Seasonal changes in light availability modify the temperature dependence of secondary production in an arctic stream

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Abstract

Light and temperature are key drivers of ecosystem productivity, but synchrony of their annual cycles typically obscures their relative influence. The coupling of annual light-temperature regimes also drives complementary seasonal cycles of energy supply (primary production) and demand (metabolism), perhaps promoting temporal stability in carbon (C) storage and food web production that may be difficult to discern in most ecosystems. Spring-fed streams in the Arctic are subject to extreme annual fluctuations in light availability but have relatively stable water temperatures, which allows assessment of the independent effects of light and temperature. We used the unusual annual light and temperature regimes of Ivishak Spring, Alaska, U.S.A. (latitude 69ºN, annual water temperature range ~4-7ºC) to test predictions about the effect of light availability on consumer productivity with minimally confounding effects of temperature. We predicted that: 1) annual patterns of secondary production would follow patterns of primary production, rather than temperature, due to organic C limitation during winter darkness when photosynthesis is effectively halted, 2) C limitation would propagate from primary producers upward through several trophic levels, 3) the lack of temperature dependence during winter darkness would be expressed as anomalous Arrhenius plots of growth rates indicating decoupled production-temperature relationships, and 4) consumer diets would reflect C limitation during winter. As predicted, we found: 1) lowest production by macroinvertebrates and *Salvelinus malma* (Dolly Varden char) at the lowest light levels rather than the lowest temperatures, 2) apparent winter C limitation propagated upwards through three trophic levels, 3) anomalous Arrhenius plots indicating lack of temperature dependence of consumer growth rates during winter, and 4) lowest consumption of diatoms (by macroinvertebrates) and invertebrate prey (by *S. malma*) during winter. Together, these results indicate that light drives annual patterns of animal production in Ivishak Spring, with stable annual temperatures likely exacerbating C limitation of ectotherm metabolism during winter. The timing and severity of winter C limitation in this unusual arctic-spring food web highlight a fundamental role for light-temperature synchrony in matching energy supply with demand in most other ecosystem types, thereby conferring a measure of stability in the metabolism of their food webs over annual time-scales.

Key words: Alaska, food webs, light, seasonality, secondary production, streams, temperature

INTRODUCTION

Light and temperature are fundamental drivers of many ecosystem processes (e.g., Roberts et al. 2007, Heffernan and Cohen 2010, Trimmer et al. 2012, McMeans et al. 2015). Although their independent effects have been assessed experimentally at small scales (Ylla et al. 2007, Dossena et al. 2012, Matheson et al. 2012), gaining understanding of their relative effects at the larger spatial scales typically used to define ecosystems (e.g., catchment scale) is more challenging because natural cycles of light and temperature are usually synchronized (Huryn et al. 2014). Temperate latitudes, for example, experience short days and low temperatures during winter and long days and higher temperatures during summer (Fig. 1). At lower latitudes, seasonal fluctuation in both day-length and temperature is reduced, while at higher latitudes these fluctuations are more extreme. Regardless, annual cycles of light and temperature remain confounded.

Recognition of the confounded effects of light and temperature on ecosystem function is important because difficulties isolating these key drivers impede understanding of how they independently affect processes such as energy flow and food-web interactions. Consider that primary productivity is maximized during periods of high light availability, which coincidently is also when metabolic demands of ectotherms are greatest due to high temperatures, and minimized during dark, cold periods when metabolic demands are lowest. This seasonal pattern of complimentary supply and demand potentially confers some measure of temporal stability in ecosystem metabolism, carbon storage, and food web production, an effect that is difficult to discern in most ecosystems due to the coupled relationship between light and temperature. Attempts to decouple light and temperature cycles, and the complementary energetic responses by consumers, to our knowledge, have not been made at the ecosystem level, presumably due to a scarcity of systems providing effective controls. One such system, however, is found in the form of arctic spring-streams where the combination of relatively stable water temperature and extreme annual fluctuations in day-length (Appendix S1: Fig. 1) provide an opportunity for advancing understanding of such relationships (Huryn et al. 2014).

Perennially flowing, spring-fed streams with relatively stable temperatures are widespread in arctic Alaska. There they provide the only open-water habitat during winter when air temperatures may be <-40°C for extended periods and other headwater streams freeze solid (Huryn et al. 2005, Parker and Huryn 2011). While the annual pattern of primary productivity in these open-canopy ecosystems shows extreme fluctuations due to seasonal cycles of light, stable temperatures result in relatively constant rates of ecosystem respiration (ER) year-round, leading to carbon (C) limitation of ecosystem metabolism during winter when photosynthesis is effectively halted (Huryn et al. 2014). This scenario contrasts with most other ecosystems where seasonal cycles of organic C demand and production are closely coupled (McMeans et al. 2015, Bernhardt et al. 2018).

Here we expand an earlier analysis (Huryn et al. 2014) of drivers of annual patterns of ecosystem metabolism in an arctic spring-stream (Ivishak Spring, Alaska) by assessing the effects of light versus temperature on secondary production. We tested several predictions. First, we predicted that patterns of secondary production would be synchronous with primary production, rather than temperature, due to C limitation during winter darkness when photosynthesis is effectively halted (Fig. 1; Huryn et al. 2014). Second, we anticipated that such C limitation would be propagated from primary producers upward through several trophic levels. Third, we predicted that lack of temperature dependence of production during winter would be shown by Arrhenius plots indicating a decoupling of the production-temperature relationship (e.g., Huryn et al. 2014). Finally, we predicted that food consumption would show annual patterns reflecting C limitation during winter.

SITE DESCRIPTION

Ivishak Spring (69.024342°, -147.721079°) is a tributary of the Ivishak River, which flows through the Arctic National Wildlife Refuge on the North Slope of Alaska, U.S.A (Appendix S1: Fig. S2). The mean annual precipitation of this region is 250+ mm yr^{-1} and the mean annual air temperature is -12°C (Huryn and Hobbie 2012). The warmest month is July (mean temperature 12-13°C); the coldest is February (mean temperature -30°C; Huryn and Hobbie 2012). The habitat structure of the 265-m stream reach selected for study consists of relatively long, uniform riffles paved with limestone particles covered with the bryophyte *Cratoneuron filicinum* (Hedw.), which is typical for North Slope spring-streams with carbonate substrata (Parker and Huryn 2006, 2011; Huryn et al. 2014). Pools are infrequent. Stream discharge shows relatively little variability (annual mean = 136 L s^{-1}), which results in high substratum stability (Parker and Huryn 2006). Water temperature ranges from a constant 7.3°C at the spring source to a mean temperature of 5.8°C with an annual fluctuation of ~3-4°C about 240 m downstream (Benstead and Huryn 2011; Appendix S1: Fig. S1). Nutrient concentrations are similar to other headwater streams of the eastern North Slope for which information is available (i.e., soluble reactive phosphorus [SRP] = 0.10 µmol L^{-1}, NH_4^+-N = 0.05 µmol L^{-1}, NO_3^--N = 5.3 µmol L^{-1}; Huryn et al. 2014). Riparian vegetation consists of willows [primarily *Salix alexensis* (Andersson)] and a sparse gallery of balsam poplar (*Populus balsamifera* L.). Predatory freshwater vertebrates include Dolly Varden char [*Salvelinus malma* (Walbaum)], the American dipper (*Cinclus mexicanus* Swainson) and the North American river otter [*Lontra canadensis* (Schreber), Parker and Huryn 2013]. Ivishak Spring provides habitat for juvenile *S. malma*. These fish migrate into Ivishak Spring from downstream spawning habitat during late spring and remain for 3+ years before beginning cyclical migrations to and from the Beaufort Sea (Huryn and Hobbie 2013; A. D. Huryn, *unpublished data*).

