, we measured patterns of ecosystem biomass and elemental stoichiometry across a large gradient of natural stream temperatures (~5°C to 25°C) and stream flow within a small geographic area in southwestern Iceland. Across this gradient, we observed two orders of magnitude variation in ecosystem biomass and relatively large variation in ecosystem biomass stoichiometry. Surprisingly, temperature showed little association with these differences and patterns of stream flow variation were most important. While among-stream differences in biomass were generally associated with changes in community structure, i.e., from dominance by large-bodied macrophyte and bryophyte communities to epilithic and detrital biomass pools, our analysis also highlighted shifts in ecosystem stoichiometry driven by changes in the relative proportions of biomass compartments and stoichiometric flexibility. These patterns highlight the importance of understanding how

warming overlays gradients in other ecosystem drivers to influence the coupling of energy and elements in ecosystems.

Keywords: *temperature, ecosystem biomass, ecological stoichiometry, flow disturbance*

Introduction

Organisms control the movement and storage of energy and elements within ecosystems through their collective metabolic processes, which can be tied to two interconnected attributes: (1) the amount and distribution of ecosystem biomass, and (2) the metabolic activities of biomass components. Although great effort has been placed on predicting ecosystem function by scaling up the metabolic activities of individuals (Peters, 1983; Brown and others, 2004) the relationships between structure and ecosystem-level fluxes are often most closely linked to overall intersystem differences in organic matter (OM) pools (e.g. Michaletz and others, 2014; Padfield and others, 2017). Organic matter and its distribution among living organisms and detrital pools is controlled by many complex processes making it difficult to predict (Polis, 1999). Yet, understanding factors that control OM and associated elemental pools will be essential for predicting how ecosystems may respond to global changes.

While the absolute size of OM pools has obvious influence on the mass of elements in ecosystems, elemental cycles are coupled through biological processes and structures (Sterner and Elser, 2002; Schlesinger and others, 2011), and this coupling can have a large influence on ecosystem function (Sistla and Schimel, 2012; Cohen and others, 2013). To date, few studies have examined patterns of OM stoichiometry at aggregated community and ecosystem-levels (but see Frost and others, 2012; Cohen and others, 2013; Teurlincx and others, 2017), leaving a significant knowledge gap regarding the range of stoichiometric variation among ecosystems and the environmental and ecological drivers. From a biological perspective, three basic processes can influence

variation in aggregate stoichiometry: (1) the gain or loss of stoichiometrically-distinct species, (2) changes in the relative abundance of species, and (3) stoichiometric flexibility within individual species. Each of these processes operate concurrently and likely have important implications for ecosystem functions (Sistla and Schimel, 2012).

Shifts in community composition through the gain or loss of species, as well as changes in species relative abundance, can have important implications for ecosystem stoichiometry because variation in elemental composition among species is large (Duarte, 1992; Townsend and others, 2008). Such variation is tied to the physiological and morphological traits of organisms (e.g. Elser and others, 1996; Woods and others, 2003; Meunier and others, 2017), and these traits relate directly to their performance along environmental and ecological gradients. For example, low nutrient availability may favor taxa that can convert nutrients into biomass efficiently (Tilman, 1982), thereby leading to elevated C:nutrient ratios in ecosystem biomass pools (i.e. nutrient use efficiency [NUE] sensu Vitousek, 1982). In contrast, short growing seasons and frequent disturbances can select for organisms with rapid growth and development rates (Elser and others, 1996) and/or smaller body sizes (Fisher and others, 1982; Klausmeier and others, 2004), which are often associated with reduced organismal C:nutrient ratios (Elser and others, 2000). These shifts in communities represent one important dimension through which aggregated ecosystem stoichiometry can change along environmental gradients.

A second important mechanism that can influence aggregate biomass stoichiometry is *intra*specific variation in elemental composition. Variation among individuals can arise from flexibility or plasticity in biomass allocation among different

structures, stoichiometric changes during ontogeny, and the extent to which organisms can store elements, each of which varies widely among taxonomic groups (Gusewell, 2004; Persson and others, 2010). While there is some evidence that organismal stoichiometry tends towards balance with nutrient delivery (Redfield, 1958; Chapin, 1980; Sterner and others, 2004), factors beyond nutrient supply may alter the relative allocation of elements within individuals. For example, temperature can systematically influence the cellular allocation of N and P relative to C in many different organisms (Rhee and Gotham, 1981; Woods and others, 2003; Yvon-Durocher and others, 2017). When aggregated across all species within an ecosystem, intraspecific stoichiometric flexibility can be a major contributor to variation among ecosystems (Duarte, 1992). Thus, characterizing this variation is an important step towards understanding broad patterns of stoichiometry across ecosystems.

Although a growing literature demonstrates that temperature can influence ecosystem OM *fluxes* through its control on primary production and respiration (Brown and others, 2004; Allen and others, 2005; Yvon-Durocher and others, 2012; Demars and others, 2016), the effects of temperature on OM *pools* are equivocal and generally not well characterized. Theory and simplified experiments (Brown and others, 2004; Savage, 2004; Bernhardt and others, 2018) predict that higher temperatures should lead to reduced population densities and biomass, but these examples are overly simplistic because they assume resource supply does not covary with temperature (Cross and others, 2015; Thomas and others, 2017). Other theoretical and empirical studies show that temperature may have minimal influence on OM pools (Allen and others, 2005;

Michaletz and others, 2014). Thus, considerable difficulty remains in developing informed predictions about the response of OM pools to temperature. Moreover, the relative importance of temperature, and the extent to which it regulates ecosystem OM mass and stoichiometry, is likely to interact with other environmental factors that shape community composition and stoichiometric traits.

One important factor that may obscure the influence of temperature is physical disturbance, long recognized as a fundamental determinant of ecosystem pattern and process (Pickett and White, 1985). In river ecosystems, water flow can be an important driver of species composition and ecosystem characteristics (Poff, 1997; Allan and Castillo, 2007). Indeed, many stream organisms have evolved specific morphological, physiological, and/or life-history attributes in response to flow regimes (e.g. Resh and others, 1988; Lytle and Poff, 2004). As such, flow may alter patterns of ecosystem OM and stoichiometry by both directly removing OM from the system and through shifts in species composition and traits. For example, a high frequency of flooding can prevent the establishment of larger-bodied primary producers such as bryophytes and macrophytes (e.g., bryophytes and macrophytes; Riis and Biggs, 2003). This shift in average body size may have large consequences for ecosystem biomass and stoichiometry, as body size is an important factor influencing both biomass (Kerkhoff and Enquist, 2006) and nutrient stoichiometry (Woods and others, 2004; Kerkhoff and others, 2005). Thus, any potential influence of temperature on patterns of biomass and stoichiometry must be considered in the context of other environmental variables—such as flow—that shape biological communities and their traits (Meunier and others, 2017).

Here, we examine patterns of ecosystem-level OM, its stoichiometry, and how it is distributed among living and detrital compartments in stream ecosystems. We leverage a 'natural geothermal laboratory' in Iceland (O'Gorman and others, 2014) that contains many small streams along a gradient of temperature and flow characteristics, but with similar chemical composition. Based on previous research demonstrating strong effects of temperature on gross primary production (Demars and others, 2011; Padfield and others, 2017; Hood and others, 2018), we expected that temperature would have primacy in shaping patterns of ecosystem OM and stoichiometry. However, we also expected variation in stream flow could modify, or even override, thermal effects through its influence on OM composition and species traits. We quantify the importance of changes in community composition, relative mass, and stoichiometric variability within OM compartments to ecosystem-level differences among streams. Our study provides a unique assessment of how whole ecosystem OM and stoichiometry emerge through shifts in individual and community-level characteristics across strong environmental gradients.

Methods

Study Area

Our study was conducted in 11 first-order streams near the Hengill geothermal field of southwestern Iceland (64°03´N 021°18´W; Figure S1), a region with high spatial heterogeneity in geothermal activity. Ten of the study streams were located within the Hengladalsá river valley, and one was located in the Hveragerði watershed ~6 km southwest. Geothermal heating of groundwater in this area is indirect (Árnason and others, 1969), resulting in large variation in stream temperatures (mean annual stream

temperature range: 4.5 – 54.0 °C), but similar water solute chemistries (Friberg and others, 2009). These streams also vary in watershed size, position, and the magnitude of surface water influx during precipitation events and snowmelt, leading to variation in stream flow characteristics (see below).

Physicochemical Measurements

We measured a number of stream physicochemical variables to include as possible covariates. We sampled water temperature and stage height across all streams every 15 minutes beginning in July 2010 through July 2016 using Onset U20-001-01 water-level loggers (Onset Computer Corp. Pocasset, MA, U.S.A). To quantify stream flow characteristics, we first estimated stream discharge using stage-discharge relationships based on salt dilution gauging (n = 7 – 13 per stream). These predictive equations were used to construct time-series of hourly discharge in all streams (Gore, 2006), and to derive important aspects of the annual stream flow regime, including; median discharge, maximum discharge, and the coefficient of variation (CV) of stream discharge. In addition, discharge time series were combined with other geomorphological variables to characterize how stream flow may interact with the stream bed and organisms. Geomorphological variables included wetted width, stream slope, and sediment size distributions. Concurrent with stream discharge measurements, wetted width (m) was measured with a meter stick at stream transects spaced every meter along the entire length of each stream reach. Wolman pebble counts were used to calculate sediment size distributions from 100 particles. Briefly, ten random particles were selected from within the stream channel using a step-toe procedure at ten transects evenly spaced

along the length of each stream reach. The intermediate axis of each particle was measured with a metric ruler and recorded. For particles that were too large to remove, the shortest axis accessible was measured.

Water surface slope (m/m) over the length of each stream reach was measured one time using a meter stick and line level. Stream slope was combined with discharge to create a time series of estimated stream power (Ω), a measure of the rate of energy dissipation against the streambed and a proxy for energy available to move sediment (Gordon and others, 2004):

$$\text{Stream power } (\Omega) = 1000 \cdot 9.8 \cdot Q \cdot S \qquad (1)$$

Here, Ω is stream power in Watts, 1000 (kg/m^3) is the density of water, 9.8 (m/s^2) is the acceleration due to gravity, Q is stream discharge (m^3/s), and S is mean channel slope.

Water samples were collected in July 2011, passed through 0.45-µm glass-fiber filters, and analyzed for ammonium-N, nitrate-N, and soluble reactive phosphorus (SRP) concentrations. Ammonium concentrations were measured using the orthophthalaldehyde fluorometric method (Holmes and others, 1999) as modified by Taylor and others (Taylor and others, 2007). Nitrate concentrations were measured using ion chromatography (Dionex ICS 2000; Dionex Corp. Sunnydale, CA, USA) and SRP concentrations were measured using the ascorbic acid method (Murphy and Riley, 1962). Mean nutrient concentrations and daily discharge measurements we used to estimate mean daily flux of nutrients from streams as a measure of nutrient supply (King and others, 2014).

Benthic Organic Matter

We sampled benthic organic matter (BOM) in each stream during August 2012 using a modified core sampler (area = 0.09 m^2, n = 5 per stream). From each core, we sampled both attached and 'loose' OM which we characterized as either 'green' epilithic OM or 'brown' detrital OM. Although the attached compartment was dominated by living primary producers, and the 'loose' category was dominated by benthic detritus (J. R. Junker, *pers. obs.*), each compartment likely contained both living and detrital components. Attached epilithic biomass was sampled by removing biomass from rock surfaces with shears and/or a wire brush. Loose detrital OM was sampled by disturbing the water and top ~10 cm of sediment within the core sampler to suspend and homogenize OM, a subsample of known volume was then quickly removed from the slurry. For both sub-compartments, samples were rinsed into a 1mm sieve to separate coarse (>1mm) and fine (<1mm) fractions. The coarse OM was further split into species or functional group using appropriate identification keys (Stefansson, 1948; Jóhannsson, 2003).Large coarse samples were subsampled (1/2 – 1/8) and the relative mass of each species or functional group was scaled to the total mass of each sample. Total water volume in the sampler was determined by measuring the water depth in three locations within the core sampler and calculating the total volume based on the core sampler dimensions. When subsamples were taken, the ratio of total sample volume to subsample volume was used to estimate total sample detrital OM from the subsample.

Following separation into compartments, OM samples were dried in an oven at 50 °C to a constant mass (>48 hours) and weighed to estimate dry mass (g). Ash-free dry mass (g AFDM) was quantified for compartments by weighing a dried subsample,

combusting the sample in a muffle furnace at 500 °C for four hours, and reweighing. The OM content was calculated as the difference between dry mass and post-combustion mass as a percentage of total initial dry mass. All OM estimates were reported on a per square meter basis.

Elemental Concentration and Stoichiometry of OM

In each stream, we measured carbon (C), nitrogen (N), and phosphorus (P) content of each species or functional group as well as other OM compartments (e.g. fine particulate OM). Subsamples of dried OM were weighed into tin capsules for analysis of %C and %N using a Costech elemental analyzer (Costech Analytical Tech. Inc. Valencia, CA, U.S.A). Acetanilide standards were used as an external standard for C and N analyses (average recovery was 98% and 99% for %C and %N, respectively). Phosphorus content was quantified using persulfate digestion and the ascorbic acid method (APHA [American Public Health Association], 1992). Bovine muscle was used as an external standard for P analysis (average recovery was 97%). Total C, N, and P for each OM compartment was quantified by multiplying the percent nutrient content of each compartment by the compartment dry mass $\cdot$ m^{-2}. Because of the large contribution of inorganic mass in fine fractions, nutrient content was adjusted to OM content (e.g., g $\cdot$ C $\cdot$ $AFDM^{-1}$ versus g $\cdot$ C $\cdot$ bulk dry $mass^{-1}$) to allow comparison of nutrient content of fine OM fractions among streams. Compartment C, N, and P mass was summed across all compartments and standardized to a g $\cdot$ m^{-2} basis to estimate total OM C, N, and P pools in each core. We described OM pools in units of g $\cdot$ C $\cdot$ m^{-2} for compartment- and

ecosystem-level OM. Elemental ratios were calculated on molar basis for OM compartments and total ecosystem OM.

Partitioning Changes in Ecosystem BOM Mass and Stoichiometry

We used a variant of the Price equation (Fox, 2006; Fox and Kerr, 2012) to quantify important contributors to differences in BOM C, N, and P mass and C:N:P stoichiometry among streams. Contributors to these differences included: (1) the gain or loss of OM compartments ("GAIN/LOSS"), (2) changes in the relative biomass of compartments ("REL-BIO"), (3) shifts in elemental concentrations within individual OM compartments ("STOIC-FLEX") and (4) shifts in both relative biomass and stoichiometry within individual OM compartments ("BIO-STOIC-INTR"). Each of these processes relate to components of the Price equation (Fox, 2006), extended to account for elemental ratios (as in Teurlincx and others, 2017). Here, the "GAIN/LOSS" component is analogous to the sum of the 'species richness effect'(SRE) and 'species composition effect' (SCE) in Fox (2006), which is only different from zero if a OM compartment is found in one system but not the other in a pair-wise comparison. If an OM compartment is present in both streams, its total effect on element mass or stoichiometry (e.g., C mass, N mass, C:N ratio) is captured by three other components (referred to in Fox (2006) as the 'context dependent effect'; CDE). This higher-level effect includes three parts, (a) changes in relative biomass ("REL-BIO" here, referred to as CDEn in Fox 2006), (b) changes in compartment stoichiometry ("STOIC-FLEX" here, referred to as CDEp in Fox 2006), and (c) the interaction between changes in relative abundance and stoichiometry. The interaction between relative biomass and stoichiometry ("BIO-

STOIC-INTR" here, referred to as CDEi in Fox 2006), represents an extension of the three biotic processes that can shift ecosystem stoichiometry. Importantly, this interaction has an ecological interpretation that connects OM compartment traits to ecological function. For example, an increase in relative biomass of a compartment that is coupled with decreasing nutrient content (i.e., a negative "BIO-STOIC-INTR" term), can suggest increased efficiency of nutrient use for that OM compartment (Vitousek, 1982).

For each pair-wise stream comparisons in the Price calculations, the 'reference site' represented the stream with the higher total BOM mass. All pair-wise comparisons were used to quantify the importance of each process across all streams. The direction and magnitude of Price components is identical to the change in element mass or molar stoichiometric ratios by that component.

Statistical Analyses

The influence of stream flow on BOM is complex because it includes direct effects of flow OM as well as indirect effects of flow on sediment movement. We therefore selected a set of variables that capture both basic characteristics of the flow environment and proxies of flow-sediment interactions. Some of these variables were correlated with one another, but together these helped to capture the complex ways that flow may influence BOM. To account for correlation of flow variables, we used a principal components analysis (PCA) to compress stream flow variables into fewer, orthogonal axes. PCA axes were then used to represent the influence of stream flow on patterns of BOM mass, composition, and stoichiometry. Variables included in the PCA

were: median discharge, median velocity, discharge CV, channel slope, maximum power, and median substrate size.

We expected that variables related to both temperature and stream flow would influence BOM mass, composition, and stoichiometry in complex and potentially interacting ways. Thus, we used a model selection framework using Akaike's Information Criterion adjusted for small data sets (AICc; Burnham and Anderson, 2002) to select among models explaining BOM characteristics. When necessary, response variables were transformed to meet model assumptions. Exploratory plots and residual variation of linear models were examined to identify potential nonlinear relationships between explanatory and response variables.

To characterize and compare the BOM pool composition among streams, we conducted non-metric multidimensional scaling (NMDS) analysis using the vegan package (Oksanen and others, 2016) in R (R Core Team, 2016). Differences among stream BOM composition were then assessed with a permutational multivariate analysis of variance on distance matrices using the adonis() function in the vegan package. We fitted environmental vectors onto the NMDS ordination using the envfit() function in vegan to examine which environmental variables may help explain variation in OM composition.

Relationships between ecosystem BOM C, N, and P pools were assessed using reduced major axis regression with the lmodel2 package in R (Legendre, 2018). Reduced major axis regression accounts for variability in both explanatory and response variables

rather than the response variables alone. The calculation of Price equation components was conducted in R using modified code from Teurlincx and others (2017).

Results

Stream Physicochemical Variables

The study streams exhibited wide variation in mean annual temperature, ranging from 4.8 to 27.2 °C (Table 2.1). Streams also varied with respect to hydrologic and geomorphological variables (Table 2.1; Figure S2.1). Dissolved nutrient concentrations were relatively low and similar among streams, ranging from 0.003 to 0.026 mg L^{-1} inorganic nitrogen (NO^{3-} + NH^{4+}) and 0.007 to 0.033 mg L^{-1} soluble reactive phosphorus (SRP; Table 2.1). Dissolved molar N:P ratios ranged from 0.2:1 to 4.4:1 (Table 2.1), markedly lower than the Redfield ratio (16:1, Redfield, 1958) suggesting high potential for nitrogen limitation in these streams (also see Friberg and others, 2009). Physicochemical variables showed relatively little association with temperature, except for SRP which was positively associated with temperature (|Spearman's ρ| = 0.02 – 0.67; Table S2.1).

Principal components analysis showed that 73% of the variation in flow characteristics was captured in the first two component axes (Figure S2.1). Principal component axes one (PC1) and two (PC2) showed little to modest association with temperature (Spearman's ρ = 0.43 and -0.05, respectively; Table S2.1), but variability around these correlation coefficients overlapped with zero.

Patterns of BOM and their Relation to Environmental Variables

Total BOM mass varied two orders of magnitude among streams (from 2.0 to 209.5 g C m^{-2}; Figure 2.1A). Although BOM mass was positively associated with temperature (Spearman's $\rho = 0.34$; Figure 2.2A), associations with flow variables were stronger (Spearman's $\rho = 0.45$ & 0.61 for PC1 and PC2; Figure 2.2B and 2.2C). Model selection showed that the flow-only (PC1+PC2) model had the most support, while the temperature-only and more complex additive and interactive models showed large increases in AICc scores (ΔAICc > 2; Table 2.2) relative to the top model. After accounting for the effects of flow (Figure 2.2E and 2.2F), mean temperature had little association with total BOM mass ($r^2 = 0.04$, Figure 2.2D).

Stream BOM Composition and its Relationships with Environmental Variables

Stream BOM composition varied among streams (PERMANOVA; $P = < 0.001$; $r^2 = 0.59$) and was generally characterized by two categories: (1) streams with relatively large-bodied communities of macrophytes, bryophytes, and colonial microbial groups, and (2) those lacking such large-bodied taxa and dominated by biofilms and detrital pools (Figure 2.1A; Figure S2.2). Of streams with large-bodied species, the bryophyte *Fontinalis antipyretica* was the most common (Figure 2.1A). Other larger bodied and colonial microbial compartments included the liverwort *Jungermannia exsertifolia*, macrophytes of the genus *Callitriche spp., Veronica sp.,* a few emergent plant species such as *Equisteum sp.*, filamentous green algae, and the cyanobacteria group *Nostoc spp.* (also see Gudmundsdottir and others, 2011).

Total BOM mass among streams was associated with the relative proportions of living epilithic and detrital pools (Figure 2.3, Figure S2.3). Generally, streams with high OM mass were dominated by larger-bodied producers (e.g. macrophytes and bryophytes) and attached epilithic biomass. In contrast, streams with low BOM mass were dominated by small-bodied producers and detrital pools.

Compartment and Ecosystem-Level Elemental Content and Stoichiometry

Among streams, C, N, and P content, as well as C:N:P stoichiometry of individual OM compartments varied widely and showed differences among compartments with respect to all elemental and stoichiometric measures (MANOVA $P < 0.001$, all ANOVA corrected $P < 0.001$; Figure S2.4). Stoichiometric variation among OM compartments was greatest for C:P (0.91 CV), followed by N:P (0.69 CV) and C:N (0.46 CV; Table S2.2). At the ecosystemllevel, variability in aggregate stoichiometry was much reduced compared to individual OM compartments (*see* Figure 2.1B-D) and CV of aggregate BOM C:N:P stoichiometry across all streams ranged from only 0.35 to 0.37 (Table S2.2).

Measures of BOM C:N:P stoichiometry showed relationships to isolated aspects of flow characteristics (PC1; Tables S2.3 and S2.4), but temperature was not an important driver for aggregate C:N or C:P ratios (Tables S2.3 and S2.4). In addition, flow characteristics were more strongly associated with BOM C:N and C:P ratios than dissolved nutrient availability (Table S2.3 and S2.4). With increasing BOM, the relative concentration of both N and P showed similar dilution, reflected in similar scaling exponents that were less than one (Figure 2.4A). When examined according to broad OM categories, nutrient dilution was only evident in ‘green’ epilithic biomass (C:N scaling

exponent (mean [95%CI lower–95%CI upper]) = 0.89 [0.84–0.94]; C:P scaling exponent = 0.82 [0.75–0.90]; Figure 2.4B). In contrast, nutrient concentrations in 'brown' detrital OM pools scaled with exponents near one suggesting isometric scaling of nutrient pools with C (C:N scaling exponent = 0.98 [0.90–1.07]; C:P scaling exponent = 1.1 [0.97–1.24]; Figure 2.4C). Thus, dilution BOM mass was likely due to a shift towards dominance of epilithic OM pools. As epilithic biomass became a larger proportion of total BOM pools, both C:N and C:P ratios of total BOM pool increased (BOM C:N r^2 = 0.37, P = 0.03; BOM C:P r^2 = 0.65, P = 0.002).

Relationships Between N:P Supply and
Ecosystem BOM N:P

BOM N:P showed little association with flow characteristics but was associated with dissolved nutrient availability (Table S2.5). Ecosystem BOM N:P appeared to track variation in N:P supply (r^2 = 0.47; P = 0.01; Figure 2.5 inset). Much of this variation was attributed to the concentration of DIN (r^2 = 0.47; P = 0.01), rather than SRP (r^2 = 0.02; P = 0.70). However, this relationship was dependent on a single stream (Figure 2.5 inset). When we removed this stream from the linear model analysis, the relationship between dissolved N:P and BOM N:P was much weaker (r^2 = -0.08, P = 0.62, slope = 0.62, 95% CI: -2.1 – 3.3). Ecosystem BOM P concentration showed a slight dilution relative to N pools at higher standing OM, but the slope was not significantly different from isometric scaling (Figure 2.5; N:P scaling exponent = 0.91 ± 0.09 SE; testing slope against 1.0; P = 0.16). Lastly, positive imbalances in BOM N:P relative to DIN:SRP (i.e., higher position of data vs. the 1:1 line, Figure 5 inset) demonstrated that all streams accumulated more N

relative to P based on nutrient delivery, with imbalances ranging from 2.5 to 11.9 (mean 7.6 ± 2.5 SD; Figure 2.5 inset).

Partitioning the Effects of BOM Composition, Compartment Relative Biomass, and Compartment Stoichiometry on Total BOM Mass and Stoichiometry

Contributors to changes in BOM elemental mass and stoichiometry varied widely when comparing streams (Table 2.3, Figure S2.5). Generally, inter-stream differences in total BOM mass (g C m^{-2}) were influenced by changes in the relative mass of OM compartments ("REL-BIO"), which had a median impact of ca. -18 g C m^{-2} (-17.6 ± 18; median ± median absolute deviation). Changes in C concentration ("STOIC-FLEX") and concurrent changes in relative mass and C concentration ("BIO-STOIC-INTR") had minimal impact on total BOM mass (-0.6 ± 9.5 and -0.4 ± 7.5, respectively). In contrast, ecosystem C:N:P stoichiometry was generally not influenced by the aggregate loss and gain of OM compartments, but more by the effects of shifting stoichiometry (Table 2.3, Figure S2.5) which had a median effect of decreasing C:N:P nutrient ratios (C:N = -15.9 ± 12.8; C:P = -161 ± 103; N:P = -5.2 ± 5.8).

Discussion

We quantified patterns of BOM mass, composition, and stoichiometry across large gradients of stream temperature and flow. We found that the influence of stream flow was more important for explaining patterns in BOM mass, composition, and stoichiometry compared to temperature. We attribute the stronger impact of stream flow to shifting dominance from large-bodied macrophytes towards biofilm- and detritus-

dominated communities with changes in stream flow characteristics. Despite wide variation in the stoichiometry of OM components, aggregate BOM stoichiometry was much less variable. While we observed large and systematic variation in BOM C:N and C:P ratios related to the distribution of OM, we found evidence for constrained BOM N:P which consistently accumulated N relative to P. Further, inter-stream differences in BOM mass were driven by shifts in the relative abundance of OM components, while differences in stoichiometry arose through concurrent shifts in species relative abundance and stoichiometry. Our study provides one of few explorations of how stoichiometry emerges at the community/ecosystem-level through multiple processes. This work demonstrates the importance of environmental context—i.e. stream flow—in predicting the impact of warming temperatures on the processing of energy and elements within ecosystems.

Temperature has long been recognized as a fundamental driver of ecosystem patterns and processes (Arrhenius, 1889), regulating organism metabolic rate (Gillooly, 2001), species ranges and distributions (e.g., Vannote and Sweeney, 1980), and species traits (e.g., nutrient content; Rhee and Gotham, 1981). Across the large thermal gradient at Hengill, we found that temperature had a relatively small influence on BOM mass and stoichiometry. This was surprising given previous work demonstrating strong relationships between temperature and stream primary production in these streams (Demars and others, 2011) and globally (Demars and others, 2016). While these studies clearly show that the rates of fluxes to stream BOM increase with temperature, BOM pool size is ultimately controlled by the relative difference between inputs (i.e. gross

primary production, upstream and allochthonous inputs) and outputs (i.e. autotrophic and heterotrophic respiration, export from stream flow) over relevant time scales. In ecosystems lacking large external inputs of OM, such as the streams studied here, whole ecosystem primary production and respiration are expected to scale similarly with temperature (Yvon-Durocher and others, 2012; Demars and others, 2016). This suggests that other biotic and abiotic processes (e.g., stream flow) likely play a larger role in determining total OM pools in our study ecosystems.

We found that flow characteristics were relatively important in explaining patterns of total BOM mass. Flow is a primary driver of ecosystem pattern and process in stream ecosystems, and organisms exhibit a number of behavioral, morphological, and life history adaptations in response to variation in flow regimes (e.g. Lytle and Poff, 2004). Previous studies suggest that variability in flow may be important in determining the size of BOM pools through several processes. First, higher frequencies and magnitude of stream flooding, one characteristic captured in our analysis, can inhibit the establishment of larger-bodied macrophyte and bryophyte species (Riis and Biggs, 2003). We found general agreement with this pattern, as flow variables were a significant determinant of BOM composition across streams. Discharge variability *per se* (CV_Q) was also a moderate determinant of BOM composition and showed negative associations with total BOM mass (Figure 2) and the relative abundance of the bryophyte *Fontinalis antipyretica* (Figure S3). Community shifts towards a larger mean organism size are expected to increase standing biomass, but reduce rates of biomass turnover (Brown and others, 2004). Further, aquatic macrophyte and bryophyte species, through their relatively

larger body size and increased structural tissues, generally have lower nutrient content and higher C:nutrient ratios (Duarte, 1992), key determinants of OM decomposition in aquatic ecosystems (Webster and Benfield, 1986). Therefore, in the absence of physical removal from high flows, shifts to larger bodied organisms may also alter the chemical properties and breakdown rates of OM entering detrital pools, leading to accrual of detritus. Thus, disturbance may be critical in setting bounds on BOM storage, as well as, mediating stream ecosystem processes such as fluxes of energy and materials (Schramski and others, 2015).

We anticipated two potential outcomes with respect to how temperature could influence the relative balance of carbon and nutrients in ecosystem-level BOM. First, based on previous experiments in these Icelandic streams (Hood and others, 2018) and elsewhere (De Senerpont Domis and others, 2014), we predicted that warmer temperatures could lead to elevated C:nutrient ratios in response to elevated primary production (O'Gorman and others, 2012; Demars and others, 2016) in combination with no change in dissolved nutrient delivery. In essence, an increase in nutrient use efficiency (Vitousek, 1982) across the thermal gradient. Alternatively, if temperature favored nitrogen-fixing taxa, as reported in mesocosm experiments in the system (Welter and others, 2015; Williamson and others, 2016), we expected elevated N flux to biomass in warm streams, leading to no change in mass-weighted C:N ratios. In the ‘acclimated’ systems studied here, any potential change in C:N ratios with warming was overridden by stream flow-mediated shifts in the distribution of OM between epilithic and detrital pools. We attributed the relationship between flow characteristics and BOM C:N and C:P

to plant community shifts from larger-bodied, lower nutrient content, macrophyte and bryophyte species to smaller, lower C:nutrient microbial communities (i.e. diatoms, filamentous algae, cyanobacteria). The shift to smaller organisms at higher temperatures is a well-established pattern within ectothermic organisms (Atkinson, 1994); however, community processes can override established intraspecific patterns leading to idiosyncratic community responses to warming as recently observed in invertebrate communities following ecosystem warming (Nelson and others, 2017). The contrasting findings between short-term warming responses within a stream and the landscape patterns we observed highlights the importance of stream disturbance as a primary moderator of stream ecosystem structure and function (Poff and others, 1997). As stream ecosystems continue to warm in the future, it will be crucial to understand how predicted changes in precipitation and flow regimes overlay changes in temperature to interactively regulate how streams store and process energy and elements.

