

Seasonality in the trophic basis of a temperate stream invertebrate assemblage: Importance of temperature and food quality

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Abstract

Ecologists have long recognized that ecosystems are open and that they receive substantial subsidies of energy and materials from beyond their boundaries. This recognition has spurred theoretical and empirical investigation of biotic and abiotic conditions that influence the importance of subsidies for recipient ecosystems. We combined temporal patterns of resource use (via stable isotope analysis), consumer–resource stoichiometry, and invertebrate production to quantify controls on the relative importance of resource subsidies (i.e., terrestrial litter) vs. in situ food resources (i.e., algae) in fueling secondary production in a highly seasonal temperate stream. Both litter subsidies and in situ primary production were important for supporting annual invertebrate production. However, temporal patterns of secondary production and trophic support varied significantly. Algae supported the majority of production (> 55%) during critical growth periods characterized by warm temperatures (5–15°C) and high primary production. In contrast, terrestrial litter supported the majority of invertebrate production (> 55%) during relatively cold months (~ 0–4°C) when primary production and metabolic demands of invertebrates were low. A model selection procedure revealed that both temperature and consumer–resource stoichiometric imbalances were important determinants of patterns of invertebrate production. Our findings highlight the important interaction of environmental conditions and resource quality in mediating how internally and externally derived resources are used to fuel invertebrate production.

Aquatic consumers are subject to extreme variation in food quantity and quality, and they often depend on resources originating from both within (autochthonous) and outside (allochthonous) the ecosystem (Minshall 1967; Marcarelli et al. 2011). Variation in autochthonous resources can result from seasonality in physical characteristics, such as temperature and light, leading to large intraannual differences in primary producer abundance and quality (Stevenson et al. 1996). Variation in allochthonous resources, however, may depend on the extent of connectivity with neighboring ecosystems and differences in the timing, duration, and quality of material subsidies (Polis et al. 1997). Although a large body of research has demonstrated the importance of both autochthonous and allochthonous resources for aquatic consumers, much less is known about how intraannual variation in environmental characteristics influences their utilization (but see McCutchan and Lewis 2002).

The relative use of subsidies vs. in situ resources by consumers may be influenced by characteristics of both the donor and recipient ecosystems, as well the ability of consumers to respond to fluctuations in resource availability (Marczak and Richardson 2008). Resource subsidies differ in their temporal dynamics; some are sustained over time, whereas others are pulsed and are only available for relatively short time periods (Yang 2004). Use of these resources may depend on whether consumers can take advantage of them, and this may be strongly influenced by physical factors, such as temperature, that affect consumer metabolic rates (Armstrong et al. 2010). In addition, patterns of resource utilization may be driven by the quality of available resources relative to consumer energetic

and nutritional demands (i.e., nutritional imbalances). Although large differences in quality may often exist between subsidies and in situ resources, few studies have examined the role of food quality in modulating the importance of subsidies (Woodward and Hildrew 2002).

In most temperate stream ecosystems, physical conditions (i.e., light, temperature, discharge) and the quantity and quality of food resources vary widely over the course of an annual cycle. Leaf fall provides a seasonal pulse of organic matter from the terrestrial landscape, in some cases greatly exceeding algal production on an annual basis (Fisher and Likens 1973; Webster and Meyer 1997). Although a number of studies have shown that leaf litter can fuel the majority of annual invertebrate production (Minshall 1967; Wallace et al. 1997), algae may be important for consumers even at low abundance (Hall et al. 2001; McCutchan and Lewis 2002) because of its relatively high food quality in comparison to detritus (Cross et al. 2003). The use of basal resources by stream consumers will depend on differences in availability and quality throughout the year, as well as on consumers' ability to effectively utilize these resources given abiotic constraints to basal metabolism, growth, and reproduction.

Measuring the ecosystem-level importance of basal resources in food webs requires a comprehensive understanding of resource use and energy flow. Resource use can be quantified using stable isotope analysis when terrestrial and aquatic resources differ in their isotopic signatures (Peterson and Fry 1987). However, stable isotopes alone do not permit a quantitative measure of energy flow and cannot provide information about the total use of different resources by the food web over a given time interval. Measurement of community-level secondary production is an important complement to isotope analysis that integrates

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several aspects of consumer life history, including abundance, biomass, individual growth rates, and survival (Benke and Hurny 2006). By combining stable isotope analysis with secondary production, one can examine the dominant pathways of energy flow through food webs, as well as fine-scale temporal changes in the utilization of food resources (McCutchan and Lewis 2002). This can be a powerful approach for examining the relative importance of subsidies vs. in situ resources in driving the dynamics of recipient food webs.

We assessed the relative importance of allochthonous leaf litter and autochthonous algae to invertebrate production at high temporal resolution in a northern Rocky Mountain stream. We quantified temporal variation in the quantity and quality of food resources, resource utilization by invertebrates, and secondary production to address the following questions: (1) How do the quantity and quality of allochthonous and autochthonous resources change throughout the year?; (2) What is the relative importance of these resources in fueling annual invertebrate production?; (3) How does the trophic basis of invertebrate production vary through time?; and (4) How do temporal changes in physical characteristics (i.e., temperature and discharge) interact with food quantity and quality to affect the trophic basis of invertebrate production? We predicted that the relative abundance of basal resources would vary throughout the year because of seasonality in light, temperature, and litter fall. These changes in resource abundance would lead to shifts in the identity (allochthonous vs. autochthonous) and quality (i.e., carbon [C]:nutrient ratios) of basal resources fueling food web production. Ultimately, we predicted that physical characteristics, such as temperature, would have primacy in driving patterns of secondary production but that food quality of basal resources would further explain seasonal variation in secondary production.

Methods

Study site—We conducted our study on West Blacktail Deer Creek in the Northern Range of Yellowstone National Park, Wyoming, from July 2008 through July 2009. This stream is surrounded by a lush riparian community consisting of woody vegetation, sedges, grasses, forbs, and shrubs. Willows (*Salix* spp.), 1–5 m high, dominate the riparian vegetation and create a canopy that provides moderate and patchy shading from mid-April to mid-November.

We studied a representative stream reach (200 m) with regard to average stream width, depth, gradient, and riparian cover located ~ 1 km south of Yellowstone's Ring Road. Stream discharge was measured at the downstream edge of the reach on each sampling date, using the midsection method. Discharge measurements were correlated with a nearby U.S. Geological Survey (USGS) gauging station (Lamar River near Tower Ranger Station, USGS No. 06188000) to estimate daily discharge between sampling dates ($p < 0.05$, $r^2 = 0.75$). Stream temperature was measured at 15 min intervals with in situ loggers (Onset Computer).

Availability of allochthonous and autochthonous food resources—We estimated direct litter fall using 15 randomly placed litter traps (0.5 m² area; mesh size 1 mm) along the stream reach. Litter traps were anchored with rebar into the incised stream bank just below the ground surface. Organic matter retained on traps was collected on a monthly or biweekly basis between July and December 2008 to estimate mean daily litter input (mg ash free dry weight [AFDW] m⁻² d⁻¹). We did not collect litter between January and June because of snow and ice cover and negligible litter inputs. For each trap, leaf litter collected over the course of the study was summed to estimate mean annual litter input per square meter of stream. Litter was oven-dried to a constant mass (60°C for > 48 h), weighed, combusted in a muffle furnace (500°C for 4 h), and reweighed to determine AFDW.