METHODS

Macroinvertebrate production and diet

Macroinvertebrates were sampled on 26 semi-monthly dates from March 2007 to August 2009. Five samples were taken at ~40-m intervals from a randomly selected start point using a Surber sampler (0.09 m^2, 243-μm mesh). Samples were preserved with ~4% formaldehyde until processing, which consisted of rinsing the sample through nested sieves, removing specimens by hand under magnification, and measuring (body length) and identifying each specimen to the lowest practical taxonomic level (see Appendix S1: Section S1 for further details). Production was estimated using the instantaneous growth method, which requires measurements of individual growth rates and population biomass over time (Benke and Huryn 2017). Individual biomass was estimated using length-mass relationships (Benke et al. 1999). Growth rates were estimated from temporal changes in mean individual biomass based on field data. Population biomass was estimated as the product of abundance and individual biomass. Diet was assessed seasonally by analyzing gut contents (Parker and Huryn 2006, 2011; see Appendix S1: Section S1 for further details) for four abundant taxa [*Rhynchelmis* (Oligochaeta), *Pagastia* (Diptera: Chironomidae), *Ecclisomyia* (Trichoptera: Limnephilidae), *Isoperla* (Plecoptera: Perlodidae)] representing a range of functional feeding groups (e.g., collector-gatherer, scraper, shredder, predator; Merritt et al. 2007). Production and biomass of omnivores was divided into primary and secondary consumer categories using areal proportions of non-animal and animal tissues occurring in their guts and the trophic-basis of production approach (Benke and Huryn 2017) using bioenergetic efficiencies summarized by Huryn (1996). Uncertainty for production statistics was estimated by bootstrapping (Benke and Huryn 2017, see Appendix S1: Section S1 for further details).

Dolly Varden production, body condition, diet and prey supply-demand budget

We sampled *S. malma* on 11 dates between May 2007 and August 2009. On the first sampling date (25 May 2007), the entire stream reach was sampled (265 m of channel length) using a Smith-Root LR-20 electrofishing machine (Smith-Root, Inc., Vancouver, WA, USA). On the subsequent 10 sampling dates, five randomly selected sub-reaches of known length and width were block-netted and sampled. The combined lengths of the sub-reaches sampled ranged from 78 to 104 m (mean length ±1 S.D. = 94 ±7 m) or 29 to 39% of the entire study reach on each date. Captured *S. malma* were anaesthetized (buffered tricaine methanesulfonate, 100 ppm), measured for standard length (SL), weighed [±0.1 g wet mass (WM)], tagged with a 1 ×2.5 mm VI Alpha tag (Northwest Marine Technology, Shaw Island, WA, USA) inserted subcutaneously along the left dentary, and released at the point of capture. Abundance was estimated from pass-depletion data (3 passes; Removal Sampling II, Pisces Conservation Ltd., Lymington, UK). Relative condition factor for each fish was estimated by dividing its WM by that predicted from the population-level length-mass relationship. Production was estimated using the instantaneous growth method (see *Macroinvertebrate production and diet,* above). Daily growth rates were obtained from recaptured, tagged individuals. Population biomass (g wet mass [WM] m^{-2}) was calculated by correcting total mass sampled from each sub-reach with the maximum-likelihood abundance estimate (mean difference between total captured and the maximum-likelihood estimate was always <5% of estimated total). Wet mass was converted to ash-free dry mass (AFDM) using an empirical coefficient of 0.17 (A. D. Huryn, *unpublished data*). Uncertainty for production statistics was estimated by bootstrapping (see *Macroinvertebrate production and diet,* above). Stomach contents of char caught with unbaited minnow traps were sampled semi-monthly (23 dates) using gastric lavage (Giles 1980). Preserved invertebrates (4% formalin) were measured (total length) and identified, and DM was calculated using published length-mass relationships (Benke et al. 1999, Sabo et al. 2002, see Appendix S1: Section S1 for further details of methods). The difference between *S. malma* prey supply and demand (mg DM m^{-2} d^{-1}) was estimated semimonthly following the approach and bioenergetic efficiencies used by Huryn (1996).

Light and water temperature

Stream temperature (Appendix S1: Fig. S1) was recorded at 15-min intervals using a digital recording pressure-transducer (Hobo U20 Water Level Data Logger, Onset Corporation, Pocasset, MA, USA) deployed in a PVC stilling well. Photosynthetically active radiation (PAR, Appendix S1: Fig. S1) was measured as photon flux density ($\mu mol \cdot m^{-2} \cdot s^{-1}$) using underwater quantum sensors (LI-190SA, LI-COR, Lincoln, NE, USA) interfaced with digital recorders. Sensors were placed ~10 cm below the surface of the water (approximate average reach depth) at two locations. The first location was approximately 20 m upstream of 0 m; the second was approximately 30 m below 200 m. PAR was measured every 5 s and data were recorded as 5-min means. Data from the two PAR sensors were averaged.

Statistical approaches

Apparent energetic coupling between trophic levels (e.g., GPP and macroinvertebrate primary consumer production, etc.) and relationships between temperature, light and secondary production and P:Bs were assessed using least-squares regression and natural log-transformed data when appropriate to improve model fit. Seasonal differences in diet were assessed using ANOVA and natural log transformed data, followed by Tukey's LSD pairwise comparisons. An apparent lack of temperature dependence of animal production during winter was used as an indication of potential C-limitation. This was assessed using Arrhenius plots (Brown and Sibly 2012, Huryn et al. 2014) of the natural log of daily P:B (d^{-1}) versus $1/kT$, where k is the Boltzmann constant and T is temperature in degrees Kelvin. Such plots provide an estimate of the activation energy of this metabolic process in eV (with the sign reversed, Brown and Sibly 2012). Our ability to estimate apparent metabolic activation energies using Arrhenius plots, however, was problematical due to the extremely small range of kT^{-1} (41.4–41.8 kT^{-1}; Huryn et al. 2014). Consequently, the temperature dependence of P:B was modeled using Arrhenius plots and fixed-slope, variable-intercept, least-square equations. The activation energy predicted for aerobic metabolic processes by eukaryotes was used as the fixed slope (-0.65 eV; Allen et al. 2005, Perkins et al. 2012). Anomalous levels of residual error producing an abrupt break in the slope (e.g., "hockey stick" pattern) in response to winter temperatures were used as an indicator of the break-down of temperature dependence and hence C-limitation of P:B (Huryn et al. 2014). To further assess the relationship between productivity, light and temperature, the residual error from the Arrhenius plots was regressed against natural log-transformed PAR to determine whether the greatest departures from the predicted activation energy occurred at lowest temperatures or the lowest PAR levels. Essentially, this procedure uses data from the Arrhenius plot to isolate the effects of temperature and light on seasonal changes in P:Bs.