The basic concept of an "ecosystem stoichiometry" faces a number of practical and definitional difficulties. On one hand, ecosystem stoichiometry can be defined as the 'chemical structure of an ecosystem" (Golley and Richardson, 1977), including largely biologically unavailable pools (e.g., air rock minerals, etc.). However, recent conceptualizations have limited its scope, drawing on concepts such as consumer-resource stoichiometric imbalances and differences in nutrient supply versus demand at the ecosystem-level (Schade and others, 2005). Here, we built on this analogy employing static comparisons of elemental ratios of aggregate OM of an ecosystem to nutrient delivery. While this approach has similar shortcomings as static vs. dynamic models of

consumer–resource imbalances ((e.g. raw imbalances vs. threshold elemental ratios; Sterner and Hessen, 1994), these comparisons have been integral in advancing stoichiometric theory (e.g., Redfield, 1958). Across all streams, BOM accumulated more N relative to P when compared to the N:P of dissolved nutrients. Considering the extremely low dissolved N:P ratios (0.2 – 4.4 N:P) and high likelihood of N-limitation in all streams, the larger accumulation of N vs P in BOM is not surprising. However, the mechanisms by which one element can accumulate relative to another may highlight the relative importance of different temperature-dependent processes and the ultimate response of ecosystems to changing temperatures. The accumulation of one element relative to another can arise through two mechanisms: (1) differential uptake and recycling of N relative to P by biota and/or (2) additional inputs of inorganic N not captured in dissolved pools, such as biological nitrogen fixation. Recent work in marine environments suggests that the temperature dependence of enzymatic activities may lead to increased N:P ratio recycled through microbial decomposition by as much as 1% per °C (Ayo and others, 2017). Although the generality of this relationship across systems is unclear, if it holds, it could translate to a ~20% increase in the N:P ratio recycled across streams in our study. In systems where elemental pools are at equilibrium, the inputs of N and P must equal the outputs of N and P and other studies in these streams have supported that steady state assumptions are justified during the timeframe of our study (late summer; see supplemental materials in Demars and others, 2016). Assuming steady state of stream BOM, an increased N:P of recycling with temperature would suggest either a decreasing imbalance between dissolved N:P and BOM N:P and/or an increase in

BOM N:P at higher temperatures, none of which we observed. On the other hand, nitrogen fixation was increasingly important in supporting primary production at higher temperatures in previous mesocosm studies in these systems (Welter and others, 2015; Williamson and others, 2016). However, inputs of N through N fixation directly enter biomass and can only influence dissolved pools following mineralization. Therefore, we speculate that the lack of relationship between temperature and dissolved N:P and BOM N:P suggests N fixation may be important in explaining the decoupling of BOM N:P from dissolved N:P and meeting biomass N demands.

Despite large among-stream differences in temperature, flow variability, BOM mass, and OM composition, BOM N vs. P scaling was near isometric and, when we removed a single outlier was not influenced by the N:P ratio of nutrient delivery. Other studies that have examined the balance of N:P in ecosystem components and whole ecosystems have, to varying extents, shown similarly conserved scaling of N:P across a range of organisms and ecosystems (Redfield, 1958; McGroddy and others, 2004; Reich and Oleksyn, 2004; Cleveland and Liptzin, 2007; Sinsabaugh and others, 2009). Yet, few have explored these patterns in benthic systems (but see Farrell and others, 2018) and even fewer have extended these patterns beyond a few OM compartments (e.g. leaves, litter, soil microbial biomass; but see Schade and others, 2005; Cohen and others, 2013). While organisms vary in the extent to which their internal stoichiometry can shift in response to variation in nutrient delivery (Persson and others, 2010), ecosystem OM, with diverse living and non-living biomass compartments, may exhibit larger flexibility in balancing nutrient supply and demand across environmental gradients (Schade and

others, 2005). Nonetheless, many questions remain about the balance of nutrient supply and demand in ecosystems, the conditions that cause supply and demand to deviate, and how stoichiometric balance/imbalance relates to other ecosystem processes (Cardinale and others, 2009)

The conceptualization of ecosystem stoichiometry as the imbalance between resource supply and aggregate ecosystem biomass allows for a much more operational framework, however, this conceptualization obscures processes that underpin much of community ecology, such as shifts in the relative abundance and traits (e.g., nutrient content) among species competing over limited resource pools and along environmental gradient. These processes operate in a complex milieu to influence the aggregate stoichiometry of ecosystem BOM, however, stoichiometric concepts have been slow to integrate into community ecology (Moe and others, 2005), with the exception of Tilman's R* concept (Tilman, 1982). Yet, understanding the relative role of these community processes and integrating them into ecosystem concepts is increasingly important in the age of a 'no-analog' ecology (Williams and Jackson, 2007). Our approach extends upon the concept of ecosystem stoichiometry to quantify the role of broad-scale community processes in shifting stoichiometry of ecosystem BOM among systems. The stoichiometry of ecosystem BOM can change through three processes: the gain and loss of BOM compartments, shifting relative mass of compartments, and flexibility in the stoichiometry of biomass compartments. Previous analyses of community stoichiometry in response to lake shoreline development (Frost and others, 2012) and shifting light and nutrient gradients (Teurlincx and others, 2017) revealed that shifts in community-level

patterns were largely driven by changes in the relative abundance of species rather than stoichiometric changes within species. We found, on average, that stoichiometric plasticity and the concurrent shifts in both the relative mass and stoichiometry were most important in driving general patterns of C:N:P stoichiometry, suggesting potential stoichiometric underpinnings of the changes in BOM composition. The communities studied by Frost and colleagues (2012) and Teurlincx (2017) and colleagues were composed of lake macrophyte and zooplankton species, taxonomic groups that show relatively fixed nutrient stoichiometry compared to other organisms (i.e. macrophytes; Demars and Edwards, 2007; zooplankton; Persson and others, 2010). In contrast, we measured changes in the relative mass and nutrient stoichiometry across diverse OM compartments including distinct macrophyte and bryophyte species, as well as detrital/microbial conglomerates such as coarse and fine BOM and filamentous algal mats. Thus, our results may reflect a sampling artifact when comparing across OM compartments at different taxonomic resolutions. However, they may also represent explicit covariance between compartment stoichiometry and biomass, resulting from, for example, shifts in nutrient use efficiency (C:nutrient ratios) associated with increasing biomass accumulation.

Predicting the effects of warming on ecosystems requires understanding how OM distribution and species traits (e.g. stoichiometry, body size) shift with increasing temperature and other environmental variables. We found, surprisingly, that flow characteristics showed primacy in determining OM mass and stoichiometric patterns despite a large gradient in stream temperature. Our research demonstrates how changes in

OM pools arise largely through changes in the relative mass of biomass compartments, but the stoichiometric coupling of nutrients in ecosystems is further modified by stoichiometric flexibility and its interaction with patterns of relative mass within OM compartments. These patterns underlie the complex processes that operate to determine the coupling of energy and elements in ecosystems. As ecosystems warm, understanding how changing temperature regimes overlay current and future flow regimes and the associated community changes is crucial to predicting patterns of OM, element storage, and coupled biogeochemical cycles within stream ecosystems.

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Table 2.1. Physical and chemical characteristics of the study streams. Temperature and discharge represent the mean annual values. CV_Q is the coefficient of variation in stream discharge.

Stream	Temperature (°C)	Median Discharge (L/s)	CV_Q	Substrate (D_{50})	Slope (cm/m)	DIN (NO_3^- + NH_4^+mg L^{-1})	SRP (SRP mg L^{-1})	DIN:SRP (molar)
hver	27.4	21.0	0.99	11.6	1.0	0.007	0.022	0.7
st8	20.5	23.1	0.12	40.3	14.5	0.006	0.030	0.4
st6	17.5	13.7	0.44	47.0	6.9	0.026	0.029	2.0
st5	15.9	22.7	0.17	21.0	3.0	0.009	0.028	0.7
st9	11.0	3.0	1.06	30.0	14.7	0.003	0.033	0.2
st1	10.7	36.4	0.40	4.0	1.8	0.006	0.007	2.0
st11U	7.4	6.6	0.98	18.0	5.5	0.004	0.016	0.6
st13	5.7	14.6	0.11	5.0	2.9	0.006	0.012	1.1
st11L	5.2	16.8	1.41	45.0	5.7	0.004	0.021	0.4
st14	4.8	12.5	2.31	39.5	4.2	0.025	0.013	4.4
st17	4.8	117.8	1.21	22.0	0.6	0.006	0.010	1.3

Table 2.2. Model selection with Akaike's Information criteria corrected for small sampled sizes (AICc) of drivers of ecosystem BOM biomass. K is the number of model terms in each model. ΔAICc represents the change in model AICc from the top model. LL represents the model log likelihood.

Modnames	K	AICc	ΔAICc	ModelLik	AICc wt.	LL	Cum. wt.
Flow	4	23.4	0.00	1.00	0.82	-4.38	0.82
Temp	3	26.8	3.35	0.19	0.15	-8.68	0.97
Flow+Temp	5	30.3	6.89	0.03	0.03	-4.16	1.00
Intercept	2	43.6	20.18	0.00	0.00	-20.59	1.00
Flow*Temp	7	47.8	24.38	0.00	0.00	1.76	1.00

Table 2.3. Summarized contributions of Price components to inter-stream differences in ecosystem BOM biomass, and C:N:P stoichiometry. The direction and magnitude of Price components represents the change in molar stoichiometric ratios by that component. Price component names have been changed from the convention of Fox (2006) to more clearly describe each component process (see methods). "GAIN/LOSS" represents the influence of biomass compartment gains and losses. For biomass compartments that are shared, their influence on ecosystem biomass and stoichiometry are partitioned into three subcomponents: changes in the relative biomass "REL-BIO", changes in compartment elemental concentration and stoichiometry "STOIC-FLEX", and concurrent changes to both relative biomass and stoichiometry "BIO-STOIC-INTR".

	C		CN		CP		NP	
	mean ± 1sd	median ± 1mad	mean ± 1sd	median ± 1mad	mean ± 1sd	median ± 1mad	mean ± 1sd	median ± 1mad
GAIN/LOSS	-22.8 ± 38.5	-9.7 ± 14.9	16.1 ± 62.6	2.5 ± 18.3	71.5 ± 244.1	-15.7 ± 149.3	-2.3 ± 3.7	-2.2 ± 3
REL-BIO	-29.8 ± 37.6	-17.6 ± 18	-25.8 ± 192.6	-3.9 ± 5.5	-132.7 ± 126.8	-111.7 ± 66.6	-5.8 ± 3.1	-5.6 ± 1.6
STOIC-FLEX	1.1 ± 12.8	-0.6 ± 9.5	-8.3 ± 36.9	-15.9 ± 12.8	-100 ± 505.1	-161.3 ± 103.2	-9.8 ± 177.6	-5.2 ± 5.8
BIO-STOIC-INTR	-2 ± 10.3	-0.4 ± 7.5	-7.4 ± 39.6	-12.7 ± 12	-133.3 ± 196.9	-150.9 ± 86.5	-0.4 ± 30.6	-6.7 ± 6

Notes: sd = standard deviation, mad = median absolute deviation

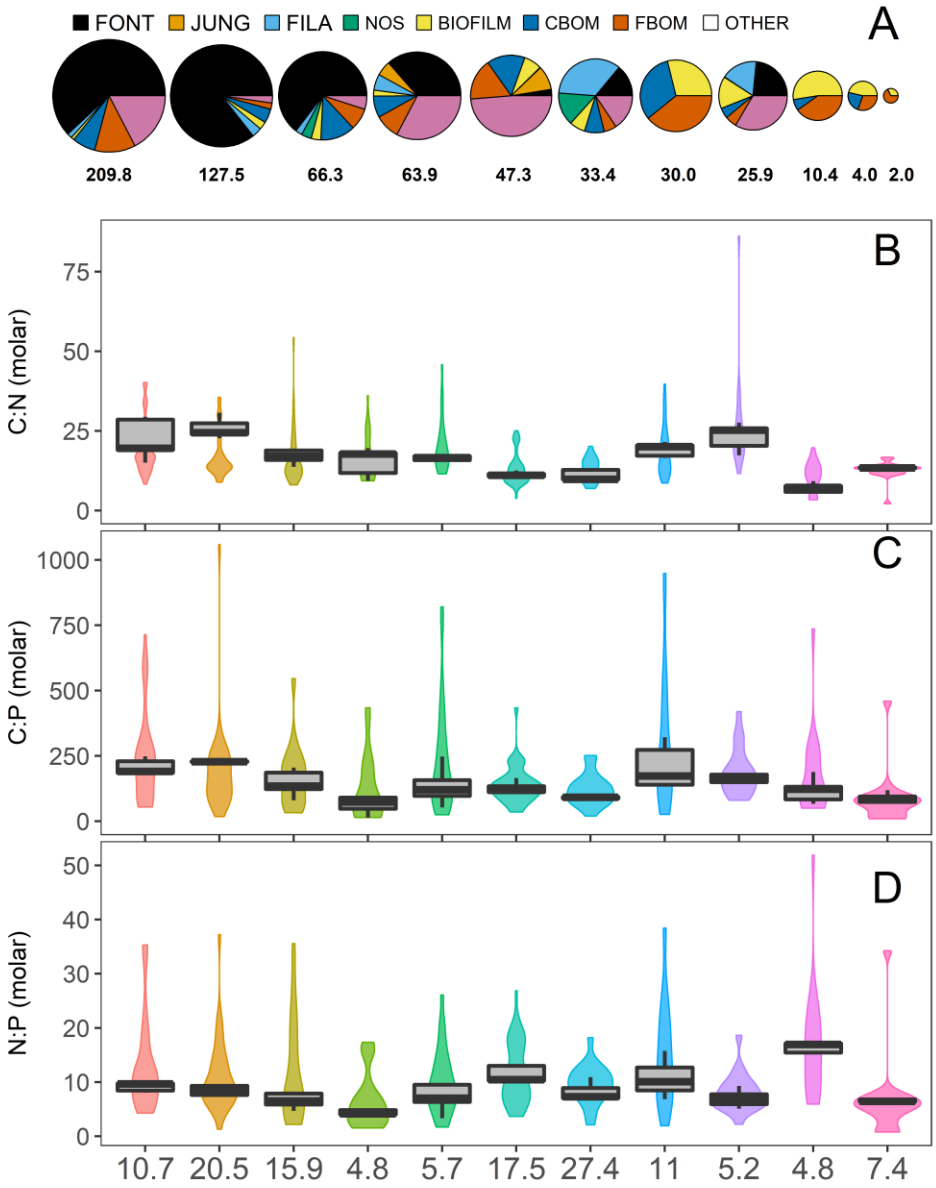

Figure 2.1. Stream ecosystem patterns of (A) total benthic organic matter biomass (BOM) and composition. The size of each pie is scaled to the total BOM biomass in g C m^{-2} (printed below each pie). Organic matter compartment abbreviation are: "FONT" = *Fontinalis antipyretica*, "JUNG" = *Jungermannia exsertifolia*, "FILA" = Filamentous algae, "NOS" = *Nostoc* spp., "BIOFILM" = epilithic biofilm, "CBOM" = coarse benthic organic matter, "FBOM" = fine benthic organic matter, and "OTHER" = other macrophyte and bryophyte species. The distribution of carbon:nitrogen:phosphorus (C:N:P) stoichiometry of aggregate ecosystem BOM (boxplots) and individual biomass compartments (violin plots). Stoichiometry is presented in molar ratios of (B) C:N, (C) C:P, and (D) N:P. Mean annual temperature (°C) of each stream is printed on the x-axis below.

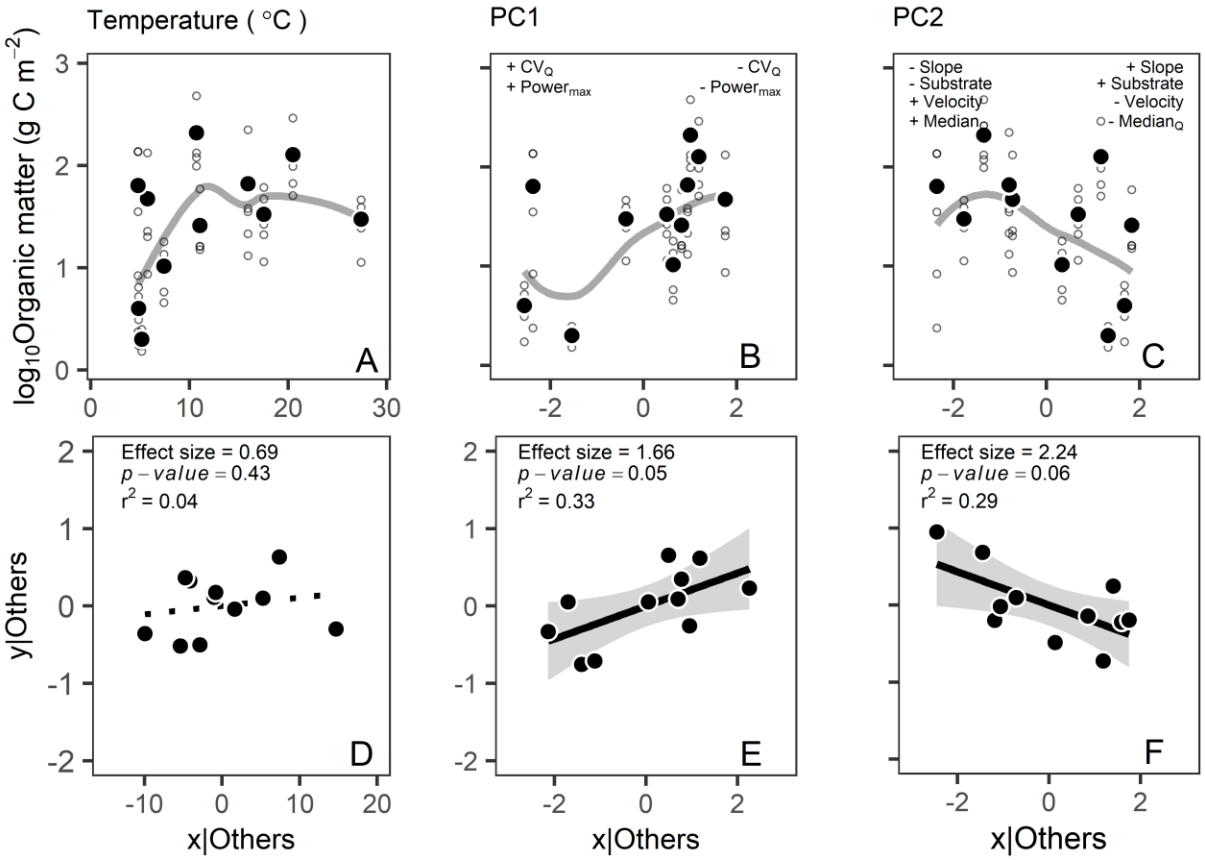

Figure 2.2. Bivariate relationships of $\log_{10}$-transformed benthic organic matter (BOM; g C m^{-2}) and flow principal components one (PC1; panel A) and two (PC2; panel B) and annual mean temperature (°C; panel C). Large filled symbols represent the mean BOM biomass for each stream, while individual samples are shown with small open symbols. Variables most strongly associated with principal component axes ($|r| > 0.40$) are listed on raw principal plots (panels A & B). Added variable plots of each variable were constructed based on the additive multivariate linear regression model: $\log_{10}$(BOM) ~ PC1 + PC2 + Temperature. Added variable plots show the relationship of $\log_{10}$-transformed BOM mass and each explanatory variable (PC1, panel D; PC2, panel E; & Temperature, panel F) while holding the other variables constant.

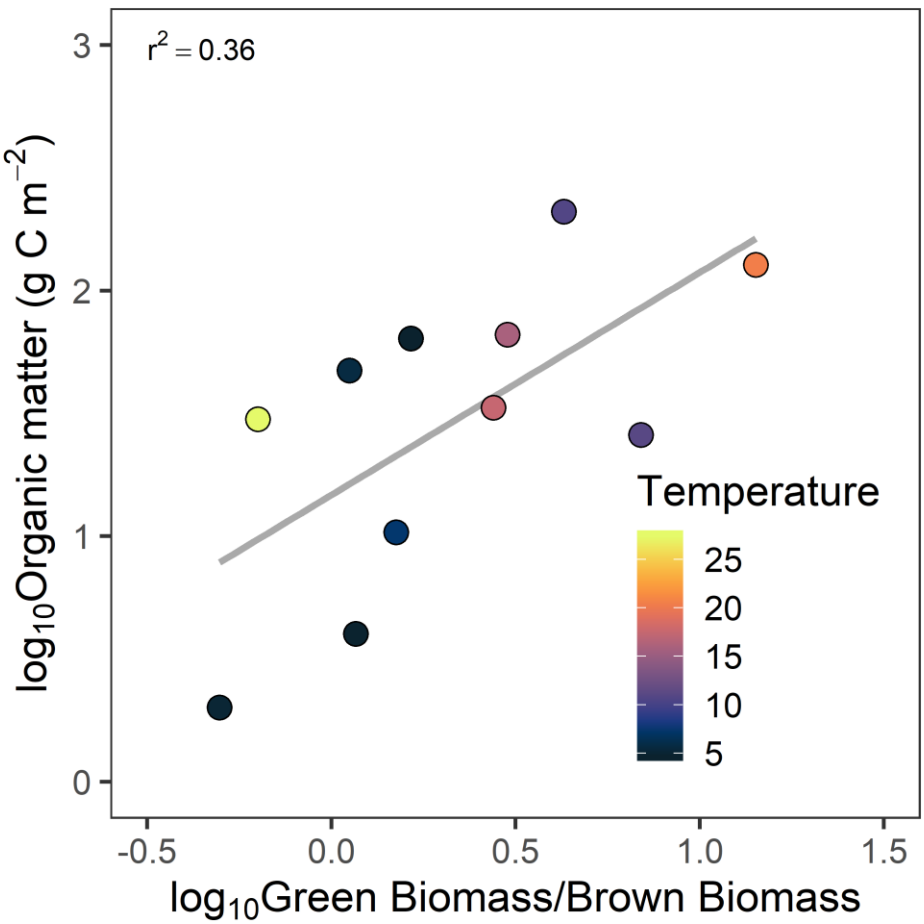

Figure 2.3. Patterns in $\log_{10}$-transformed benthic organic matter biomass compared to the $\log_{10}$-transformed ratio of attached epilithic biomass to detrital biomass (G/B). Annual mean temperature (°C) is represented by the fill color of points.

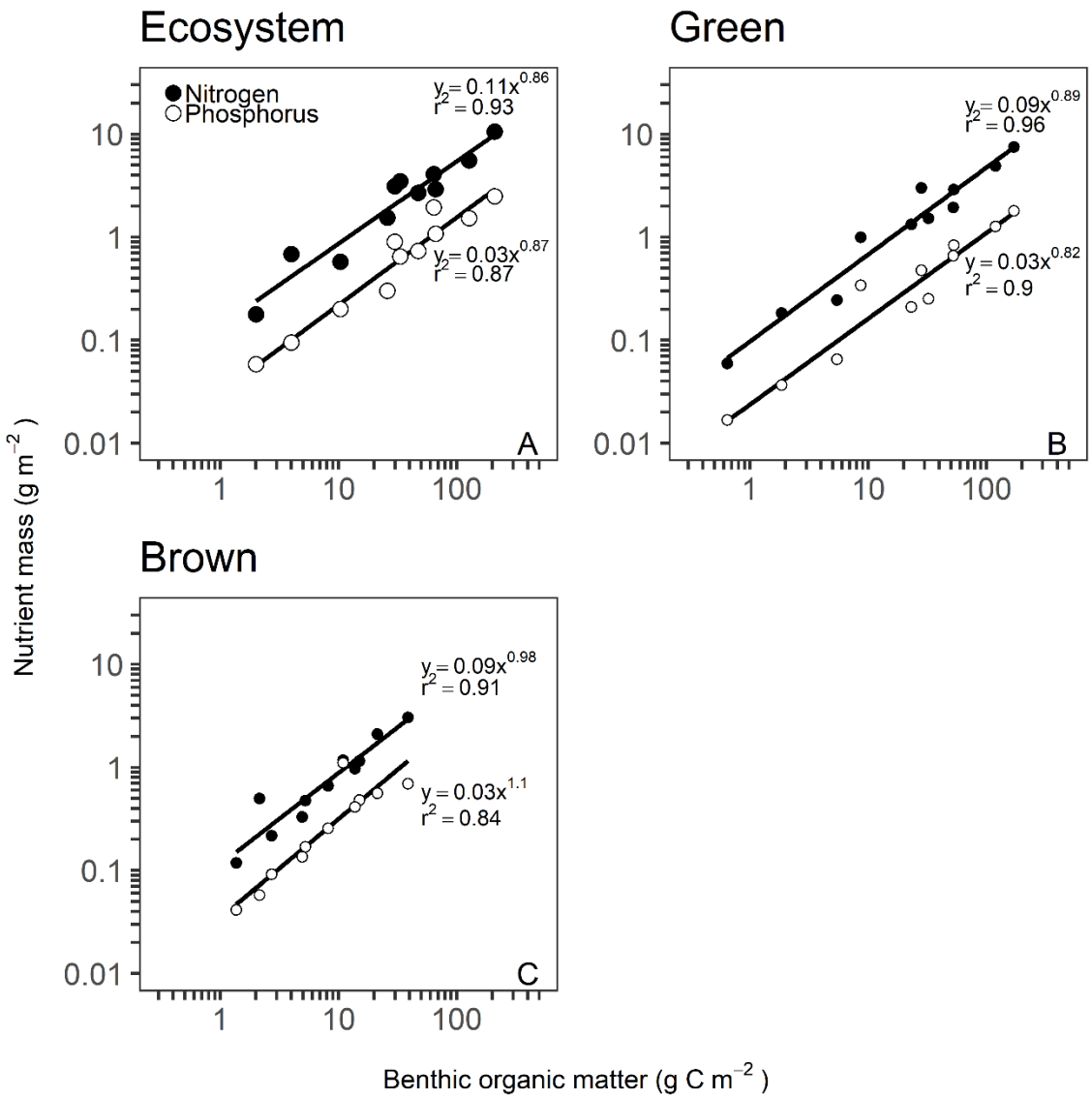

Figure 2.4. The scaling of nitrogen (filled symbols) and phosphorus (open symbols) in ecosystem benthic organic matter (BOM; A) and of attached epilithic biomass (Green; B) and detrital biomass (Brown; C). All scaling relationships were fit with reduced major axis regression on $\log_{10}$-transformed nutrient mass (g m^{-2}) and total BOM (g C m^{-2}).

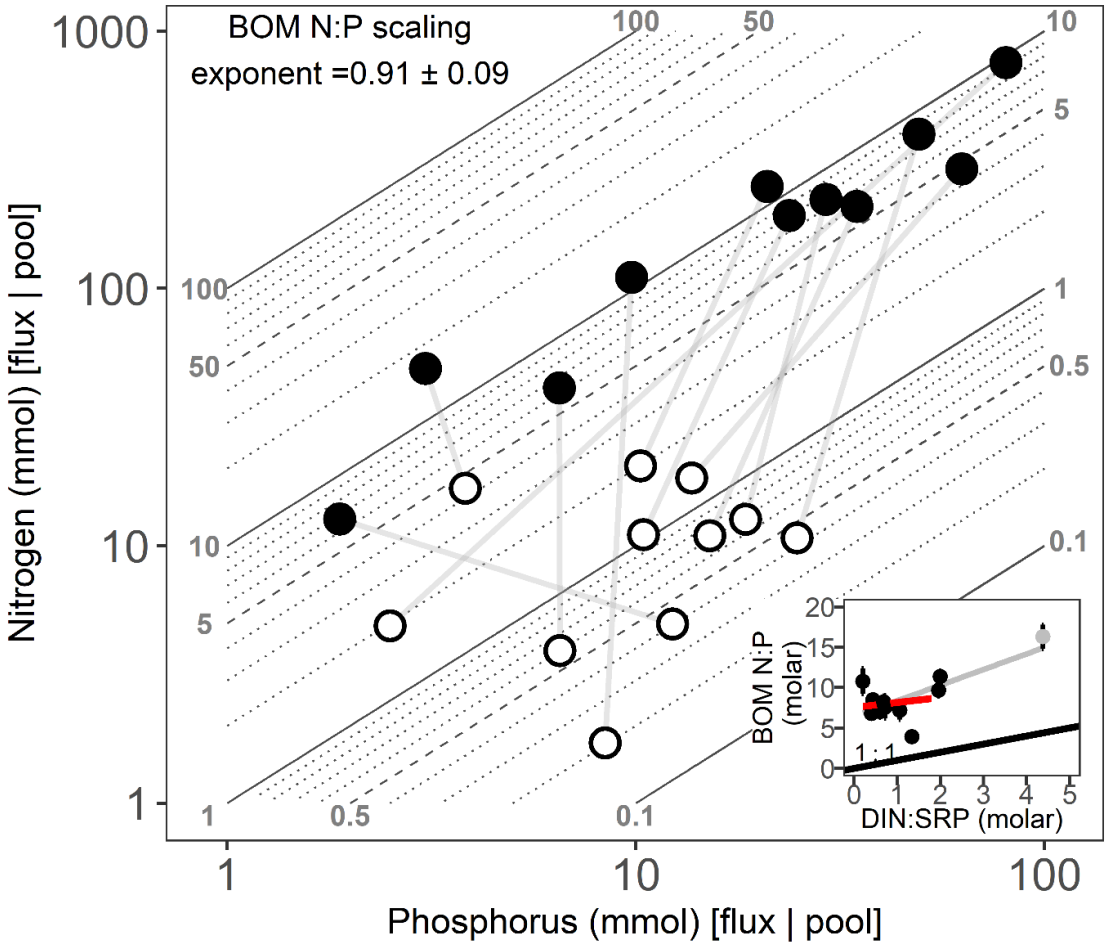

Figure 2.5. Median daily molar dissolved element delivery (mmol m^{-2} d^{-1}; open circles) and benthic organic matter (BOM) elemental standing stock (mmol m^{-2}; closed circles) across all study streams. Grey lines in the main plot window connect the dissolved elemental delivery flux and BOM element standing stock within a stream. Thin black and dashed lines represent stoichiometric isoclines. The inset displays the relationship between molar dissolved DIN:SRP ratios and BOM N:P (mean ± SE), the lower black line is 1:1 and the solid grey line represents the linear relationship between dissolved and BOM N:P. BOM N:P ~ 6.4 (±1.0SE) + 1.94 (±0.62SE) * DIN:SRP with all streams included. When we removed the single outlying stream, the relationship between dissolved N:P and BOM N:P (dashed red line) was indistinguishable from zero with a mean difference of 8.1 in BOM N:P compared to dissolved N:P.

CHAPTER THREE

RESOURCES GOVERN THE TEMPERATURE-DEPENDENCE OF ANIMAL PRODUCTION AT MULTIPLE TIMESCALES

Contribution of Authors and Co-Authors

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Manuscript Information

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Running head: Temperature-dependence of secondary production

Abstract

Increasing global temperatures have motivated a critical need to understand how temperature influences the movement of energy and materials through ecosystems. We used a metabolic scaling framework to quantify the temperature-dependence of animal production and its constituent components standing biomass (*B*) and production:biomass (*P:B*) ratios from individuals to communities and on daily to annual timescales. Leveraging a large natural temperature gradient in streams, we show divergent patterns in the relationship between temperature and animal production from individuals to communities and on daily and annual timescales. The apparent temperature-dependence of animal production was steeper than canonical predictions of the metabolic theory of ecology, driven by differences in light and resource availability within and among streams. Our work addresses important temporal environmental and basal resource dynamics that modify temperature-productivity relationships in ecosystems.

Introduction

Increasing temperatures are influencing patterns and processes in Earth's ecosystems with potentially large consequences for the provision of ecosystem goods and services (Costanza and others, 1997; Montoya and Raffaelli, 2010). Many important services provided by ecosystems (e.g., food and fiber production) are closely tied to the fluxes of energy and materials through trophic networks, including the conversion of solar energy to living biomass by primary producers and the consumption and decomposition of fixed biomass by microbial and animal consumers. Although significant research has focused on how warming influences heterotrophic microbes and their role in energy and material cycling (Allison and others, 2010; Song and others, 2018), less effort has been placed on the roles of animals, perhaps owing to the perception that their influence at the ecosystem-level is less pronounced. Yet, this view is changing (Schmitz and others, 2018), as many studies have demonstrated strong effects of animals on ecosystems (e.g., (Carpenter and others, 1985; Wallace and Webster, 1996; Schmitz and others, 2013), underscoring the need to understand how warming influences energy and material flux through animal communities (Petchey and others, 1999; Brose and others, 2012).

An effective approach for linking animal community structure to ecosystem processes is the quantification of secondary production (Waters, 1969; Waters, 1977; Benke and Huryn, 2010). Broadly, secondary production, or the formation of heterotrophic biomass over time, is an ecosystem flux that incorporates individual and population-level characteristics (e.g., individual size and growth, biomass, reproduction, survivorship) each of which may be influenced by temperature (Benke, 1993; Brown and

others, 2004). Thus, understanding the role of animals in ecosystems, particularly in response to warming, requires understanding how temperature affects these characteristics, as well as how thermal responses scale from individuals (i.e., individual growth and metabolism) to whole communities.