Benthic organic matter (BOM; $\geq 250 \mu\text{m}$) standing stock was quantified from 10 replicate benthic samples collected approximately monthly throughout the study (see "Macroinvertebrate biomass and secondary production" below). AFDW of BOM was quantified as described above after removal of invertebrates. Our sampling method did not take into account organic matter $< 250 \mu\text{m}$, and we likely underestimated total availability of allochthonous BOM. This likely skewed our estimates of proportional consumption by invertebrates (see below); however, we were more interested in capturing temporal patterns of BOM storage and consumption than the absolute amounts on any given date.

On each sampling date, we collected epilithic material from 10 randomly selected transects within the study reach. At each transect, three to four stones were scrubbed, the slurry combined, and subsamples filtered onto separate pre-ashed glass fiber filters (Whatman GF/C 1.2 μm pore size) for quantification of epilithic AFDW and chlorophyll *a* (Chl *a*). We quantified Chl *a* by extraction in buffered acetone, measurement on a calibrated fluorometer, and correction for pheophytin through acidification. Stones selected for each sample were photographed in the field using a ruler for scale, and stone surface areas were quantified with digital image analysis (ImageJ version 1.42q).

To estimate algal primary production (mg AFDW m⁻² d⁻¹), we used the modeling approach of Morin et al. (1999), which estimates daily gross primary production (GPP; mg C m⁻² d⁻¹) using Chl *a* biomass (mg Chl *a* m⁻²) and stream temperature (°C). The study of Morin et al. (1999) included a large number of temperate streams from a variety of systems and contained Chl *a* values that were similar to our empirical measurements. We assumed that net primary production (NPP) constituted 50% of GPP (Likens 1975). Estimates of NPP (mg C m⁻² d⁻¹) were converted to AFDW using our measured ratio of dry mass (DM):AFDW and the mean %C ($13 \pm 5\%$ DM; mean \pm standard deviation [SD], see below) of epilithic algal samples collected throughout the study. We estimated primary production throughout the year, including winter months when the stream was buried under a thick layer of snow and ice (~ 0.5–1.5 m). Such conditions are not well represented in the model of Morin et al.; thus, our winter

estimates of NPP may be biased high. Although this modeling approach has obvious shortcomings compared to direct measurements of primary production, our estimates of GPP fell within the range observed in streams of similar size within the region (Hall and Tank 2003). Importantly, this analysis allowed us to estimate temporal patterns of NPP that could be compared to patterns of invertebrate production and trophic support.

Macroinvertebrate biomass and secondary production—We collected benthic samples monthly between July 2008 and June 2009 with a Surber sampler (0.096 m², 250 μm mesh) at 10 randomly selected locations. Samples were immediately preserved in 70% ethanol and transported to the laboratory. We separated samples into coarse (> 1 mm) and fine fractions (< 1 mm, > 250 μm) using nested metal sieves. Invertebrates were manually removed from both fractions using a dissecting microscope (15X magnification). Samples were subsampled ($1/2-1/16$) when necessary, using a Folsom plankton splitter (Wildlife Supply Company). Fine fractions were suspended with forced air in a known volume of water in a modified Imhoff cone (Wards Natural Science) and were subsampled with a graduated wide-mouthed plastic syringe. We identified individuals to the lowest possible taxonomic group, generally genus, and assigned taxa to functional feeding groups (FFGs; Cummins and Klug 1979) using our knowledge of these taxa and information reported in Merritt et al. (2008). Individuals were counted, and their body lengths were measured to the nearest mm (first 30 encountered of each taxon). Individuals counted but not measured were assumed to follow the same size distribution as those directly measured on that date. Biomass of individuals was determined using length–mass regressions from Benke et al. (1999). Monthly and annual abundance and biomass were calculated on a per square meter basis.

We estimated annual (mg AFDW m⁻² yr⁻¹) and daily (mg AFDW m⁻² d⁻¹) macroinvertebrate production using the instantaneous growth method (Gillespie and Benke 1979). Production of Chironomidae was determined using the size- and temperature-specific growth rate equation in Huryn (1990). For taxa with easily identifiable cohorts, we used changes in size–frequency distributions to calculate daily growth rates between sampling dates. We then used these growth rates to build an empirical model that predicts growth based on body size and temperature (Eq. 1).

$$g = 0.0107(\pm 0.003) - 0.0019(\pm 0.0018) \times (m) + 0.0193(\pm 0.0004) \times T; \quad (1)$$

$$r^2 = 0.45; p < 0.001$$

where g is the instantaneous growth rate (d⁻¹, mean ± standard error [SE]), m is individual mass in AFDW (mg), and T is the mean stream temperature (°C) for a given interval. We used our model to estimate daily growth rates of other taxa that lacked distinguishable cohorts. Taxa used to derive our model represented approximately 30% of total annual invertebrate production.

To estimate uncertainty in invertebrate abundance, biomass, and production, we calculated 95% confidence

intervals (CIs) using bootstrap analysis as described in Benke and Huryn (2006). Briefly, for each taxon, size-specific abundance data from replicate samples on each date were randomly resampled with replacement 1000 times to generate vectors of mean abundance and biomass. To generate estimates of invertebrate production in the interval between sampling dates, each of the biomass estimates was multiplied by size-specific growth rates (Eq. 1) and the number of days between sampling dates. We summed production vectors across all taxa and time intervals to generate a vector of total annual production estimates and 95% CIs. Annual production was estimated on a per square meter basis.

Elemental concentrations and stable isotope analysis of food web components—On each sampling date, we measured C, nitrogen (N), and phosphorus (P) content, as well as natural abundances of stable C and N isotope ratios of invertebrates and basal resources. Dominant invertebrate taxa were collected with a kick net (1 mm mesh), identified in the laboratory, and stored in cryogenic vials at -20°C until preparation for analysis. Prior to analysis, frozen invertebrate samples were lyophilized and homogenized; and lipids and bicarbonates were removed, following methods adopted from Logan et al. (2008) and Jacob et al. (2005), respectively. Subsamples were then weighed into tin capsules for analysis of %C, %N, and δ¹³C and δ¹⁵N (units are ‰, Peterson and Fry 1987). For the remaining taxa, we applied mean %C, %N, and δ¹³C and δ¹⁵N values from taxa in similar FFGs (e.g., collector-gatherers, scrapers, shredders). All samples for C and N content and stable isotope signatures were analyzed at the University of California–Davis with a PDZ Europa automated N and C analysis for gas, solids, and liquids (ANCA-GSL) elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon). Nylon and glutamic acid were used as external standards for C and N analyses (recovery was 100% and 98% for %C and %N, respectively; standard sample SDs were 0.07 and 0.26 for δ¹³C and δ¹⁵N, respectively). P content was quantified using persulfate digestion and the ascorbic acid method (APHA 1992). Bovine muscle was used as an external standard for P analysis (average recovery 93%). On each date, taxa included in the elemental and stable isotope analyses represented > 60% of total interval production (range 61–81%).