RESULTS

Macroinvertebrate community members and life cycles—Eighteen taxa of nominal primary consumers and six taxa of nominal predators (Merritt et al. 2007) were identified (Table 1). Life cycles were diverse, including bivoltine (e.g., *Eukieferiella gracei* species group, *Pagastia*, *Thienemanniella*), univoltine, and semivoltine (e.g., *Isoperla* with a 15- to 18-month life cycle*,* *Zapada* with an 18- to 20-month life cycle). Most taxa were characterized by rapid growth during spring and summer and little or no growth during winter, even when larvae were present (e.g., *Baetis*, most chironomids). Five taxa, however, showed significant growth (i.e., >60% of total growth) during winter (*Dicranota, Ecclisomyia*, *E. gracei* group, *Pericoma*, *Tvetenia*).

Macroinvertebrate diet

The four taxa selected for diet analysis together contributed 40% to total macroinvertebrate primary consumer production, when averaged over both years of study [*cf.* Table 1; *Rhynchelmis* (Oligochaeta, 6.1%), *Pagastia* (Diptera: Chironomidae, 7.1%), *Ecclisomyia* (Trichoptera: Limnephilidae, 12.1%), *Isoperla* (Plecoptera: Perlodidae, 14.7%)]. Diatoms were prominent components of the diet for each of the four taxa for which gut contents were analyzed. Strong seasonality was apparent, however. During April, diatoms dominated the gut contents for each taxon analyzed (% of total particle area): Oligochaeta (74.2%±7.0%, mean ± 95% C.I.), *Isoperla* (79.6%±11.5%), *Ecclisomyia* (80.2%±1.9%), and *Pagastia* (72.1%±14.9%). During January, however, amorphous organic matter dominated gut contents while diatoms were minor contributors: Oligochaeta (7.1%±11.3%, mean ±95% C.I.), *Isoperla* (1.5%±2.6%), *Ecclisomyia* (0.9%±1.3%), and *Pagastia* (10.9% ±14.2%). Quantities of diatoms in guts of all four taxa were lower in January than other months ($P<0.05$, ANOVA, Tukey's LSD, Fig. 2). In addition to diatoms, invertebrate tissue fragments occurred in the gut contents of *Isoperla* (range among individuals analyzed = 0.0 to 96.4% of total μm^2 particle area mg^{-1} individual DM) and *Pagastia* (range = 0.0 to 81.2%). Bryophyte (range = 1.6 to 89.3%) and vascular plant (range = 0.0 to 51.6%) fragments were common components of *Ecclisomyia* gut contents. Amorphous organic matter was an important diet item for *Pagastia* (range = 6.5 to 96.5%) and the Oligochaeta (range = 9.3 to 100.0%). With the exception of diatoms, however, no significant seasonal patterns of consumption were detected.

Macroinvertebrate biomass, production and P:Bs—Production by macroinvertebrate primary consumers from 24 May 2007-29 May 2008 was 10.1±1.6 g DM m^{-2} (mean±95% CI), mean biomass was 2.6±0.3 g DM m^{-2}, and the P:B was 3.9±0.7 (Table 1). Production from 29 May 2008-25 May 2009 was 17.4±2.2 g DM m^{-2}, mean biomass was 4.2±0.4 g DM m^{-2}, and the P:B was 4.2±0.7. Both production and mean biomass from 29 May 2008-25 May 2009 were greater than for 24 May 2007-29 May 2008 ($P>0.05$, 2-sample randomization test; Manly 1991). P:Bs, however, did not differ significantly, indicating that the greater level of production during 29 May 2008-25 May 2009 was due to biomass accumulation rather than altered growth rates. Production by macroinvertebrate secondary consumers from 24 May 2007-29 May 2008 was 1.9±0.5 g DM m^{-2}, biomass was 0.9±0.2 g DM m^{-2}, and the P:B was 2.2±0.7 (Table 1). Production from 29 May 2008-25 May 2009 was 4.9±1.0 g DM m^{-2}, biomass was 1.3±0.2 g DM

m^{-2}, and the P:B was 3.9±1.0. Biomass, production and P:Bs of secondary consumers were all greater in the interval from 29 May 2008-25 May 2009 than 24 May 2007-29 May 2008 ($P<0.05$).

Seasonal patterns of total macroinvertebrate production, biomass and P:Bs—Daily interval production and P:Bs for macroinvertebrate primary consumers showed seasonal cycles, with the highest levels from May-August and lowest from October-January (Fig. 3). Although seasonal cycles of total primary consumer biomass were in general synchrony with production and P:Bs, there was also a trend of increasing biomass over the study (see "*Macroinvertebrate biomass, production and P:Bs*" above). Daily production and P:Bs for the macroinvertebrate secondary consumers showed seasonal cycles similar to primary consumers, but the overall pattern was more muted and variable (Fig. 3). The temporal pattern of macroinvertebrate secondary consumer biomass showed little seasonality. Biomass tended to increase over the study, however, as observed for primary consumers.

Salvelinus malma *abundance and biomass*—A total of 1,454 individual *S. malma* were sampled on 11 dates between May 2007 and August 2009. The SL of captured fish ranged from 5.5 to 19.0 cm ($\overline{X}$=9.2±0.1 cm, n=1,454) and AFDM ranged from 0.4 to 19.0 g ($\overline{X}$=3.3±0.1 g, n=1,452). Mean abundance ranged from 0.10±0.01 to 0.72±0.17 ($\overline{X}$±SE, n=5) individuals m^{-2}, while biomass ranged from 0.27±0.03 to 3.09±0.87 g AFDM m^{-2}.

Salvelinus malma *growth and condition factor*— Individual growth rates showed strong seasonal fluctuations, with peaks during May - June, while growth rates measured over winter were negative (Fig. 4). Mean condition factor also showed strong seasonal variation (e.g., 1.2 in May 2007 to lows of <0.8 in March 2008 and February 2009). Mean condition factor was typically >1 during May - August, and condition declined sharply during both winters of the study.

Salvelinus malma *production*— Estimates of production for *S. malma* were problematic due to low numbers of recaptured individuals (102 total) allowing calculation of growth rates, particularly during the second year of study (~May 2008-May 2009). To counter this, mean individual growth rates were estimated using quadratic regression over quasi-annual periods. Daily growth rates (d^{-1}) from marked individuals were regressed against the midpoint date of their marking and recapture. The first period spanned 20 March 2007-26 May 2008. The equation describing mean daily growth during this period was: g (d^{-1}) = 523.6 - 26.6 × date + 0.337 × date^2 ($P<0.0001$, n=60 recaptures, R^2=0.48), where "date" = Excel© date/1000. The second period spanned 4 July 2008-4 August 2009. The equation describing growth rates during this period was: g (d^{-1}) = 234.3 – 11.8 × date + 0.148 × date^2 ($P\leq 0.001$, n=42 recaptures, R^2=0.29). Although the R^2 values are relatively low, the residual error was distributed symmetrically around the fitted plots, indicating accurate trends of changing g over time.