The metabolic theory of ecology (MTE) provides a useful framework for understanding the influence of temperature on animal metabolism and secondary production. This theory focuses on two fundamental drivers of individual metabolic rate—body size and temperature (Brown and others, 2004; Schramski and others, 2015). The effects of body size, M_i (grams), and temperature, T (degrees Kelvin), on individual metabolic rates are described by the equation:

$$I = i_0 M_i^{0.75} e^{-E/kT}, \quad (1)$$

where, I is individual metabolic rate (Watts), i_0 is a taxon-level normalization constant, E represents the mean activation energy of respiratory processes (0.60–0.70 eV K^{-1}; in this formulation, negative values of E correspond to a positive relationship with temperature and vice-versa), and k is the Boltzmann constant (8.62 10^{-5} eV; Gillooly, 2001; Brown and others, 2004). This equation describes the total metabolic energy demands of an organism, including energy required for maintenance, heat loss, tissue synthesis and growth. Assuming a constant proportion of metabolism is directed towards production of somatic and reproductive biomass, this equation may be extended to make predictions about secondary production at higher levels of organization.

In order to move from individual to population-level predictions about secondary production, we must consider two factors, the product of which is population-level secondary production: population biomass (B) and biomass turnover (production to

biomass ratio; *P:B*), as well as how these factors are influenced by mean body size and temperature (Cross and others, 2015). With respect to *B*, the MTE predicts:

$$B \approx [R]\, M^{0.25} e^{E/kT}, \tag{2}$$

where *[R]*, represents a generic term for resource supply. With a fixed resource supply, this equation predicts that total biomass of a population should increase with average body size (i.e., $M^{0.25}$) and decrease with temperature at a slope approximating the activation energy of respiration (i.e. E = 0.60–0.70 eV K^{-1}; Savage and others, 2004).

Population biomass turnover (*P:B*), which is analogous to instantaneous growth rate (Waters, 1977), is predicted by the MTE as:

$$P{:}B \approx M^{-0.25} e^{-E/kT}, \tag{3}$$

where turnover is expected to decline with body size at a negative, but similar slope (i.e. -0.25), and increase with temperature at a positive, but similar slope to that of *B* (i.e., 0.6 – 0.7). Because secondary production is the product of *B* and *P:B*, population-level production is predicted to be both body size- and temperature-independent, assuming fixed resources (Damuth, 1987; Huryn and Benke, 2007; Cross and others, 2015). The predicted temperature-independence of secondary production can be extended from individual populations to the summed production of all populations (i.e. community-level secondary production); however, doing so requires further assumptions (e.g., constant resource quantity and quality, food web structure) that may alter predictions when moving from the population to the community.

One critical assumption underpinning the predicted temperature-independence of secondary production is that of fixed resources (i.e., no change in *[R]*). This assumption is likely violated, both among populations within a community, and for the community as

a whole, at seasonal timescales that are relevant for animal production. For instance, factors that alter the division of resources among species (e.g., interspecific competition) should lead to unequal production among co-existing populations (Taper and Marquet, 1996). Thus, population-level predictions described above are only informative if the resources acquired by each population is known. Yet, when applied to trophic groups or whole communities feeding on a common, fixed resource pool, temperature-independence may still manifest, because any decrease in resource use by a given species is offset by elevated resource use by other species in the community, as long as total resource use by the consumers community is consistent (Van Valen, 1973; Isaac and others, 2012; Padfield and others, 2018a). Further, resources are rarely distributed equally in time and likely covary with changes in light, temperature, and inorganic nutrient availability. Such variation should give rise to large temporal variation in consumer metabolism, biomass, and secondary production (Hill and others, 2010; Junker and Cross, 2014; Huryn and Benstead, 2019), particularly in the context of life history evolution and strong selection for temporal coherence between consumer demands and resource availability (Ross, 1963; Winder and Schindler, 2004). Ultimately, the emergence of temperature-productivity relationships on annual and seasonal timescales hinge on the interplay between variables that constrain the timing (e.g. seasonal resource availability) and potential magnitude (e.g. temperature, resource quality) of consumer production. Thus, resource availability must be considered within the framework of metabolic ecology to realize its utility in predicting responses to warming.

Here, we quantified the apparent temperature-dependence of invertebrate secondary production, from the individual to the community and on daily and annual timescales

across a natural stream temperature gradient (5.0–28.0 °C annual mean temperature) in Iceland. Previous research in these streams has shown a strong positive effect of temperature on primary production, both among streams of different temperatures (Demars and others, 2011) and within streams across seasons (O'Gorman and others, 2012; Hood and others, 2018). Thus, we were aware that predictions based on MTE must account for spatial and temporal variation in the resource base. At the individual-level, we expected that empirically-derived growth rates would follow theoretical expectations for metabolic rates (Brown and others, 2004), given differences in body size and temperature. At the population-level, we had no *a priori* prediction for each population, given the likely interspecific differences in the proportion of total resources used. At the community-level, we expected that secondary production would vary strongly over space and time in response to variation in resources, leading to a steeper apparent temperature-dependence of secondary production, driven by resource limitation during periods of low light availability. However, after accounting variation in resource availability *among* and *within* streams, we predicted that community-level secondary production would exhibit temperature-invariance. Our results demonstrate that seasonality in resource availability governs life histories and the timing of population- and community-level metabolic activity, thus shaping patterns and temperature-dependence of secondary production.

Methods

We studied six headwater streams in the Hengill geothermal field of southwestern Iceland (64°03´N 021°18´W). The Hengill region is characterized by indirect geothermal heating of groundwater (Árnason and others, 1969), which creates spatial heterogeneity

in stream temperatures (4.5–54.0 °C). Importantly, these streams maintain similar water solute chemistries (Friberg and others, 2009), creating a unique natural laboratory to isolate the impacts of temperature on secondary production (Hannesdóttir and others, 2013; O'Gorman and others, 2014; Nelson and others, 2017b). We selected a subset of streams within and near the Hengill watershed to maximize our range of stream temperatures, while minimizing differences in structural aspects of the basal resource community (i.e., minimal biomass of large macrophyte primary producers). In each stream, we measured temperature and stage height every 15 minutes from July 2010 through August 2012 (Onset #U20-001-01 water-level logger, Onset Computer Corp. Pocasset, MA, USA). Over the course of the study, average light availability in the watershed was also measured every 15 minutes from atmospheric stations located within the Hengill watershed (Onset HOBO pendant temperature/light UA-002-64).

Invertebrate community sampling

We sampled macroinvertebrate communities approximately monthly from October 2010 to October 2011 in two streams from a previous study (*see* Nelson and others, 2017b, a) and July 2011 to August 2012 in four other streams. Inter-annual comparisons of primary and secondary production in previous studies showed minimal differences among years in unmanipulated streams suggesting that inclusion of data collected the year prior would not significantly bias our results (Nelson and others, 2017b; Hood and others, 2018). In each study, we collected five replicate Surber samples (0.023 m^{-2}, 250 µm mesh) from randomly-selected locations within each stream reach. Inorganic substrates in the surface ~10cm were disturbed and invertebrates and organic matter were removed with a brush before field preservation with 5% formaldehyde. In the

laboratory, we split samples into coarse (>1mm) and fine (1mm > x >250 µm) fractions using nested metal sieves and then removed invertebrates from each fraction with the aid of a dissecting microscope (10–15x magnification). For particularly large samples, fine fractions were sub-sampled (1/2 – 1/16) using a modified Folsom plankton splitter and invertebrates were removed from subsamples. Subsamples were scaled to the rest of the sample by assuming a similar abundance and body size distribution. Invertebrates were identified to the lowest practical taxonomic level (usually genus) from relevant taxonomic keys (Peterson, 1977; Merritt and others, 2008; Andersen and others, 2013). Body lengths of individuals were measured to the nearest 0.25 mm and body size estimated using length–mass regressions (Benke and others, 1999; O'Gorman and others, 2012; Hannesdóttir and others, 2013). Estimates of taxon-specific abundance and biomass were then scaled to a per meter basis by dividing by the sampler area.

Individual-Level Secondary Production
(Instantaneous Growth Rates)

Growth rates of macroinvertebrate taxa were estimated empirically using multiple approaches. For common taxa (i.e. *Radix balthica*, *Simulium* spp., and dominant Chironomidae species), live individuals (n = 5–15) were collected in the field, separated into relatively small size categories (~1mm range in length), and photographed digitally next to a field micrometer. Individuals were then placed into clear PVC tubes with mesh on both ends (0.5 – 0.25 mm depending on taxa) that had been conditioned in the stream for >7 days. Individuals were removed after 7-15 days and photographed as above. Body lengths were measured from initial and final photographs, using image processing software (ImageJ; Schindelin and others, 2012). Body lengths were converted to mass

(mg ash-free dry mass [AFDM]) using published and calculated length-mass regressions (see sources above). Instantaneous growth rates (g; d^{-1}) were estimated by changes in mean body size divided by the time between initial and final photographs using the following equation:

$$g = \frac{\mathrm{Ln}(W_{t+\Delta t}/W_t)}{\Delta t} \quad (4)$$

For taxa with distinguishable cohorts, we examined temporal changes in size-frequency distributions and calculated growth rates and uncertainty using a bootstrap technique similar to that described in Benke and Huryn (2017). Briefly, size-frequency histograms were visually inspected for distinguishable and directional changes in body size distributions. For each date, size-frequency distributions were resampled with replacement (n = 500) and growth rates between dates were estimated using equation 4 to create vectors of taxon-, body size-, and date-specific growth rates. We prevented calculation of negative growth rates by requiring that body size_{t+1} > body size_t between intervals during resampling.

To estimate growth rates of additional taxa for which we could not measure growth, we developed stream-specific growth equations using multivariate linear regressions that included body size and temperature. These equations independently estimated the effects of temperature and body size on mass-specific growth rates.

Population- and Community-Level Secondary Production

We applied individual estimates of growth to quantify daily population-level production using the instantaneous growth method (Benke and Huryn, 2006). For a given

taxon, daily production of each size class (mg AFDM m^{-2} d^{-1}) was calculated using the empirically-estimated growth rates derived above. To estimate uncertainty, we used a bootstrap technique that resampled instantaneous growth rates, as well as abundance and size distributions from individual Surber samples. For each of 1000 iterations, size-specific growth rates were multiplied by mean interval biomass for each size class and the numbers of days between sampling dates to estimate total size class production for each sampling interval. Size classes were summed for each taxon to calculate total population-level production for each time interval. Within each time interval, bootstrapped vectors were summed across populations to estimate community-level production and divided by the number of days between sampling events to obtain daily production estimates (mg AFDM m^{-2} d^{-1}). For annual estimates, population and community production were summed across all time intervals.

Epilithic Biomass

To quantify potential food resource availability, chlorophyll *a* was quantified on five randomly selected stones on each sampling date. The area of a 35-mm slide mount (8.05 cm^2) was scrubbed with a wire brush into a tray and rinsed into a plastic amber bottle. Subsamples of the epilithic slurry were filtered onto glass-fiber filters (Whatman GF/F; 0.7um pore size) for quantification of chlorophyll *a*. Total chlorophyll *a* was measured on a Turner *Aqua*Fluor fluorometer (Turner designs, Sunnyvale, CA USA) and standardized to a per-meter basis. While chlorophyll *a* biomass represents only a portion total of basal resource availability, previous work has shown that macroinvertebrate diets are dominated by components of epilithon (e.g. diatoms, green algae, and amorphous

detritus) and thus chlorophyll *a* biomass may represent an adequate proxy of spatial and temporal variation in resources available to consumers.

Temperature and Body Size Scaling of
Community Secondary Production, B, and P:B

The 'apparent' temperature-dependence (Anderson-Teixeira and others, 2008) of annual secondary production was estimated by ordinary least squares (OLS) regression of ln-transformed annual secondary production against annual mean Boltzmann-temperature (*1/kT*). To estimate the temperature-dependence of annual community *B* and *P:B*, we corrected for body size differences among communities by first calculating the annual mean body size for each taxon. We then derived an average body size for the whole community weighted by the relative biomass of all taxa within the community (Yvon-Durocher and Allen, 2012; Barneche and others, 2014). Uncorrected invertebrate community *B* or *P:B* was then multiplied by the weighted community body size raised to the predicted body size scaling in equations 1 and 2 (i.e., ± 0.25; Yvon-Durocher and Allen, 2012). Corrected *B* and *P:B* were then ln-transformed and regressed against Boltzmann-temperature to estimate the temperature-dependence of secondary production *among* streams. We used bootstrapping techniques to estimate variability in the temperature-dependence of mean annual community secondary production, *B*, and *P:B*. From the bootstrapped estimates of secondary production, *B*, and *P:B* in each stream (see above), we randomly selected with replacement a single estimate of community production, *B*, or *P:B.* For each of these sets, we calculated the OLS slope coefficient between Boltzmann temperature and community secondary production, *B,* or *P:B*, and then repeated this procedure 10,000 times to create a vector of slope coefficient

estimates. We then estimated the lower and upper 95% confidence bounds as the 2.5% and 97.5% quantiles of these vectors.

Body size corrections to community *B* and *P:B* were repeated for each time interval to calculate the temperature-dependence of community *B* and *P:B* *within* streams. The apparent temperature-dependence of secondary production, *B*, and *P:B* within each stream was estimated using multivariate regression allowing for unique slope and intercepts. We were interested in the slope of the relationships between secondary production, *B*, or *P:B* and Boltzmann-temperature and we thus had no *a priori* predictions about the intercept. As such, we performed all analyses on uncentered Boltzmann-temperature ($1/kT$), rather than centering the data on an arbitrary temperature as in previous studies (Yvon-Durocher and others, 2012; Padfield, 2017).

Responses of Secondary Production to Variation in Resource Availability

Relationships between ln-transformed annual community secondary production and annual chlorophyll *a* biomass were assessed with ordinary least squares (OLS) regression. We predicted resource availability would be an important modifier of patterns of secondary production both within and among streams. True resource availability, i.e., resource *production* (e.g., GPP), is a product of resource biomass and biomass turnover. While we measured a proxy for resource biomass (chlorophyll *a*), we did not directly measure resource turnover or GPP. To explore how resource *production* among and within streams may influence daily secondary production, we constructed a multivariate model that included our proxy of resource biomass (chlorophyll *a*) and another driver of resource turnover—light availability. To quantify the temperature-dependence of

secondary production, after accounting for resource availability, we included Boltzmann temperature in the model. The best model of daily secondary production within and across streams was selected based on model selection with Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002). For all analyses, we use Boltzmann-temperature ($1/kT$) unless otherwise noted for consistency with MTE.

Results

Mean annual stream temperatures ranged from 5.0 to 27.2 °C, and daily mean temperature showed moderate covariation with light availability (Pearson's r = 0.67 – -0.09, mean r = 0.42; Figure 3.1 and Table S3.1 in Supporting Information). Relative temperature differences among streams were generally maintained throughout the year (i.e., stream temperature minima: 0.01 – 9.3 °C, maxima: 12.7 – 35.1 °C; Figure 3.1).

Individual-Level Secondary Production

Instantaneous growth rates of individuals showed relatively large variation but generally followed theoretical expectations with body size and temperature (multivariate regression r^2_{adj} = 0.18; Figure S3.1A & S3.1B). Estimates of scaling coefficients for body size and temperature overlapped values predicted by the MTE (log(body size) = -0.18 [95% CI:-0.25 – -0.12] vs -0.25 predicted and Boltzmann-temperature [$1/kT$] = -0.64 [95% CI:-0.82 – -0.47] vs -0.65 predicted).

Population- and Community-Level Secondary Production

Annual production varied up to eight orders of magnitude among populations within streams (Figure S3.2). The distribution of ranked population secondary production values was most even at moderate temperatures, while the coldest—and especially the warmest—streams showed a steeper decline in ranked production among taxa (Figure S3.2).

Annual community-level secondary production (mg AFDM m^{-2} y^{-1}) was positively associated with mean annual temperature among streams, increasing ~45-fold between the coldest and warmest streams (range: 0.45 – 20.1 g AFDM m^{-2} y^{-1}; Figure 3.2A). The temperature-dependence, i.e., the apparent activation energy, of community production was -0.83 eV (95% CI: -0.94 – -0.73 eV) corresponding to a ~12% increase in mean production for each 1°C increase in stream temperature. Because secondary production is the product of standing biomass (*B*) and biomass turnover (*P:B*), we examined the temperature-dependence of these components independently. Controlling for differences in body size distributions, both *B* and *P:B* ratios exhibited consistent sign (i.e. positive and negative), but steeper temperature-dependence than predicted by MTE (log(*B*) = 0.79 eV [95% CI: 0.65 – 0.95] vs 0.65 and log(*P:B*) = -1.62 eV [95% CI: -1.76 – -1.52] vs -0.65; Table 3.1; Figure 3.2B). Yet, *B* was less sensitive to temperature and more variable than community *P:B* ratios.

Seasonality of Community Secondary Production

We predicted that intra-annual covariation in temperature, light, and resource availability would shape the timing of secondary production and consumer metabolic demand. In support of this prediction, we observed wide temporal variation in daily production within streams (Figure 3.3A). Minimum production ranged from 0.08 – 13.4 mg AFDM m^{-2} d^{-1}, while peak production ranged from 4.3 – 190.0 mg AFDM m^{-2} d^{-1}.

The relationship between temperature and daily community secondary production within streams was generally steeper than the relationship among streams on an annual basis (i.e., colored lines vs. black line in Figure 3.3B). The apparent temperature-dependence of daily secondary production ranged from -6.0 (95% CI: -8.9 – -3.0; stream 7, mean temperature: 5.8 °C) to -1.1 eV (95% CI: -3.0 – 0.8; stream 6, mean temperature: 17.6 °C; mean response among all streams: -2.8 ± 0.8 SE; Figure 3.3B; Table 3.1).

Intra-annual patterns of *B* and *P:B* suggested variation in *B* was much more important in explaining patterns of community production (Figure 3.4A). Mass-corrected *B* showed largely positive relationships with temperature, counter to annual patterns and theoretical expectations. The apparent temperature-dependence of mass-corrected *B* ranged from -4.0 eV (95% CI: -8.9 – -1.0) – 0.1 eV (95% CI: -2.2 – 2.5; mean response -1.9 ± 0.6 SE eV; Figure 3.4A, Table 3.1). In contrast, the relationships between daily community *P:B* ratios and temperature were often weak and variable across streams (Figure 4B), ranging from -1.8 eV (95% CI: -4.3 – 0.6) – 1.4 eV (95% CI: 1.1 – 4.3; mean response -0.3 ± 0.4 SE eV; Figure 3.4B; Table 3.1).

Relationships Between Community Secondary Production, Basal Resource Biomass, and Drivers of Resource Biomass Turnover

Epilithic chlorophyll *a* biomass varied ~180-fold and across streams mean annual chlorophyll *a* biomass was positively associated with mean annual stream temperature (apparent temperature-dependence of chlorophyll *a* biomass: -0.55 eV; 95% CI: -1.22 – -0.11; Figure 3.5A; $r^2 = 0.47$). Annual community secondary production was strongly associated with mean annual chlorophyll *a* biomass ($r^2 = 0.89$; Figure 3.5B). On average, a 10% increase in annual mean chlorophyll *a* biomass corresponded with a ~12.9 % (95% CI: 7.1% – 19.1%) increase in annual secondary production (Figure 3.5B; log-log slope = 1.13; 95% CI: 0.72 – 1.83). Within streams, there was no seasonal relationship between Boltzmann temperature and chlorophyll *a* biomass (Figure 3.5A). Similarly, community secondary production within streams was weakly related to chlorophyll *a* biomass (Figure 3.5B; Table 3.2).

Community secondary production across all sampling periods in all streams was best explained by an additive model that included ln-transformed chlorophyll *a* biomass, ln-transformed light availability, and Boltzmann temperature (Table 3.2). This global model explained ~66% of the variation in daily secondary production among and within streams. After accounting for the effects of resource biomass and light availability, the apparent temperature-dependence of secondary production was -0.80 (95% CI: -1.09 – -0.52; Table S3.2; Figure S3.3). The global model predicted patterns of community secondary production well in all but one stream (i.e., st9), explaining between 14.6 and 83.1% of the within stream variability in secondary production. The estimated 95%

confidence intervals between predicted and actual secondary production overlapped one in all streams and did not overlap zero in all streams except one (i.e., st9).

Discussion

We quantified the temperature-dependence of secondary production from individuals to communities on daily and annual timescales. We aimed to use a metabolic scaling framework to examine how basal resource dynamics *within* and *across* ecosystems alter emergent patterns of animal production across biological levels of organization. We found that while growth rates of individuals followed expected relationships with body size and temperature, these relationships did not scale to patterns predicted by MTE at population- and community-levels. Secondary production among populations within streams varied widely, suggesting variation in the availability and acquisition of basal resources among species (Taper and Marquet, 1996; Isaac and others, 2013). At the community-level, secondary production did not appear to follow predicted temperature-independence at annual or daily timescales. At annual timescales, the covariance between temperature and chlorophyll *a* biomass likely explained the deviation from temperature-independence, as chlorophyll *a* biomass was strongly associated with annual community secondary production (Figure 3.5B). Within a stream, however, chlorophyll *a* biomass was a poor predictor of secondary production. Seasonal variation in light availability and temperature, along with chlorophyll *a* biomass, best explained secondary production within and among streams. Here, low light availability likely reduced basal resource growth rates, which coincided with low consumer community biomass. As light availability increased, consumer biomass also increased leading to a

much steeper relationship between temperature and daily community production *within* most streams. Yet, even after we accounted for the effects of basal resource biomass and light availability, we still observed a positive relationship between secondary production and temperature, an increase that was steeper than the measured temperature-dependence of primary production in these systems (Demars and others, 2016), suggesting deviations from temperature-independence predicted under the MTE.

Metabolic scaling theory has proven a useful framework to link ecosystem structure and function using information on community size structure and ecosystem temperature (Brown and others, 2004; Yvon-Durocher and Allen, 2012; Padfield and others, 2018b). Here, we explored an under-recognized prediction of the metabolic scaling framework, i.e., the temperature-independence of secondary production (Huryn and Benke, 2007; Cross and others, 2015). Predicted temperature-independence of secondary production is an extension of a more widely cited 'rule' of ecology—energy-equivalence (Damuth, 1987)—wherein population energy use and production does not vary systematically among organisms of vastly different body sizes (Ernest and others, 2003). The emergence of temperature-independence of secondary production, similar to energy-equivalence with body size, arises from the opposing relationships between individual energy use and population density with changes in body size or temperature. However, the large range of population-level secondary production values observed here supports recent critiques that the rule of energy- or production-equivalence may not be a useful schema in many cases, at least at the population-level (Isaac and others, 2013). At the community-level, we do find qualitative support for the mechanisms of compensation that underlie energy-equivalence. Specifically, community biomass and rates of biomass

turnover showed opposing patterns across ecosystem temperatures on an annual timescale. Similar qualitative patterns have been observed in planktonic communities within experimentally-warmed mesocosms (Padfield and others, 2018a) and in stream macroinvertebrate communities (Nelson and others, 2017b). However, our multi-stream survey highlights important differences in how patterns of, and deviations from, predicted production-equivalence emerge *among* and *within* ecosystems through spatial and temporal dynamics of basal resources.

Resource availability is an important determinant of production of higher trophic levels (Cyr and Pace, 1993). We presented multiple lines of evidence supporting the prediction that seasonal and interstream differences in resource availability modify consumer production. Namely, community secondary production showed positive relationships with both epilithic chlorophyll *a* biomass and light availability (Table 3.2 & Figure S3.3). While chlorophyll *a* biomass on epilithic surfaces is a rough and incomplete proxy for basal resource availability (i.e. gross primary production [GPP]), it does represent a snapshot of critical resources for consumers, especially in the biofilm-dominated food webs of our study streams (O'Gorman and others, 2014; Nelson and others, in review). Further, previous studies in this system have shown that light availability is a strong seasonal determinant of GPP in these systems (O'Gorman and others, 2012; Hood and others, 2018). Still, after correcting for the effects of epilithic chlorophyll *a* biomass and light availability, secondary production showed a positive relationship with temperature, suggesting a deviation from predicted temperature-independence. Part of this deviation may be attributable to the temperature-dependence of GPP. A previous extensive survey of streams within the Hengill watershed—including

many of the streams sampled here—show that during light saturated periods stream ecosystem GPP, on average, showed a positive relationship with temperature (activation energy of GGP = -0.57 eV; Demars and others, 2016). These two lines of evidence suggest that secondary production within a stream, after accounting for basal resource biomass, can be partially explained by patterns of basal resource *production* driven by seasonal light availability and temperature.

The apparent activation energy of annual secondary production (-0.83 eV, Figure 3.2A) showed a large deviation from expected temperature-independence (Cross and others, 2015). This strong positive association with temperature differs from a recent whole-stream experiment in the Hengill watershed that found no observable change in secondary production following short-term experimental warming of ~3°C (Nelson and others, 2017b). In this experiment, a disproportionate increase in production of large-bodied organisms countered increased P:B ratios in response to warming, leading to no change in community production, despite a tripling of annual primary production (Hood and others, 2018). Interestingly, increased primary production was largely attributable to a single species of green algae, *Ulva* sp., which was not an important food resource for consumers (Nelson and others, in review). In our study, streams were dominated by epilithic producer communities largely composed of diatoms, green algae, and some cyanobacteria (Gudmundsdottir and others, 2011; Chapter 2). These epilithic communities are more accessible to consumers than the large macro-producers which dominated the experimental stream post-warming. Such differences in primary producer community structure may explain why consumer secondary production more closely followed increased primary producer biomass and increases in GPP with temperature in

these long-term ‘thermally-acclimated’ systems of our study, compared to short-term warming responses (O'Gorman and others, 2014; Nelson and others, 2017b).

Seasonal variation in light likely caused a steepening of the apparent temperature-dependence of secondary production when viewed at an intra-annual time scale. This strong seasonality was more closely tied to temporal variation in community abundance and biomass, than patterns of biomass turnover (*P:B*; Figure 3.4A). During the winter, we found that all streams exhibited lower community biomass, when light availability and resource production was low. Reduced community biomass during darker and cooler winter months led to an apparent temperature-dependence of community biomass that countered MTE predictions *within* streams, despite *among* stream patterns that qualitatively followed MTE predictions. We attribute this counter scaling *within* streams, to adaptive coupling between species life-histories—specifically, the timing of biomass accumulation—and predictable seasonal production of basal resources (Ross, 1963). Such seasonal coupling of consumer energy demand and basal resource production may be a common attribute of mid- to high-latitude ecosystems, with and without strong covariance between temperature and light regimes (e.g., Junker and Cross, 2014; Huryn and Benstead, 2019).

There is a long history recognizing temperature as a fundamental determinant of ecosystem patterns and processes (e.g., Arrhenius, 1889). Our work has shown that temperature had a strong apparent influence on multiple biological facets of the ecosystem, including community biomass, production:biomass ratios, and the timing and magnitude of basal resource availability. Because of the strong covariance between temperature and basal resource availability, annual community secondary production

showed a steep positive relationship with stream temperature. However, temperature *per-se* had little relationship with annual secondary production after accounting for the influence of basal resource availability. On a seasonal timescale, temperature operated in concert with basal resource availability and light availability to influence organism life-history, leading to a steeper apparent temperature-dependence *within* streams versus *among* streams. In addition to the importance of temperature, this work highlights the role of covariation in environmental controls on resource availability and biological controls on consumer community metabolic demands (i.e. life-history, community biomass, growth rates) that modulate the temperature–productivity relationships in ecosystems. Further incorporation of temporal resource dynamics into metabolic scaling theory is necessary to fully leverage these conceptual frameworks. As global temperature regimes change in response to anthropogenic activities, predicting the response of secondary production requires a greater recognition of potential covariation between temperature, light, and the provision of resources that support metazoan demands (Huryn and others, 2014; Huryn and Benstead, 2019).

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Table 3.1. Apparent temperature-dependence (mean estimate and 95% confidence intervals) of secondary production, biomass (*B*), and production:biomass (*P:B*) ratios within (intra-annual) and among (Annual) streams. Mean annual temperature (°C) are shown in parentheses following the stream ID. Estimated activation energy and coefficients of determinations (r^2) are derived from the relationship between the natural-logged variables and Boltmann-temperature (1/*kT*). Community biomass (*B*) and *P:B*, which have expected body size scaling, were mass-corrected by mean biomass weighted body size of the community.

	Intra-annual		**Annual**	
	E (95% CI)	r^2	*E* (95% CI)	r^2
Secondary Production	--	--	-0.83 (-0.94 – -0.73)	0.64
hver (27.2)	-1.3 (-4.3 – -2.4)	0.84	--	--
st6 (17.6)	-1.1 (-3.0 – 0.8)	0.10	--	--
st9 (11.2)	-3.8 (-5.7 – -1.9)	0.90	--	--
st7 (5.8)	-6.0 (-8.9 – -3.0)	0.73	--	--
oh2 (5.5)	-3.0 (-4.4 – -1.5)	0.74	--	--
st14 (5.0)	-1.5 (-2.8 – -0.1)	0.46	--	--
Biomass$_{mass\text{-}corrected}$	--	--	0.79 (0.65 – 0.95)	0.22
hver	-2.5 (-6.7 – -3.3)	0.81	--	--
st6	-0.6 (-3.9 – 2.6)	0.05	--	--
st9	-3.1 (-3.6 – -0.1)	0.46	--	--
st7	-4.0 (-8.9 – 1.0)	0.18	--	--
oh2	-1.2 (-3.6 – 1.3)	0.31	--	--
st14	0.1 (-2.2 – 2.5)	0.001	--	--
P:B$_{mass\text{-}corrected}$	--	--	-1.62 (-1.76 – -1.52)	0.59
hver	1.4 (1.1 – 4.3)	0.40	--	--
st6	-0.3 (-3.5 –2.9)	0.03	--	--
st9	-0.07 (-3.3 – 3.1)	0.001	--	--
st7	-0.8 (-5.7 – 4.1)	0.03	--	--
oh2	-1.8 (-4.3 – 0.6)	0.25	--	--
st14	0.004 (-2.3 – 2.3)	<0.001	--	--

Table 3.2. Model selection analysis of daily community secondary production within and among streams. For all models, the response variable was natural log-transformed daily secondary production. 'Chla' represents the mean chlorophyll *a* biomass (µg m^{-2}), 'Light' is the cumulative light (lux) between sampling dates, and 'Temp' is mean Boltzmann temperature over the sampling interval. 'K' represents the number of estimated parameters in each model, 'AICc' is the Akaike's Information Criterion adjusted for small sample sizes, 'ΔAICc' is the change in AICc score from the top model, 'AICcWt' is the relative AICc model weight, 'LL' is the log-likelihood of each model, and 'Cum.Wt' is the cumulative Akaike weight.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**	**LL**	**Cum.Wt**
Chla+Light+Temp	5	154.10	0	0.89	-71.4	0.89
Chla*Light*Temp	9	159.28	5.18	0.07	-68.5	0.96
Temperature	3	160.15	6.05	0.04	-76.82	1
Chla+Light	4	178.51	24.42	0	-84.83	1
Chlorophyll *a* (Chla)	3	190.07	35.97	0	-91.78	1
Light	3	200.13	46.03	0	-96.82	1
Intercept	2	205.58	51.48	0	-100.67	1

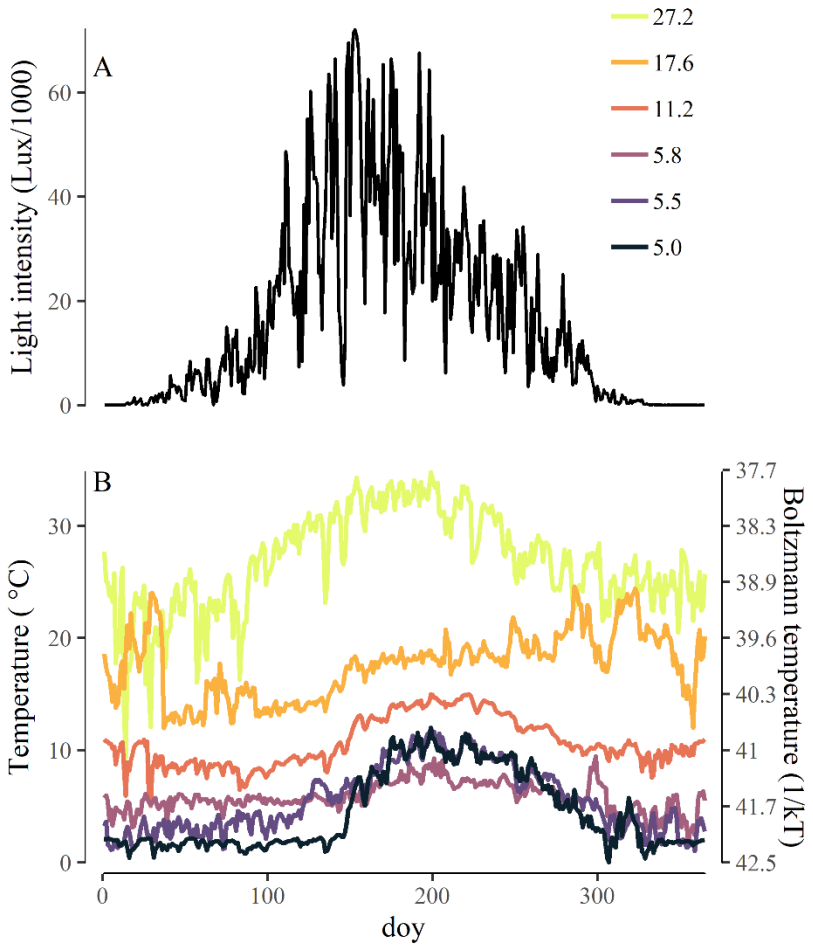

Figure 3.1. Annual patterns of light intensity (A) in the broader Hengill watershed and stream temperature (B) regimes of study streams. Mean annual temperatures can be found in Appendix B: Table S3.1.