For elemental and stable isotope analysis of allochthonous resources, leaf litter from litter traps was subsampled, dried, homogenized, weighed, and analyzed as above. Previous work suggests that the stable isotope ratios of unconditioned, senesced litter do not substantially differ from litter-derived stream BOM because much of the enrichment in litter occurs before or during leaf abscission, with minimal change during decomposition (Finlay 2001). For analysis of algal food resources, we randomly selected a subset of four epilithon samples for each date and isolated epilithic diatoms from bulk epilithon by centrifugation through colloidal silica (Hamilton et al. 2005). Algal fractions were then filtered onto pre-ashed glass fiber filters (Whatman GF/C 1.2 μm pore size), dried, and prepared for

analysis as described above. Elemental content and stable isotope ratios were analyzed as described for invertebrate consumers. Nylon and peach leaves were used as external standards for C and N analysis, and poplar leaves were used for P analysis (average recovery 102% for C and N, 89% for P).

Trophic basis of invertebrate production—We used a Bayesian mixing model approach, Stable Isotope Analysis in R (SIAR; Parnell et al. 2010), to determine the contributions of allochthonous and autochthonous organic matter to invertebrate biomass. SIAR uses Bayesian inference to estimate the most likely proportional contributions of sources to a mixture—in this case, food sources to a consumer. A Dirichlet distribution is used to ensure that the proportions sum to 1, while still treating each source input as independent (Parnell et al. 2010). This model has advantages over other models in that it accounts for many sources of variation, including isotopic variation among samples of resources and individual consumers, trophic enrichment (fractionation), resource nutrient concentration (Koch and Phillips 2002), and unidentified sources of variation (i.e., physiological variation or unidentified minor dietary sources; Parnell et al. 2010).

When combining stable isotope analysis with secondary production, it is important to account for differences in the timescale between these measurements. Secondary production is a flow that is calculated on multiple timescales (e.g., daily, monthly, annual), whereas isotope measurements are integrative but are measured at a single point in time. Importantly, the stable isotope signature of a consumer integrates a variable amount of the past diet, which depends on body size, growth, and tissue turnover rates (Fry and Arnold 1982). These factors determine how quickly consumers mirror changes in isotope signatures of their food resources. Thus, when quantifying resource use by invertebrates, it is critical to account for these factors, especially when isotope signatures of food resources change more rapidly than the rate of consumer tissue equilibration. We found large variability in the consumer growth rates and isotopic signature of epilithic diatoms over time. To account for changes in the isotopic end-members and differences in biomass accrual among taxa and across time, we adjusted the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of our mixing model end-members, epilithic diatoms, and terrestrial litter. For each taxon on each date, we calculated the amount of time prior to that date that would be equivalent to complete tissue turnover (assumed to scale linearly with growth rate; McCutchan and Lewis 2002). This amount of time differed widely among taxa, based on differences in growth rates (e.g., a short time span for rapidly growing taxa). Next, we calculated an “average” value for the algal isotopic end member that integrated this time by weighting previous algal isotope values by the amount of tissue turnover that occurred during those intervals. This method allowed us to estimate the proportions of algal vs. terrestrial food resources that contributed to biomass on any given date.

We estimated the mean and 95% CIs of the trophic basis of production for each taxon over a given interval using bootstrap analysis, as described above. For each taxon, we

randomly resampled from the “proportional contribution” distributions that were generated by the isotope mixing model and multiplied them by the vector of interval production estimates. This yielded an estimate of the amount of production attributed to allochthonous and autochthonous organic matter during a given time interval. Annual trophic basis of community production was calculated by summing across all taxa and intervals.

Resource consumption and elemental imbalance—For each taxon, we estimated consumption of allochthonous vs. autochthonous resources between sampling dates from measurements of trophic basis of production and assumed gross production efficiencies for leaf detritus and diatoms (0.05 and 0.15, respectively; Benke and Wallace 1980). Whereas these values may not be exact, the error associated with these trophic efficiencies is often minimal compared to other large sources of error, such as abundance or biomass measurements (Cross et al. 2007 supplementary material). The elemental composition (i.e., C:N:P content) of consumed resources was calculated based on the elemental content of allochthonous and autochthonous food resources weighted by their respective proportional contributions to taxon-specific consumption. Community-wide elemental imbalance was calculated as the production-weighted difference in molar C:nutrient ratios between consumers and consumed food resources during a given interval.

Statistical analysis—We tested for differences in the stable C and N isotope ratios of terrestrial litter and diatoms using analysis of variance (ANOVA). Pairwise comparisons for each date were tested using Tukey’s honestly significant difference (HSD) test. To evaluate factors that explained variation in interval community production, we used a generalized linear model with a model selection procedure. In this analysis, interval community production was the response variable; and temperature, C:N imbalance, and C:P imbalance were used as the explanatory variables. We used a variant of Akaike’s Information Criterion corrected for small data sets (AICc) to select the model that best explained variation in interval production during the study. We then used linear regression analysis to examine the relationship between interval production and the variables selected through AICc. In this analysis, the relationship between production and temperature is somewhat self-evident because temperature was included as a variable in our production model. However, our growth model was derived from growth rates that were calculated independently of temperature by examining size–frequency distributions of individual taxa over time. This approach allowed us to examine the potential role of food quality in driving patterns of production while accounting for other important factors such as temperature. Statistical analyses were performed in R (R Development Core Team 2009).

Results

Daily stream discharge and temperature varied seasonally and followed patterns typical of a snowmelt-driven temperate stream (Fig. 1A). Stream discharge ranged from