Production by *S. malma* showed dramatic seasonal cycles, with consistently high levels during May-August [e.g., range = 4.6±2.1 to 16.3±7.9 mg AFDM m^{-2} d^{-1} (±95% C.I.), Fig. 4]. The lowest levels of production occurred during October-February (e.g., range = 0.4±0.9 to 1.5±2.2 mg AFDM m^{-2} d^{-1}, Fig. 4). During these latter intervals the 95% C.I.s include zero. Annual *S. malma* production from 24 May 2007-29 May 2008 was 1,985±647 (±95% C.I.) mg AFDM m^{-2} and production from 29 May 2008-25 May 2009 was 1,711±727 mg AFDM m^{-2}. The P:B from 24 May 2007-29 May 2008 was 1.56±0.29 and the P:B from 29 May 2008-25 May

2009 was 1.75±0.41. Annual production or P:Bs did not differ significantly between years (*P*>0.05, 2-sample randomization test). Semimonthly estimates of *S. malma* prey demand and supply (mg DM m^{-2} d^{-1}) indicated that prey production during October – February was generally not sufficient to support demand (Fig. 5).

Salvelinus malma *diet*—Mean prey taxon richness in stomach contents ranged from 2-6 during November – February to 8-12 during April – August. Similarly, mean prey items individual^{-1} ranged from <20 during November – February to ~40 to ~90 during April – August and prey biomass individual^{-1} ranged from <10 mg DM from November – February to >60 mg DM from April – August (Fig. 6, Table 2). Terrestrial invertebrates contributed to prey biomass during May – September, with greatest levels reached in early July [e.g., 65±49% ($\overline{X}$±95% CI)]. Essentially no terrestrial prey were consumed during October – May. A comparison of diets during summer (May-June) and winter (January-February) indicates that diets were dominated (i.e., >75% of mean DM gut^{-1}) by five taxa (*Baetis*, *Ecclisomyia*, *Isoperla*, *Limnophora*, *Zapada*; Table 2), with *Baetis* larvae comprising the highest proportion of the diet during summer (~59% of mean DM gut^{-1} during summer versus ~4% during winter) and *Isoperla* larvae comprising the highest proportion during winter (~15% during summer versus ~49% during winter). Other seasonal differences included the consumption of adult *Zapada* only during summer, and larval *Zapada* and *Limnophora* only during winter.

Light and temperature as correlates of consumer production—Daily interval production by the macroinvertebrate primary-consumer assemblage was positively related to both PAR (mg DM m^{-2} d^{-1} =2.247 × $PAR^{0.563}$, R^2=0.73, *P*<0.0001, *n*=23) and temperature (mg DM m^{-2} d^{-1} = 0.107 ×

$^{\circ}C^{3.259}$, R^2=0.21, P=0.03, n=23). Daily interval production by the macroinvertebrate secondary-consumer assemblage was not related to either PAR (P=0.20, n=23) or temperature (P=0.43, n=23). Daily interval production by *S. malma* was positively related to both PAR (mg AFDM m^{-2} d^{-1} =0.296 × $PAR^{0.514}$, R^2=0.50, P<0.001, n=23) and temperature (mg AFDM m^{-2} d^{-1} =0.00001 × $^{\circ}C^{7.101}$, R^2=0.82, P<0.0001, n=23).

Apparent energetic coupling of trophic levels—Daily macroinvertebrate primary consumer production was closely related to the productivity of their putative food source [gross primary production, GPP (mg C m^{-2} d^{-1}; Huryn et al. 2014); mg DM m^{-2} d^{-1} = 9.040 + 0.020 × GPP, R^2=0.64, P<0.0001, n=23, Fig. 7]. Predaceous macroinvertebrate production (mg DM m^{-2} d^{-1}) was significantly related to primary consumer production (mg DM m^{-2} d^{-1}; predator production = 1.962 × primary consumer $\text{production}^{0.457}$, R^2=0.31, P<0.006, n=23) and *S. malma* production (mg AFDM m^{-2} d^{-1}) was significantly related to prey production (i.e., total macroinvertebrate production, mg DM m^{-2} d^{-1}; *S. malma* production = 1.789 × prey $\text{production}^{0.263}$, R^2=0.45, P<0.0004, n=22).

Patterns of apparent temperature versus light dependence of consumer growth and productivity—Arrhenius plots of daily P:Bs for macroinvertebrate primary consumers, predators, and *S. malma* generally showed similar “hockey stick” patterns, indicating a decoupling of the temperature-P:B relationship as temperatures decrease (Figs. 8a, 8c, 8e). Plots of consumer P:B within a range of 41.4 – 41.6 kT^{-1} (i.e., ~7ºC to 5ºC) were consistent with plots of least-square fitted equations with slopes fixed as the activation energy predicted for aerobic metabolic processes by eukaryotes (-0.65 eV [Allen et al. 2005], Figs. 8a, 8c, 8e). At kT^{-1} >41.6 (i.e., <

~5ºC), however, the apparent temperature dependence broke down, indicating that factors other than temperature were primary drivers of P:B during winter. Arrhenius plots also showed that P:B increased from its nadir as the coldest annual temperatures were approached (i.e., the lowest P:Bs were not observed at the lowest temperatures; Figs. 8a, 8c, 8e). This pattern is consistent with light availability rather than temperature being the driver of the lowest consumer P:B as the lowest levels of light occur in December, while the lowest water temperatures occur in February and March (Appendix S1: Fig. S1; Huryn et al. 2014). Furthermore, the analysis of the residual error from the Arrhenius plots revealed positive relationships between PAR and P:Bs for macroinvertebrate primary consumers (residual error = $0.502 \times \ln(\mathrm{PAR}) - 2.703$, $R^2=0.76$, $P<0.0001$, Fig. 8b) and *S. malma* (residual error = $0.411 \times \ln(\mathrm{PAR}) - 2.319$, $R^2=0.69$, $P<0.01$, Fig. 8f). In both cases, the maximum negative deviation from the regression model occurred at the minimum PAR measured. The plot of residuals derived for the predaceous macroinvertebrates showed a similar pattern, but was not statistically significant (residual error = $0.544 \times \ln(\mathrm{PAR}) - 0.716$, $R^2=0.12$, $P=0.10$, Fig. 8d).

DISCUSSION

How productive is Ivishak Spring?