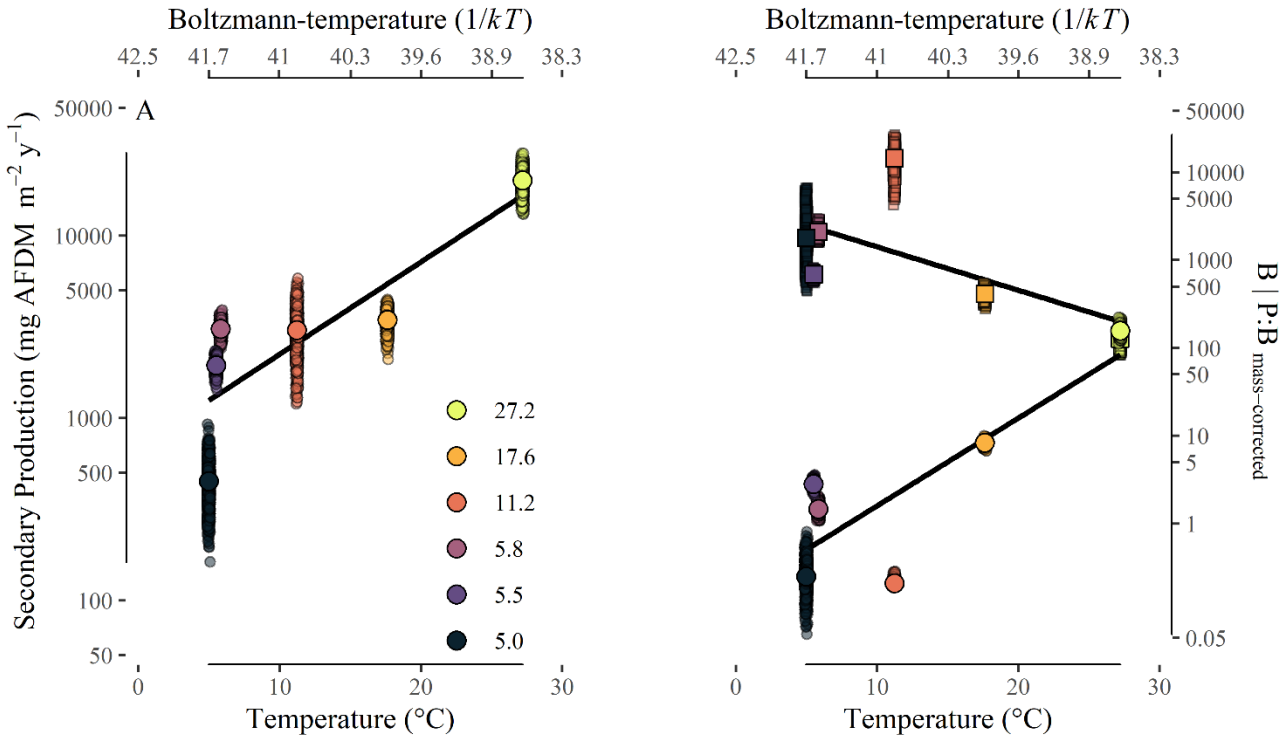

Figure 3.2. Temperature scaling of annual community secondary production (panel A; mg AFDM m^{-2} y^{-1}) and annual mass-corrected community biomass (*B*; mg AFDM m^{-2}; panel B; square points and top line) and production:biomass ratio (*P:B*; panel B, circle points and bottom line). The mean annual measurement within each stream is represented by the larger points, while all 1000 bootstrapped estimates are shown by small points. The apparent temperature-dependence of annual production and annual *B* and *P:B* can be found in Table 3.1.

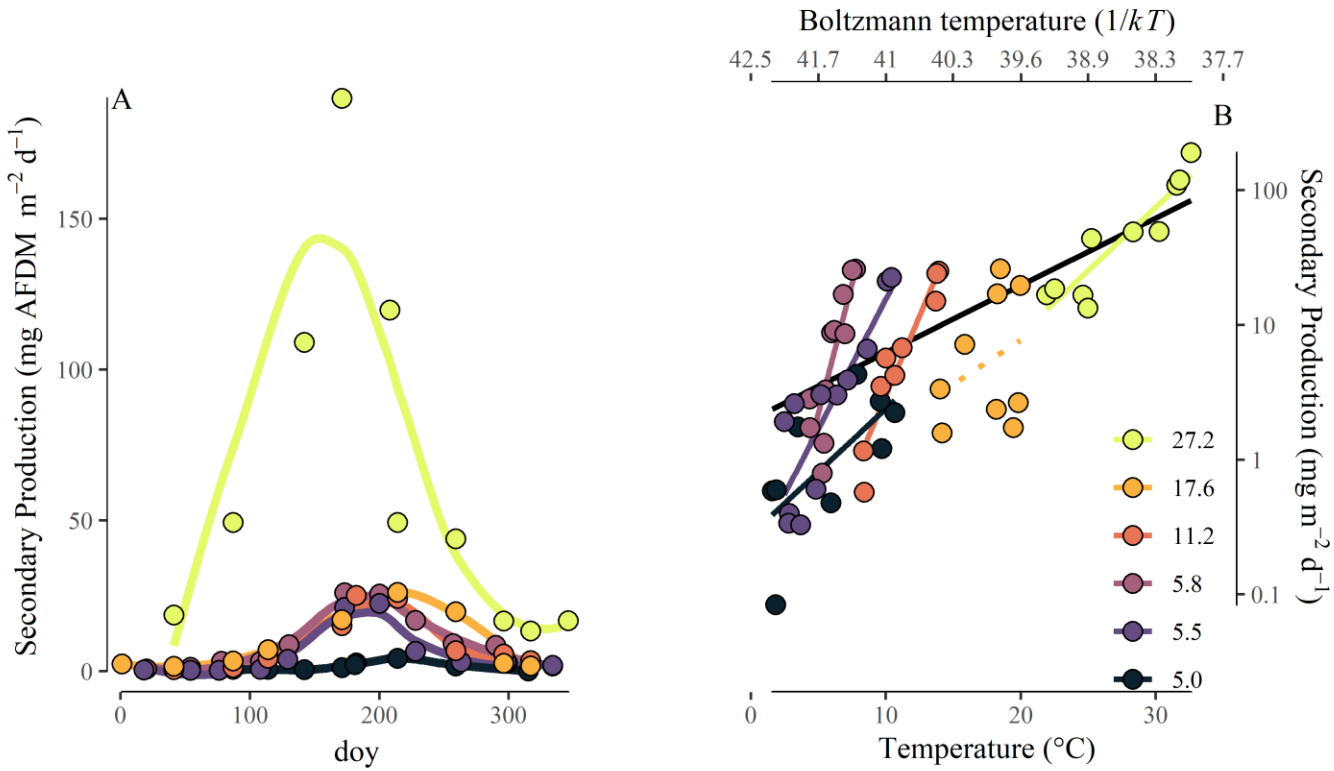

Figure 3.3. Within-stream patterns of daily community secondary production (mg AFDM m^{-2} d^{-1}) through the year (panel A, for visualization purposes LOESS lines are fit to temporal patterns of secondary production within streams, span = 0.70) and the relationship between interval temperature and ln-transformed daily secondary production (panel B). The black line represents the annual relationship between temperature and secondary production across streams, while the temperature dependence within each stream is described by the colored lines and corresponding points. Broken lines of intra-annual relationships between temperature and secondary production represent streams where the 95% CI of the estimated temperature-dependence overlaps zero. Apparent temperature-dependence coefficients of secondary production on annual and intra-annual timescales can be found in Table 3.1 of the main text.

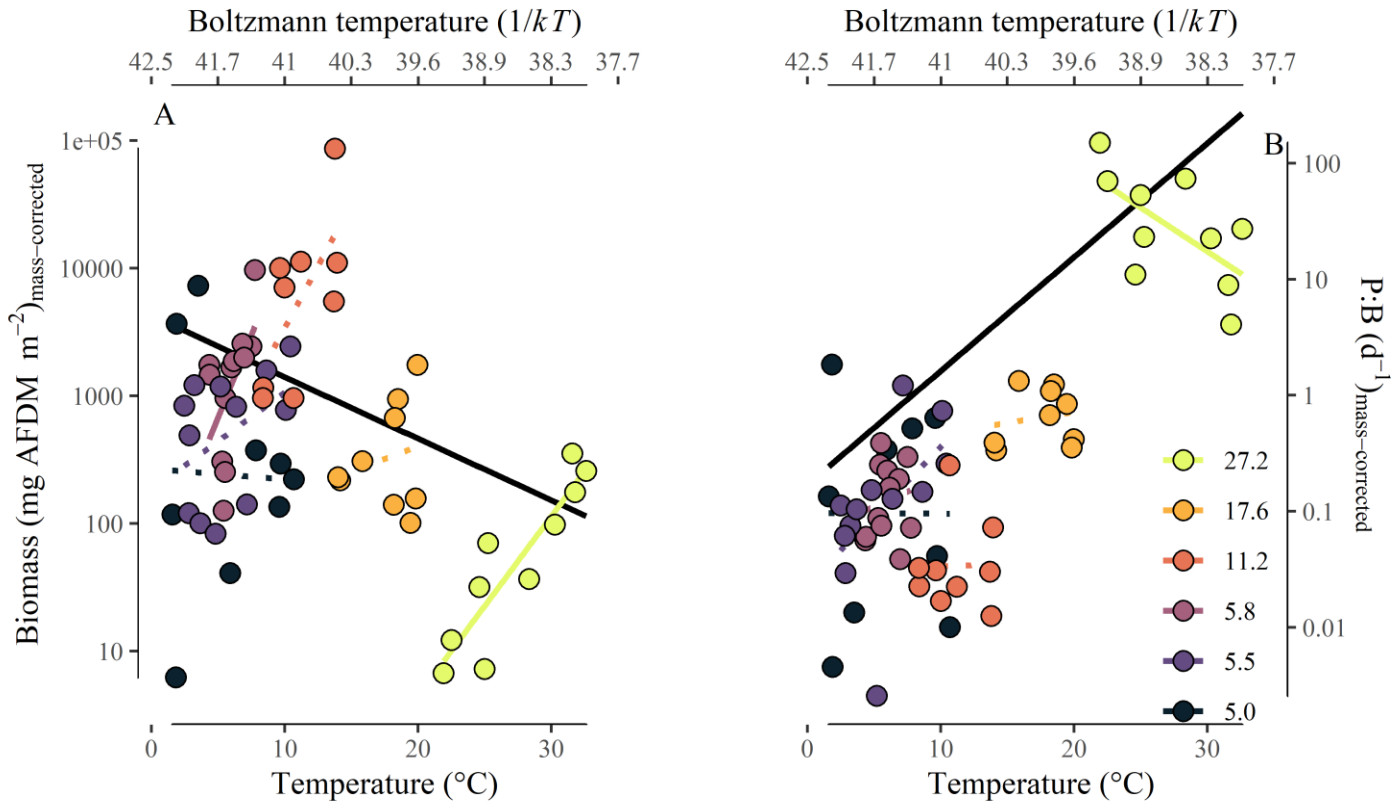

Figure 3.4. Intra-annual patterns between stream temperature and ln-transformed community biomass (*B*; mg AFDM m^{-2}; panel A) and production:biomass ratio (*P:B*; panel B) after correcting for the average community body size. Annual patterns across streams are shown by solid black lines through all data. The estimated intra-annual relationship between interval temperature and community *B* and *P:B* are represented by colored lines and corresponding points. Broken lines show streams wherein 95% CI of the estimated temperature-dependence of community *B* or *P:B* overlap zero. Coefficients of the temperature-dependence of *B* and *P:B* on annual and intra-annual timescales are found in Table 3.1 of the main text.

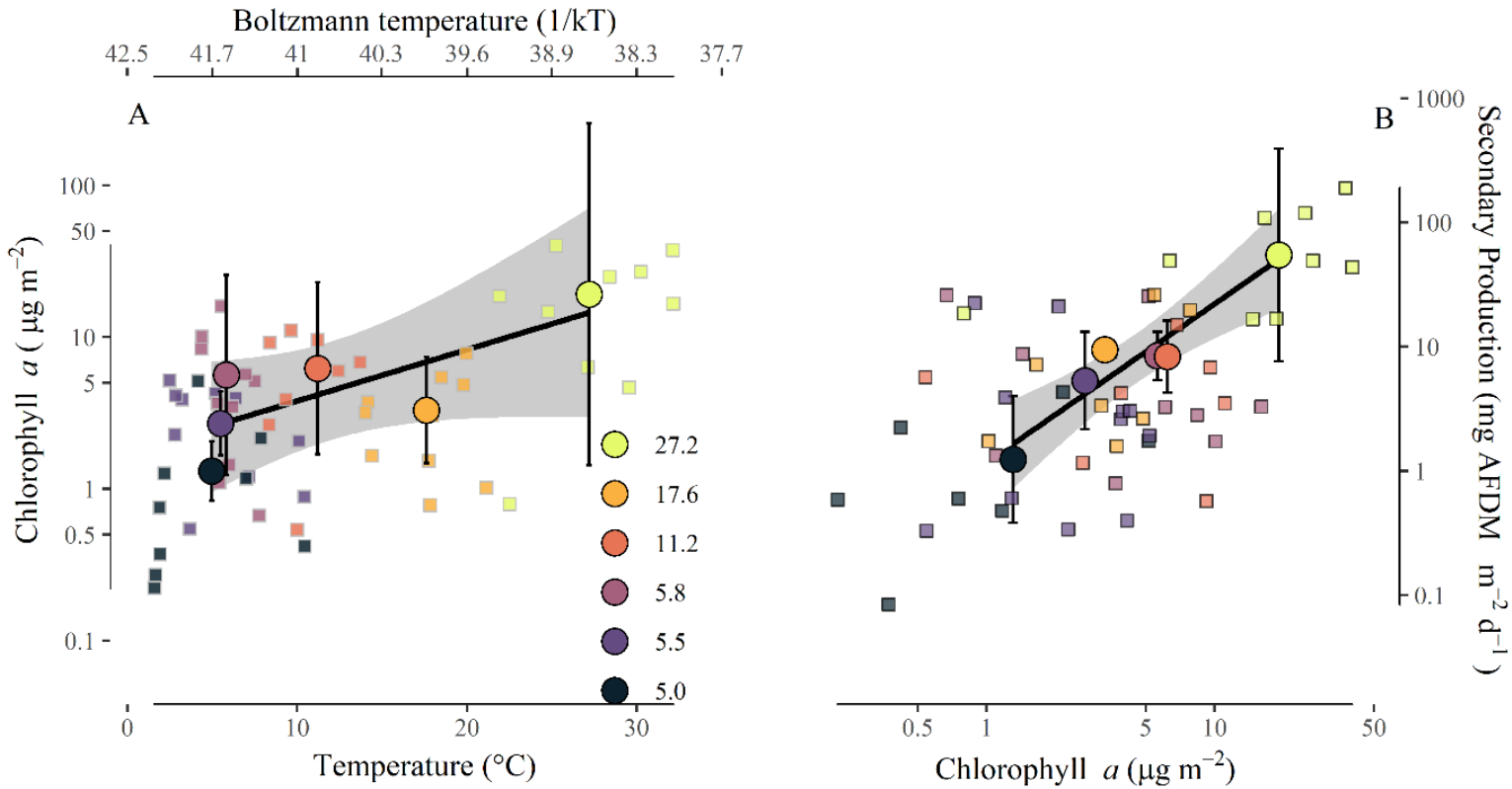

Figure 3.5. (A) Patterns of ln-transformed chlorophyll *a* biomass (mean ± 1 SD; µg m^{-2}) and annual stream temperature (large points). The temperature-dependence of annual mean chlorophyll *a* biomass among streams was -0.55 eV (95% CI: -1.22 – 0.11; r^2 = 0.45). Within streams (small square points, mean * $interval^{-1}$; µg m^{-2}) chlorophyll *a* showed little relationship with temperature. (B) Annual chlorophyll *a* biomass was positively related to annual secondary production across streams (r^2 = 0.89). Annual production was scaled to day^{-1} by dividing by 365 days to allow for comparisons with daily secondary production estimates. Within streams (small square points), chlorophyll *a* biomass was not associated with secondary production. The standard Ordinary least squares regression lines are fit to the data in each plot (mean ± 1SE).

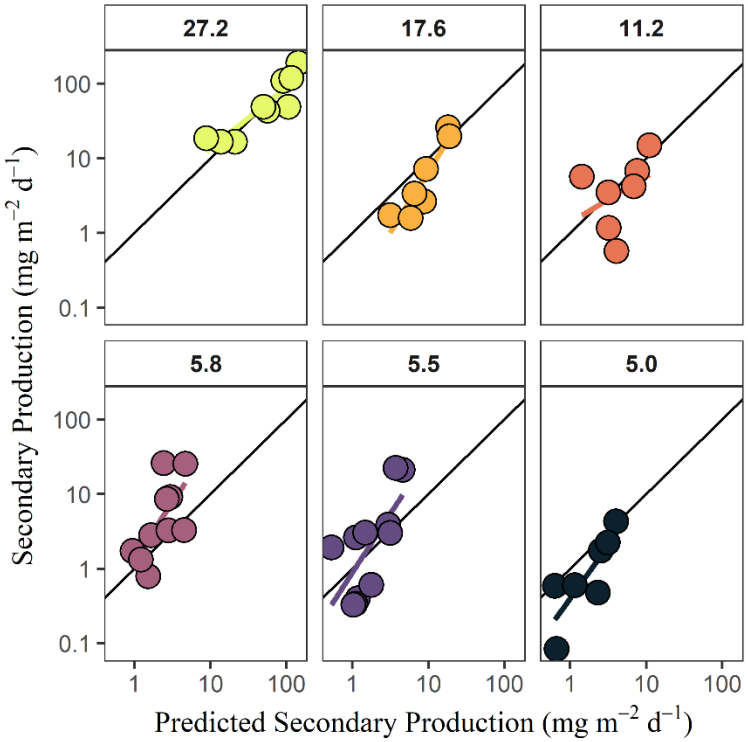

Figure 3.6. Predicted versus actual daily secondary production (mg m^{-2} d^{-1}) across all dates within each stream based on the multivariate model of: ln(secondary production)~ln(chlorophyll *a*) + log(light availability) + Boltzmann temperature. Mean annual stream temperature in of each stream is shown above each plot and the 1:1 line is shown solid black.

CHAPTER FOUR

RESPONSES OF FOOD WEB ORGANIC MATTER FLUXES TO TEMPERATURE AND THEIR IMPLICATIONS FOR FOOD WEB STABILITY

Contribution of Authors and Co-Authors

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Contributions: Designed the study, collected the data, performed analyses, interpreted results, and wrote the manuscript.

Co-Author: Wyatt F. Cross

Contributions: Conceived the study, procured funding, discussed results and interpretation, edited earlier draft of the manuscript.

Co-Author: Jonathan P. Benstead

Contributions: Conceived the study, procured funding, discussed results and interpretation, provided comments on an earlier draft of the manuscript.

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Contributions: Provided feedback on sampling design, collected the data, provided feedback on results and interpretation, provided comments on an earlier draft of the manuscript.

Co-Author: Daniel Nelson

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Manuscript Information

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Abstract

Global warming is likely to modify ecosystem functions by both altering organismal metabolic rates and restructuring biological communities and the network of interactions that sustain and stabilize them. However, understanding and predicting warming effects on ecosystems is difficult because of the shear complexity of multispecies systems as well as the underdeveloped data and theory connecting processes that drive ecosystem function (e.g., metabolism and production) with factors that sustain them (e.g., populations and community structure). Here, we quantified organic matter fluxes through stream macroinvertebrate food webs across a 20 °C natural temperature gradient. Total consumption fluxes increased two orders of magnitude with stream warming. Across all streams, consumption was constrained to periods with high light availability, but shifted forward a month between the warmest and coldest streams. Using these consumption measurements, we calculated consumer-resource interaction strengths and combined these with consumer:resource biomass ratios to examine temporal patterns in interaction strengths, the fate of organic matter fluxes, and consumer-resource coupling. Warmer streams were generally more simplified with stronger interaction strengths and a greater proportion of taxa with faster turnover rates. Warming also led to tighter coupling between consumers and resource biomass, which manifested as stable interaction strength distributions and reduced variation in consumer:resource biomass ratios. Our research demonstrates how warming can restructure food webs and ecosystems, but also, how function may be maintained in the face of environmental variation in a warmer world.

Introduction

Increasing global temperatures are changing how organisms interact with the environment and each other, potentially altering the stability and functioning of ecosystems (Costanza et al. 1997, Woodward et al. 2010b). The provision and maintenance of ecosystem functions are underpinned by the network of species interactions across which energy, materials, and information are exchanged (de Ruiter et al. 1995, Thompson et al. 2012). However, predicting the responses of complex species interaction networks to perturbations is notoriously difficult (Walther et al. 2002, Woodward et al. 2010a, O'Gorman et al. 2012), because interactions are determined by multiple physiological and ecological traits, each of which may exhibit unique responses to environmental drivers such as temperature (Dell et al. 2013). As such, even relatively small shifts in temperature can have large, cascading effects on food webs and ecosystems.

Ecosystem functionality, and its response to warming, is closely tied to the magnitudes and relative distribution of energy fluxes among species and trophic levels (Barnes et al. 2018). Previous work has shown clear connections between perturbations that alter structure of communities and how energy is partitioned among taxa and trophic groups (Benke and Wallace 1980, Hall et al. 2000, Cross et al. 2007, Cross et al. 2013). This research suggests that energy-based approaches can help to illuminate mechanisms and specific interactions that drive broader changes at the community-level. In addition, detailed characterization of energy fluxes can provide a window into the temporal variability of food web interactions and trophic basis of production (McCutchan and

Lewis 2002, Junker and Cross 2014). Unfortunately, empirical measures of energy flux are rare because they are data intensive and require considerable time and effort. Nevertheless, the study of energy flux is critical for confronting food web theory with data and advancing our understanding of how communities respond to global changes (Ledger et al. 2013, Barnes et al. 2018).

Although much of food web theory has been built on a population-dynamic perspective (i.e., May 1973), recent efforts have been made to bridge classical population-based approaches with ecosystem energetics (Paine 1980, McCann 2012). Of considerable promise is the notion that the patterning of energy and material fluxes in food webs can provide an empirical estimation of interaction strengths, and these measures can be made compatible with food web theory and community stability analysis (de Ruiter et al. 1995, Wootton 1997, Neutel et al. 2002, McCann 2012). This realization has helped to bridge disparate perspectives in ecology and, most importantly, it has advanced our ability to quantify the effects of perturbations on both ecosystem function and community stability (de Ruiter et al. 1995, Neutel et al. 2002, Rip and McCann 2011). Such a blending of perspectives may be necessary to advance our understanding of how energy flux, interaction strengths, and community stability simultaneously respond to perturbations such as warming (Gilbert et al. 2014)

In general, consumer energy fluxes are predicted to increase with temperature in response to changes in primary production and resource availability (Allen et al. 2005, Schramski et al. 2015). This prediction hinges upon the relative stasis and maintenance of the food web structure along which energy and materials move. Yet, warming may

disrupt food webs by restructuring the community and the relative energetic requirements among different taxa or trophic groups. Indeed, stronger thermal sensitivity of heterotrophic metabolism vs. photosynthesis (Allen et al. 2005, Lopez-Urrutia et al. 2006) should increase energy demands of herbivores relative to primary producers (O'Connor et al. 2011), strengthening top-down control and the strength of interactions of consumers on their resources. Here, increased organic matter fluxes to consumers that are not offset by losses (e.g. predation, mortality, emigration) tend to increase the ratio of consumer biomass to resource biomass (i.e., B_{cr} Rip and McCann 2011) and this general condition is known to destabilize consumer-resource interactions in a modeling framework (Rosenzweig 1971, McCann 2012). If temperature-induced shifts in energetic requirements pushes consumer-resource interactions towards instability, ecosystem functions may become especially vulnerable to further natural and anthropogenic perturbations.

Spatial and temporal variation is the rule for natural ecosystems and lies at the heart of many pressing questions in ecology (Levin 1992). Yet, most predictions derived from consumer-resource theory assume constant, equilibrium conditions that are rarely maintained in nature (White and Hastings 2018)—especially in highly seasonal ecosystems. Indeed, previous work has shown that environmental variation can lead to food web outcomes which run counter to basic expectations under equilibrium conditions (e.g., communities are stabilized by asynchrony in stable environments and increased synchrony under variable environments Vasseur and Fox 2007). Thus, predicting

responses to warming must take into account natural variation—whether predictable or stochastic—which is likely to modify responses to temperature (Hastings 2010).

In ecosystems with extreme temporal variation in resource availability (e.g., high-latitude light-driven ecosystems), seasonal changes in temperature, consumer life-histories, and metabolic demands can lead to wide variation in the coupling of resource availability and consumer energetic demand (Huryn et al. 2014, Huryn and Benstead 2019). When resource availability and consumer demand (i.e., organic matter fluxes to consumers) are perfectly coupled (Figure 4.1A), interaction strengths—i.e., the per capita influence of consumers on resources (Bascompte et al. 2005)—and the ratio of consumer to resource biomass are predicted to remain constant over time (Figure 4.1A). Conversely, if these factors are completely decoupled (Figure 4.1C), interaction strengths should vary over time in response to shifts between periods of high demand and low resource availability vs. those with low demand relative and an abundance of resources. Other alternatives exist between these extremes (e.g., Figure 4.1B). Such seasonal variation in interaction strength may have consequences for food web stability, potentially dampening or enhancing predictions derived from model equilibrium assumptions. Thus, understanding when and how consumer-resource dynamics support or erode stability in the face of environmental variation will be crucial for predicting ecological responses to warming.

Here, we quantified organic matter fluxes throughout the year in six stream food webs along a natural temperature gradient (5 – 27 °C). We tracked temporal shifts in consumer consumption through detailed diet analysis and quantification of secondary

production. This allowed us to quantify patterns in total and resource-specific organic matter fluxes among individual taxa, trophic groups, and whole food webs on seasonal and annual timescales. We coupled this information with patterns of basal resource availability to calculate variation in consumer-resource interaction strengths and consumer-resource biomass ratios. We predicted that annual organic matter fluxes would increase with temperature despite large changes in species composition and trophic structure. On shorter timescales, we predicted that organic matter fluxes in all streams would exhibit strong seasonality, with the majority of fluxes occurring during critical periods of high light and basal resource availability. With respect to the strength of interactions, we predicted a general simplification of food webs with warming and a strengthening of average interaction strengths, consistent with equilibrium theory and previous research. However, at short-term timescales, we expected considerable variation in the coupling of resource availability and consumer demand in response to temperature with potential consequences for the distribution of biomass between consumer and resources. Our study demonstrates the strong role of seasonality in modifying consumption fluxes, the distribution of ecosystem biomass, and the patterns and strengths of food web interactions.

Methods

Study Site

We studied six headwater streams in the Hengill geothermal area of southwestern Iceland (64°03´N 021°18´W). This region is characterized by indirect geothermal heating of groundwater (Árnason et al. 1969), which creates spatial heterogeneity in stream

temperatures (4.5–54.0 °C). Importantly, these streams exhibit similar water solute chemistries (Friberg et al. 2009), creating a unique natural laboratory to isolate the influence of temperature on stream ecosystem structure and function (Friberg et al. 2009, O'Gorman et al. 2012, Nelson et al. 2017b, Hood et al. 2018). We selected a subset of streams across a wide range of mean annual temperature, while also attempting to standardize structural aspects of the basal resource community (i.e., minimal biomass of large macrophyte primary producers; *see* Chapter 2). In each stream, we measured temperature every 15 minutes from July 2010 through August 2012 (Onset #U20-001-01 water-level logger, Onset Computer Corp. Pocasset, MA, USA), along with a suite of physicochemical variables (Table 4.1). Over the course of the study, average light availability in the watershed was also measured every 15 minutes from multiple atmospheric stations located within the Hengill watershed (Onset HOBO pendant temperature/light UA-002-64).

Macroinvertebrate Sampling

We sampled macroinvertebrate communities approximately monthly in six streams. Two streams, used in a previous study, were sampled between October 2010 to October 2011 (Nelson et al. 2017a, b). Four other streams were sampled between July 2011 and August 2012. Inter-annual comparisons of primary and secondary production in the two streams from previous studies showed minimal differences among years in unmanipulated streams, suggesting comparisons of data collected during different years would not significantly bias our results (Nelson et al. 2017b, Hood et al. 2018). In each stream, we collected replicate Surber samples (n = 5; 0.023 m^2; 250 µm mesh size) from

randomly-selected locations. Inorganic substrate in the top ~10 cm was disturbed and invertebrates and organic matter were removed with a plastic scrub brush. Samples were then preserved in the field with 5% formaldehyde. In the laboratory, samples were split into coarse (>1 mm) and fine (1 mm> x >250 µm) fractions with nested sieves and macroinvertebrates were removed with the aid of a dissecting microscope (10–15X magnification). For particularly large samples, fine fractions were subsampled (1/2–1/16th) using a modified Folsom plankton splitter prior to removal of invertebrates. Subsamples were scaled to the rest of the sample assuming similar abundance and body size distributions. Macroinvertebrates were identified to the lowest practical taxonomic level (usually genus) with taxonomic keys (Peterson 1977, Merritt et al. 2008, Andersen et al. 2013). Taxon-specific abundance and biomass were scaled to a per meter basis by dividing by the Surber sampler area.

Secondary Production

Daily secondary production of invertebrate taxa was calculated using the instantaneous growth rate method (IGR; Benke and Huryn 2006). Growth rates were determined using multiple approaches described in Chapter 3. Briefly, growth rates of common taxa (e.g., Chironomidae spp., *Simulium* spp., *Radix balthica*, etc.) were determined using *in-situ* chambers, repeat photography, and changes in size-frequency distributions. Variability in growth was estimated using a bootstrapping technique that resampled individuals with replacement from each date (n = 500). Body lengths were converted to mass (mg ash-free dry mass [AFDM]) using published length-mass regressions (Benke et al. 1999, O'Gorman et al. 2012, Hannesdóttir et al. 2013). Growth

rates (g) were calculated by the changes in mean body size (W) over a given time interval (t) divided by the number of days in the interval with the following equation:

$$g = \frac{\mathrm{Ln}\left(\frac{W_{t+\Delta t}}{W_t}\right)}{\Delta t} \quad (1)$$

For those taxa in which growth could not be estimated empirically, we developed stream-specific growth rate models by constructing multivariate linear regressions of empirical growth data against body size and temperature within each stream.

To estimate uncertainty in production of each taxon, we used a bootstrapping technique that resampled measured growth rates, in addition to abundance and size distributions from individual samples. For each iteration (n = 1000), size-specific growth rates were multiplied by mean interval biomass for each size class and the number of days between sample dates to estimate size class-specific production. For each interval, size classes were summed for each taxon to calculate total population-level production. Intervals were summed to estimate annual secondary production.