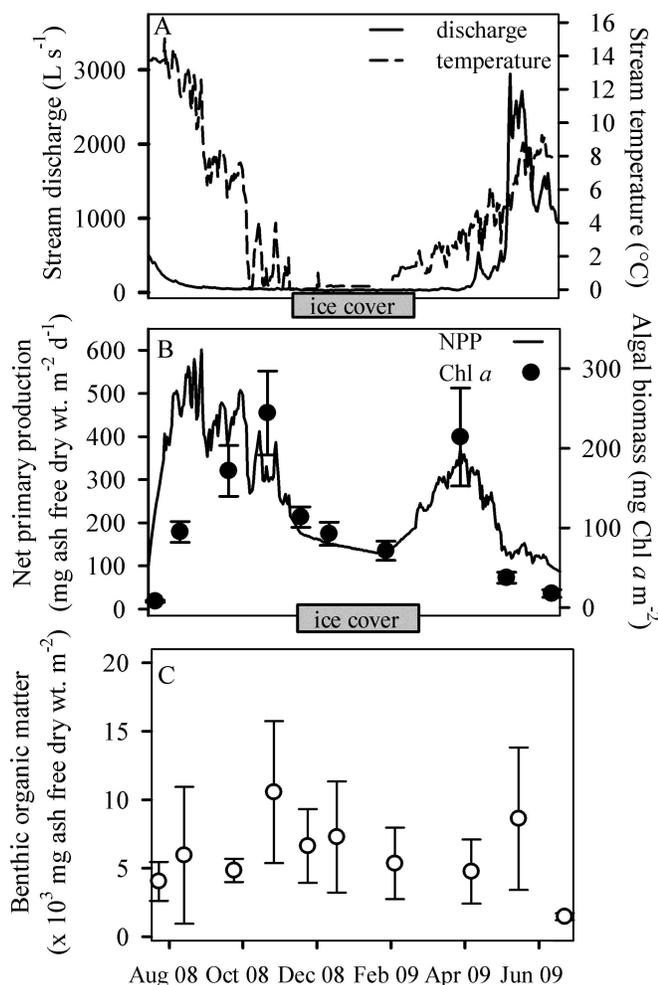


Fig. 1. Temporal patterns of (A) stream discharge and temperature, (B) daily net primary production and chlorophyll *a* biomass (mean and 95% CI; $n = 10$), and (C) benthic organic matter (mean and 95% CI; $n = 10$) in West Blacktail Creek throughout the study.

24 L s⁻¹ to 2900 L s⁻¹. Minimum discharge occurred in January, and peak discharge coincided with snowmelt in May. The mean daily stream temperature ranged from near 0°C (December to March) up to ~15°C (August; Fig. 1A).

Inputs, availability, and quality of allochthonous and autochthonous resources—Epilithic Chl *a* biomass and NPP exhibited a bimodal temporal pattern with peaks in early fall and spring (Fig. 1B). Peak algal biomass in the fall exceeded the highest values observed in spring. Although modeled estimates of NPP roughly mirrored patterns in Chl *a*, reduced stream temperatures in the fall led to an earlier peak in NPP relative to Chl *a*.

Inputs of particulate allochthonous detritus were overwhelmingly dominated by willow litter (> 90% willow leaves and catkins by mass) and occurred from mid-September to mid-November, with peak litter input during October (965 mg AFDW m⁻² d⁻¹; 95% CI, 580–1351). Inputs of particulate detritus from December to July were

negligible. Annual litter inputs were 187,100 mg m⁻² yr⁻¹ (95% CI, 122,000–252,200).

BOM standing stock varied widely, both within and among dates. Mean BOM standing stock ranged from 1500 to 10,600 mg AFDW m⁻² throughout the year (Fig. 1C). Due to the large variability within dates, any seasonal trends were difficult to distinguish; however, the highest values occurred shortly after pulsed litter inputs in November, whereas the minimum standing stock of BOM occurred after peak discharge (i.e., in July 2009).

Macroinvertebrate biomass and secondary production—Thirty invertebrate taxa (22 families) were collected during the study, but relatively few contributed substantially to biomass and production. Total invertebrate biomass averaged 1458 mg AFDW m⁻² (95% CI, 1338–1587), over 50% of which was attributed to four dominant taxa (Elmidae, Chironomidae, *Cinygmula* sp., *Classenia* sp.; Table 1). Mean annual production was 7598 mg AFDW m⁻² yr⁻¹ (95% CI, 6979–8258; Table 1), and the mean annual community production: biomass ratio was 5.2.

Invertebrate biomass and production varied through time and had contrasting temporal patterns. Biomass was lowest in July (416 mg AFDW m⁻²; 95% CI, 295–538) and highest in November (2521 mg AFDW m⁻²; 95% CI, 1933–3110; Fig. 2A). Daily production ranged from 8.2 mg AFDW m⁻² d⁻¹ in January (95% CI, 6.8–9.8) to 44.8 mg AFDW m⁻² d⁻¹ in August (95% CI, 37.0–53.5; Fig. 2B). Total community production was highly seasonal, with > 50% of annual production occurring from July to October. The taxon with the highest annual biomass, Elmidae, was consistently the most productive taxon, representing between 20% and 40% of total invertebrate production during all intervals (Fig. 2B). Relatively few other taxa contributed substantially to community production, and these included *Cinygmula* sp., *Serratella* spp., *Sweltsa* spp., and Chironomidae, which together represented ~20–40% of interval secondary production (Table 1; Fig. 2B).

Elemental concentrations and stable isotope analysis of food web components—Elemental concentrations varied widely between detritus and diatoms. Diatoms also displayed large variation among dates in contrast to minimal differences observed in detritus (Table 2). Terrestrial detritus was a nutrient-poor food resource, with mean molar C:N and C:P ratios of 70 (95% CI, 58–80) and 1313 (95% CI, 1290–1336), respectively. Stream diatoms had consistently lower C:N and C:P ratios than terrestrial detritus and ranged from 6.2 to 10.3 and 107 to 333 for C:N and C:P, respectively (Table 2). C:N ratios of diatoms varied over time, with the highest values in July, following spring spates, and a generally decreasing trend throughout the year to a minimum in April before snowmelt (Table 2). Patterns of diatom C:P ratios showed a similar trend but had higher spatial variability within each sampling date.

Stable isotope values of terrestrial litter and diatoms showed consistent differences on each sampling date (Fig. 3A). However, stable isotope values of terrestrial litter were not significantly different among sampling dates

Table 1. Mean and 95% confidence intervals of annual abundance (N; individuals m^{-2} ; $n = 10$), biomass (B; mg AFDW m^{-2} ; $n = 10$), secondary production (P; mg AFDW $m^{-2} yr^{-1}$; $n = 10$), production : biomass ratios (P : B; yr^{-1}), and annual percent contribution from allochthonous (allo) and autochthonous (auto) resources of macroinvertebrate taxa in West Blacktail Deer Creek, Wyoming.

