

TROPHIC BASIS OF INVERTEBRATE PRODUCTION IN A NORTHERN ROCKIES
STREAM WITH RECENT WILLOW RECOVERY

by

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ABSTRACT

Ecologists have long recognized that ecosystems are not isolated in the landscape and can receive inputs of energy, materials, and organisms from beyond their boundaries. The role of these inputs for consumers in receiving ecosystems depends on biotic and abiotic characteristics of both the donor and recipient ecosystems. In streams, the influence of leaf litter input from terrestrial environments on stream structure and function has received much study. Recently, riparian vegetation in Yellowstone National Park has undergone increases in growth and distribution in many areas, however the implications for food webs of adjacent stream ecosystems has remained unexplored. In this study, we combined stable isotope ratios of food web components with estimates of invertebrate secondary production to measure the relative importance of terrestrial organic matter and algae to stream invertebrate production. We found stable isotope ratios of terrestrial litter were relatively constant throughout the annual cycle. In contrast, algae showed varying patterns of enrichment and depletion likely driven by changes in light, discharge, and sources of dissolved carbon and nitrogen. Mean annual secondary production was $7.5 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ (95% CI; 7.0-8.2), and the majority of this production was supported by stream algae (58%; terrestrial detritus supported 42%). Invertebrate production varied seasonally, with >50% of annual production occurring between July and September. Relatively high quality algae supported the majority of production during this critical growth period characterized by warm temperatures and high NPP. Terrestrial litter supported the majority of invertebrate production (57%) during cold months between October and May, when stream NPP and metabolic demands of invertebrate consumers were low. Our findings demonstrate that high quality resources support invertebrate production during periods of high metabolic demand, while terrestrial litter provides an abundant resource to support invertebrate consumer production when higher quality resources are scarce and metabolism is reduced. This study provides a quantitative measure of the importance of allochthonous and autochthonous resources to an invertebrate community of a northern Rocky Mountain stream, and provides a benchmark to assess the potential impacts of changing riparian vegetation on streams within the northern Rocky Mountains.

TROPHIC BASIS OF INVERTEBRATE PRODUCTION IN A NORTHERN ROCKIES STREAM WITH RECENT WILLOW RECOVERY

Introduction

Ecologists have long recognized that ecosystems are not isolated in the landscape and can receive large inputs of energy, materials, and organisms from beyond their boundaries (e.g., Elton 1927). These allochthonous resources, often referred to as resource subsidies, may have significant impacts on the structure and function of recipient ecosystems (Polis and Hurd 1996), influencing community composition (Vannote et al. 1980), food web dynamics (Polis and Strong 1996), ecosystem stability (Huxel and McCann 1998), and primary and secondary productivity (Wipfli et al. 1998). A growing body of theoretical and empirical studies demonstrates that consumers may exhibit varied responses to resource subsidies (Polis et al. 1997, Vanni et al. 2004, Holt 2008). How resource subsidies vary in both space and time in relation to physical (i.e., temperature, perimeter:area ratio; Polis and Hurd 1996) and functional (i.e., productivity; Marczak et al. 2007) characteristics of the recipient ecosystem may determine the relative importance of resource subsidies in recipient food webs. In particular, the magnitude, quality, timing and duration of subsidies relative to autochthonous resources may modulate their importance for recipient ecosystems (Polis et al. 1997, Polis et al. 2004, Marczak et al. 2007).

In temperate ecosystems, leaf litter fall into streams provides a seasonal pulse of organic matter from the terrestrial landscape. In some streams, inputs of

allochthonous detritus greatly exceed autochthonous algal production on an annual basis (Fisher and Likens 1973, Webster and Meyer 1997). Many studies have shown that terrestrial litter can fuel the majority of stream consumer production (Minshall 1967, Wallace et al. 1997, Hall et al. 2001) and may influence energy flow and community composition (Vannote et al. 1980). However, autochthonous resources may be important for consumers even at relatively low abundance (Minshall 1978, Hall et al. 2001, McCutchan and Lewis 2002) because they are often a higher quality food resource than allochthonous detritus (Cross et al. 2003). How consumers utilize allochthonous and autochthonous resources will depend on the availability and quality of these resources throughout the year, as well as the ability of consumers to effectively utilize these resources given abiotic constraints to metabolism as they strive to meet their requirements for basal metabolism, growth, and reproduction. Alterations in terrestrial landscapes may directly and indirectly affect resource dynamics in stream ecosystems and will likely alter consumer-resources interactions and production dynamics.

The loss of riparian vegetation through deforestation and changing land-use practices is widespread (Gregory et al. 1991). However, in systems with relatively low anthropogenic influence, natural disturbance and terrestrial herbivores can have a large influence on riparian vegetation dynamics (Naiman and Decamps 1997). For example, periodic flood disturbances of varying intensity may help maintain diversity of riparian plants (Duncan 1993), while, changes in herbivore (e.g., elk) abundance can have strong effects on plant

community composition and productivity (Pastor et al. 1988). In the northern range of Yellowstone National Park, many riparian plant communities have experienced rapid increases in growth and distribution over the past 10-15 years (Ripple et al. 2001). Recent work suggests these changes may be attributed, in part, to top-down (Beyer et al. 2007, Creel and Christianson 2009), and/or bottom-up (Tercek et al. 2010) factors. However, the effect of these changes on consumer-resource interactions in adjacent stream ecosystems has remained largely unexplored.