Gut Content Analysis

Macroinvertebrate diets were quantified for dominant taxa in each stream. We focused on numerically abundant taxa and/or taxa with relatively high annual production. We selected a minimum of five individuals from samples, and, when possible included individuals of different size classes to account for ontogenetic shifts in diet, including individuals from different seasons to capture concurrent ontogenetic and seasonal changes. For small-bodied taxa, we combined multiple individuals (n = 3–5) to ensure samples contained enough material for quantification. We used methods outlined in Rosi-

Marshall et al. (2016) to remove gut tracts and prepare gut content slides. Briefly, we removed the foregut from each individual or collection of individuals, suspended gut contents in water and sonicated for 30 seconds. Gut content slurries were filtered onto gridded nitrocellulose membrane filters (Metricel GN-6, 25 mm, 0.45µm pore size; Gelman Sciences, Ann Arbor, MI, USA), dried at 60 °C for 15 mins, placed on a microscope slide, cleared with Type B immersion old, and covered with a cover slip. We took 5–10 random photographs under 200–400x magnification, depending on the density of particles using a digital camera mounted on a compound microscope. From these photographs we identified all particles within each field and measured the area of particles (μm^2) using image analysis software (Schindelin et al. 2012). We identified particles as diatoms, green and filamentous algae, cyanobacteria, amorphous detritus, vascular and non-vascular plants (bryophytes), and animal material. We calculated the proportion of each food category in the gut by dividing their summed area by the total area of all particles. Gut contents of many predators were empty or contained unidentifiable, macerated prey. For these taxa, we assumed 100% animal material.

Organic Matter Consumption Estimates

Consumption fluxes (grams m^{-2} $time^{-1}$) were calculated using the trophic basis of production method (Benke and Wallace 1980). Taxon-specific secondary production estimates were combined with measured diet proportions, assumed diet-specific assimilation efficiencies (AE_i, diatoms = 0.30, filamentous algae = 0.30, green algae = 030, cyanobacteria = 0.15, amorphous detritus = 0.10, vascular and non-vascular plants (bryophytes) = 0.1, and animal material = 0.7), and assumed net production efficiencies

(NPE = 0.50) to estimate consumption of organic matter. For each food category, *i*, diet proportions were multiplied by the gross growth efficiency ($GGE_i = AE_i * NPE$) to calculate the relative production attributable to each food category. The relative production from each food type was then multiplied by the interval-level production and finally divided by GGE_i to estimate consumption of organic matter from each food category by a consumer (Benke and Wallace 1980). Consumption was calculated for each taxon across sampling intervals (typically ~1 month). Total interval consumption was calculated by summing across all taxa, while annual consumption was calculated by summing across all taxa and intervals.

Quantification of basal resource availability

We measured epilithic chlorophyll *a* biomass (mg m^{-2}) as a proxy for bulk basal resource availability. While this proxy represents an imperfect measure of true basal resource availability (i.e. gross primary production of edible resources), previous research in the Hengill watershed has demonstrated that stream food webs are largely fueled by autochthonous primary production. Furthermore, diets of primary consumers typically include epilithic diatoms, amorphous detritus, and limited green algae, with minimal contributions from vascular and non-vascular plants or cyanobacteria (O'Gorman et al. 2012, O'Gorman et al. 2017, Nelson et al. *in review*). As such, epilithic chlorophyll *a* biomass likely represents a conservative approximation of resource availability when large macrophytes are absent, as in the study streams (see Chapter 2). Chlorophyll *a* was quantified in each stream approximately monthly by scraping a known area (8.05 cm^2) on five stones with a plastic stiff-bristled brush. The removed epilithic slurry was rinsed into

amber Nalgene bottles with a known volume of water and kept cool until returning to the laboratory for further processing. In the laboratory, subsamples were filtered onto glass-fiber filters (Whatman GF/F, 0.7 µm pore size), extracted in 90% acetone overnight, and chlorophyll *a* measured on a Turner *Aqua*Fluor fluorometer (Turner designs, Sunnyvale, CA USA). Total chlorophyll *a* was standardized to a per meter basis by dividing by the area scraped.

Consumer-Resource Interaction Strengths and
Biomass Ratios (B_{CR})

To summarize patterns of interaction strengths and biomass ratios on annual and interval scales, we used summarized community measures which incorporated aspects of taxon-level and whole consumer community biomass, total resource biomass, and total organic matter flux. This simplification produced aggregate metrics that are consistent with theoretical two species consumer-resource modules (Rosenzweig 1971, Murdoch et al. 2003). To quantify the daily biomass-specific interaction strength of each consumer on autochthonous basal resources, we used the interaction strength formulation of Bascompte et al. (2005). This equation calculates the portion of resource biomass eaten per unit consumer biomass each day as:

$$Interaction\ strength\ = \frac{(Q/B)_j * DC_{ij}}{R_i} \quad (3)$$

where, *Q/B* is total daily consumption (*Q*) divided by mean consumer biomass (*B*) (or the number of times the population of consumer *j* eats its own mass in resources per day), DC_{ij} is the proportion of resource *i* in the diet of consumer *j*, and R_i is the mean biomass of resource *i* (epilithic chlorophyll *a* biomass). We estimated the proportion of resources,

DC_{ij}, from the summed contribution of diet categories found within epilithic biofilms, namely: diatoms, filamentous algae, and cyanobacteria. Further, we excluded predatory taxa and those that did not consume epilithic primary producers (e.g., diatoms, filamentous algae, etc.). Here, we report community-level interaction strength as the median of $\log_{10}$-transformed interaction strength for a given stream. The second metric we assessed was the ratio of summed consumer biomass to resource biomass, B_{CR} (Rip and McCann 2011) as:

$$B_{CR} = \frac{log_{10}(Consumer\ biomass)}{log_{10}(Resource\ biomass)} \quad (2)$$

Statistical Analyses

To examine how organic matter consumption varied with stream temperature, the relationship between annual stream temperature and total consumed organic matter was assessed with ordinary least squares regression. Total consumption was natural log transformed to normalize residuals. We also analyzed how organic matter consumption was distributed among species and in relation to species attributes such as body size, P:B ratio, and population biomass among streams. However, interspecific differences in annual consumption spanned multiple orders of magnitude and stream communities had varying levels of species richness, making meaningful cross-system comparisons difficult using the raw consumption values. To account for this, we used rank-rank plots to standardize species attributes and consumption across streams. In this analysis, species-level attributes (e.g., mean annual body size, annual P:B, or annual mean population biomass) were ranked within each stream. Ranked consumption values were then plotted against species rank for each attribute. This analysis provided a standardized metric that

is robust to large differences in consumption, species richness, and evenness of consumption. Importantly, the slope of the relationship is bounded between -1 and 1, with larger absolute values related to the relative importance of species attributes in determining the magnitude and direction organic matter fluxes within a community. For each stream, we calculated the ordinary least squares slopes of these relationships and their coefficients of determination (R^2).

To test if the timing in consumer demand among consumer was correlated in time within a stream (e.g., temporal synchrony among consumer populations) we calculated the temporal synchrony of consumer consumption using the formulation of Loreau and de Mazancourt (2008), implemented in the "codyn" package (Hallett et al. 2019). This estimation is robust to differences in species richness present among these streams (Chapter 3, Friberg et al. 2009). To examine whether temporal synchrony in demand varied systematically with temperature, we calculated the bivariate correlation between annual stream temperature and the estimated temporal synchrony (*see below*).

Lastly, we were interested in the relationships between temperature and annual or seasonal variability in consumer-resource interaction strength and consumer:resource biomass ratios (B_{cr}). Temporal variability in each stream was assessed by the standard deviation of each variable across all time intervals. We then calculated the bivariate correlation between mean annual stream temperature and annual consumer-resource interaction strength and B_{cr}, as well as the variability in interaction strength and B_{cr} within a stream. For all bivariate correlations, we use Pearson's correlation coefficient (r). When bivariate plots suggested that the data were not described well by a bivariate

normal distribution, we also used Spearman's rank correlations (ρ) as a more robust statistic. All statistical analyses were conducted in R (R Core Team 2016).

Results

Annual Consumption and Production Fluxes

Mean annual consumption of organic matter by the whole invertebrate community ranged two orders of magnitude from 3.0 to 185.4 g AFMD m^{-2} y^{-1} (Figure 4.2A). Total consumption was positively associated with mean annual stream temperature, corresponding to a ~13% increase in consumption on average for each 1 °C increase (95% CI: 1.0 – 27.6%). These patterns of consumption fluxes mirrored changes in secondary production across the thermal gradient (13% increase in consumption vs. 12% increase in secondary production for each 1 °C increase in annual mean stream temperature; Figure 4.2A).

Consumer Diets, Trophic Basis of Production, and Organic Matter Consumption

Consumer diets were dominated by diatoms, amorphous detritus, and animal material which made up between 46 – 66%, 10 – 27%, and 0 – 23% of consumer diets (diatoms: 55% ± 27 mean ± standard deviation (SD), amorphous detritus: 18% ± 14, animal material: 15% ± 8; Appendix C: Table S4.2). The community-level trophic basis of production generally followed trends in diet composition with diatoms fueling the largest proportion of total secondary production (63% ± 15 mean ± SD; range: 39 – 81%; Figure 4.2B). However, differences in assimilation efficiency among diet items led to some divergence between diets and the trophic basis as animal material (14% ± 11.0

mean ± SD; range: 0.003 – 27.4%) and green algae (12% ± 7.1 mean ± SD; range = 5.8 – 19.5%) tended to fuel a greater amount of secondary production than amorphous detritus (7.9% ± 5.6 mean ± SD; range = 1.5 – 18.0%; Figure 4.2B; Appendix C: Table S4.3).

Annual consumption of diatoms ranged from 1.1 – 81.5 g AFDM m^{-2} y^{-1}, while consumption of the least important food item, cyanobacteria, ranged from 0 – 2.8 g AFDM m^{-2} y^{-1} (Appendix C: Table S4.4). The consumption of animal prey by secondary and tertiary consumers ranged from 0.002 – 2.7 g AFMD m^{-2} y^{-1}, representing between <0.001 to 12% of total organic matter flux. The contribution of predation to total annual consumption showed a highly variable but weak negative association with stream temperature (Spearman's r = -0.42; 95% CI -0.92 – 0.59; Figure 4.2C), with a notably small amount of predation in the warmest stream.

Interspecific Patterns of Organic Matter Flux

Consumption varied over 6 orders of magnitude among populations and streams (>0.0001 – 83 g AFDM m^{-2} y^{-1}; Appendix D: Table S4.1). Annually, food webs were relatively simplified at high temperatures where only 14 species contributed to fluxes, compared with 29 – 43 at cool and moderate temperatures (Figure 4.3). Generally, the relative magnitude of annual consumption by a population was unrelated to individual body size (Figure 4.3A; Table 4.2) but showed a modest increase with increasing annual P:B ratio (Figure 4.3B; Table 4.2). Further, rank-rank slopes between population annual P:B ratios and consumption showed a moderate, positive relationship with stream temperature (Pearson's r = 0.70). Patterns in the coldest stream (st14, annual mean temp = 5.0) were somewhat different, with a strong positive association between individual

body size and consumption (estimate: 0.67, $R^2 = 0.58$) and a weak but *negative* association between annual P:B ratios and consumption (Figure 4.3A & B, Table 4.2). Mean population biomass had a consistently positive effect on taxon-level consumption in all streams (Figure 4.3C, Table 4.2).

Temporal Patterns of Community-level Flux

Community-level consumption varied intra-annually within streams and in relation to temperature, but the majority of consumption occurred during the arctic summer when light availability, temperature, and consumption rates were high (Figure 4.4A & B, Appendix C: Figure S4.1). Cumulative organic matter consumption between the spring and fall equinox accounted for ~70 – 80% of total annual consumption. Increased fluxes during the summer partially reflected higher temperatures during this period (Appendix C: Figure S4.2); however, there was considerable variability around these relationships. The timing and accumulation of consumption was shifted earlier in the warmest stream and delayed in the coldest (estimated time to 50% annual consumption: ~210 days at 5.0 °C and ~175 days at 27.2 °C; Figure 4.4A), but the timing of consumption in other streams were similar.

The percent of total consumption by the dominant taxa varied among streams and within each stream throughout the year (Figure 4.5). Despite large variability in the contribution of individual taxa to organic matter fluxes over time, most taxa showed similar temporal patterns in consumption leading to high temporal synchrony of fluxes within streams (community synchrony = 0.70 ± 0.11 mean ± SD; range: 0.54 to 0.87).

Temporal synchrony in consumption showed a positive, but highly variable, association with mean annual stream temperature (Pearson's $r = 0.26$; 95% CI: -0.70 – 0.88).

Chlorophyll *a* Biomass

Epilithic chlorophyll *a* biomass varied ~180-fold (Figure 4.6) and was positively related to temperature across streams and seasons (Pearson's $r = 0.23$, Appendix C: Figure S4.3). However, variability in chlorophyll *a* biomass over the year, measured as the standard deviation, was higher in warmer systems (Pearson's $r = 0.82$, 95% CI 0.03 – 0.98, range: 1.6 – 13.9) and this relationship was robust to parametric assumptions (Spearman's $\rho = 0.77$).

Consumer-Resource Interaction Strengths and Biomass Ratios (B_{cr})

Among and within streams variation in basal resource biomass and consumer biomass and consumption led to large variation in food web structure and consumer-resource interaction strengths among and within streams. Annual median interaction strengths ranged from -2.58 to -0.42 (raw values: 0.003 – 0.38) and showed a positive, but weak association with mean annual stream temperature (Pearson's $r = 0.41$, 95% CI -0.60 – 0.92, Figure 4.7A). Within a stream, there was considerable variation in interaction strengths throughout the year and streams showed variable patterns of seasonality (i.e., concave, convex, and stable; Figure 4.8; Appendix C: Figure S4.5), but these relationships were not clearly related to within stream temperature (Appendix C: Figure S4.6). Interestingly, stream temperature had a significant negative influence on

intra-annual variability of median interaction strengths (Pearson's r = -0.82, 95% CI -0.98 – -0.02, Spearman's ρ = -0.66, Figure 4.7B).

Consumer:resource biomass ratios were weakly but negatively related to median interaction strengths across and within streams (Pearson's r = -0.17, 95% CI -0.41 – 0.09). At an annual timescale, B_{cr} ranged from 0.6 to 1.34 (mean ± SD: 0.98 ± 0.24) and showed a negative association with mean temperature (Pearson's r = -0.54, 95% CI -0.94 – 0.49). However, this relationship appeared more unimodal due to a single stream with high B_{cr} at moderate temperatures (Appendix C: Figure S4.7). Within a stream, B_{cr} generally peaked around the middle of the year when light and temperature were highest, but temporal patterns varied among streams (Figure 4.9). Within-stream variability in B_{cr} was negatively associated with mean annual temperature (Pearson's r = -0.66, 95% CI -0.95 – 0.32; Spearman's ρ = -0.86).

Discussion

We combined empirical measurements of energy flux, community structure, diets, and interaction strengths to infer changes in food webs driven by environmental warming. We showed that a ~20 degree warming of stream temperature increased the annual flux of materials through food webs by nearly two orders of magnitude. Warming also influenced the timing of fluxes, as well as the identities and importance of dominant taxa in sustaining these fluxes. In all streams, energy demands were generally highest during periods of high light and temperature, and differences in the phenology of energy fluxes were most pronounced in the warmest (earlier) and coldest (later) streams. Despite the large increase in fluxes with warming, these elevated fluxes were supported by more

simplified food webs with fewer taxa, reduced predation, and higher biomass turnover rates. There was also a trend towards tighter coupling and reduced variability in the warm streams, suggesting a potential stabilizing mechanism that may counteract otherwise destabilizing characteristics associated with food web simplification. Together, shifts in warm streams towards higher biomass turnover and tighter coupling between consumer and resource populations may represent an adaptive state in which ecosystem functions may persists despite time periods of potentially large energetic mismatches.

Across the stream temperature gradient, patterns of energy flux were governed largely by basal resource availability. Two main lines of evidence support this point. First, total annual energy flux increased with temperature, qualitatively supporting the general prediction that total ecosystem fluxes should mirror changes in primary production (Schramski et al. 2015). However, this increase was steeper than predicted from the temperature-dependence of photosynthesis alone (-0.88 vs. -0.32 eV K^{-1}; Allen et al. 2005), suggesting that additional factors may influence the efficiency of transfer between primary producers and consumers. The second line of evidence for the importance of basal resources in governing food web fluxes is that variation in fluxes among streams on annual and intra-annual timescales was explained by factors that fundamentally control resource productivity (e.g., resource biomass, light availability, and temperature; Chapter 2). Our results contrast with recent experimental work in soils (Schwarz et al. 2017), where warming had a variable, but mostly negative, influence on bulk energy fluxes. These differences may be partially attributed to the inclusion of heterotrophic microbes in soil experiments. When microbes were excluded, energy fluxes

through soil macrofauna actually increased in response to a 3.4 °C warming in most treatments (Schwarz et al. 2017). Results from a recent whole-stream warming experiment at our study site also contrasted with our work, reporting no change in total fluxes with warming, but a shift in the distribution of fluxes to towards larger-bodied macroinvertebrate consumers (Nelson et al. 2017a, in review). While both of these experiments measured fluxes across a much smaller temperature gradient than our study (~3.5 vs. 20 °C), these examples demonstrate the importance of the *distribution* and *identity* of energetic pathways in explaining the responses of energy fluxes to warming (Petchey et al. 1999).

Variation in consumer energy demand over time was driven by interactions between temperature and other sources of environmental variability, in this case light and associated changes in resources. In all streams, the majority of total annual flux (>70 %) occurred during the six months of the year with more than 12 hours of daylight. This pattern was evident despite a ~15 °C temperature difference between the warmest and coldest stream that was maintained during months of low light (Appendix A: Figure S4.1). Temperature did appear to shift the phenology of fluxes as 50% of cumulative annual consumption in the warmest stream occurred ~35 days earlier than in the coolest streams (~175 vs 210 days; Figure 4.4A). Resource biomass in the warmest stream began to increase in May (~150 days) and remained high until October (~300 days). In contrast, resource biomass in the coldest stream was notably low until July (~200 days, Appendix A: Figure S4.4). This pattern suggests that the time of consumer life histories may evolve to track resource availability (e.g., Ross 1963). The other four streams had similar

patterns in the timing of consumption, suggesting this pattern may only manifest at relatively extreme temperatures at the boundaries of thermal ranges. Nonetheless, the clear divergence in flux phenology between the warmest and coldest streams demonstrates that temperature may interact with other drivers of environmental variability (e.g., light availability) to shift the timing and length of time over which ecological interactions can manifest.

High latitude ecosystems with large seasonal variation in light may experience periods of resource scarcity during the winter months that can limit the productivity of multiple trophic levels (Huryn and Benstead 2019). Time periods of resource scarcity may also act as a strong selection agent, setting the bounds for species presence, persistence, and diversity (McNamara and Houston 2008, Tonkin et al. 2017). Species that persist in such environments must be able to thrive during resource booms and persist during times of extreme scarcity. In warm streams at our study site, organic matter fluxes were shunted towards taxa with relatively high instantaneous growth rates and annual biomass turnover rates (P:B). This effect was not simply an artifact of elevated P:B of the same taxa ratios at warmer temperatures, but occurred independently, likely as a consequence of changes in species composition and life-history traits (Figure 4.3B). Such a pattern has been reported in other highly variable ecosystems such as flashy desert streams (Fisher and Gray 1983) and experimental streams exposed to drought (Ledger et al. 2011). The fact that this effect was most pronounced in our warm streams suggests that warming may intensify energetic mismatches during periods of resource scarcity, thus shortening the amount of time when consumer energy demands can be met and

selecting for ‘fast’ life history traits. Lifespan, voltinism, and body size are all related to annual P:B (see references and discussion in Huryn and Wallace 2000) and our results, in conjunction with other traits such as reduced maximum body size (i.e., temperature-size rule Atkinson 1994), support the notion that temperature may speed up ecosystem processes in ways that are both direct (metabolic) and indirect (changes in communities, species traits).

Trophic interactions lie at the core of food web theory and their strengths and patterning play a critical role in species persistence and community stability (Paine 1980, McCann et al. 1998). Recent theory has begun to unravel how changes in temperature might alter interaction strengths and stability (Vasseur and McCann 2005, Gilbert et al. 2014). In general, warming is predicted to increase average interaction strengths, leading to higher amplitude population cycles and reduced food web stability (Vasseur and McCann 2005, O’Connor et al. 2011). Among our study streams, we demonstrated a slight increase in the annual mean interaction strength with temperature—consistent with previous studies (O'Gorman et al. 2012, O'Gorman et al. 2017, O'Gorman et al. 2019) and the destabilization of food webs. Strong to weak interactions often align along the spectrum of ‘fast’ and ‘slow’ energy channels (Rooney et al. 2006) and we found that energy flux in warm streams (>15 °C annual mean temperature) tended to favor ‘fast’, high P:B taxa, supporting this as a mechanism for warming to destabilize food webs. Understanding how these seemingly unstable ecosystem states persist may give insight into the general impacts of warming on ecosystem stability and function.

Food web instability that is driven by high interaction strengths arises, in part, because of decoupling between consumers and resources and the potential for 'over-fueling' consumer populations (e.g., paradox of enrichment; Rosenzweig 1971, Rip and McCann 2011). Yet, high per capita fluxes (i.e., interaction strengths) that are measured at one point in time may not represent interactions that unfold at finer timescales or among seasons. In systems with high interaction strengths and strong internal feedbacks, consumer demand and resource availability should be tightly coupled in time, leading to consistent interaction strength distributions in time (Figure 4.1A). We found that warmer streams, while exhibiting higher mean interaction strength, also had lower temporal variability in interaction strength distributions. This pattern suggests that consumers tracked changes in resource abundance in warm streams. In addition, low variation in B_{cr} at higher temperatures supports the idea that even with large per capita fluxes to consumers, consumer biomass accumulation and resource growth were more in balance and resource declines during low light periods were associated with concomitant reductions in consumer biomass (e.g., mortality, emergence, emigration). In cold streams consumer demand and resource availability were more decoupled, despite lower absolute variability in basal resource biomass. In some cases, the mismatch between consumer demand and resource biomass led to per capita interaction strengths in cooler streams that were as strong or stronger than in warmer streams. Temporal comparisons between consumer-resource interactions and biomass distribution reveal important information about food web processes and the ultimate fates of energy flux in ecosystems. Continued

exploration of these patterns at fine timescales in other ecosystems could provide important insights into the responses of ecosystems to warming.

Our research provides a comprehensive empirical assessment of how temperature influences energy flux in stream food webs. Our work also provides a novel quantification of interaction strengths at different temporal scales in an effort to understand how warming may influence food web stability. We show that other sources of environmental variation, independent of temperature, can play an important role in regulating the timing of fluxes. In addition, we show that environmental variability and temperature may interact to structure species diversity, food web structure, patterns of life-history, and consumer-resource interactions. The consideration of all of these factors will ultimately determine how temperature controls the distribution of energy flux in food webs. However, these questions can only be addressed by studying food webs at timescales that are relevant with respect to environmental variation. Recent efforts to combine biomass estimates with mechanistic models of organism metabolism represent an important step towards closing this gap (Barnes et al. 2018). Yet, given the wide variation in statistical and mechanistic models of organismal metabolism and production (Benke 1993, Tilman et al. 2004), empirical measurements of energy flux are still necessary, as is, the further integration of energy flux and species-dynamic approaches in conceptual and mechanistic models of food webs. Moreover, embracing the environmental variation that is inherent in most natural ecosystems is crucial if we are to understand and predict the short- and long-term influence of warming on food webs, ecosystems and the goods and services they provide.

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Table 4.1. Physical and chemical characteristics of the study streams. Temperature represents the annual mean temperature in degrees Celsius and discharge is represented by the annual median values. Temp-light correlation represents Pearson's correlation coefficient between daily light intensity and temperature.

Stream	Temperature (° C)	Median Discharge (L/s)	DIN ($NO_3^- + NH_4^+$ mg L^{-1})	SRP (mg L^{-1})	DIN:SRP (molar)	Temp–Light correlation (Pearson's *r*)
hver	27.2	21.0	0.007	0.022	0.7	0.67
st6	17.6	13.7	0.026	0.029	2.0	-0.09
st9	11.2	3.0	0.003	0.033	0.2	0.48
st7	5.8	3.9	0.027	0.033	1.8	0.41
oh2	5.5	12.5	0.008	0.050	0.4	0.57
st14	5.0	12.5	0.025	0.013	4.4	0.47

Table 4.2. Estimated ordinary least squares slopes and coefficients of determination (R^2) for rank-rank relationships between species-level mean body mass (mg AFDM ind^{-1}), production-to-biomass ratio (y^{-1}), and mean annual population biomass (mg AFDM m^{-2}) versus mean annual consumption fluxes (mg AFDM m^{-2} y^{-1}). Streams are ordered in descending order of mean annual stream temperature from warmest to coldest.

	Bodysize		P:B		Biomass	
Stream	**Estimate**	**R^2**	**Estimate**	**R^2**	**Estimate**	**R^2**
hver	0.29	0.08	0.95	0.91	0.78	0.61
st6	0.13	0.02	0.20	0.04	0.79	0.63
st9	0.27	0.07	0.45	0.20	0.66	0.44
st7	0.17	0.03	0.42	0.17	0.75	0.69
oh2	0.01	>0.001	0.35	0.13	0.78	0.61
st14	0.67	0.58	-0.20	0.04	0.86	0.93

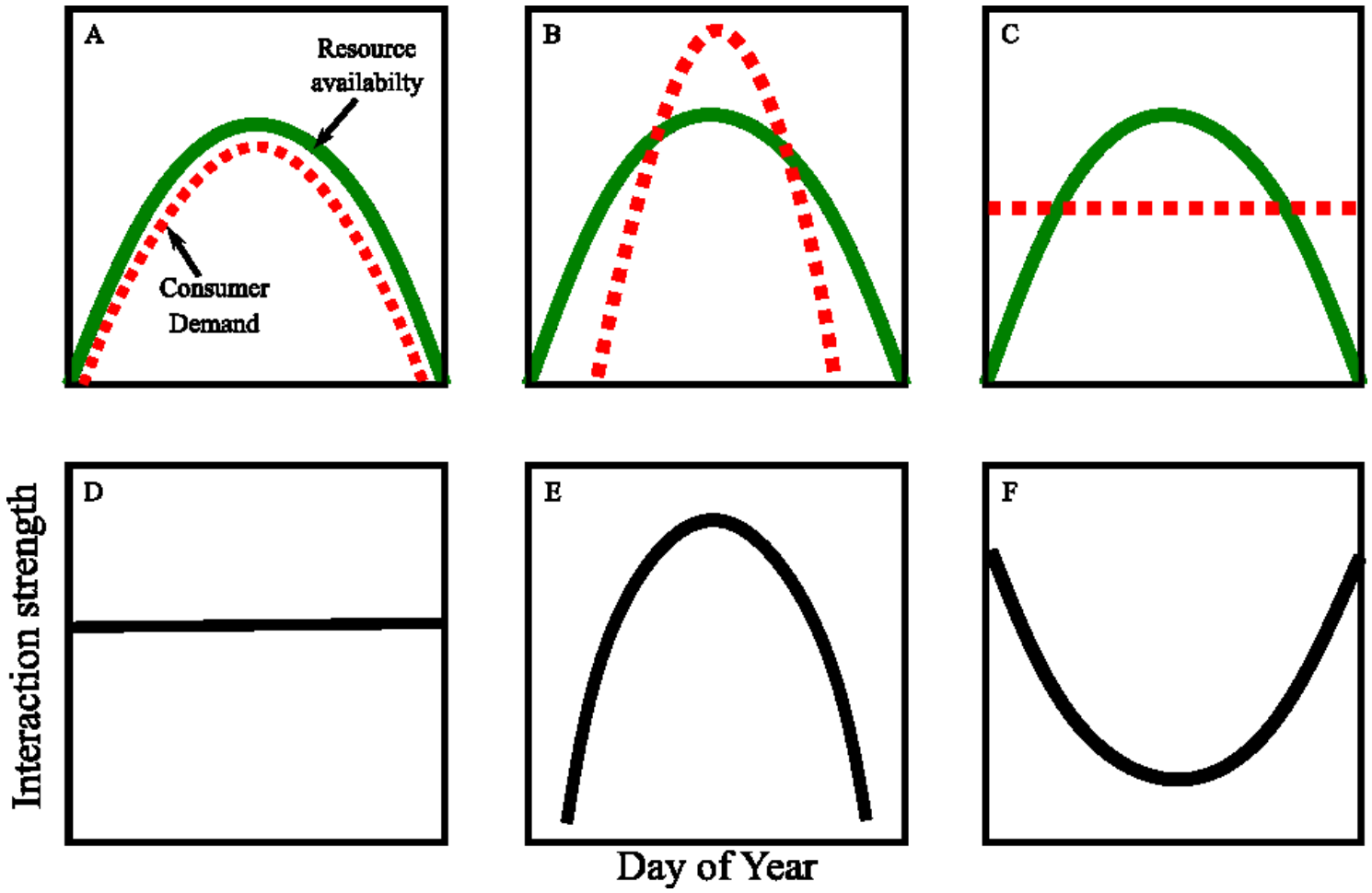

Figure 4.1. Conceptual model of the coupling of resource availability and consumer demand in seasonal ecosystem. The top panels (A – C) depict variation in resource availability (solid green line) when temporal patterns are controlled by extrinsic environmental driver (e.g., light availability in high latitude systems). The hypothetical patterns of consumer demand range from A) completely coupled, B) lagged, over-shoot dynamics, and C) constant demand completely decoupled from resources. Each of these scenarios leads to distinct qualitative patterns in interaction strengths through time (panels D – F).

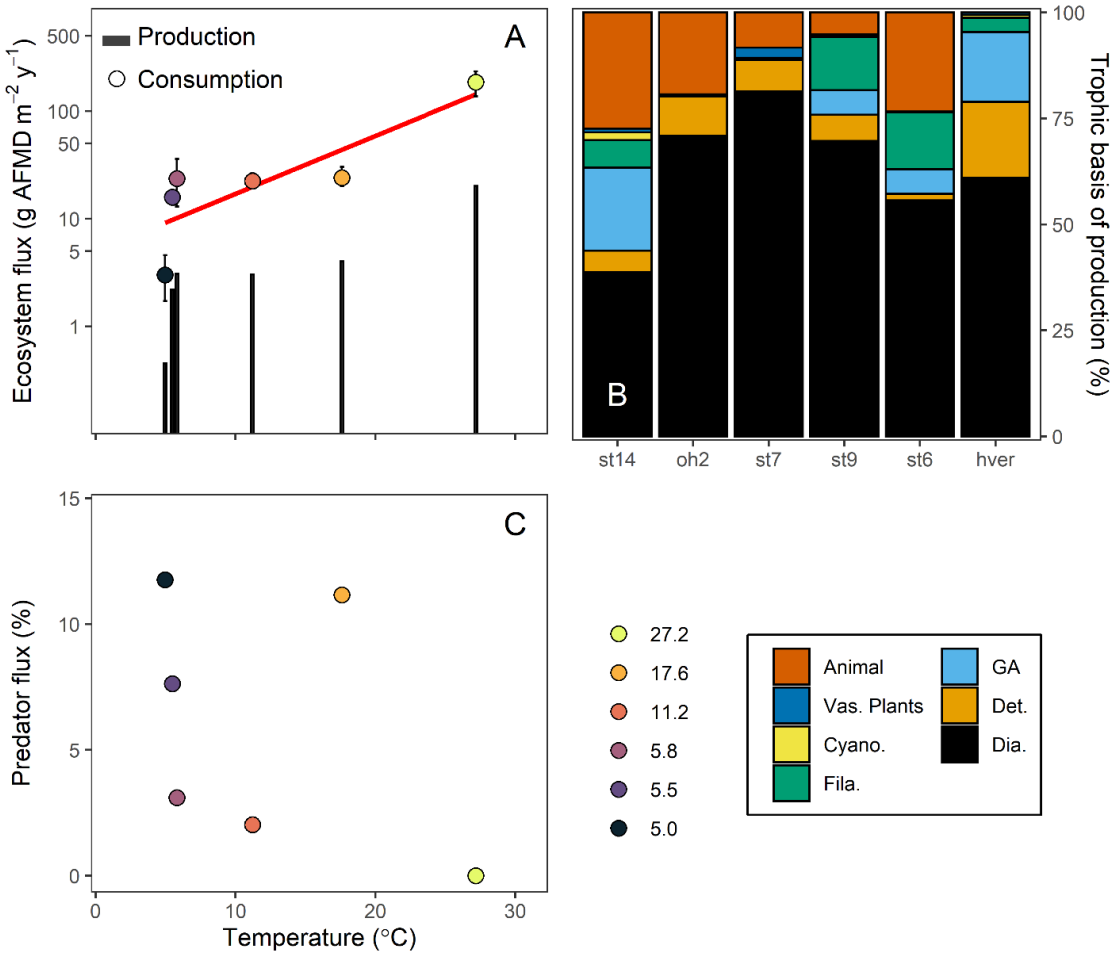

Figure 4.2. A) The relationship between temperature and whole-community consumption and secondary production (mg AFDM m^{-2} y^{-1}); B) the relative contribution of diet items to secondary production (i.e. trophic basis of secondary production; %); and C) the proportion of total annual consumption by predators. Point fill is ordered by mean annual stream temperature (°C) shown in legend labels. Diet category abbreviations for panel b are: "Animal" = animal material, "Vas. Plants" = vascular plant material, "Cyano." = cyanobacteria, "Fila." = filamentous algae, "GA" = green algae, "Det." = amorphous detritus, "Dia." = diatoms.