Taxon	N	B	P	P : B	% allo	% auto
Elmidae	960(796–1129)	412(351–482)	2623(2167–3169)	6.13(5.64–6.60)	33	67
<i>Cinygmula</i> sp.	253(190–325)	142(108–180)	790(610–979)	5.58(5.19–6.00)	54	46
<i>Serratella</i> spp.	252(198–313)	85(61–111)	459(333–592)	5.40(5.04–5.81)	56	44
Chironomidae	1145(868–1462)	166(126–210)	455(311–627)	2.75(2.00–3.60)	47	53
<i>Sweltsa</i> spp.	211(156–271)	66(47–91)	420(276–636)	6.31(5.49–7.22)	55	45
<i>Acentrella</i> sp.	753(565–943)	51(40–62)	361(275–455)	7.06(7.23–7.44)	51	49
<i>Drumella doddsi</i>	71(55–88)	58(41–76)	295(293–298)	5.09(4.74–5.46)	57	43
Elmidae (adult)	50(40–58)	38(30–46)	260(204–320)	6.80(6.36–7.19)	36	64
Rhyacophilidae	55(40–74)	70(44–100)	214(158–277)	3.08(2.47–3.82)	49	51
<i>Baetis</i> spp.	276(203–365)	26(20–34)	190(136–248)	7.26(6.68–7.85)	50	50
<i>Classenia</i> spp.	13(8–19)	108(45–187)	188(110–281)	1.94(0.90–3.95)	48	52
<i>Epeorus</i> spp.	314(225–410)	27(18–36)	186(116–270)	6.87(5.85–7.78)	47	53
<i>Ephemerella</i> sp.	80(58–105)	31(22–40)	175(123–228)	5.61(5.13–6.07)	56	44
Perlodidae	30(17–46)	15(9–23)	110(61–167)	7.16(6.36–8.02)	62	38
<i>Barbaetis</i> spp.	86(59–115)	13(7–21)	103(50–174)	7.75(6.26–8.81)	46	54
Leptophlebiidae	193(135–262)	15(11–19)	93(67–119)	6.61(5.61–6.76)	48	52
Simuliidae	112(62–169)	10(5–17)	91(34–164)	8.44(7.03–9.38)	43	57
<i>Zapada</i> spp.	75(46–109)	15(9–23)	88(52–129)	5.90(5.02–6.89)	41	59
<i>Ameletus</i> spp.	35(17–63)	10(6–15)	78(41–127)	7.58(6.60–8.66)	47	53
Hydropsychidae	10(5–16)	31(15–50)	57(34–84)	1.95(1.07–3.35)	43	57
<i>Pericoma</i> spp.	159(124–197)	8(6–11)	49(36–66)	5.95(5.51–6.40)	57	43
<i>Drumella</i> spp.	16(10–24)	9(6–13)	47(29–70)	5.24(4.63–5.95)	55	45
<i>Rhithrogena</i> spp.	30(16–46)	7(5–10)	47(30–68)	6.67(5.87–7.57)	52	48
Tipulidae	10(6–15)	18(10–28)	35(17–59)	1.99(0.95–3.41)	60	40
<i>Suwallia</i> spp.	25(16–35)	5(4–7)	32(23–44)	6.33(5.74–6.84)	63	37
Glossosomatidae	7(4–12)	8(3–15)	28(13–47)	3.62(2.91–5.02)	42	58
<i>Brachycentrus</i> spp.	91(69–116)	4(3–6)	23(17–30)	5.65(4.89–6.54)	51	49
Other	117(91–146)	10(8–12)	77(67–89)	—	—	—
Sum all taxa	5429(5016–5871)	1458(1338–1587)	7598(6979–8258)	5.21	48	52

(ANOVA, $p > 0.05$). Willow litter was consistently depleted in ^{13}C relative to diatoms, whereas $\delta^{15}N$ signatures were similar for most dates. In contrast, patterns of diatom $\delta^{13}C$ and $\delta^{15}N$ showed wide variation through time (Fig. 3A). Stable isotope $\delta^{13}C$ values of diatoms were statistically higher than those of litter on all sampling dates (Tukey's HSD pairwise comparison, $p < 0.001$). Stable isotope ratios of consumers also varied considerably across the year, with some evidence that consumers tracked changes in algal isotope signatures (Fig. 3B). Invertebrates showed a slight enrichment in ^{13}C during the summer and late fall, when diatom isotope values were enriched in ^{13}C . However, consumers were consistently depleted in ^{13}C relative to diatoms (Fig. 3B).

Trophic basis of secondary production—Annual invertebrate production was nearly equally supported by autochthonous (52%) and allochthonous (48%) resources, but there was substantial variation in trophic support over time (Fig. 2B). The amount of invertebrate production supported by autochthonous resources roughly followed patterns of NPP (Table 3; Fig. 2B). Over the course of the year, algal food resources supported 3950 mg AFDW $m^{-2} yr^{-1}$ of annual secondary production, but 66% of this occurred between July and October, a time of high algal production and temperature (Table 3). Daily production attributed to

algal resources ranged from 3.2 mg AFDW $m^{-2} d^{-1}$ (95% CI, 3.4–4.3; December) to 27.9 mg AFDW $m^{-2} d^{-1}$ (95% CI, 25.3–30.5; August). Secondary production derived from allochthonous detritus was less variable throughout the year, ranging from 4.9 mg AFDW $m^{-2} d^{-1}$ (95% CI, 3.4–6.1) in December to 19.5 mg AFDW $m^{-2} d^{-1}$ (95% CI, 12.6–26.3) in July. However, the percentage of total interval production supported by detritus was significantly greater in December (60%; 95% CI, 57–64) than July (44%; 95% CI, 38–49; Fig. 2B; Table 3) and ranged from 36% (August) to 64% (April).

Temporal patterns of community-level trophic basis of production result from both changes in taxon-specific resource use and the contribution of individual taxa to total production. In an effort to understand the relative importance of these factors, we plotted daily production and the proportion of secondary production derived from allochthonous leaf litter for the five most productive taxa (Fig. 4A,B). Patterns of daily production demonstrate that variation in total production was driven largely by changes in the most productive taxon, Elmidae (Fig. 4A). In contrast, there was much less temporal variation in allochthonous support (Fig. 4B), although all five taxa tended to rely more on detritus during colder months. Together, these patterns suggest that variation in community-level trophic basis of production was more strongly associated with the

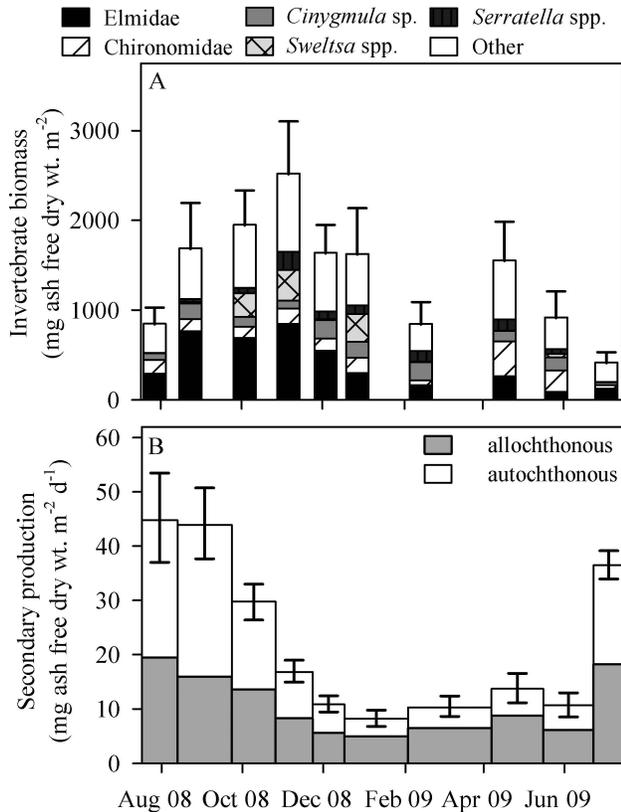


Fig. 2. (A) Invertebrate community biomass (mean and 95% CI; $n = 10$), highlighting the amount of total community biomass contributed by the most productive taxa. (B) Daily secondary production (mean and 95% CI; $n = 10$) of the invertebrate community in each time interval supported by autochthonous and allochthonous food resources.

production and diet of Elmidae, rather than with consistent changes in resource use of the community.