Levels of production estimated for the macroinvertebrate primary consumers (10.1–17.4 g DM m^{-2} yr^{-1}) of Ivishak Spring were surprisingly high, particularly given its location above the Arctic Circle (69ºN). The mean annual level reported here, for example, exceeds 58% of the community estimates of macroinvertebrate annual production reported worldwide in a recent meta-analysis (Patrick et al., *in press*), despite annual mean water temperatures ranging from only 4.2 to 7.6ºC (Appendix S1: Fig. S1). Similarly, the production of *S. malma* measured here is relatively high compared with many other salmonid streams. Our estimates of 1.7 – 2.0 g AFDM m^{-2} yr^{-1} are equivalent to ~100 –118 kg WM ha^{-1} yr^{-1}, which is within the range of levels used to define highly productive trout streams (~100 – 300 kg WM ha^{-1} yr^{-1}; Waters 1988, 1992). Although some macroinvertebrate taxa had bivoltine life cycles and, consequently, relatively high annual P:Bs (i.e., >10), the majority of production was attributed to taxa with annual P:Bs <5.0, showing that their total productivity is primarily dependent on high biomass rather than high growth rates, as shown for spring-stream communities elsewhere (Berg and Hellenthal 1991). The high primary consumer productivity shown for Ivishak Spring also supports an unusually long food chain (mean length = 3.2 steps) for arctic headwater streams (i.e., the longest food chain length of 19 arctic stream communities analyzed by Parker and Huryn 2013), with documented predators including other macroinvertebrates, *S. malma*, American dipper (*C. americanus*), and North American river otter (*L. canadensis*), which is a predator of *S. malma* (Parker and Huryn 2013). Although the level of secondary production we measured here is notable, given the arctic context, it is perhaps not unexpected as GPP measured during summer (>4.0 g C m^{-2} d^{-1}) compares favorably with the highest rates reported for headwater streams at much lower latitudes (Huryn et al. 2014).

Drivers of annual cycles of production in Ivishak Spring

In a study of the ecosystem metabolism of Ivishak Spring, Huryn et al. (2014) revealed apparent C limitation of ER during winter when rates of photosynthesis and GPP were at their lowest levels. Two lines of evidence were used to support this conclusion: 1) a strong relationship between gross GPP and ER showing that these processes were closely coupled, and 2) an Arrhenius relationship (White et al. 2012) between temperature and ER that, rather than being linear, showed a “hockey stick” pattern consistent with a deviation from an apparent relationship with temperature that was both sudden and synchronous with a seasonal reduction of light availability. As we show below, the results of our analyses of secondary production indicate a close correspondence to the analyses of drivers of ecosystem metabolism by Huryn et al. (2014).

Close coupling of consumer production and energy availability—Temporal patterns of production by macroinvertebrate primary consumers, predaceous macroinvertebrates and *S. malma* were all significantly and positively related to temporal patterns of their food supplies. Although examples are uncommon, similar coupling of production between trophic levels has been shown for other stream ecosystems. For example, strong bottom-up control of primary consumer production that, in turn, controlled predator production was shown for a temperate forest stream ecosystem by Wallace et al. (1999, 2015) in a multi-year experiment that altered organic matter supply. Although an experimental approach was not used in our study, a similar pattern of resource variation was apparently induced by seasonal changes in light and consequent fluctuations in GPP (Fig. 7). This cyclical fluctuation in resource base was then propagated upward through the food web to drive temporal patterns of production by predaceous macroinvertebrates and *S. malma*. Although speculative, the close coupling between secondary production and primary production we document provides support for possible C-limitation during periods of winter darkness, as observed previously for ER (Huryn et al. 2014).

Arrhenius plots showing a P:B-temperature anomaly—The rapid decline of production from summer to winter combined with comparatively minor reductions in water temperature suggests that seasonal C limitation of consumer growth in Ivishak Spring is possible. Assessing this, however, is complicated because water temperature and light availability are confounded, even though the range of water temperature during our 30-month study was only 2.8ºC. As a consequence, the control of seasonal patterns of productivity due to temperature, via direct thermal-kinetic effects, or light availability via its control of primary productivity, could not be directly measured. When temporal patterns of daily P:Bs ranging across several trophic level are visualized using Arrhenius plots, however, insight into potential controlling factors is gained. Arrhenius plots of the P:Bs of macroinvertebrate primary consumers, predaceous macroinvertebrates, and *S. malma* each showed similar, relatively slow, linear declines in rates as water temperatures decreased from ~7°C to 5°C, followed by abrupt declines to very low rates as temperatures fell below ~5°C, followed by an increase in rates as temperatures approach the lowest levels measured (≤4.5ºC). Consequently, analyses of the residual error from the Arrhenius plots for both macroinvertebrate primary consumers and Dolly Varden showed strong relationships with PAR, with the greatest negative departures at the lowest levels of light rather than at the coldest temperatures.

A further analysis of Arrhenius plots of GPP and ER reported by Huryn et al. (2014) showed temperature anomalies similar to those observed for P:Bs (i.e., GPP showed a rapid decline below 5.6°C followed by an increase as temperatures fell below 4.7°C; ER showed a rapid decline below 5.6°C followed by an increase as temperatures fell below 4.9°C; Figs. 9a, 9c). Moreover, an analysis of the residuals of the Arrhenius plots [i.e., departures from least-square regression with the slope constrained to ~0.3 eV, which approximates activation energy of photosynthesis as constrained by RuBisCO carboxylation (Allen et al. 2005, Anderson-Teixeira and Vitousek 2012), or -0.65 eV, which approximates the expected activation energy of aerobic catabolism (Allen et al. 2005, Perkins et al. 2012)] showed relationships with PAR essentially identical to those shown for consumer P:Bs, with the greatest negative departures from predicted values occurring at lowest levels of light rather than coldest temperatures (GPP residual error = 0.205 × ln(PAR) – 1.248, R^2=0.81, P<0.0001, Fig. 9b; ER residual error = 0.080 × ln(PAR) – 0.607, R^2=0.17, P=0.055, Fig 9d). The fact that ecosystem metabolism and consumer P:Bs were estimated using independent approaches, combined with the close synchrony of their annual cycles and similar anomalous Arrhenius relationships, provides strong support for the conclusion that temporal patterns of secondary production and ER in Ivishak Spring are both controlled by seasonal light cycles rather than temperature. By combining temperature thresholds for the breakdown of temperature dependence of ER and consumer production with daily records of water temperature, the periods when apparent C-limitation affects these processes can be estimated. Although there is year-to-year variation, ER is generally affected by apparent C-limitation from ~October to April, whereas the apparent C-limitation of secondary production is of shorter duration, extending from ~December to March.

Seasonal patterns of food consumption

Although direct evidence of C-limitation of macroinvertebrate production during winter is lacking, diet and prey supply-demand analyses provide insight into this possibility. Two observations regarding diet are significant. The first is the serial omnivory documented for *Isoperla petersoni*, the most productive species at Ivishak Spring. The second is the seasonality of diatom consumption by the other taxa analyzed. Although omnivory has been reported previously for *I. petersoni* (Stewart and Stark 2002), its extreme seasonality at Ivishak was striking and provides an example of the importance of the temporal axis when analyzing food web structure (McMeans et al. 2015; Fig. 2). Diatoms, for example, made up almost the entire diet of *I. petersoni* during April (~85%), whereas invertebrate prey were more prevalent during other months (i.e., April ~5% vs. July ~81%, October ~45%, January ~81%). It is important to note that >50% of *I. petersoni* production occurred during the April-June period when diatom consumption was maximized (Fig. 2). *Pagastia*, *Ecclisomyia* and *Rhynchelmis* showed similar patterns, with maximum diatom consumption during April (e.g., range of mean % diatoms among taxa ~74 – 85%), whereas gut contents were essentially devoid of diatoms during January (e.g., range among taxa ~0 – 5%, Fig. 2). Given the correlation between the seasonality of diatom consumption and production by primary consumers, it is possible that low diatom availability limited their production during winter. Although speculative, diatoms may disproportionately contribute to the pool of essential fatty acids required to support production by the macroinvertebrate primary consumers in Ivishak Spring. Diatoms have relatively high levels of total fatty acids, compared with other primary producers (Brett and Müller-Navarra 1997) and their near absence in the winter diet of macroinvertebrates may have resulted in low levels of production rather than C-limitation *per se*.