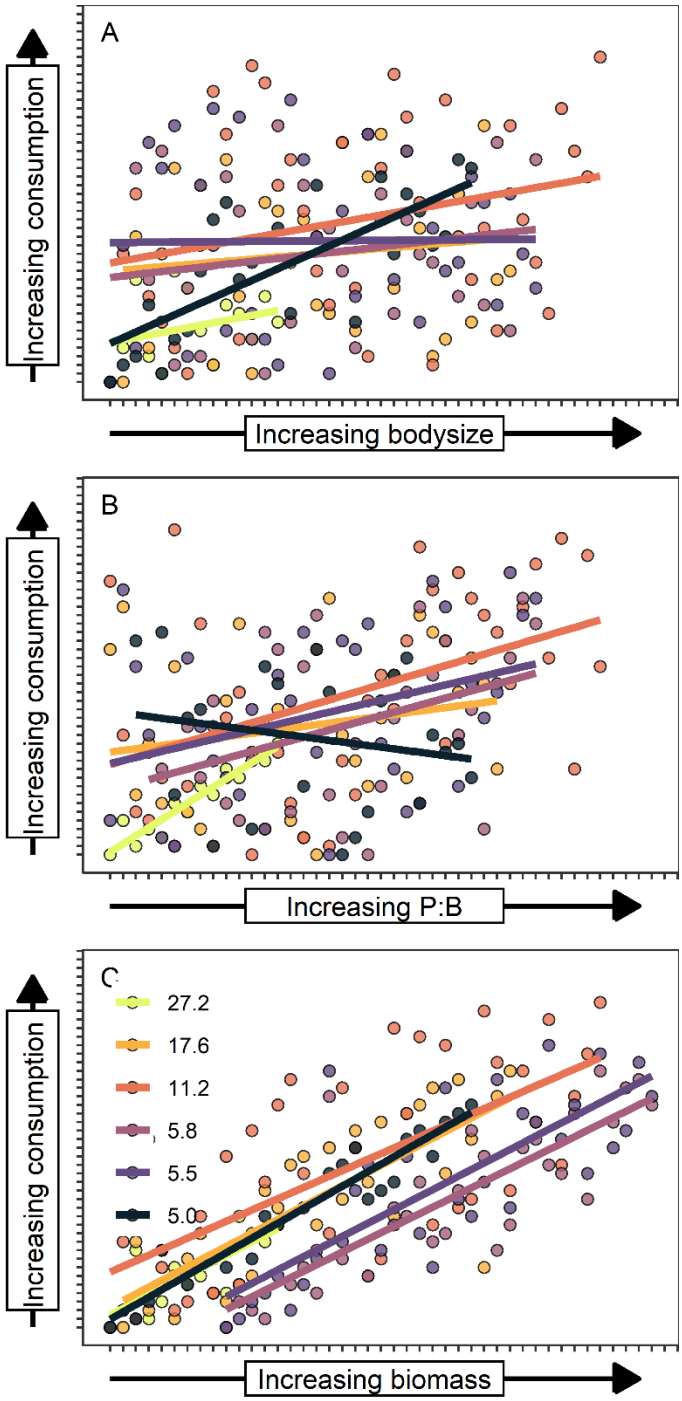

Figure 4.3. Rank-rank plots of annual consumption (mg AFDM m^{-2} y^{-1})in relation to three taxon-level attributes: A) mean individual body size (mg AFDM ind^{-1}), B) annual production to biomass ratio (P:B; y^{-1}), and C) mean annual population biomass (mg AFDM m^{-2}). Point fill is ordered by mean annual stream temperature (°C) shown in legend labels. Each point represents a single population's rank position rather than absolute values. Estimates of correlations and coefficients of determination are found in Table 4.2.

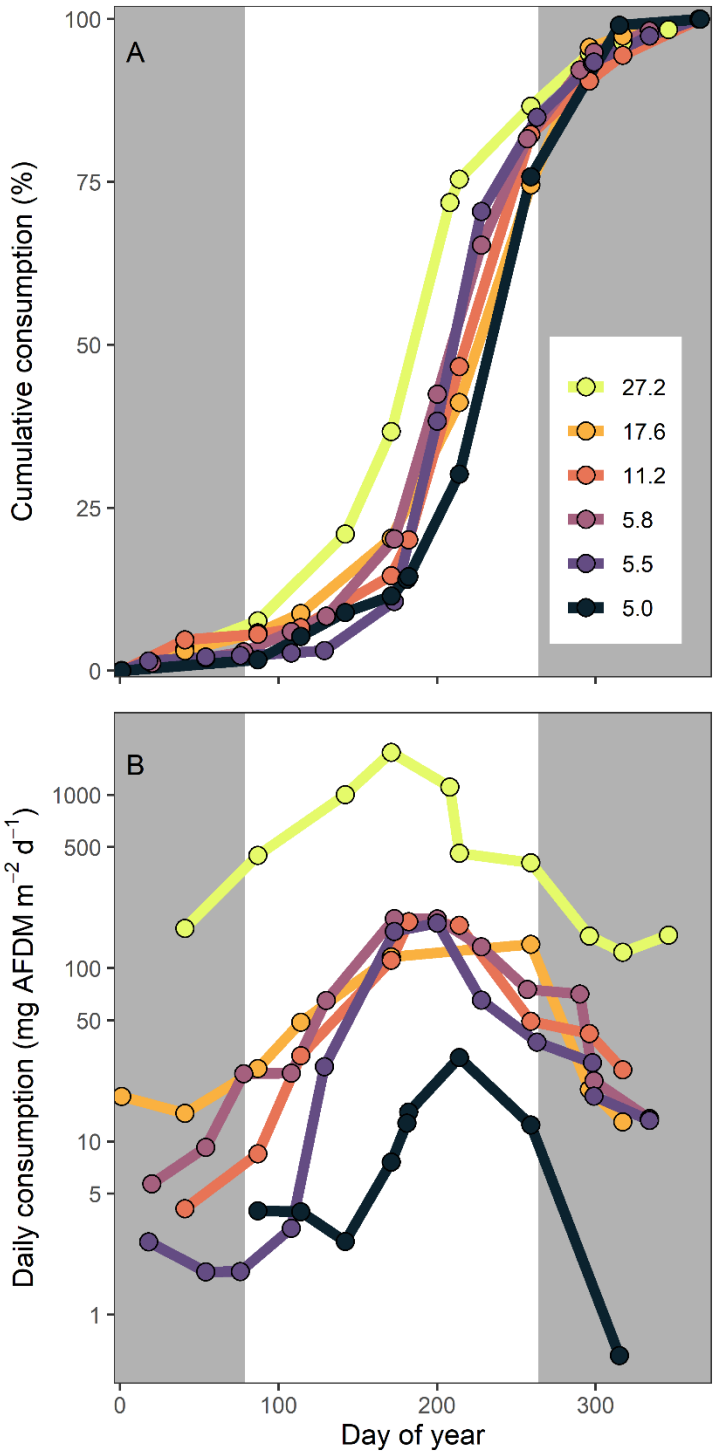

Figure 4.4. Temporal patterns in A) cumulative consumption (as % of total annual consumption) among streams and B) daily consumption rates (mg AFDM m^{-2} d^{-1}) throughout the year. Shaded regions represent times of the year with ≥12 hours of darkness between the fall and spring equinox. Point fill is ordered by mean annual stream temperature (°C) shown in legend labels.

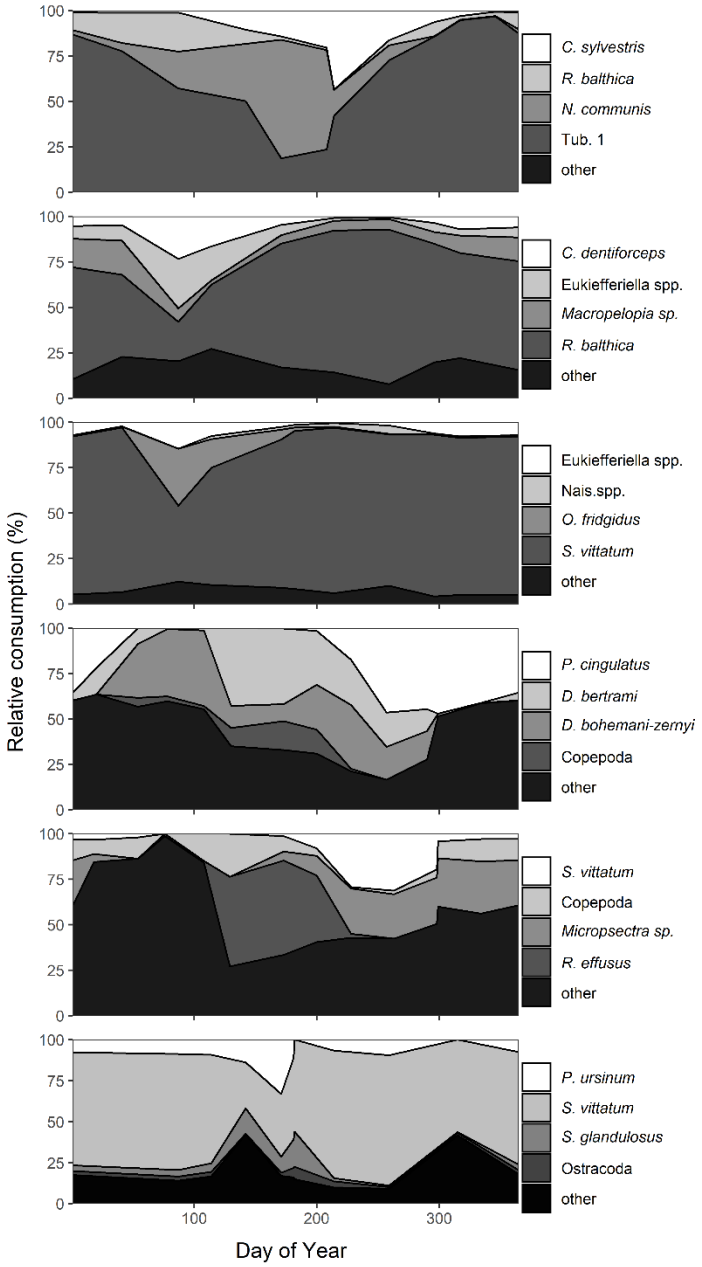

Figure 4.5. The percent contribution of dominant taxa to total community-level consumption fluxes over the year. The contribution of the four most dominant taxonomic groups are highlighted with different grayscales. The summed contribution of all other taxa is represented by black shading. Each panel represents a single study and panels are arranged by descending annual stream temperature (top: Hver = 27.2 °C, bottom: st14 = 5.0 °C).

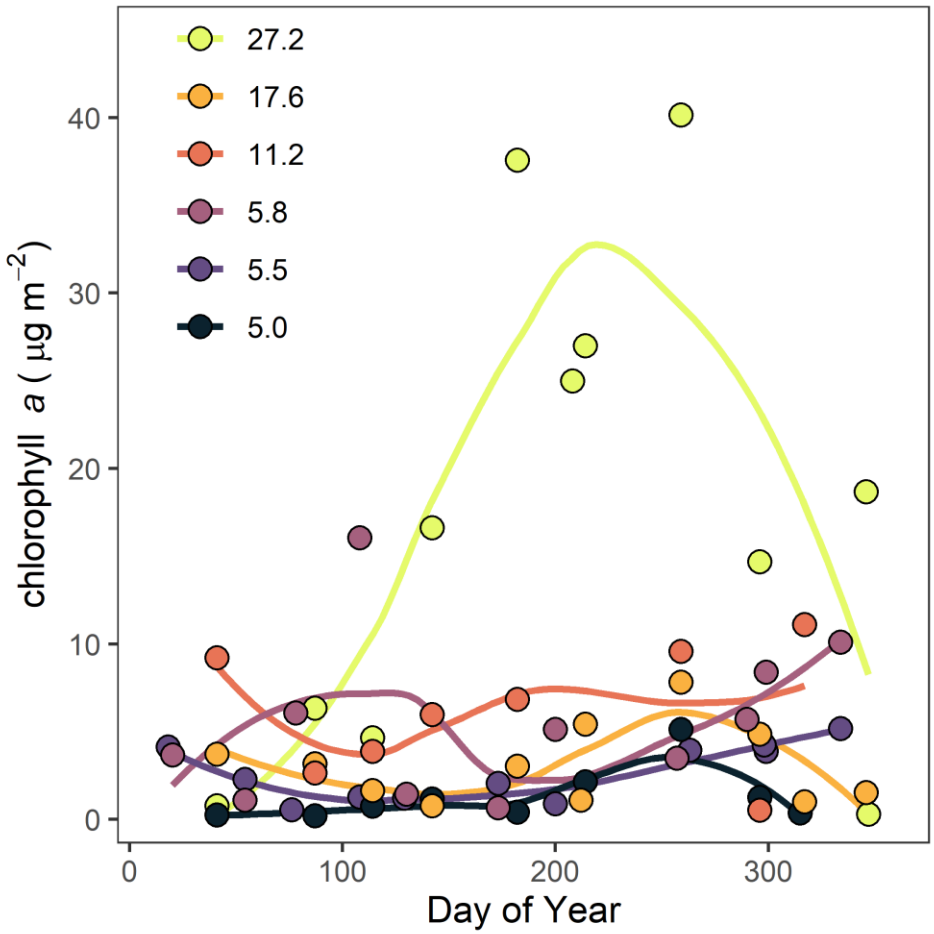

Figure 4.6. Intra-annual patterns of chlorophyll *a* biomass in all study streams. Locally estimated scatterplot smoothing (LOESS) was added to ease visualization (span = 0.90). Point fill is ordered by mean annual stream temperature (°C) shown in legend labels.

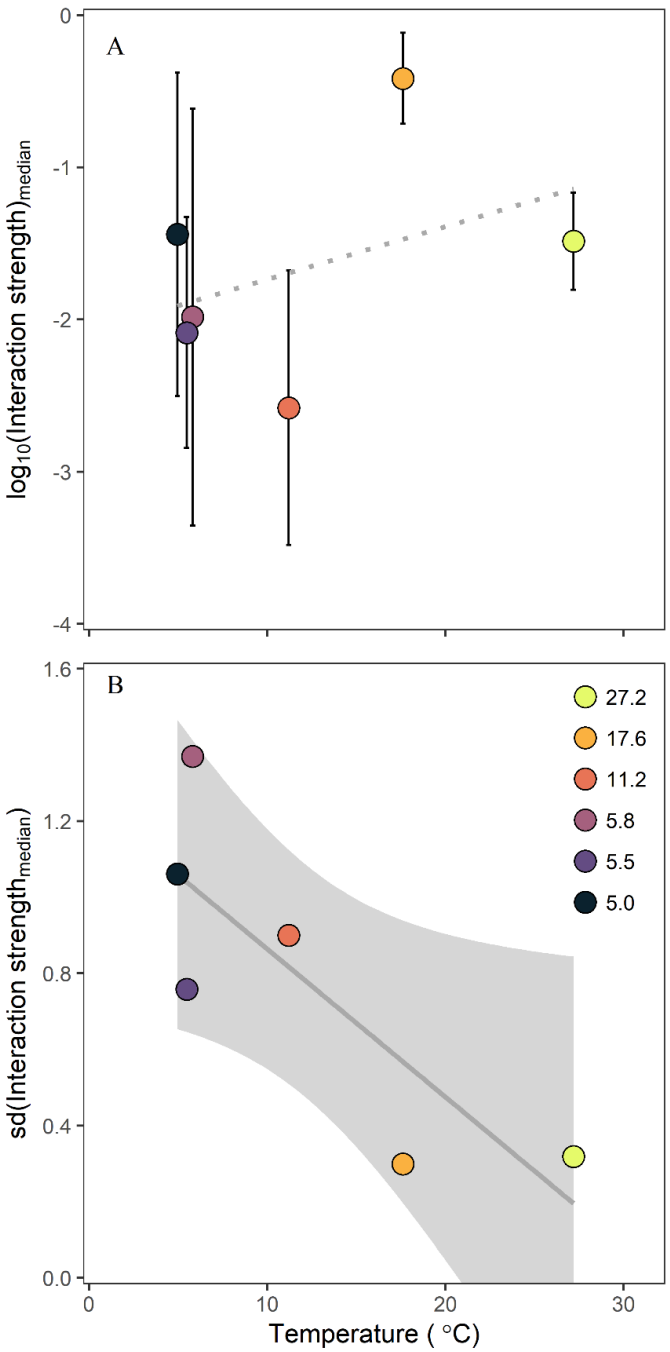

Figure 4.7. Bivariate relationship between mean annual temperature and A) $\log_{10}$-transformed interaction strengths of invertebrate consumers on basal resources. Error bars represent the standard deviation in the median $\log_{10}$-transformed interaction strength among intervals; and B) standard deviation in the median interaction strength as a function of mean annual temperature. The ordinary least squares linear relationship and 95% confidence bands of the relationship between the standard deviation in median interaction strength and mean annual stream temperature are shown. Point fill represents mean annual stream temperature (°C) shown in legend labels.

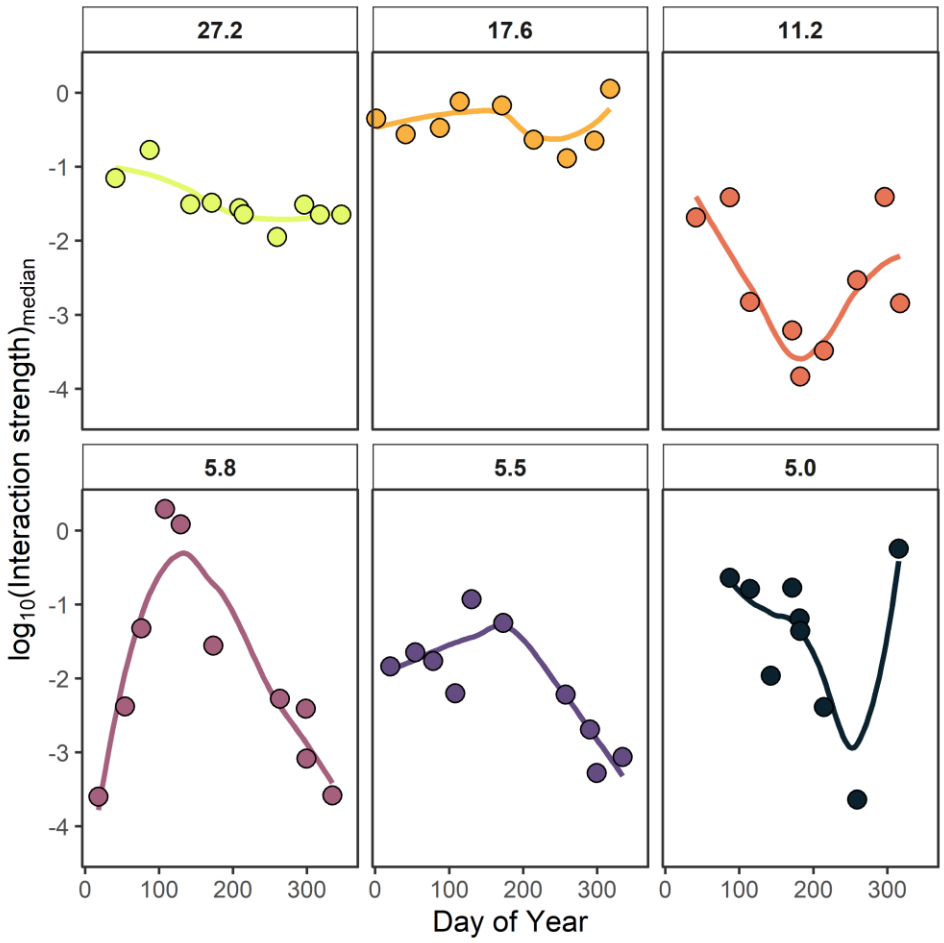

Figure 4.8. Within-stream temporal patterns of median interaction strength (log_{10}-transformed) of consumers on basal resources. Full interaction strength distributions are shown in the supplemental material Figure S4.8. Each point represents the median interaction strength from the distribution of all taxon-level interaction strengths. Locally-estimated scatterplot smoothing (LOESS) lines are shown to aid interpretation (span = 0.90). Point fill is ordered by mean annual stream temperature (°C) shown in plot titles.

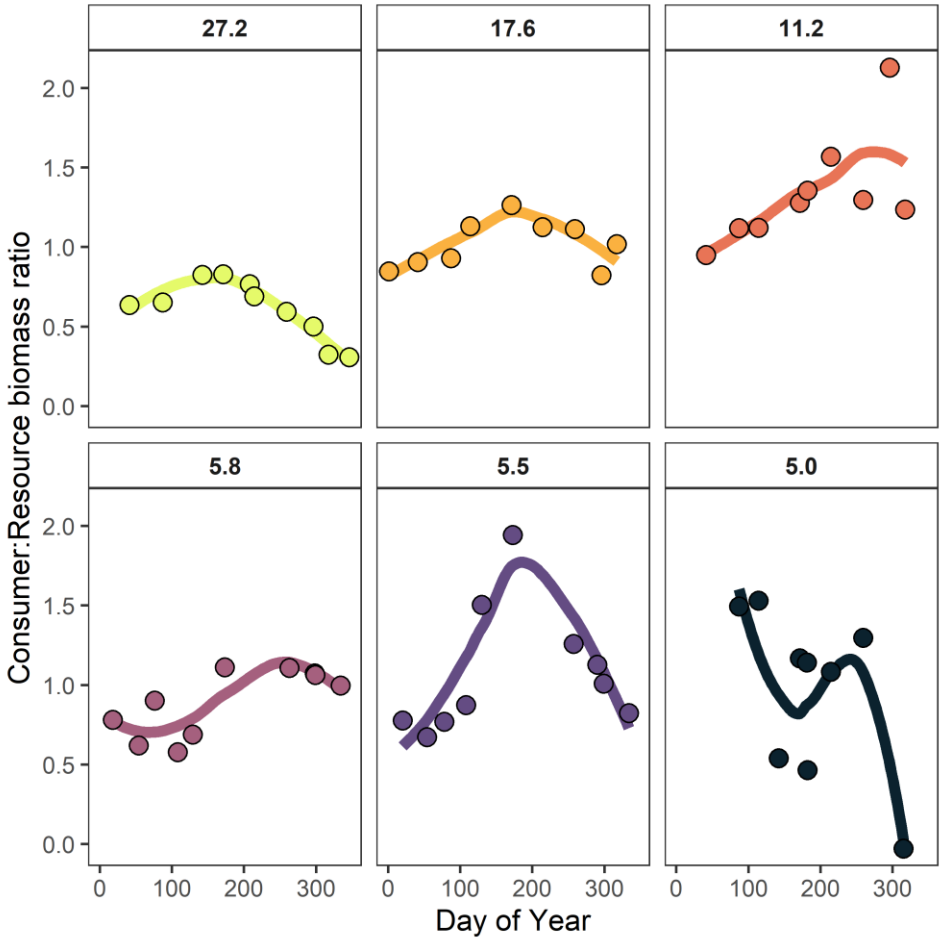

Figure 4.9. Within-stream temporal patterns of consumer:resource biomass ratios (B_{cr}). B_{cr} was calculated as the ratio of $\log_{10}$-transformed mean biomass on each sampling date. Locally-estimated scatterplot smoothing (LOESS) lines are plotted to aid interpretation (span = 0.90). Point fill is ordered by mean annual stream temperature (°C) shown in plot titles.

CHAPTER FIVE

GENERAL CONCLUSIONS

A growing body of work is beginning to disentangle the effects of temperature on aquatic ecosystem structure and function (e.g., Hogg and Williams, 1996; Friberg and others, 2009; Woodward and others, 2010; Yvon-Durocher and others, 2010; Gudmundsdottir and others, 2011; Yvon-Durocher and others, 2011; O'Gorman and others, 2012; Hannesdóttir and others, 2013; Welter and others, 2015; Demars and others, 2016; Williamson and others, 2016; Nelson and others, 2017a, b; O'Gorman and others, 2017; Padfield and others, 2017; and Hood and others, 2018 *as a non-exhaustive and highly biased subset of work*). These studies have highlighted important mechanisms through which temperature influences ecosystems; however, many represent snapshots or patterns over relatively short time periods. Further, studies of patterns over longer time periods (i.e., intra-annual) often represent experimental warming experiments, where transient patterns may not capture longer-term processes that may modify the effects of warming over the next century. The research in this dissertation emphasized the influence of temperature both in the context of other environmental drivers and throughout an annual cycle. My specific questions were: 1) what is the relative influence of temperature and stream flow on whole-ecosystem biomass and element storage? 2) how does temperature shape patterns of animal production *across* streams and *within* a stream throughout the year? and 3) how does temperature modify the seasonal patterns of consumer-resource interactions in stream food webs? The first two chapters examined aspects of distinct ecosystem compartments—epilithic primary producers and

macroinvertebrate consumers. These data, along with information on consumer diets, were used to construct material flow food webs through time allowing me to follow the dynamics of food webs in systems of widely varying temperature. Each of these chapters led to new insights into the control of temperature on patterns and processes in stream ecosystems.

The first study (chapter 2), started with an observation early in the course of the study that patterns of 'stuff' within streams was not obviously related to temperature. Conspicuous plants such as bryophyte and macrophyte species, seemed to occur more frequently and at higher biomass in warmer streams, but there were marked deviations from this pattern. Findings from this chapter showed that temperature, while the most obvious gradient among the streams in the watershed, played a secondary role to stream flow in determining patterns of organic matter among streams. The large variation in organic matter pool size was the main determinant of element pools and was associated with a systematic decrease in the relative concentration of nitrogen (N) in larger biomass pools. However, the stoichiometry of N and phosphorus (P) was relatively fixed despite large differences in total organic matter mass and composition. These findings highlight the importance of shifting precipitation and stream flow gradients which overlay temperature changes in determining the storage and cycling of organic matter and elements in ecosystems.

Based on the findings in chapter 2, I chose to narrow the focal streams in chapter 3 to maintain consistent primary producer communities, at least functionally. Within this subset of streams, I aimed to test a specific extension of the metabolic theory of ecology (Brown and others, 2004)—that of the temperature-independence of secondary

production. To my knowledge, this is the first explicit and robust test of this prediction. I showed qualitative support for some predictions of MTE, that consumer biomass should decrease, and consumer biomass turnover rates should increase with temperature. However, these changes were more pronounced than expected and occurred at different magnitudes, leading to both qualitative and quantitative deviations from the MTE predictions and a strong positive relationship between temperature and secondary production. However, measurement of basal resource availability showed a similarly strong positive relationship with temperature. Interestingly, basal resource biomass explained the patterns in community secondary production at the annual timescale yet was a relatively poor predictor at intra-annual timescales. Throughout the year, incorporating drivers of basal resource *production*, i.e., light availability and temperature, improved the prediction of secondary production both across and within streams. This showed that basal resource availability was important on both annual and intra-annual timescale in shaping patterns of secondary production. Further, explicit attention should be paid to defining what 'resource availability' means to realize the full utility of the MTE.

The final study, chapter 4, brought together information from chapters 2 and 3 to 'connect the dots' of feeding relations within the food webs. Here, given the drastic seasonality of light availability within these streams I focused on how temperature alters the response of food webs to seasonal changes in light and basal resource availability. I found that consumer demands and basal resource availability were strongly coupled in time at higher temperatures compared to cooler streams. This manifested as consistent interaction strengths and consumer:resource biomass ratios in warmer streams. These

patterns suggest that the influence of temperature on energetic requirements of consumers shaped consumer life history, production, and mortality around the seasonal availability of basal resources. In contrast, at cooler temperatures organism growth and life history showed weaker relationships with basal resource availability in time. As stream ecosystems continue to warm, the higher metabolic demands of consumers might shift population and community traits to track basal resource dynamics. In a world where variability is the rule (Levin, 1992; White and Hastings, 2018), key information for predicting animal production of warmer ecosystems will be characterizing the spatial and temporal scales of variability in basal resources and their drivers.

Together, the research in this dissertation showed that there is much work to be done if we are to understand the complete influence of current and future warming on Earth's ecosystems. If I were to highlight a single common thread, it is that the effects of temperature are mediated through interactions with other ecosystem drivers and their variability in space and time. Understanding how patterns of warming overlay other environmental gradients is crucial, as is their explicit recognition and measurement when designing future research programs.

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APPENDICES

APPENDIX A

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 2

Table S2.1. Correlation between physicochemical stream variables and mean annual stream temperature among streams. PC1 and PC2 represent the first and second principal component axis of stream flow variables.

	Spearman's *p*	p-value
DIN (mg NO_3 L^{-1})	0.28	0.40
SRP (mg SRP L^{-1})	0.67	0.03
CV_Q	-0.50	0.12
Median Q (L s^{-1})	0.03	0.95
Stream power (Watts)	-0.52	0.11
Median substrate (mm)	0.03	0.95
PC1	0.43	0.19
PC2	-0.05	0.88

Table S2.2. Patterns of mean values and measures of variability in molar C:N, C:P, and N:P ratios of individual OM compartments and aggregate organic matter pools from the current study and previous literature.

		CN			CP			NP		
	#	mean	sd	cv	mean	sd	cv	mean	sd	cv
Ecosystem BOM*	11	17.0	6.0	0.35	143	53	0.37	8.8	3.2	0.36
Individual OM compartments*	199	16.8	7.7	0.46	184	167	0.91	10.8	7.5	0.69
Aquatic plant communities[1]	72	20.1	2.8	0.28	805	348	0.43	29.2	14.0	0.35
Individual aquatic plants[1]	184	20.6	5.8	0.28	815	484	0.60	39.2	21.0	0.55
Terrestrial plants[2]	406	36.0	23.0	0.64	968	731	0.75	28.0	15.0	0.54
Freshwater seston[2]	267	10.2	3.0	0.29	307	212	0.69	30.2	16.0	0.53
Boreal periphyton[3]	279	13.5	2.5	0.18	733	654	0.89	49.7	29.0	0.58

Note: sd = 1 standard deviation, cv = coefficient of variation *This study; [1]Frost et al 2012; [2]Elser et al. 2000; [3]Frost 2006

Model selection of ecosystem biomass stoichiometry

Given the potential for complex relationships between ecosystem stoichiometry and environmental variables, we used Akaike's information criterion corrected for small sample sizes (AICc) to describe the environmental variables that best explained ecosystem biomass stoichiometry. For these models, in addition to a null 'intercept-only' model, we compared models representing a suite of competing hypotheses about the determinants of ecosystem stoichiometry. These models included a full 'Flow' model including the first and second principal component axes (PC1 + PC2), a temperature-only model ('Temp'), along with additive (PC1+PC2+Temp) and interactive (PC1+PC2+Temp+PC1:Temp+PC2:Temp) flow–temperature models. In addition, we included nutrient models that included the dissolved concentrations or ratios of relevant nutrients (mg $NH_4 + NO_3$ L^{-1} for C:N, mg SRP L^{-1} for C:P, and $NH_4 + NO_3$:SRP ratio for N:P). Finally, we also tested models including only single components of the flow principal component analysis (PC1). We included this model due to the inherent penalty associated with adding model variables within the AICc framework. Here, values of ΔAICc ~2 but with an additional variable represent similarly supported models. Models with ΔAICc <2 and additional variables suggest models with higher support.