Resource consumption and elemental imbalance—Allochthonous detritus was the dominant food resource consumed by invertebrates throughout the year, but consumption of algae was relatively high during the

summer months (Table 3). Only a small fraction of NPP was necessary to support invertebrate production during most months (i.e., $\leq 13\%$, Table 3), yet nearly 30% of NPP was required to fuel secondary production in June. During most intervals, the amount of detritus necessary to support production was much greater than the measured standing stock (Table 3), demonstrating the importance of other pools of detritus (e.g., fine detritus $< 250 \mu\text{m}$) that were not measured in our benthic samples.

Our AICc model selection analysis demonstrated that temperature and community-level C:P imbalances were important explanatory variables in the top model to predict secondary production (Table 4). Interval invertebrate production showed a strong positive relationship with mean monthly stream temperature ($r^2 = 0.66$, $p = 0.003$), and this relationship was strengthened by removal of a single outlier (June) that coincided with peak stream discharge ($r^2 = 0.84$, $p < 0.001$; Fig. 5A). In addition, the residual variation was partially explained by community-level C:P imbalance ($r^2 = 0.65$, $p = 0.005$; Fig. 5B), demonstrating the important secondary influence of food quality on temporal patterns of secondary production.

Discussion

Subsidies of allochthonous leaf litter have long been recognized as an important basal resource for consumers in many stream ecosystems, often greatly exceeding autochthonous production (Minshall 1967; Hall et al. 2000). However, an increasing number of studies have shown that autochthonous resources can be disproportionately important to consumer production relative to their availability (Mayer and Likens 1987; McCutchan and Lewis 2002). Our detailed temporal analysis revealed strong seasonal variation in the relative importance of allochthonous and autochthonous resources to stream consumer production. Seasonal patterns in stream temperature were strongly correlated with community production over sampling intervals, and residual variation in this relationship was associated with the elemental imbalance between consumers and consumed resources. Our results highlight the

Table 2. Patterns of food resource elemental concentrations (mean and 95% CI; $n = 5$) and consumer–resource elemental imbalances throughout the study. All elemental ratios are molar.

Date	Epilithic algae		Terrestrial litter		Elemental imbalance	
	C:N	C:P	C:N	C:P	C:N	C:P
Jul 08	10.3(8.8–12.4)	234(120–347)	*	*	50.0	1130
Aug 08	7.9(7.0–8.8)	153(98–218)	*	*	45.3	1026
Sep 08	8.1(7.2–9.0)	196(167–224)	68(25–110)	1279(1270–1289)	50.5	1096
Oct 08	7.5(7.0–8.1)	136(48–261)	72(61–83)	1296(1286–1306)	51.1	1152
Nov 08	9.4(8.7–10.2)	107(65–148)	75(54–95)	1323(1306–1341)	52.3	1164
Dec 08	7.1(6.5–7.6)	155(63–391)	66(54–78)	1353(1337–1369)	55.2	1222
Feb 09	6.9(5.6–8.1)	167(115–219)	*	*	56.0	1258
Apr 09	6.2(5.4–6.9)	127(101–153)	*	*	57.3	1228
May 09	9.2(8.3–9.6)	185(164–205)	*	*	55.7	1224
Jun 09	9.8(8.9–10.7)	333(123–543)	*	*	53.2	1156
Annual	7.5(6.4–8.5)	179(137–221)	70(59–81)	1313(1290–1336)	—	—

* No data available due to negligible litter inputs over these dates.

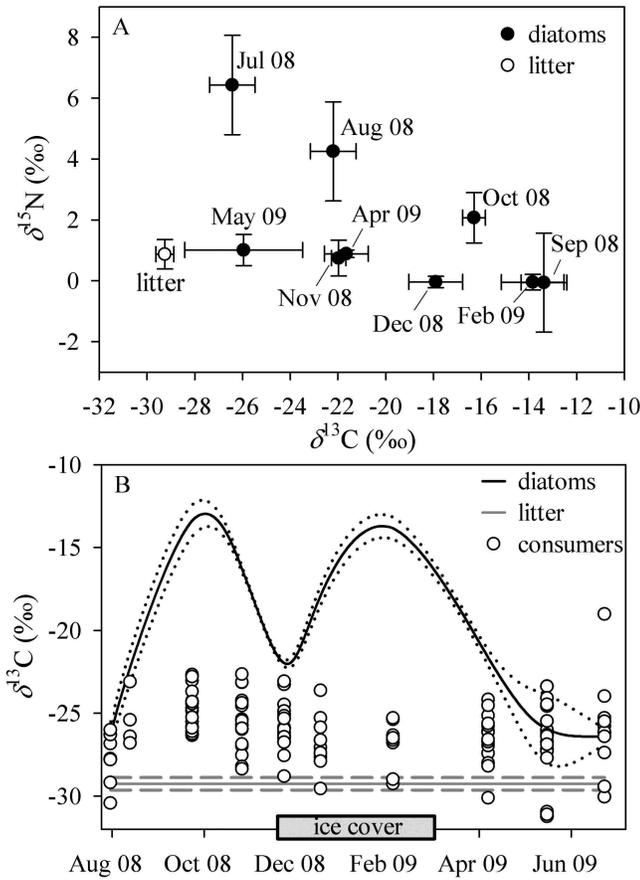


Fig. 3. (A) Stable carbon and nitrogen isotope ratios (mean and 95% CI; $n = 4$) of diatoms and terrestrial litter throughout the study. (B) Carbon stable isotope ratios of basal resources and consumers collected on each sampling date. The relationship between nitrogen stable isotope values of resources and consumers is not shown because $\delta^{15}\text{N}$ values of terrestrial litter and algae were similar on most dates.

important roles of environmental variation and resource quality in modulating the importance of resource subsidies in recipient food webs (Marecchelli et al. 2011).

Temperature plays an important role in determining metabolic demands of invertebrate consumers. Growth rates of poikilothermic organisms generally increase with temperature (within tolerance boundaries; Brown et al. 2004), and high growth rates require acquisition of nutrients that make up the machinery (e.g., P-rich ribonucleic acid) and building blocks (e.g., N-rich proteins) of new tissue (Sterner and Elser 2002). Because invertebrates are relatively homeostatic with regard to their body nutrient content (Persson et al. 2010), high amounts of nutrients in food are required during times of rapid growth. We found that invertebrate production was strongly related to temperature and was highly variable among seasons, with > 50% of annual production occurring over a few months, from July to October. This period of rapid growth coincided with relatively warm temperatures and the highest rates of primary production. Interestingly, we could explain additional variation in consumer production

Table 3. Temporal patterns in the proportion (mean and 95% CI; $n = 10$) of macroinvertebrate community production supported by allochthonous and autochthonous food resources, total consumption between sampling dates (g AFDW interval⁻¹) of allochthonous (allo) and autochthonous (auto) resources, the percentage of available resources consumed, and the relative consumption of allochthonous and autochthonous resources.