Similar to the macroinvertebrates, *S. malma* showed substantial seasonal variation in diet composition, although only five prey taxa contributed ≥75% to gut content DM during both summer and winter. In addition to differences in taxonomic richness, the biomass of stomach contents also declined significantly from a high of >60 mg DM during April – August to <10 mg DM from November – February. Although seasonal patterns of growth and condition may have been affected by seasonal differences in prey type (e.g., dominance of *Baetis* larvae during summer), coincident patterns of extremely low gut content DM and low body condition suggest that fasting during winter was the primary driver of the significant losses of individual *S. malma* biomass observed from ~November – February. Although resting metabolic rates of salmonids may be reduced during periods of winter food scarcity in north temperate rivers, which offsets metabolic losses of biomass (Auer et al. 2016), the effects of fasting on individual biomass and condition in Ivishak Spring are presumably exacerbated during winter due to stable water temperatures that drive relatively constant metabolic demands despite declining prey consumption.

Potential factors controlling prey biomass consumed by *S. malma* during November – February include the lack of terrestrial invertebrates and a reduction of foraging efficiency due to long periods of darkness. Although the absence of terrestrial prey contributed to lower total prey biomass during winter (e.g., ~8 to 20% during July – August, ~0 to 1% during November – February), most of the reduction in consumption was due to lower quantities of ingested aquatic prey. Whether this is due to an inability to capture prey effectively or due to prey scarcity is unknown, although our analysis of prey supply versus demand indicated that macroinvertebrate production during the winter months (e.g., October – February; Fig. 5) was insufficient to support *S. malma* production or maintain body condition. Although information specific for *S. malma* is limited, several studies have shown that stream salmonids tend to forage for benthic prey when drifting prey are uncommon (Dunham et al. 2008) or during periods of darkness (Hagan and Taylor 2001). Furthermore, some studies have shown that foraging during darkness has a lower probability of prey capture than daytime foraging (Fraser and Metcalfe 1997, Watz et al. 2014). Nevertheless, studies of arctic char (*Salvelinus alpinus*) and juvenile Atlantic salmon (*Salmo salar*) have shown that nocturnal feeding is a common overwintering strategy (Alanärä and Bränäs 1997, Amundsen et al. 2000). Although data allowing the definitive separation of different factors are lacking, it is likely that the reduction in prey biomass consumed during winter is due to a combination of the lack of terrestrial prey, inefficient foraging during darkness, and low levels of aquatic prey production. Nevertheless, the results of our semi-monthly prey supply-demand analysis indicate that the latter factor is preeminent (Fig. 5).

Light availability, not temperature, drives cycles of productivity in Ivishak Spring

Extreme seasonal cycles of light and temperature are key exogenous drivers (e.g., Valett et al. 2008) of ecological processes occurring in most arctic ecosystems (Thomas et al. 2008). Arctic spring-streams, however, maintain relatively constant temperatures year-round, which provides an unusual energetic context in which ectothermic consumers are subject to relatively stable metabolic demands while energy supplies undergo annual cycles forced by light availability (Huryn et al. 2014). These factors together result in cycles of C limitation that drive patterns of consumer productivity that are uncoupled from cycles of temperature. In support of this scenario, we found: 1) lack of temperature dependence of daily P:Bs during winter, 2) lowest levels of GPP and daily P:Bs of consumers at lowest light levels rather than lowest water temperatures, 3) minimal consumption of primary producers by macroinvertebrates and prey by *S. malma* during winter, 4) biomass loss by *S. malma* due to fasting during winter, as indicated by direct measurements of individual growth rates and body condition, and 5) a prey supply versus demand budget indicating that macroinvertebrate production was insufficient to support *S. malma* production or maintain body condition during winter.

In conclusion, we found light, not temperature, to be the apparent driver of annual cycles of secondary production in Ivishak Spring. Our results provide evidence for C limitation of consumer productivity due to changes in the rate of photosynthesis as light waned and waxed through the winter months (consistent with Fig. 1d). We used the unusual annual light and temperature regimes of this arctic spring to test predictions about the effect of seasonal light availability on consumer productivity – with minimally confounding effects of temperature. This exceptional combination of extreme seasonal fluctuations in light and relatively constant and moderate temperatures perhaps raises questions about whether the results of our study can be generalized to other ecosystem types. Although arctic springs are uncommon and remote, they offer a “natural manipulation” of exogenous drivers that are difficult or even impossible to alter experimentally at appropriate scales. By capitalizing on the unusual energetic context of Ivishak Spring, we were able to demonstrate how the almost universal synchrony between annual light and temperature regimes conceals mechanisms by which these two drivers interact to control energy flow through ecosystems. In particular, the timing and severity of winter C limitation we have documented in this spring-stream hints at a fundamental role for light-temperature synchrony in matching ecosystem-level energy supply with demand in most other ecosystem types. This widespread seasonal supply-demand synchrony potentially confers an important measure of stability in the metabolism of food webs over annual time-scales.

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Literature cited

Alanärä, A. and E. Bränäs. 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 54:2894-2900.

Amundsen, P.A., H.M. Gabler, T. Herfindal and L.S. Riise. 2000. Feeding chronology of Atlantic salmon parr in subarctic rivers: consistency of nocturnal feeding. Journal of Fish Biology 56:676-686.

Auer, S.K., K. Salin, G.J. Anderson and N.B. Metcalfe. 2016. Flexibility in metabolic rate and activity level determines individual variation in overwinter performance. Oecologia 182:703-712.

Benke, A.C. and A.D. Huryn. 2017. Secondary production and quantitative food webs. Pp. 235-254 *in* (F.R. Hauer, G.A. and G.A. Lamberti, *eds*.) *Methods in Stream Ecology, 3rd Edition. Volume 2: Ecosystem Function.* Academic Press, San Diego.

Benke, A.C., A.D. Huryn, L.A. Smock and J.B. Wallace 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308-343.

Benstead, J.P. and A.D. Huryn. 2011. Extreme seasonality of litter breakdown in an arctic spring-fed stream is driven by shredder phenology, not temperature. Freshwater Biology 56:2034-2044.

Berg, M.B. and R.A. Hellenthal. 1991. Secondary production of Chironomidae (Diptera) in a north temperate stream. Freshwater Biology 25:497-505.

Bernhardt, E.S., J.B. Heffernan, N.B. Grimm, E.H. Stanley, J.W. Harvey, M. Arroita, A.P. Appling, M.J. Cohen, W.H. McDowell, R.O. Hall Jr. and J.S. Read. 2018. The metabolic regimes of flowing waters. Limnology and Oceanography 63:99-118.

Brett, M.T., and D.C. Müller-Navarra. 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biology 38:483-499.