Table S2.3. Model selection of environmental drivers of ecosystem BOM C:N ratios. The 'Flow*' model represents a model including only the first principal component axis (PC1) compared to the full 'Flow' model with both the first and second axes (PC1 + PC2). The nutrient model represents dissolved DIN concentration (mg NH_4 + NO_3 L^{-1}). AICc represents Akaike's Information Criterion adjusted for small sample sizes, K is the number of variables included in each model, ΔAICc is the change in AICc from the top model, ModelLik represents the relative model likelihood, AICc wt. is the model weight, LL is the model log likelihood, and Cum. wt. is the cumulative model weights.

Model	K	AICc	Δ AICc	ModelLik	AICc wt.	LL	Cum. wt.
Flow*	3	71.5	0.00	1.00	0.60	-31.05	0.60
Nutrients	3	73.4	1.90	0.39	0.23	-32.00	0.83
Intercept	1	74.9	3.38	0.18	0.11	-34.71	0.94
Flow	4	76.7	5.14	0.08	0.05	-31.01	0.98
Temp	3	78.8	7.25	0.03	0.02	-34.68	1.00
Flow+Temp	5	83.0	11.50	0.00	0.00	-30.52	1.00
Flow*Temp	7	106.8	35.27	0.00	0.00	-27.74	1.00

Table S2.4. Model selection of environmental drivers of ecosystem BOM C:P ratios. The 'Flow*' model represents a model including only the first principal component axis (PC1) compared to the full 'Flow' model with both the first and second axes (PC1 + PC2). The nutrient model represents dissolved SRP concentration (mg SRP L^{-1}). AICc represents Akaike's Information Criterion adjusted for small sample sizes, K is the number of variables included in each model, ΔAICc is the change in AICc from the top model, ModelLik represents the relative model likelihood, AICc wt. is the model weight, LL is the model log likelihood, and Cum. wt. is the cumulative model weights.

Model	K	AICc	Δ AICc	ModelLik	AICc wt.	LL	Cum. wt.
Flow*	3	119.2	0.00	1.00	0.59	-54.89	0.59
Flow	4	120.7	1.49	0.47	0.28	-53.02	0.86
Intercept	1	122.9	3.68	0.16	0.09	-58.70	0.96
Nutrients	3	125.8	6.55	0.04	0.02	-58.17	0.98
Temp	3	126.5	7.32	0.03	0.02	-58.55	0.99
Flow+Temp	5	128.0	8.79	0.01	0.01	-53.00	1.00
Flow*Temp	7	154.2	34.95	0.00	0.00	-51.42	1.00

Table S2.5. Model selection of environmental drivers of ecosystem BOM N:P ratios. The 'Flow*' model represents a model including only the first principal component axis (PC1) compared to the full 'Flow' model with both the first and second axes (PC1 + PC2). The nutrient model represents dissolved molar DIN:SRP ratio. AICc represents Akaike's Information Criterion adjusted for small sample sizes, K is the number of variables included in each model, ΔAICc is the change in AICc from the top model, ModelLik represents the relative model likelihood, AICc wt. is the model weight, LL is the model log likelihood, and Cum. wt. is the cumulative model weights.

Model	K	AICc	Δ AICc	ModelLik	AICc wt.	LL	Cum. wt.
Nutrients	3	57.1	0.00	1.00	0.85	-23.83	0.85
Intercept	1	61.3	4.22	0.12	0.10	-27.91	0.96
Flow*	3	65.1	7.98	0.02	0.02	-27.82	0.97
Temp	3	65.2	8.14	0.02	0.01	-27.90	0.99
Flow	4	65.5	8.39	0.02	0.01	-25.41	1.00
Flow+Temp	5	72.2	15.07	0.00	0.00	-25.08	1.00
Flow*Temp	7	100.3	43.23	0.00	0.00	-24.49	1.00

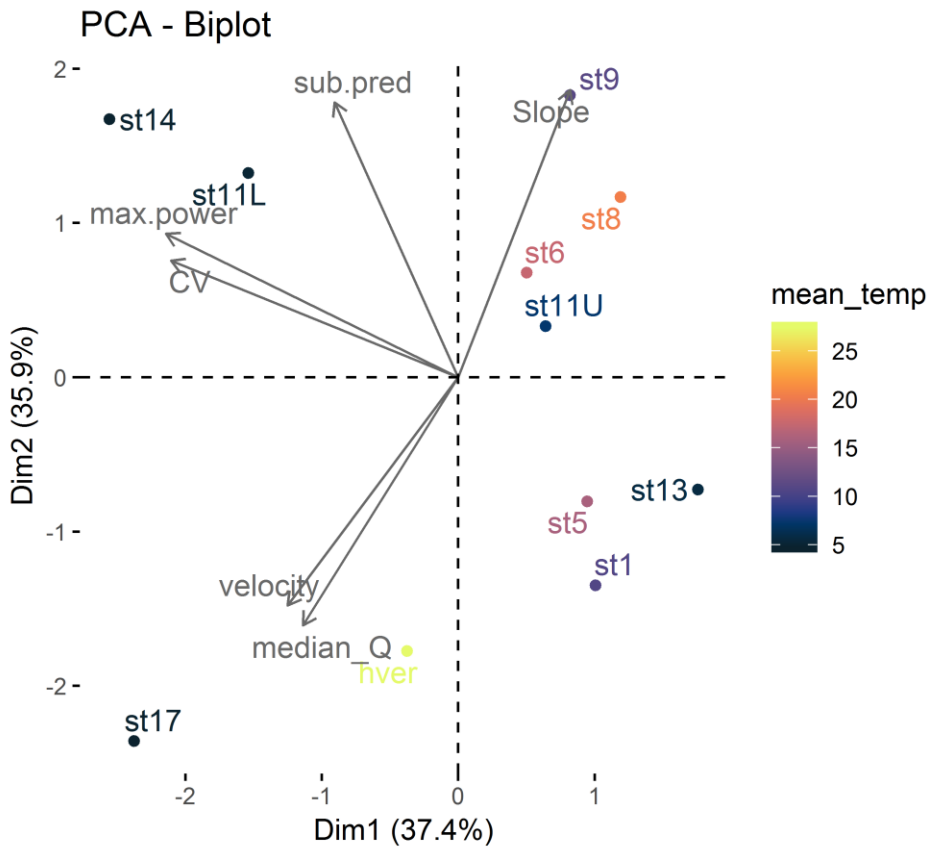

Figure S2.1. Biplot of the first two principal component axes of stream flow characteristics. Annual mean temperature is represented by point and label color.

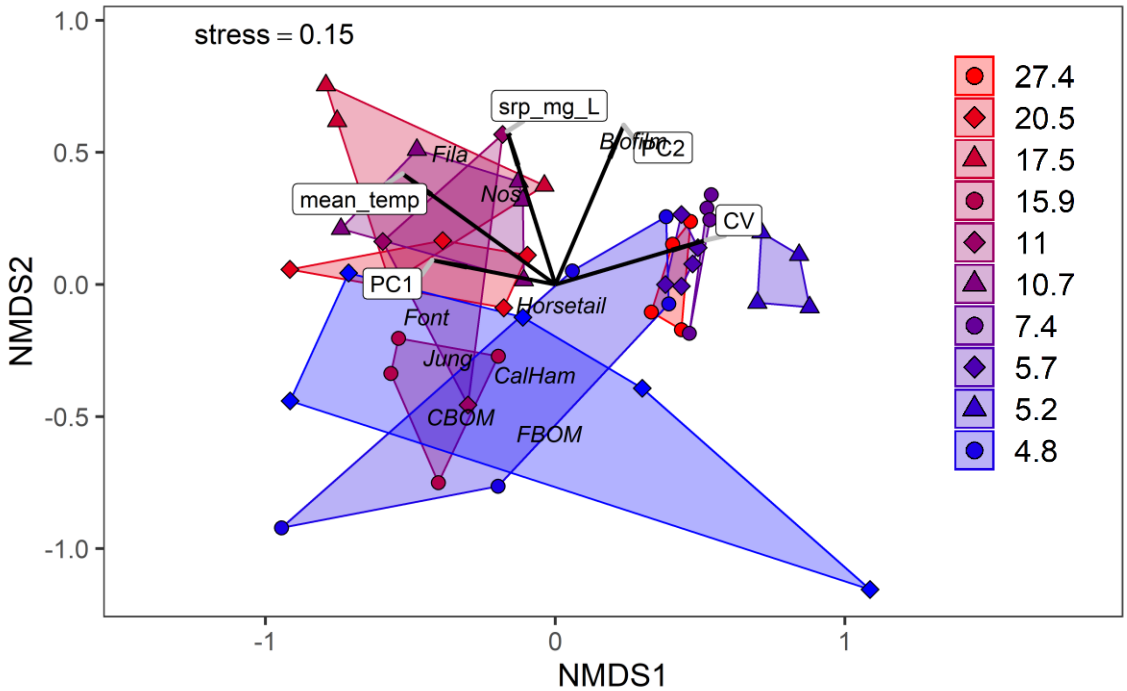

Figure S2.2. Non-metric multidimensional scaling plot of benthic organic matter communities. Streams are arranged from highest to lowest annual mean temperature and samples within streams are distinguished by similar color and point shapes. Convex hulls enclose the multidimensional space encompassed by each stream community. Vectors of environmental variables associated with differences among stream communities relate to the point in multidimensional space with the strongest correlation. Similarly, OM compartments contributing to community differences among streams are plotted at the point in space of strongest correlation. Organic matter categories are abbreviated as: "FONT" = *Fontinalis antipyretica*, "JUNG" = *Jungermannia exsertifolia*, "FILA" = Filamentous algae, "NOS" = *Nostoc* spp., "BIOFILM" = epilithic biofilm, "CBOM" = coarse benthic organic matter, "FBOM" = fine benthic organic matter, "CALHAM" = *Callitriche* spp., and "HORSETAIL" = *Equisetum* spp.

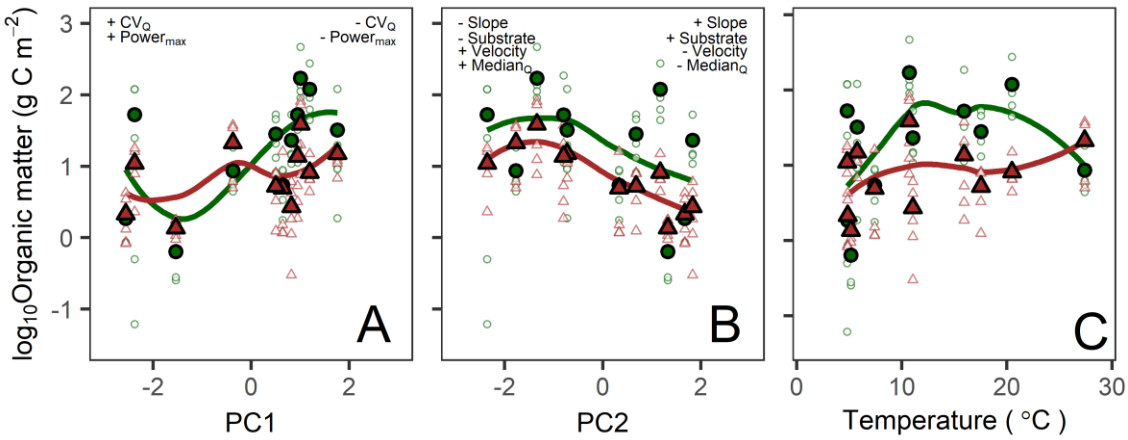

Figure S2.3. The relationships between $\log_{10}$-transformed epilithic (green circles and lines) and detrital (brown triangles and lines) biomass and principal components one (A), principal component two (B), and annual mean temperature (C). Mean values of each stream are shown in large points, while individual samples are displayed in small open circles. Environmental variables most strongly associated with principal components ($|r| > 0.40$) are displayed in text of principal component plots (A and B).

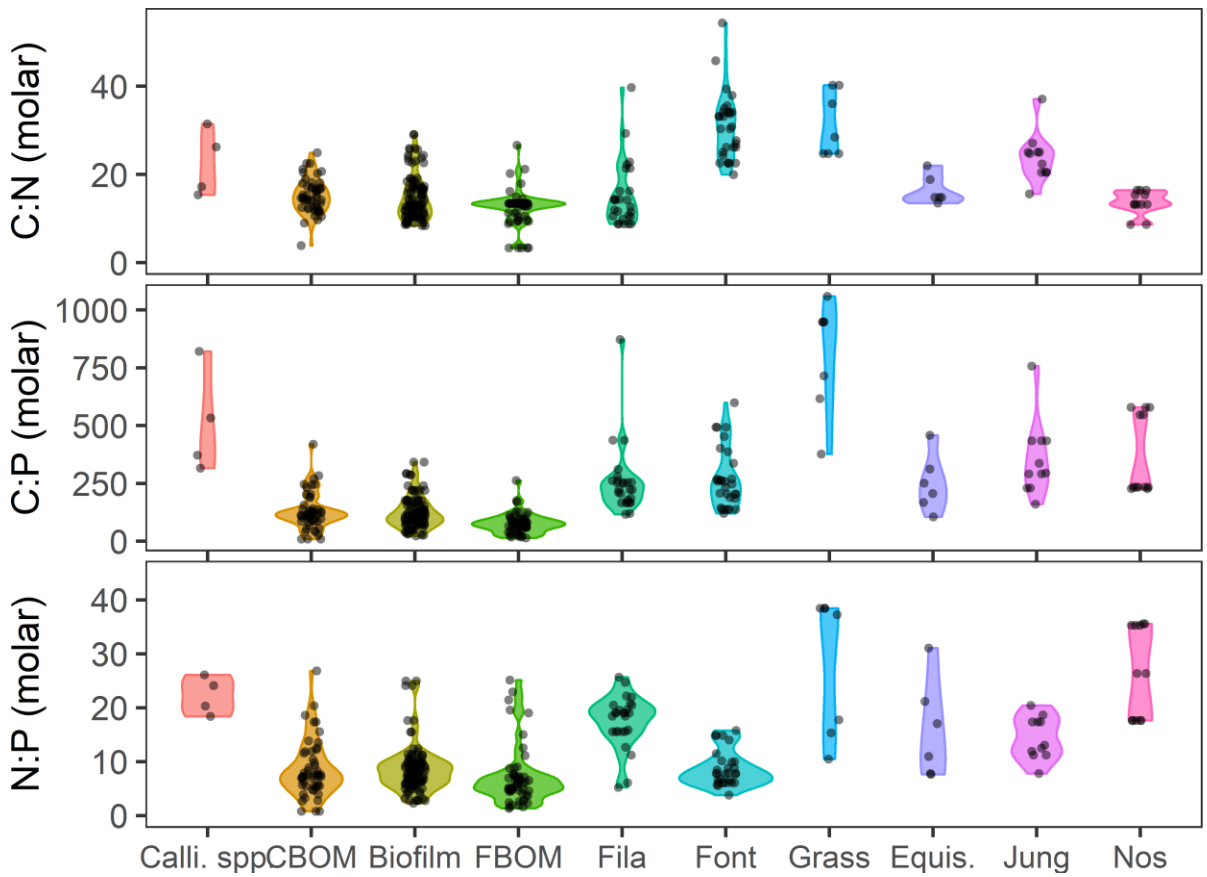

Figure S2.4. Patterns in compartment-level molar C:N:P stoichiometry across all streams. "Calli. spp." = species of the genus *Callitriche*, "CBOM" = coarse benthic organic matter, "FBOM" = fine benthic organic matter, "Fila" = filamentous algae, "Font" = *Fontinalis antipyretica*, "Grass" = *Bromus* spp., "Equis." = *Equisetum* spp., "Jung" = *Jungermannia exsertifolia*, and "Nos" = *Nostoc* spp.

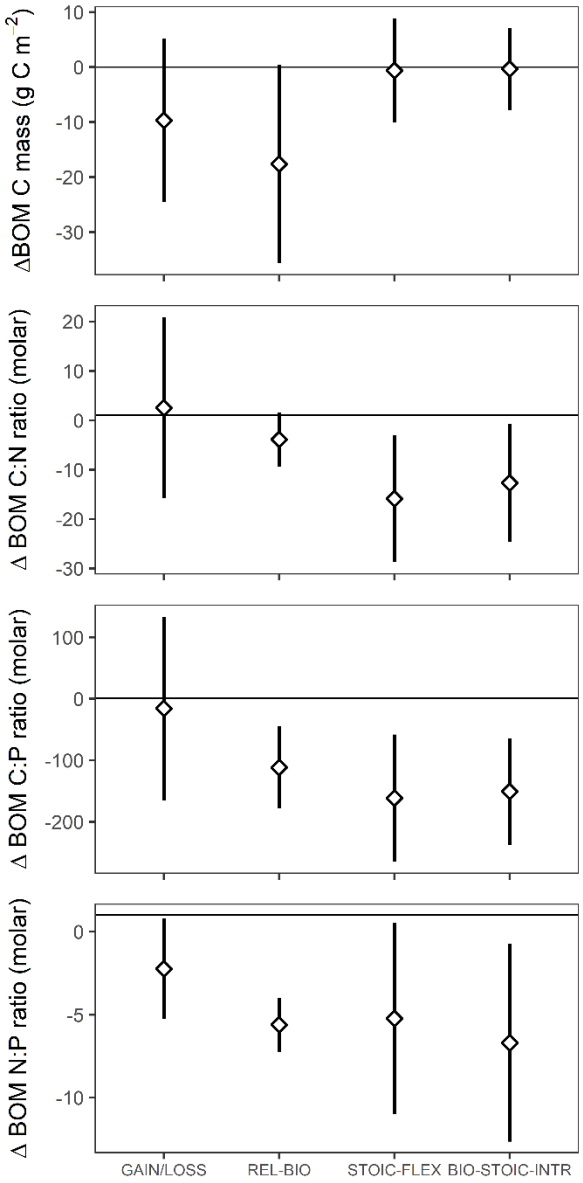

Figure S2.5. Distributions of the influence of Price components on the total benthic organic matter biomass and C:N:P stoichiometry. Open diamonds represent the median influence of each price component across all inter-stream comparisons and error bars represent one median absolute deviation.

APPENDIX B

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 3

Table S3.1. Physical and chemical characteristics of the study streams. Temperature represents the mean annual temperature in degrees Celsius and discharge represents the median annual values. Temp-light correlation represents Pearson's correlation coefficient between daily light intensity and temperature.

Stream	**Temperature (° C)**	**Median Discharge (L/s)**	**DIN (NO_3^- + NH_4^+mg L^{-1})**	**SRP (mg L^{-1})**	**DIN:SRP (molar)**	**Temp–Light correlation (Pearson's *r*)**
hver	27.2	21.0	0.007	0.022	0.7	0.67
st6	17.6	13.7	0.026	0.029	2.0	-0.09
st9	11.2	3.0	0.003	0.033	0.2	0.48
st7	5.8	3.9	0.027	0.033	1.8	0.41
oh2	5.5	12.5	0.008	0.050	0.4	0.57
st14	5.0	12.5	0.025	0.013	4.4	0.47

Table S3.2. Multivariate regression model coefficients for predicting daily community secondary production (mg AFDM m^{-2} d^{-1}) among and within streams. 'Light' represents the cumulative light over an interval (cumulative light $interval^{-1}$), 'Temperature' is Boltzmann-temperature ($1/kT$). Added-variable plots of these relationships are shown in Figure S3.3.

Term	**Estimate**	**95% confidence interval**	**P**	**R^2**
Intercept	30.7	18.0 – 43.3	<0.001	
ln(chlorophyll *a*)	0.33	0.05 – 0.60	<0.02	
ln(light)	0.25	0.07 – 0.42	0.007	
Boltzmann-temperature	-0.80	-1.09 – -0.52	<0.001	
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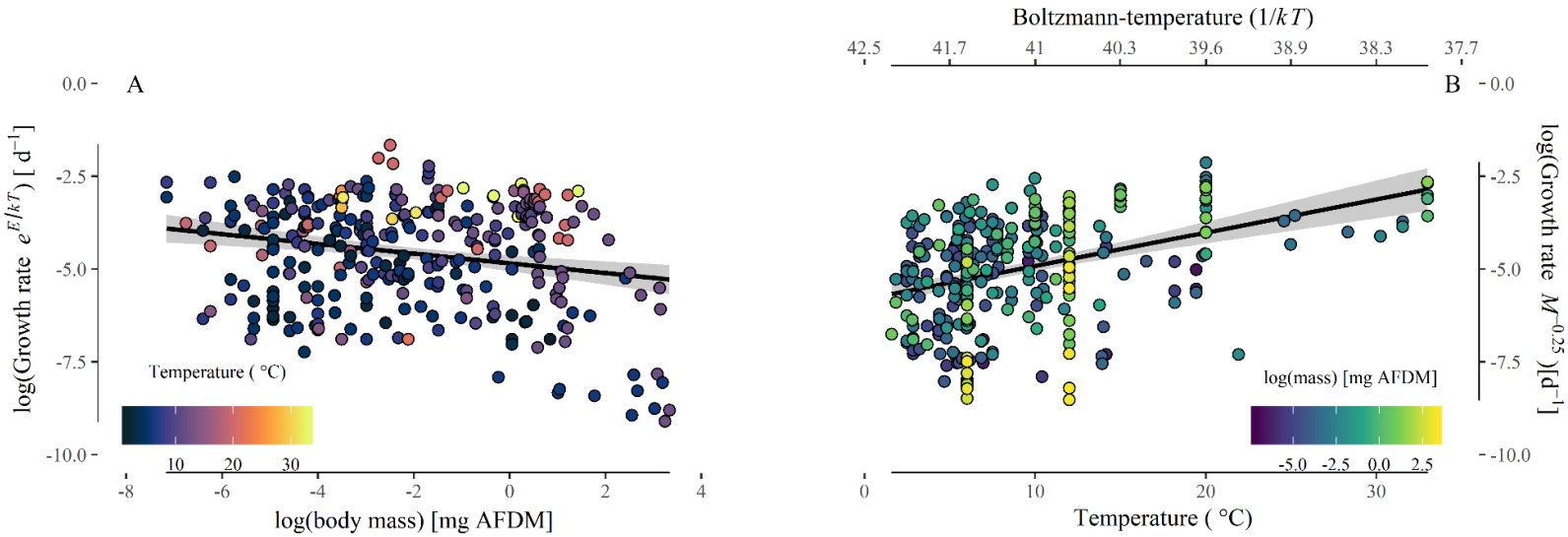

Figure S3.1. Individual instantaneous growth rates (g; d^{-1}) determined from in-situ measurements and bootstrapped body mass changes of identified cohorts against individual body mass after correcting for the influence of temperature (A) and against stream temperature while over the observation period (B). Each point represents the mean growth estimate for a unique stream-date-taxa combination. Mean and 95% confidence intervals of the multivariate linear regression fit of growth data with body size and temperature were described by the equation: log(g) ~ 21.5 [14.4 – 28.6] – 0.18 [-0.25 – -0.12]* log(*body size*) – 0.64 [-0.82 – -0.47]**1/kT*, where, *body size* is individual or mean cohort body size in mg AFDM, k represents the Boltzmann-constant ($8.2 \cdot 10^{-5}$ eV $\cdot$ K^{-1}), and T is absolute temperature in Kelvin.

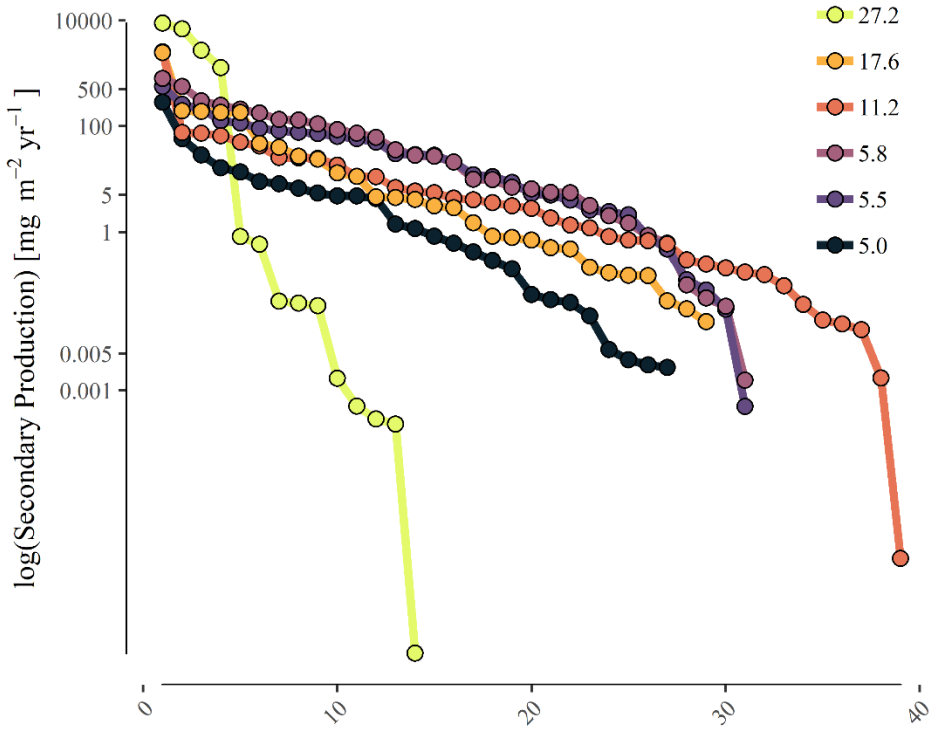

Figure S3.2. Rank-production of ln-transformed annual secondary production (mg AFDM m^{-2} y^{-1}) among taxa within streams.

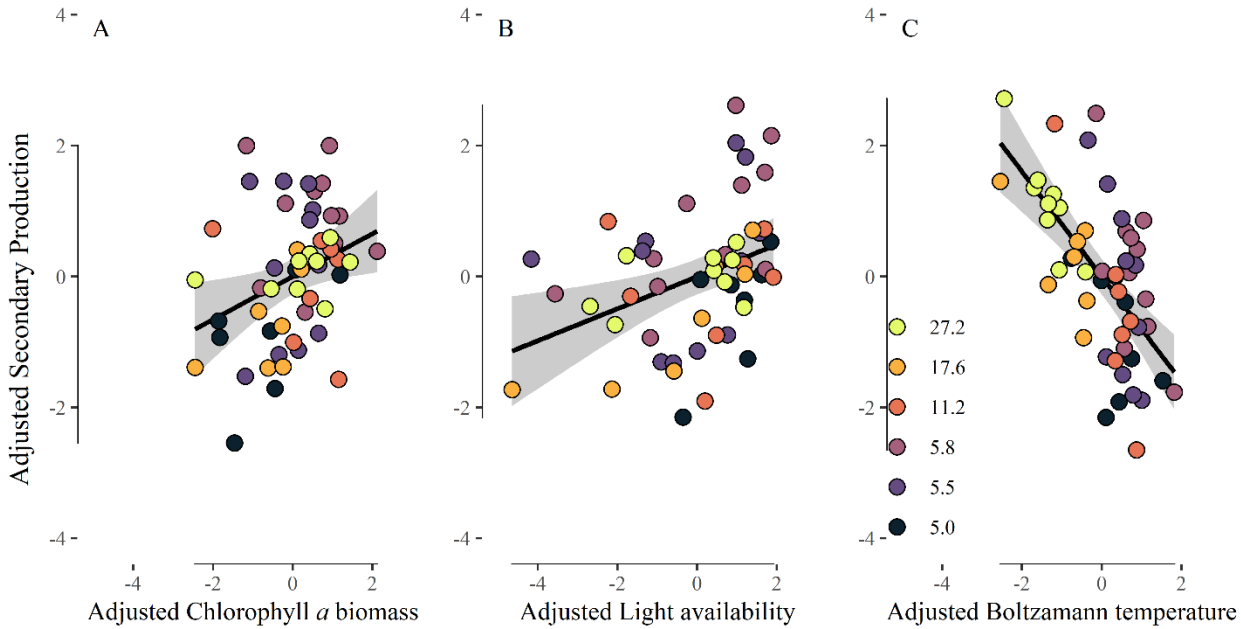

Figure S3.3. Added variable plots of the relationship between daily community secondary production (mg m^{-2} d^{-1}) and (A) chlorophyll *a* biomass (µg m^{-2}), (B) interval light availability (Lux $interval^{-1}$), and (C) Boltzmann temperature ($1/kT$) after accounting for the effects of other variables in the multivariate model.

APPENDIX C

SUPPLEMENTARY FIGURES AND TABLES FOR CHAPTER 4

Table S4.1. Community-level mean diet proportions for all study streams. SD = standard deviation.

Diet category	Proportion (mean ± SD)
Diatom	0.56 ± 0.07
Amorphous detritus	0.18 ± 0.06
Animal material	0.15 ± 0.08
Green algae	0.14 ± 0.07
Filamentous algae	0.05 ± 0.04
Vascular plants	0.04 ± 0.02
Cyanobacteria	0.02 ± 0.03

Table S4.2. Mean annual diet proportions (± standard deviation) for all consumers in each study stream. Mean annual temperature in Celsius (°C) is shown in parentheses for each stream.

stream	Amorphous detritus	Animal material	Cyanobacteria	Diatom	Filamentous algae	Green algae	Vascular plant
hver (27.2)	0.27 ± 0.2	0 ± 0	0.01 ± 0.01	0.59 ± 0.28	0.03 ± 0.03	0.13 ± 0.01	0.03 ± 0.03
st6 (16.7)	0.1 ± 0.10	0.18 ± 0.32	0.01 ± 0.01	0.55 ± 0.33	0.09 ± 0.08	0.22 ± 0.43	0.03 ± <0.01
st9 (11.2)	0.16 ± 0.09	0.07 ± 0.05	0.02 ± 0.02	0.66 ± 0.1	0.08 ± 0.15	0.06 ± 0.05	0.08 ± 0.14
st7 (5.8)	0.12 ± 0.15	0.23 ± 0.41	0 ± 0	0.6 ± 0.35	0.01 ± 0.03	0 ± 0	0.04 ± 0.10
oh2 (5.5)	0.22 ± 0.16	0.23 ± 0.44	0 ± 0	0.52 ± 0.32	<0.01 ± 0.01	0 ± 0	0.02 ± 0.06
st14 (5.0)	0.2 ± 0.12	0.06 ± 0.08	0.08 ± 0.11	0.46 ± 0.19	0.09 ± 0.10	0.17 ± 0.16	0.04 ± 0.03

Table S4.3. Annual community-level trophic basis of production in the study streams (%). Streams are arranged by descending annual mean stream temperature in degrees Celsius.

stream	Diatom	Amorphous detritus	Animal material	Green algae	Filamentous algae	Vascular plants	Cyanobacteria
hver	60.9	18	0	16.5	3.3	0.6	0.7
st6	55.7	1.5	23.4	5.9	13.5	0.1	0
st9	69.7	6.1	5.2	5.8	12.6	0.3	0.3
st7	81.4	7.4	8.3	NA	0.5	2.4	0
oh2	70.9	9.3	19.3	NA	0.1	0.3	0
st14	38.7	5.1	27.4	19.5	6.5	0.9	1.8

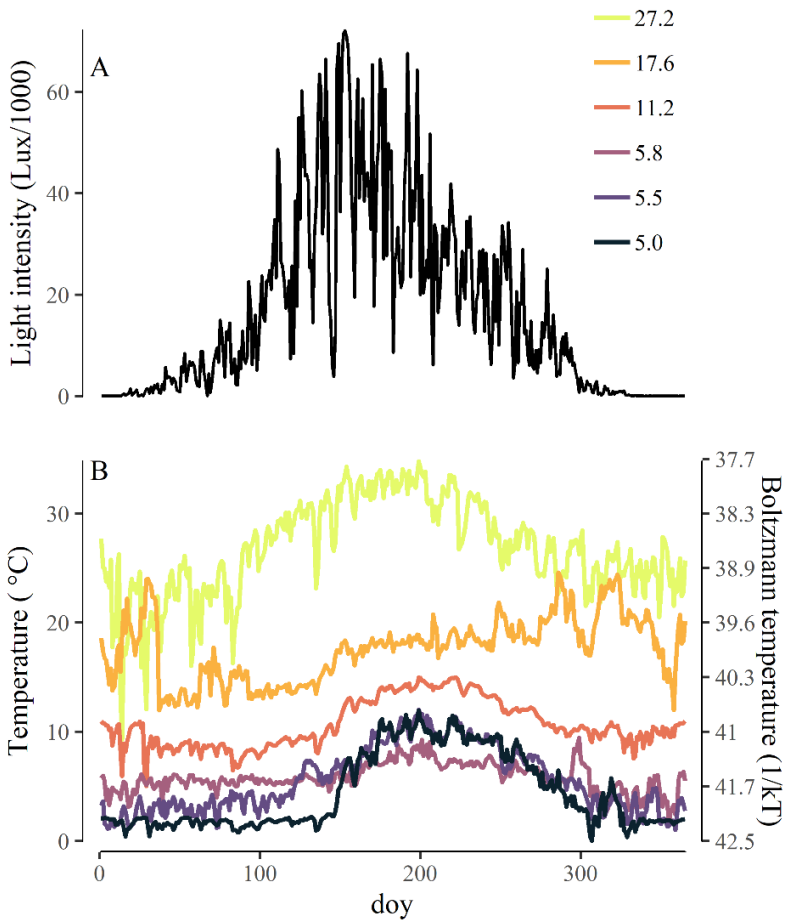

Figure S4.1. Mean daily A) light intensity and B) stream temperatures. Light intensity (Lux/1000) was measured from weather stations located within the Hengill watershed. Legend labels represent the annual mean temperature in degrees Celsius (°C).