Date	Trophic support		Resources consumed		% of available resources consumed*		Allo : auto consumption ratio
	Allo	Auto	Allo	Auto	Allo	Auto	
Jul 08	0.44(0.38–0.49)	0.56(0.51–0.62)	14.3(11.9–17.0)	4.9(4.0–5.9)	355	13	2.9
Aug 08	0.36(0.30–0.42)	0.67(0.58–0.70)	17.8(15.3–20.6)	8.3(7.1–9.6)	300	13	2.2
Sep 08	0.46(0.33–0.58)	0.54(0.42–0.67)	12.2(10.9–13.5)	3.9(3.4–4.3)	253	10	3.2
Oct 08	0.49(0.47–0.52)	0.51(0.48–0.53)	6.3(5.6–7.1)	1.6(1.4–1.8)	60	6	4.0
Nov 08	0.52(0.50–0.53)	0.48(0.47–0.50)	3.7(3.2–4.2)	0.9(0.8–1.1)	55	3	4.0
Dec 08	0.60(0.57–0.64)	0.40(0.36–0.43)	6.5(5.3–7.8)	1.1(0.9–1.3)	89	9	5.8
Feb 09	0.63(0.58–0.67)	0.37(0.33–0.42)	11.0(9.4–13.3)	1.8(1.5–2.1)	207	4	6.3
Apr 09	0.64(0.58–0.70)	0.36(0.30–0.42)	9.3(7.6–11.3)	1.4(1.1–1.7)	196	3	6.7
May 09	0.58(0.53–0.63)	0.42(0.37–0.47)	6.4(5.1–7.8)	1.2(1.0–1.5)	74	7	5.2
Jun 09	0.50(0.38–0.62)	0.50(0.38–0.62)	11.9(11.1–12.8)	3.2(2.9–3.4)	819	28	3.8
Annual	0.48(0.41–0.55)	0.52(0.45–0.59)	99.5(91.8–108.0)	28.1(25.7–31.0)	167	10	3.5

* Some values exceed 100%, demonstrating that our estimates of “available detritus” are biased low and do not include fine particles < 250 μm .

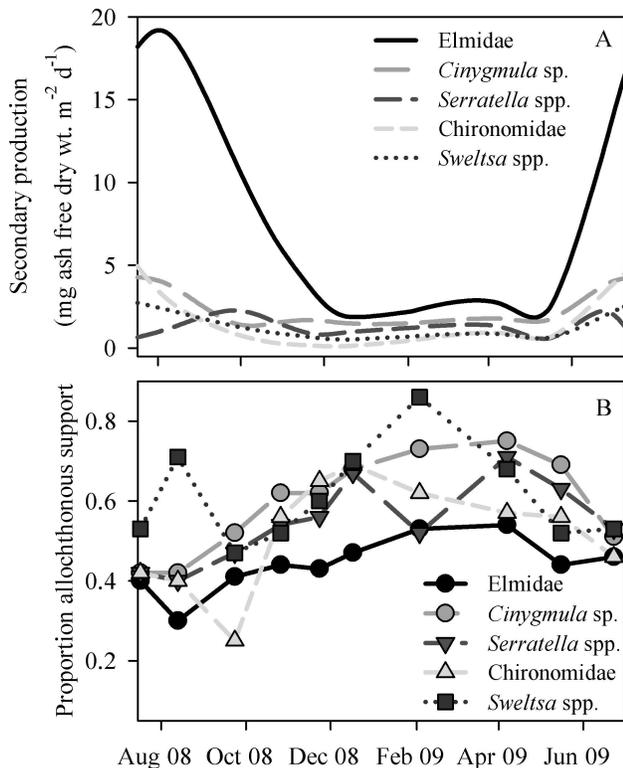


Fig. 4. Temporal patterns of (A) daily production (mg AFDW $m^{-2} d^{-1}$) and (B) model-estimated production derived from allochthonous organic matter of the five most productive taxa.

when we examined consumer–resource elemental imbalances (Fig. 5B). The abundance of high-quality autochthonous resources in summer and early fall likely reduced stoichiometric constraints on invertebrate growth during periods of warm temperatures.

Some studies have suggested that temperature and food quality may interact to influence organism growth. For example, Persson et al. (2011) found that the risk of growth limitation by P was much greater at higher temperatures for some species of *Daphnia*. Thus, during cold months, the availability of high-quality resources may not be as critical, because temperature likely limits the growth rates of consumers and ingested resources are largely dedicated to fueling basal metabolism instead of new tissue growth. Others, however, have shown that food quality effects on growth may be greater at cold temperatures and can vary across species (McFeeters and Frost 2011). Such an effect may be driven by constraints on physiological mechanisms for countering poor food quality at cold temperatures. In our study, although temperature and food quality both explained patterns in community production, we did not observe a temperature–food quality interaction. Further, greater consumer–resource imbalances during cold months were associated with lower than predicted community production, suggesting that food quality may still be important at low temperatures. Clearly, additional studies are needed to better understand how temperature and food quality affect secondary production in highly seasonal systems.

Table 4. Results of model selection based on the linear model of interval production and temperature and food quality variables. AIC wt., Akaike weight; LL, log likelihood.

Model variables	AICc	Δ AICc	AIC wt.	LL
Temperature + C:P	66.30	0.00	0.93	-25.15
Temperature + C:N	72.60	6.30	0.04	-28.30
Temperature \times C:P	74.08	7.78	0.02	-24.54
Temperature + C:P + C:N	74.86	8.56	0.01	-24.93
Temperature only	79.11	12.81	0.00	-34.56
Temperature \times C:N	81.55	15.25	0.00	-28.28
C:P only	82.01	15.72	0.00	-36.01
C:N only	82.39	16.09	0.00	-36.19

The recognition that consumer response to resource subsidies should not be similar across ecosystems has directed work toward understanding the nuanced response of recipient food webs to subsidies. For example, a number of studies have identified physical and biological characteristics that may mediate the importance of subsidies, including ecosystem perimeter : surface area ratio (Polis and Hurd 1996), productivity (Polis et al. 1997), the trophic position where resource subsidies enter the food web (Huxel et al. 2002), and physical characteristics (e.g., temperature) of the recipient ecosystem (Armstrong et al. 2010). Marczak and others (2007) found that changes in consumer abundance and biomass increased as the ratio of subsidy resources to trophically similar ambient resources increased. Whereas we found nearly equal importance of both resource subsidies and in situ food resources to macroinvertebrate community production on an annual basis, there was wide variation in the relative abundance and importance of these resources through time. Subsidies were less important for consumers during periods when higher quality resources were relatively abundant (July–October). In contrast, subsidies were more important during periods of low temperature and ice cover, when estimated benthic algal production was low and the relative abundance of detritus was high. Terrestrially derived organic matter supported a majority of invertebrate consumer production during these periods, demonstrating that the abundance of internally derived resources within the recipient ecosystem may play a crucial role in determining the timing of subsidy use by invertebrates, potentially altering food web dynamics (Takimoto et al. 2002).