Brown, J.H., and R.M. Sibly. 2012. The metabolic theory of ecology and its central equation. Pages 21-33 *in* J.H. Brown, R.M. Sibly, and A. Kodric-Brown, editors. Metabolic ecology: a scaling approach. Wiley-Blackwell, West Sussex, UK.

Dossena, M., G. Yvon-Durocher, J. Grey, J.M. Montoya, D.M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. Proceedings of the Royal Society: B-Biological Sciences 279:3011-3019.

Dunham, J., C. Baxter, K. Fausch, W. Fredenberg, S. Kitano, I. Koizumi, K. Morita, T. Nakamura, B. Rieman, K. Savvaitova and J. Stanford. 2008. Evolution, ecology, and conservation of Dolly Varden, white spotted char, and bull trout. Fisheries 33:537-550.

Fraser, N.H.C. and N.B. Metcalfe. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. Functional Ecology 11:385-391.

Giles, N. 1980. A stomach sampler for use on live fish. Journal of Fish Biology 16:441-444.

Hagen, J. and E.B. Taylor. 2001. Resource partitioning as a factor limiting gene flow in hybridizing populations of Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 58:2037-2047.

Heffernan, J.B., and M.J. Cohen. 2010. Direct and indirect coupling of primary production and diel nitrate dynamics in a subtropical spring-fed river. Limnology and Oceanography 55:677-688.

Huryn, A.D. 1996. An appraisal of the Allen Paradox in a New Zealand trout stream. Limnology and Oceanography 41:243-252.

Huryn, A.D., J.P. Benstead & S.M. Parker. 2014. Seasonal changes in light availability modify the temperature dependence of ecosystem metabolism in an arctic stream. Ecology 95:2826-2839.

Huryn, A.D., and J.E. Hobbie. 2012. Land of extremes: a natural history of the arctic North Slope of Alaska. University of Alaska Press, Fairbanks, Alaska, USA.

Huryn, A.D., K.A. Slavik, R.L. Lowe, S.M. Parker, D.S. Anderson, and B.J. Peterson 2005. Landscape heterogeneity and the biodiversity of Arctic stream communities: a habitat template analysis. Canadian Journal of Fisheries and Aquatic Sciences 62:1905-1919.

Manly, B.F.J., 1991. Randomization and Monte Carlo Methods in Biology. Chapman and Hall, London, UK.

McMeans, B.C., K.S. McCann, M. Humphries, N. Rooney and A.T. Fisk. 2015. Food web structure in temporally-forced ecosystems. Trends in Ecology and Evolution 30:662-672.

Merritt, R.W., K.W. Cummins and M.B. Berg (eds.). 2007. Introduction to the Aquatic Insects of North America, 4th Edition. Kendall Hunt.

Parker, S.M. and A.D. Huryn. 2013. Disturbance and productivity as codeterminants of stream food web complexity in the Arctic. Limnology and Oceanography 58:2158-2170.

Parker, S.M., and A.D. Huryn. 2006 Food web structure and function in two Arctic streams with contrasting disturbance regimes. Freshwater Biology 51:1249-1263.

Parker, S.M., and A.D. Huryn. 2011. Effects of natural disturbance on stream communities: a habitat template analysis of Arctic headwater streams. Freshwater Biology 56:1342-1357.

Patrick., C.J., D. McGarvey, W.F. Cross, D. Allen, A.C. Benke, T. Brey, A.D. Huryn, J. Jones, C. Murphy, C. Ruffing. P. Saffarinia, M.R. Whiles, J.B. Wallace and G. Woodward. In press. Precipitation and temperature drive continental to global patterns of stream invertebrate production. Science Advances.

Perkins, D.M., G. Yvon-Durocher, B.O.L. Demars, J. Reiss, D.E. Pichler, N. Friberg, M. Trimmer, and G. Woodward. 2012. Consistent temperature dependence of respiration across ecosystems contrasting in thermal history. Global Change Biology 18:1300-1311.

Roberts, B.J., P.J. Mulholland, and W.R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10:588-606.

Sabo, J.L., J.L. Bastow and M.E. Power. 2002. Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336-343.

Stewart, K.W. and B.P. Stark. 2002. Nymphs of North American stonefly genera (Plecoptera). The Caddis Press, Columbus, Ohio.

Thomas, D.N., G.E. Fogg, P. Convey, C.H. Fritsen, J.-M. Gili, R. Gradinger, J. Laybourn-Parry, K. Reid and D.W.H. Walton. 2008. The Biology of Polar Regions: Biology of Habitats. Oxford University Press.

Valett, H.M., S.A. Thomas, P.J. Mulholland, J.R. Webster, C.N. Dahm, C.S. Fellows, C.L. Crenshaw, and C.G. Peterson. 2008. Endogenous and exogenous control of ecosystem function: N cycling in headwater streams. Ecology 89:3515-3527.

Wallace, J.B., S.L. Eggert, J.L. Meyer and J.R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409-442.

Wallace, J.B., S.L. Eggert, J.L. Meyer and J.R. Webster. 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. Ecology 96:1213-1228.

Waters, T.F. 1988. Fish production-benthos relationships in trout streams. Polskie Archiwum Hydrobiologii 35:545-561.

Waters, T.F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient for management of trout in streams. North American Journal of Fisheries Management 12:34-39.

Watz, J., J. Piccolo, E. Bergman and L. Greenberg. 2014. Day and night drift-feeding by juvenile salmonids at low water temperatures. Environmental Biology of Fishes 97:505-513.

White, E.P., X. Xiao, N.J.B. Isaac, and R.M. Sibly. 2012. Methodological tools. Pages 9-20 *in* J.H. Brown, R.M. Sibly, and A. Kodric-Brown, editors. Metabolic ecology: a scaling approach. Wiley-Blackwell, West Sussex, UK.

Table 1. Mean annual biomass (B, mg DM m^{-2}±95% C.I.), production (P, mg DM m^{-2} yr^{-1}±95% C.I.) and P:B (yr^{-1}± 95% C.I.) for macroinvertebrates occurring in Ivishak Spring, AK. Y1 = 24 May 2007 to 29 May 2008, Y2 = 29 May 2008 to 25 May 2009. Taxa are primary consumers unless otherwise indicated as †=omnivore or ††=predator. Cases where P:B could not be calculated are indicated as "n.c."