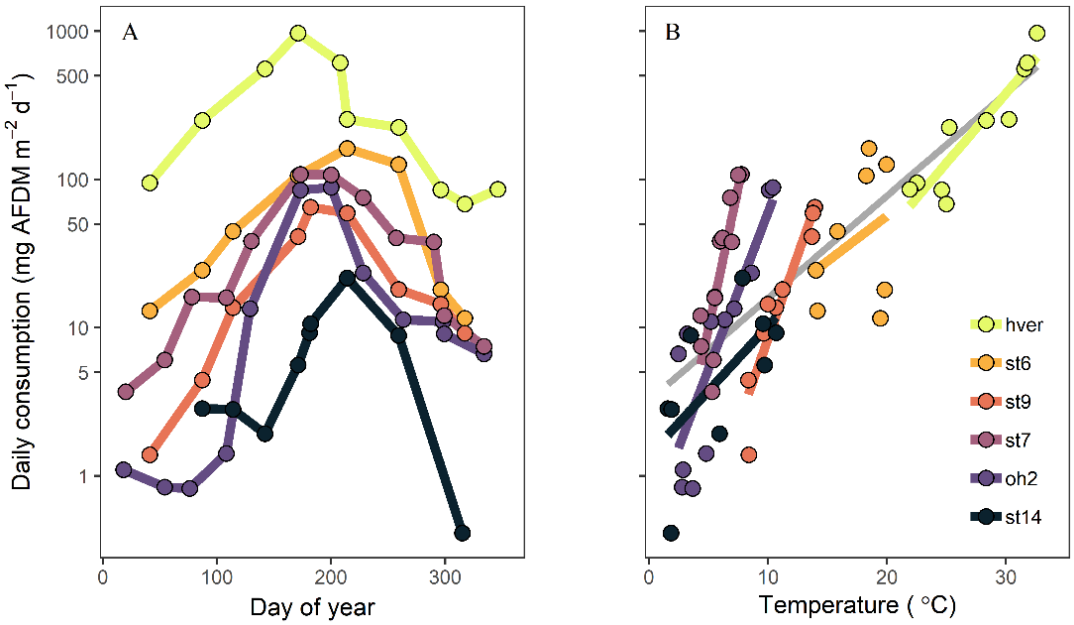

Figure S4.2. Total daily organic matter consumption by stream consumers plotted A) by day of year and B) in relation to stream temperature. Legend labels represent the annual mean temperature in degrees Celsius (°C).

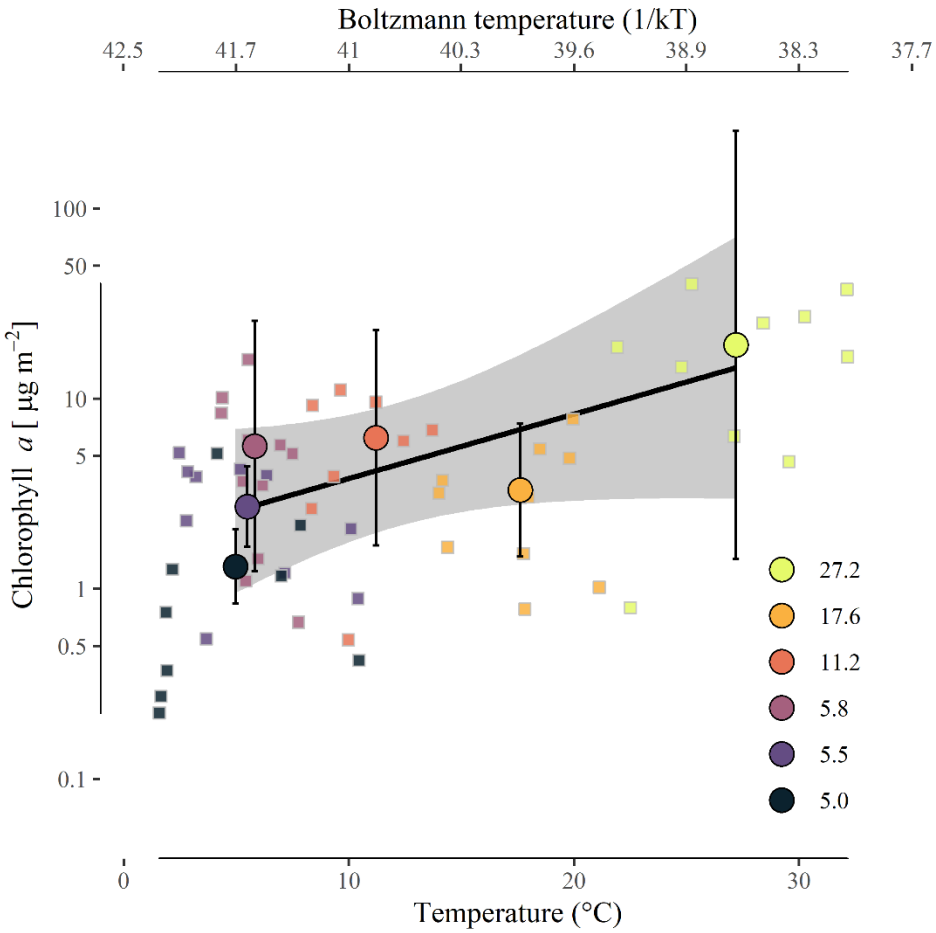

Figure S4.3. Relationship between stream temperature and chlorophyll *a* biomass (µg m^{-2}) across all study streams and dates. Mean annual chlorophyll *a* biomass is represented by large circle points and intra-annual measurements are shown by small square points. Legend labels represent the annual mean temperature in degrees Celsius (°C). The black line and shading are the ordinary least square regression and 95% confidence bands between ln-transformed chlorophyll *a* biomass and temperature.

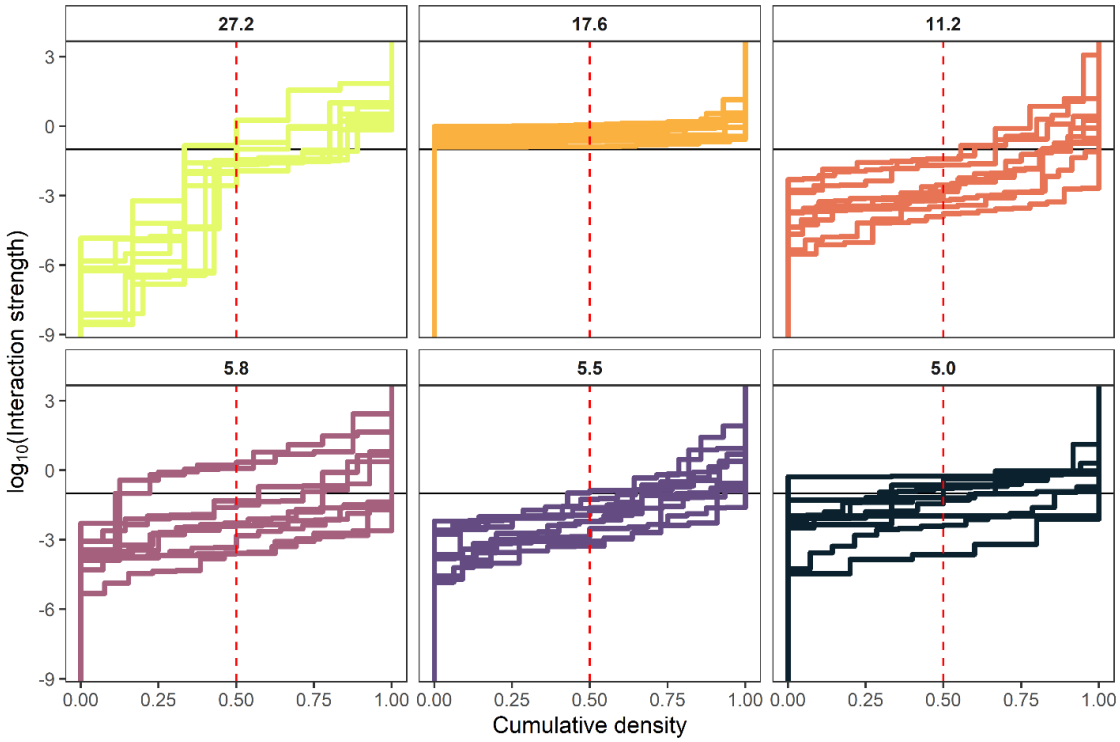

Figure S4.4. Within-stream cumulative distributions of $\log_{10}$-transformed interaction strengths throughout the year. Each line represented the empirical cumulative distributions for a single sample interval with a stream. The red dashed line represents the median of the distribution. The solid black line in the background represents an interaction strength of 0.1 ($\log_{10} = -1$), an arbitrary, but widely used cutoff for 'strong' interactions. Streams are ordered by descending mean annual temperature in degrees Celsius.

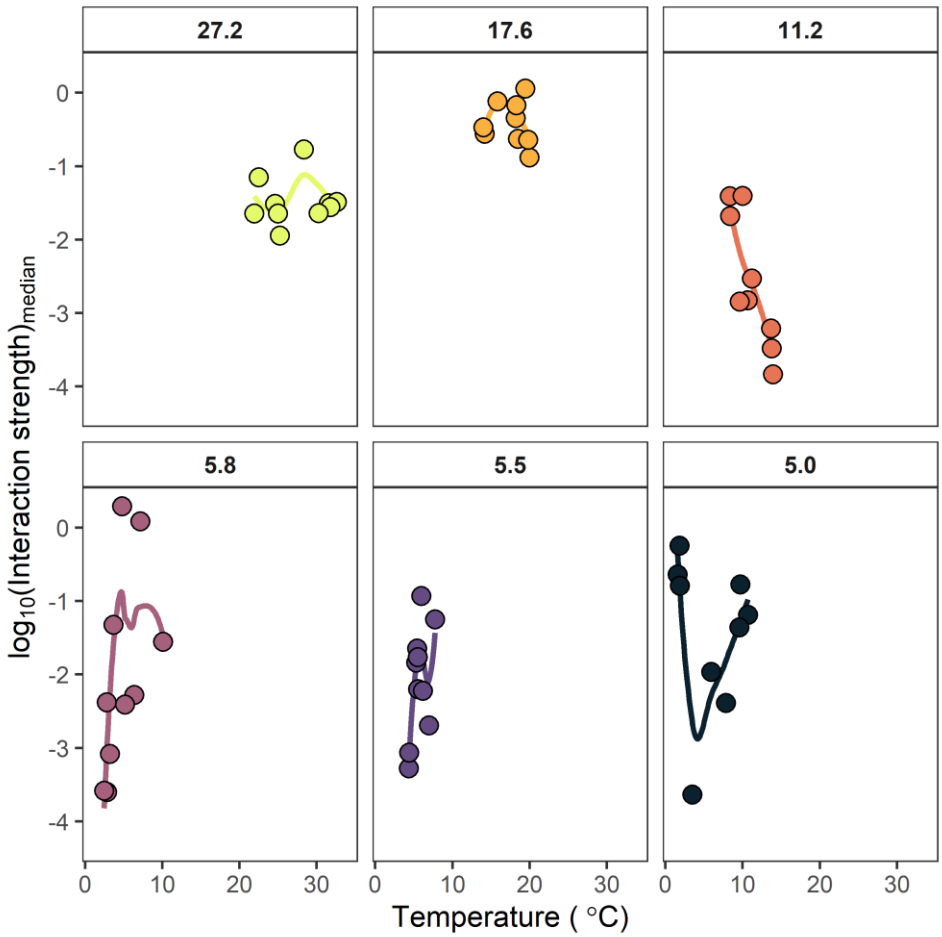

Figure S4.5. Within-stream relationships between stream temperature and median log10-transformed interaction strength. Mean annual stream temperature is shown in panel titles. Locally weighted scatterplot smoothing lines (span = 0.9) are drawn to ease visualization of the relationship between temperature and median interactions strength.

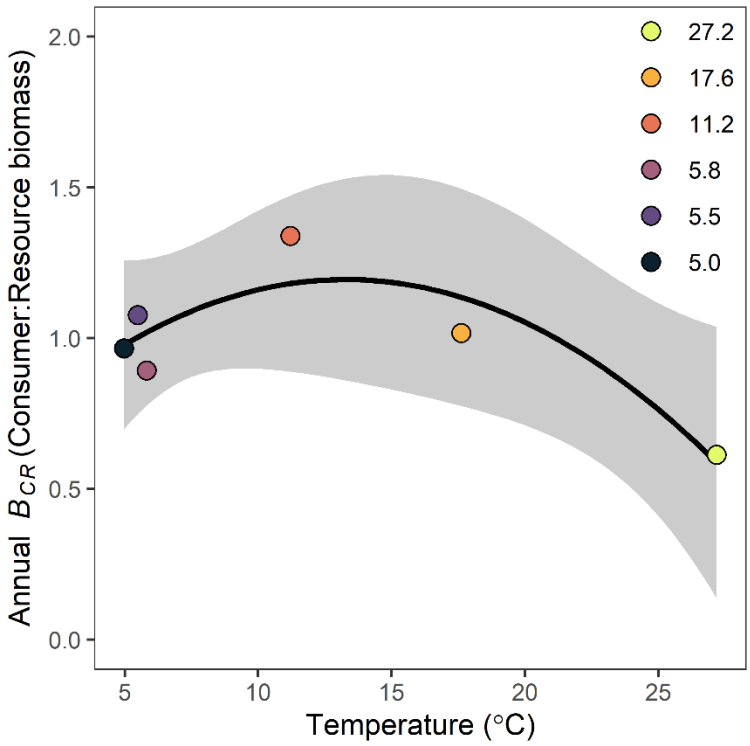

Figure S4.6. Annual consumer:resource biomass ratios among study streams was unrelated to mean annual stream temperature. Consumer:resource biomass ratios exhibited a unimodal response to temperature. The modeled relationship and 95% confidence bands of $y \sim x^2$ explained 65% of the variation in B_{CR} and is shown by the black line and shaded region. Legend labels represent the annual mean temperature in degrees Celsius (°C).

APPENDIX D

ANNUAL DIET-SPECIFIC CONSUMPTION BY CONSUMERS

Table S4.1. Annual consumption of diet items by individual taxa across all streams in the study (mg AFDM m^{-2} y^{-1}). "Cyanos" represent cyanobacteria and "Fila. Algae" represent filamentous algae.

Stream	Taxon	Amorphous detritus	Animal material	Cyanos	Diatom	Fila. algae	Green algae	Vascular plants
hver	*Cricotopus sylvestris*	10761.8	0	460.5	11780.8	486.7	2212.4	241.5
hver	Hirudinea	0.001	0	0	0.001	0	0	0
hver	*Limnophora riparia*	0	1.7	0	0	0	0	0
hver	Lumbricidae 3	0.2	0	0.007	0.2	0.01	0.04	0.006
hver	Midge Indet.	3.0	0	0.1	3.6	0.2	0.6	0.1
hver	*Nais* spp.	25382.2	0	1003.9	30926.5	1521.3	5240.7	821.0
hver	Nematoda	0.001	0	0	0.001	0	0	0
hver	Oribatid 1	0.006	0	0	0.008	0	0.001	0
hver	Ostracoda	0	0	0	0	0	0	0
hver	*Radix balthica*	3350.4	0	76.3	6230.5	456.2	707.3	280.3
hver	*Simulium vittatum*	0.2	0	0.006	0.2	0.01	0.03	0.005
hver	*Sperchon glandulosus*	0	0.1	0	0	0	0	0
hver	Thysanoptera	0.002	0	0	0.002	0	0	0
hver	Tubificid 1	32635.8	0	1290.8	39764.5	1956.1	6738.4	1055.6
oh2	*Capnia vidua*	51.9	0	0	121.5	0.5	0	3.7
oh2	Ceratopogonidae A	1.2	0	0	2.7	0.01	0	0.9

oh2	Ceratopogonidae B	0	0	0	0	0	0	0
oh2	*Chaetocladius* sp.	283.7	0	0	662.6	2.9	0	20.4
oh2	*Clinocera stagnalis*	0	80.8	0	0	0	0	0
oh2	Collembola	0.3	0	0	0.7	0.003	0	0.02
oh2	Copepoda	315.1	0	0	736.0	3.2	0	22.7
oh2	*Diamesa bertrami*	71.6	0	0	167.2	0.7	0	5.2
oh2	*Diamesa bohemani-zernyi*	74.9	0	0	174.9	0.8	0	5.4
oh2	Dicranota	0	209.8	0	0	0	0	0
oh2	Dytiscidae Adult	0	0	0	0	0	0	0
oh2	Dytiscidae Larva	27.5	0	0	64.1	0.3	0	2.0
oh2	*Eukiefferiella claripennis*	24.2	0	0	72.5	0	0	0
oh2	*Eukiefferiella minor*	100.7	0	0	302.0	0	0	0
oh2	*Galba truncatula*	0	0	0	0	0	0	0
oh2	Hirudinea	0	0	0	0	0	0	0
oh2	*Limnephilus sparsus*	0	0	0	0	0	0	0
oh2	*Limnophora riparia*	0	260.9	0	0	0	0	0
oh2	*Limnophyes* spp.	0.1	0	0	0.2	0.001	0	0.006

oh2	*Limonia* spp.	6.4	0	0	15.0	0.07	0	0.5
oh2	*Macropelopia* spp.	0	14.3	0	0	0	0	0
oh2	*Metriocnemus* spp.	0.2	0	0	0.5	0.002	0	0.01
oh2	*Micropsectra* sp.	444.4	0	0	1575.7	0	0	0
oh2	Nematoda	0.5	0	0	1.2	0.005	0	0.04
oh2	Oligochaeta A	275.0	0	0	297.9	0	0	0
oh2	Oligochaeta B	13.1	0	0	30.5	0.1	0	0.9
oh2	Oligochaeta C	6.0	0	0	14.0	0.06	0	0.4
oh2	*Orthocladius frigidus*	86.3	0	0	489.0	0	0	0
oh2	*Orthocladius oblidens*	2.0	0	0	4.6	0.02	0	0.1
oh2	Ostracoda	0.001	0	0	0.003	0	0	0
oh2	*Parochlus* sp.	5.2	0	0	12.2	0.05	0	0.4
oh2	*Potamophylax cingulatus*	114.9	0	0	168.8	0	0	75.4
oh2	Predatory Oligochaeta	0	0	0	0	0	0	0
oh2	*Prosimulium ursinum*	0	0	0	0	0	0	0
oh2	*Radix balthica*	36.9	0	0	42.6	2.5	0	0
oh2	*Rheocricotopus effusus*	1483.7	0	0	3302.5	0	0	0
oh2	*Simulium aureum*	0	0	0	0	0	0	0

oh2	*Simulium vernum*	160.2	0	0	373.8	0	0	0
oh2	*Simulium vittatum*	302.4	31.8	0	1257.3	0	0	0
oh2	*Sperchon glandulosus*	0	613.1	0	0	0	0	0
oh2	Thaumaleidae	0	0	0	0	0	0	0
oh2	*Thienemanniella* sp.	203.9	0	0	476.2	2.1	0	14.7
oh2	Tipula	9.9	0	0	23.0	0.1	0	0.7
st14	*Antocha* sp.	0	19.1	0	0	0	0	0
st14	Ceratopegonid	0.1	0.02	0.03	0.2	0.03	0.04	0.01
st14	Copepoda	0.4	0.1	0.1	1.1	0.2	0.2	0.07
st14	*Diamesa bohemani_zernyi*	0.5	0	0.3	1.6	0.6	0.3	0
st14	*Eukiefferiella* spp.	8.1	0	0.3	23.6	0.2	4.7	2.8
st14	*Limnophora riparia*	0	46.7	0	0	0	0	0
st14	Lumbricidae	10.3	3.0	3.9	32.1	4.7	5.8	1.9
st14	*Micropsectra* sp.	0.8	0	0.3	3.2	0.1	0.4	0
st14	Nematoda	0.3	0.07	0.1	0.8	0.1	0.1	0.05
st14	Oribatid 1	0.005	0.001	0.002	0.02	0.002	0.003	0.001
st14	Oribatid 2	0.007	0.002	0.003	0.02	0.003	0.004	0.001
st14	Oribatid 3	0.004	0.001	0.001	0.01	0.002	0.002	0.001
st14	*Orthocladius dentiformes*	0.02	0.006	0.03	0.1	0.007	0.003	0

st14	*Orthocladius fridgidus*	1.1	0	0.3	2.8	0.3	2.05	0
st14	Ostracoda	17.3	5.0	6.6	53.8	7.9	9.7	3.13
st14	*Potamophylax cingulatus*	11.3	3.3	4.3	35.2	5.1	6.3	2.1
st14	*Prosimulium ursinum*	27.8	0.2	4.9	172.5	4.7	3.2	0.5
st14	*Radix balthica*	0.1	0.02	0.03	0.3	0.04	0.05	0.02
st14	Hydracarina	0.003	0.001	0.001	0.01	0.002	0.002	0.001
st14	*Rheocricotopus effusus*	2.5	0	0.2	8.1	0.2	0.3	0
st14	*Simulium aureum*	6.0	1.8	2.3	18.8	2.8	3.4	1.1
st14	*Simulium vittatum*	357.5	103.8	136.6	1113.4	162.6	199.7	64.8
st14	*Sperchon glandulosus*	0	166.4	0	0	0	0	0
st14	Thysanoptera	5.4	1.6	2.1	16.9	2.5	3.03	1.0
st14	*Thienemanniella* sp.	2.1	0.2	1.1	4.2	1.5	0.2	0.5
st14	Tubificid 2	0.1	0.02	0.02	0.2	0.03	0.03	0.01
st14	Tubificid 1	6.8	2.0	2.6	21.3	3.1	3.8	1.2
st6	*Antocha* sp.	0	11.8	0	0	0	0	0
st6	*Chaetocladius dentiforceps*	164.2	197.8	5.3	626.6	39.6	39.8	19.9
st6	Ephydridae sp.	0	0.4	0	0	0	0	0

st6	*Eukiefferiella claripennis*	0	0	0	13.7	0	771.8	0
st6	*Eukiefferiella minor*	0	0	0	9.1	0	514.6	0
st6	*Galba trunculata*	1.3	1.6	0.04	5.1	0.3	0.3	0.2
st6	*Limnophora riparia*	0	2.4	0	0	0	0	0
st6	Lumbricidae	0	0	0	245.5	20.9	0	0
st6	*Macropelopia* spp.	0	1396.5	0	0	0	0	0
st6	*Micropsectra* sp.	42.2	50.8	1.4	160.9	10.2	10.2	5.1
st6	*Corynoneura* sp.	4.0	4.8	0.1	15.3	1.0	1.0	0.5
st6	*Chaetocladius dentiforceps*	24.2	29.2	0.8	92.4	5.8	5.9	2.9
st6	*Cricotopus sylvestris*	10.1	12.1	0.3	38.5	2.4	2.4	1.2
st6	*Diamesa bertrami*	0.5	0.5	0.02	1.7	0.1	0.1	0.05
st6	*Rheocricotopus effusus*	0.6	0.8	0.02	2.4	0.1	0.2	0.08
st6	Midge indet.	3.2	3.9	0.1	12.4	0.8	0.8	0.4
st6	*Nais* spp.	163.5	197.0	5.3	624.0	39.4	39.6	19.8
st6	Nematoda	0.03	0.04	0.001	0.1	0.008	0.008	0.004
st6	Oribatid 1	4.1	5.0	0.1	15.8	1.0	1	0.5
st6	Oribatid 2	0.1	0.2	0.004	0.5	0.03	0.03	0.02

st6	*Orthocladius frigidus*	0.4	0.5	0.01	1.6	0.1	0.1	0.05
st6	*Orthocladius oblidens*	68.5	82.6	2.2	261.6	16.5	16.6	8.3
st6	Ostracoda	0.02	0.02	0.001	0.07	0.004	0.004	0.002
st6	*Potamophylax cingulatus*	0.2	0.2	0.005	0.6	0.04	0.04	0.02
st6	*Radix balthica*	483.1	368.3	0	12175.9	3451.1	54.08	0
st6	*Simulium* spp.	0.04	0.05	0.001	0.2	0.01	0.01	0.005
st6	*Simulium vittatum*	200.01	250.3	6.9	608.4	12.8	1.6	22.9
st6	*Sperchon glandulosus*	0	37.8	0	0	0	0	0
st6	*Thienemanniella* sp.	21.2	25.6	0.7	81.1	5.1	5.1	2.6
st6	Tubificid 2	0.2	0.2	0.006	0.7	0.05	0.05	0.02
st6	Tubificid 1	2.8	3.4	0.09	10.6	0.7	0.7	0.3
st7	*Capnia vidua*	2.5	0	0	12.2	0.3	0	0.8
st7	Ceratopogonidae A	0	0	0	0	0	0	0
st7	Ceratopogonidae B	0	0	0	0	0	0	0
st7	*Chaetocladius* spp.	32.8	0	0	162.2	3.8	0	11.2
st7	*Clinocera stagnalis*	0	16.0	0	0	0	0	0

st7	Collembola	0.1	0	0	0.3	0.008	0	0.02
st7	Copepoda	299.7	0	0	1482.0	34.8	0	102.7
st7	*Diamesa bertrami*	1766.3	0	0	4775.6	0	0	0
st7	*Diamesa bohemani-zernyi*	1253.1	0	0	3387.9	0	0	0
st7	Dicranota	0	102.6	0	0	0	0	0
st7	Dytiscidae Adult	0	0	0	0	0	0	0
st7	Dytiscidae Larva	0	0	0	0	0	0	0
st7	*Eukiefferiella claripennis*	16.8	0	0	403.7	0	0	0
st7	*Eukiefferiella minor*	36.0	0	0	864.6	0	0	0
st7	*Galba truncatula*	0	0	0	0	0	0	0
st7	Hirudinea	0	0	0	0	0	0	0
st7	*Limnephilus sparsus*	0	0	0	0	0	0	0
st7	*Limnophora riparia*	0	18.8	0	0	0	0	0
st7	*Limnophyes* sp.	0.1	0	0	0.6	0.01	0	0.04
st7	*Limonia* sp.	12.1	0	0	59.7	1.4	0	4.1
st7	*Macropelopia* spp.	0	0	0	0	0	0	0
st7	*Metriocnemus* sp.	1.0	0	0	5.1	0.1	0	0.4
st7	*Micropsectra* sp.	2.7	0	0	36.2	0	0	0

st7	Nematoda	0	0	0	0	0	0	0
st7	Oligochaeta A	305.2	0	0	1081.9	0	0	0
st7	Oligochaeta B	11.8	0	0	58.4	1.4	0	4.0
st7	Oligochaeta C	253.8	0	0	1255.2	29.5	0	87.0
st7	*Orthocladius frigidus*	154.5	0	0	137.0	0	0	0
st7	*Orthocladius oblidens*	0	0	0	0	0	0	0
st7	Ostracoda	0.002	0	0	0.009	0	0	0.001
st7	*Parochlus* sp.	0.05	0	0	0.2	0.006	0	0.02
st7	*Potamophylax cingulatus*	203.2	0	0	1596.8	0	0	1103.3
st7	Predatory Oligochaeta	0	0	0	0	0	0	0
st7	*Prosimulium ursinum*	5.1	208.1	0	238.5	0	0	55.8
st7	*Radix balthica*	2.5	0	0	17.7	2.8	0	0
st7	*Rheocricotopus effusus*	103.9	0	0	513.9	12.1	0	35.6
st7	*Simulium aureum*	0	0	0	0	0	0	0
st7	*Simulium vernum*	77.6	0	0	441.7	0	0	77.6
st7	*Simulium vittatum*	7.3	0	0	125.3	13.1	0	0
st7	*Sperchon glandulosus*	0	383.8	0	0	0	0	0
st7	Thaumaleidae	0.7	0	0	3.7	0.09	0	0.3

st7	*Thienemanniella* sp.	8.5	0	0	42.2	1.0	0	2.9
st7	*Tipula* sp.	1.8	0	0	8.8	0.2	0	0.6
st9	*Antocha* sp.	0	0.7	0	0	0	0	0
st9	Ceratopegonid A	1.0	0	0.03	0.05	0.4	3.7	0.3
st9	*Clinocera stagnalis*	0	0.8	0	0	0	0	0
st9	Copepoda	5.0	0	0.2	0.3	2.1	19.4	1.3
st9	*Diamesa bohemani-zernyi*	7.8	0	0.3	0.4	3.2	30.2	2.1
st9	*Eukiefferiella* spp.	105.7	0	3.5	5.8	43.4	410.3	27.9
st9	Hydra	0.1	0	0.004	0.007	0.06	0.5	0.04
st9	*Limnophora riparia*	0	52.6	0	0	0	0	0
st9	Lumbricidae	4.0	0.4	0.1	0	1.0	20.0	12.1
st9	*Macropelopia* sp	0	188.6	0	0	0	0	0
st9	*Micropsectra* sp.	40.6	0	0	4.4	0.8	264.8	0
st9	*Orthocladius frigidus*	38.6	0	1.3	2.1	16.5	150.1	10.1
st9	*Orthocladius oblidens*	103.3	0	3.4	5.6	42.4	400.8	27.2
st9	*Orthocladius* spp.	34.2	0	1.1	1.9	14.1	132.8	9.0
st9	Thaumaleidae	1.9	0	0.06	0.1	0.7	7.3	0.5

st9	*Rheocricotopus effusus*	3.9	0	0.1	0.2	1.6	15.1	1.0
st9	*Parochlus* sp.	8.3	0	0.3	0.5	3.4	32.4	2.2
st9	Midge indet.	4.4	0	0.1	0.2	1.8	17.0	1.2
st9	*Nais* spp.	70.0	0	2.3	3.8	28.8	271.8	18.5
st9	Oribatid 1	1.1	0	0.04	0.06	0.5	4.4	0.3
st9	Oribatid 2	0.03	0	0.001	0.002	0.01	0.1	0.008
st9	Oribatid 3	0.002	0	0	0	0.001	0.01	0.001
st9	Ostracoda	0	0	0	0	0	0	0
st9	*Potamophylax cingulatus*	0.02	0	0.001	0.001	0.008	0.08	0.005
st9	*Prosimulium ursinum*	0.8	0	0.03	0.05	0.3	3.2	0.2
st9	*Radix balthica*	43.0	0	0.5	0.9	13.6	140.5	1.03
st9	*Simulium aureum*	0.3	0	0.01	0.02	0.1	1.1	0.08
st9	*Simulium* spp.	0.2	0	0.007	0.01	0.09	0.8	0.06
st9	*Simulium vernum*	0.03	0	0.001	0.001	0.01	0.1	0.007
st9	*Simulium vittatum*	3209.4	189.5	170.7	554.1	2362.1	12624.7	26.6
st9	*Sperchon glandulosus*	0	19.7	0	0	0	0	0
st9	Thysanoptera	1.0	0	0.03	0.05	0.4	3.8	0.3
st9	*Thienemanniella* sp.	37.3	0	1.2	2.03	0	153.8	9.8
st9	Tubificid 2	0.06	0	0.002	0.003	0.02	0.2	0.02
st9	Tubificid 1	1.7	0	0.06	0.09	0.7	6.5	0.4