Inputs of terrestrial detritus may stabilize food webs in stream ecosystems by increasing resource diversity and alleviating volatile fluctuations in autochthonous resource availability (Huxel et al. 2002). Wetzel (1995) suggested that detrital resources might also stabilize ecosystem functions, such as secondary production, because of their relatively slow and constant metabolism in comparison to the widely fluctuating dynamics of algae and algal-based food webs. In our study, allochthonous detritus was available through times of wide fluctuations in NPP, and we observed an increase in the relative consumption of detritus during periods when NPP was low. In some cases, consumption of allochthonous food resources was estimated to be greater than the standing stock of BOM. This

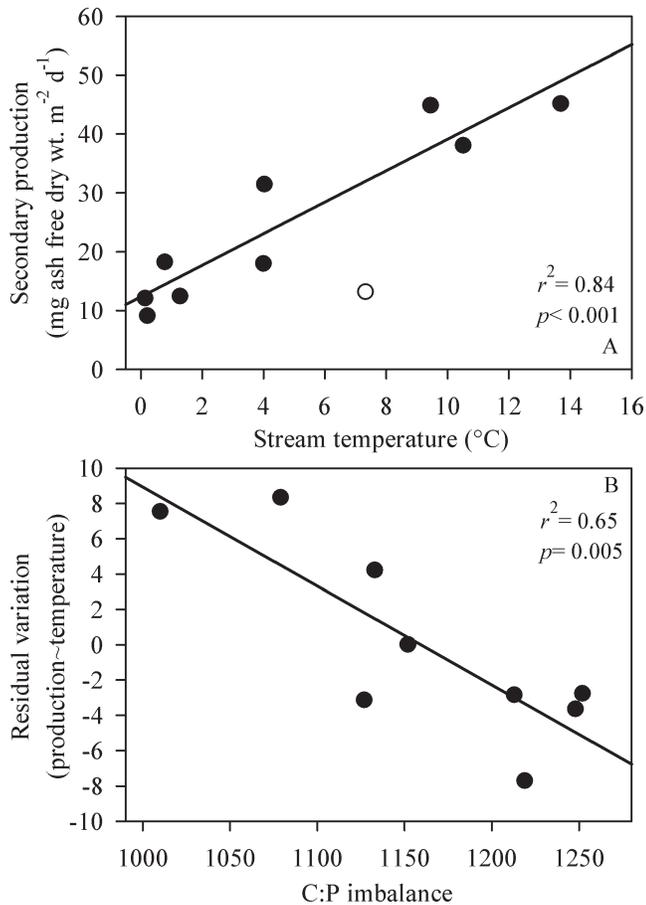


Fig. 5. (A) Relationship between mean interval stream temperature and invertebrate community secondary production throughout the study. The open point represents an outlier in June 2009 that was removed from the regression. (B) The relationship between the residual variation from the production–temperature relationship (outlier removed) and community-level consumer–resource C:P imbalance.

likely reflects a large pool of organic matter $< 250 \mu\text{m}$ that was unaccounted for in our sampling. We also observed a large amount of spatial variability in the BOM pool within sampling dates, and our estimates of consumption fell within the 95% CIs of our BOM standing stock estimates on all but three dates (July 2008, October 2008, and June 2009). This discrepancy may have also resulted from an underestimation of the assimilation efficiency of leaf litter. Nonetheless, the increase in the proportion of consumer production supported by allochthonous food resources during periods of autochthonous resource scarcity suggests that resource subsidies may provide a stable, albeit low-quality, food resource for consumers.

Frequent sampling of food web stable isotope ratios was necessary for capturing temporal changes in food web characteristics and accounting for temperature-driven differences in growth and tissue turnover. Previous studies have observed that C stable isotope ratios of algal resources often vary widely relative to terrestrial litter (Finlay 2001). This is thought to reflect the variable sources in the dissolved inorganic C (DIC) pool and the extent of

discrimination against ^{13}C , likely determined by the supply of DIC relative to algal demand (Finlay et al. 1999). Whereas we did not characterize the $\delta^{13}\text{C}$ of the DIC pool and are unable to address the extent of discrimination by algal resources, we did find wide variation in algal C isotope ratios. Algal ^{13}C signatures exhibited a range of approximately 14‰ throughout the year, a similar range as that observed in other Rocky Mountain streams (McCutchan and Lewis 2001). This wide variation in food–resource isotope ratios can be a large concern when estimating the importance of food resources to consumers. For example, small and quickly growing consumers will mirror dietary isotope ratios much more quickly than larger and slower growing consumers (Fry and Arnold 1982). This required us to scale the resource values to better characterize the contribution of allochthonous and autochthonous food resources to consumer growth. Without accounting for the large seasonal changes in algal isotope signatures and consumer growth rates, our estimates of the importance of basal resources to consumers may have been highly skewed (Woodland et al. 2012). Our study gives further evidence that isotopic food web analysis may require intensive sampling of resources on a timescale relevant to seasonal patterns of consumer growth rates (McCutchan and Lewis 2001).

By combining stable isotope analysis with temporally detailed estimates of community-level production, we were also able to capture changes in the pathways of energy flux within the food web. The quantification of energy flows is especially crucial for understanding the importance of resources in seasonally variable ecosystems with few quantitatively dominant pathways of energy flow. Applying stable isotope analysis alone would have led to overestimates in the importance of litter for consumers, and we would have missed important dynamics in invertebrate community energy flux. For example, although invertebrate isotopes largely reflected detrital C during the cold months, secondary production was relatively low, indicating minimal flux of detritus to invertebrates. In addition, our production estimates demonstrated that few taxa (i.e., Elmidae) dominated invertebrate production and that these taxa represented key “gate-keepers” of energy flow through the stream food web, particularly during warm months.

The relationship we demonstrated among temperature, food quality, and invertebrate production may be disrupted by changes to other physical aspects of the ecosystem, such as flow disturbance. Disturbance has long been recognized as a “master variable” that limits the abundance and distribution of aquatic organisms (Resh et al. 1988). In our study, temperature and food quality explained patterns of macroinvertebrate community production throughout most of the year. However, a single outlier of secondary production during June, coinciding with peak discharge, did not fit this pattern (Fig. 5A). In snowmelt-dominated systems of the northern Rocky Mountains, spring and early summer flows dominate annual water budgets. This period of high flow is seasonally predictable and is generally orders of magnitude greater than base flow conditions. Because the timing, magnitude, and predictability of

high-flow events can modulate the effects of disturbance on ecosystem dynamics (Sabo and Post 2008), river systems exposed to different disturbance regimes may not exhibit the strong relationships we observed among temperature, food quality, and secondary production.

Our findings document the importance of both autochthonous and allochthonous resources for stream food webs in northern temperate streams. Temporal variation in community production was largely explained by variation in temperature, but we found that additional variation could be explained with consumer–resource elemental imbalances. High-quality autochthonous resources supported invertebrate production during abbreviated periods of high temperatures and rapid consumer growth rates. In contrast, allochthonous resources supported consumers during periods of slow growth and relative scarcity of autochthonous resources. These findings highlight the critical roles of both resource quality and the environmental template in modulating the importance of resource subsidies. Our results also suggest that widely differing resources from spatially distinct habitats can serve complementary, but dissimilar, roles in fueling food-web production in seasonally variable ecosystems.

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