Class	Order	Family	Genus	Y1 B	Y2 B	Y1 P	Y2 P	Y1 P:B	Y2 P:B
Turbellaria††				60±19	91±27	64±33	129±76	1.1±0.7	1.5±1.0
Clitellata	Lumbriculida	Lumbriculidae	*Rhychelmis* sp.	277±96	428±172	447±211	526±255	1.7±1.0	1.3±0.8
			Misc.	69±35	333±113	141±146	562±568	2.1±1.9	1.7±1.6
Insecta	Ephemeroptera	Baetidae	*Baetis cf. foemina*	256±48	332±74	1398±492	2058±643	5.5±2.2	6.3±2.4
	Plecoptera	Nemouridae	*Zapada haysi*	275±77	342±81	1064±414	822±229	3.9±1.9	2.4±0.9
		Perlodidae	*Isoperla petersoni*†	812±218	1009±196	2172±724	4743±1266	2.7±1.2	4.8±1.6
	Diptera	Chironomidae	*Corynoneura* sp	5±3	8±6	5±4	49±54	1.2±1.7	6.7±10.1
			Diamesa sp.	13±18	19±8	26±58	34±45	5.9±5.9	1.9±2.8
			Eukiefferiella brehmi grp.	15±8	25±10	51±69	211±178	3.8±5.7	8.9±8.2
			Euk. devonica grp.	64±26	168±52	330±212	1398±536	5.4±4.4	8.6±4.4
			Euk. gracei grp.	23±7	81±50	192±135	637±448	8.5±6.4	8.7±8.7
			Micropsectra sp.	75±36	153±68	738±748	1648±894	10.4±12.0	11.4±8.4
			Orthocladius s.s.	85±50	85±49	326±404	222±186	5.8±6.3	4.6±3.1
			O.(Euorthocladius) sp.	28±11	129±44	1±1	673±493	0.0±0.0	5.4±4.5
			Pagastia sp.†	204±64	459±107	772±553	1517±771	3.9±3.1	3.4±1.9
			Rheocricotopus sp	35±27	19±10	434±324	220±101	15.3±23.5	12.4±9.8
			Tvetenia sp.	0±0	20±13	0±0	87±70	n.c.	5.0±5.6
			Thienemanniella sp.	11±4	12±5	108±85	75±61	10.5±9.5	6.7±6.4
		Simuliidae	*Prosimulium* sp.	55±39	38±30	792±638	273±193	17.0±22.0	8.9±11.3
		Psychodidae	*Pericoma* sp.	469±122	515±119	1044±388	1469±478	2.3±1.0	2.9±1.2
		Tipulidae	*Dicranota* sp.†	43±26	53±15	49±30	150±65 1.	3±1.1	2.9±1.6
		Empididae	*Chelifera* sp.††	242±51	321±59	494±166	1312±434	2.1±0.8	4.1±1.5
			Oreogeton sp.††	0±0	98±46	0±0	531±331	n.c.	5.8±4.9
		Muscidae	*Limnophora* sp.††	123±61	207±97	362±249	696±450	3.2±2.9	3.6±3.1
	Trichoptera	Limnephilidae	*Ecclisomyia conspersa*	239±79	517±151	1085±467	2251±708	4.7±2.6	4.5±2.0

Table 2. Summary of Dolly Varden stomach contents from individuals sampled monthly in Ivishak Spring during May-July (2007, 2008, 2009) and January-February (2008, 2009). The taxa shown represent the most common prey items among stomach contents and collectively make up >75% of total mean prey biomass (74.5% for May-July samples, 92.9% for January-February samples). Values are grand means based on estimates of monthly mean stomach content biomass ± 1 S.E. See Table 1 for information regarding the taxonomic classification of listed taxa.

	May-July	January-February
Taxon	mg DM gut^{-1}	mg DM gut^{-1}
Baetis cf. foemina	20.7 ± 5.8	0.3 ± 0.2
Isoperla petersoni	5.2 ± 2.7	3.4 ± 1.0
Zapada haysi (larva)	0.0 ± 0.0	0.5 ± 0.3
Zapada haysi (adult)	2.4 ± 1.2	0.0 ± 0.0
Empididae (adult)	5.7 ± 4.3	0.0 ± 0.0
Limnophora sp.	0.0 ± 0.0	0.8 ± 0.5
Ecclisomyia conspersa	2.2 ± 1.3	2.3 ± 0.7
Total	35.1 ± 6.0	7.0 ± 1.1

Figure captions

FIG. 1. Conceptual model (modified from Huryn et al. 2014) summarizing anticipated annual patterns of primary and secondary production in arctic spring-stream ecosystems. GPP = gross primary production, a.) Coupled pattern of light availability and temperature that normally occurs in high-latitude ecosystems. b.) Decoupling of light and temperature that occurs in arctic springs. c.) De-coupled pattern of annual GPP (controlled by light availability) and consumer metabolism (controlled by temperature). d.) Quasi-coupled pattern of annual GPP (controlled by light availability) and secondary production (controlled by both organic C supplied by GPP and the effect of temperature on consumer metabolism).

FIG. 2. Temporal patterns of diet composition measured as particle area of gut contents for four abundant macroinvertebrate taxa in Ivishak Spring, AK [*Rhynchelmis* (Oligochaeta), *Pagastia* (Diptera: Chironomidae), *Ecclisomyia* (Trichoptera: Limnephilidae), *Isoperla* (Plecoptera: Perlodidae)]. OM = organic matter. Open symbols are the individual data points (*n* = 5-8 individuals).

FIG. 3. Temporal patterns of macroinvertebrate primary consumer (a) production and (b) production:biomass ratio and of macroinvertebrate secondary consumer (c) production and (d) production:biomass ratio in Ivishak Spring, AK. Length of box represents measurement period and height of box represents 1 S.E. either side of the mean. Smoothing function (dark grey line) is a locally weighted regression ± 1. S.E. (shaded).

FIG. 4. Temporal patterns of (a) specific growth rate, (b) daily production and (c) daily production:biomass ratio for Dolly Varden char (*S. malma*) in Ivishak Spring, AK. In plot (a) bars represent individual char and their length shows the measurement period for growth rate.

In plots (b) and (c) length of box represents measurement period and height of box represents 1 S.E. either side of the mean.

FIG. 5. Estimated prey surplus (± 95% CIs) for Dolly Varden char (*S. malma*) in Ivishak Spring. Prey surplus was calculated as the difference between interval invertebrate production and energetic demand based on interval char production and assumed gross production efficiency (see Huryn 1996). Dashed line indicates zero surplus.

FIG. 6. Temporal patterns of aquatic and terrestrial prey consumption measured as mean dry mass (± 1 S.E.) of stomach contents of Dolly Varden char (*S. malma*) in Ivishak Spring. Smoothing function (dark grey line) is a locally weighted regression ± 1. S.E. (shaded).

FIG. 7. Relationship between mean daily interval production of primary consumers and mean daily gross primary production in Ivishak Spring. Fitted line is a linear least-squares regression ± 1 S.E. (shaded).

FIG. 8. Arrhenius plots of daily production:biomass ratio (d^{-1}) vs. Boltzmann temperature for (a) primary consumer macroinvertebrates, (c) secondary consumer macroinvertebrates and (e) Dolly Varden char (*S. malma*) measured semi-monthly in Ivishak Spring, AK (March 2007-August 2009). Dashed lines are least-square fits with slopes constrained to the activation energy predicted for aerobic anabolic metabolism (i.e., ~0.65 eV). Panels (b), (d) and (f) plot residual error from the Arrhenius plots vs. photosynthetically active radiation (PAR).

FIG. 9. Arrhenius plots of (a) GPP (g C m^{-2} d^{-1}) and (c) ER (g C m^{-2} d^{-1}) measured semi-monthly in Ivishak Spring, AK (March 2007-August 2009). Dashed lines are plots of least-square fit equations with slopes constrained to the activation energies predicted for GPP (i.e., activation energy of RuBisCO carboxylation ~0.3 eV) and ER (i.e., ~0.65 eV), respectively. Panels (b)

and (d) plot residual error from the Arrhenius plots vs. photosynthetically active radiation (PAR).