Measuring the importance of allochthonous and autochthonous resources in food webs requires a comprehensive understanding of the linkages between resources and consumers. Stable isotopes of carbon (C) and nitrogen (N) represent powerful tools for examining resource use by stream consumers when terrestrial and aquatic resources differ in their isotopic signatures (e.g., Rounick et al. 1982, Winterbourn et al. 1986, Hamilton et al. 1992). Analysis of stable isotopes has advantages over other methods (i.e., gut analysis) because isotope signatures reflect material assimilated as opposed to ingested, and food resources often differ greatly in efficiency of assimilation by consumers (Benke and Wallace 1980). However, stable isotopes alone do not provide a complete picture when measuring the importance of resources to a community because they cannot provide a quantitative measure of energy flow through food webs (Benke and Wallace 1980). Given that many stream invertebrate life histories have evolved to coincide temporally with the availability of particular food resources (Ross 1963, Cummins et al. 1989) fluxes of different materials through

food webs may vary considerably among seasons (Benke and Wallace 1997). Measurements of community-level secondary production can capture changes in energy flow through a food web over time (Benke 1993). By combining stable isotope analysis with secondary production one can incorporate shifts in energy flow through food webs, as well as changes in resource use which may occur with changing availability of allochthonous and autochthonous resources (McCutchan and Lewis 2002).

In our study, we used this approach to investigate the relative importance of allochthonous and autochthonous resources in a northern Rockies stream with recent and rapid recovery of riparian vegetation. We addressed the following questions: (1) What is the relative availability of allochthonous and autochthonous resources throughout the year?; (2) What is the relative importance of these resources for annual invertebrate production?; and (3) Does the trophic basis of invertebrate production vary through time? We found that while autochthonous production supported the majority of secondary production on an annual basis, allochthonous resources may play a critical role in maintaining invertebrate production during periods of low temperatures and reduced primary production.

Methods

Study Site

We conducted this study on West Blacktail Deer Creek in the Northern Range of Yellowstone National Park, Wyoming, USA (Figure 1) from July 2008

through July 2009. West Blacktail Deer Creek is surrounded by a lush riparian community consisting of woody vegetation, sedges, grasses, forbs, and shrubs. Willow (*Salix* spp.), 1-5 meters high, dominate the riparian vegetation and create a canopy that provides moderate and patchy shading from mid-April to mid-November. Previous research on this stream has explored physicochemical responses following a 1988 fire (Minshall et al. 1997). More recent work conducted along West Blacktail Deer Creek has explored changes in riparian vegetation over the past few decades (Beyer et al. 2007) and possible bottom-up constraints (i.e., water availability) to growth of riparian vegetation (Bilyeu et al. 2008).

We sampled a single 100 meter stream reach during the course of the study. The stream reach was representative of West Blacktail Deer Creek regarding stream size, gradient, and riparian cover. We measure discharge on each sampling date using the midsection method (Gore 2006). Discharge measurements were related to a nearby USGS gauging station (Lamar River near Tower Ranger Station, USGS #0618800) to estimate discharge between sampling dates ($p < 0.05$, $r^2 = 0.75$). We measured daily stream temperature continuously with in situ loggers (Onset Computer Corp. MA, USA).

Quantifying Inputs and Availability of Allochthonous and Autochthonous Resources

We estimated direct litter fall into West Blacktail Creek 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 bi-weekly basis between July and December 2008 to estimate mean daily litter input (mg ash-free dry mass [AFDM] m⁻² d⁻¹). We did not collect litter between January and June because of snow cover and no inputs occurring. We summed the average leaf litter collected in traps at each sampling date to estimate annual litter input into the stream. Organic matter was oven-dried (60°C for 5 days), weighed, combusted in a muffle furnace (500°C for 4 hours), and reweighed to determine AFDM.

Benthic organic matter standing stock, measured as coarse particulate organic matter (CPOM, ≥1mm) and fine particulate organic matter (FPOM, <1mm≥250µm) was quantified from 10 replicate benthic samples collected approximately monthly throughout the study (see *Macroinvertebrate Abundance, Biomass, and Secondary Production* below). Ash-free dry mass of benthic organic matter was quantified as described above. Together, CPOM and FPOM were assumed to represent allochthonous organic matter available to invertebrate consumers during each time interval.

On each sampling date, we quantified AFDM, chlorophyll *a* (Chl *a*), natural abundance stable carbon (C) and nitrogen (N) isotopes, and %C (see *Stable Isotope Analysis and Trophic Basis of Production* below) from epilithon samples collected at 10 randomly-selected transects along the study reach. At each transect, 3-4 cobble or gravel-sized rocks were scrubbed, the slurry combined, and subsamples filtered onto pre-ashed glass fiber filters (Whatman GF/C 1.2µm

pore size). Separate filters were analyzed for epilithic AFDM, Chl *a*, and stable C and N isotopes. We quantified epilithic AFDM as described above for allochthonous organic matter. Chlorophyll *a* was extracted from filters with acetone and quantified using the fluorometric acidification method (Steinman et al. 2006). Rocks selected for each sample were photographed in the field using a ruler for scale, and rock surface areas were quantified with digital image analysis (ImageJ version 1.42q). Chlorophyll *a* was expressed on an areal basis ($\text{mg Chl } a \cdot \text{m}^{-2}$).

To estimate algal primary production ($\text{mg AFDM m}^{-2} \text{d}^{-1}$) available to invertebrates throughout the study, we used a modeling approach (Morin et al. 1999). This approach, based on empirical measurements from a broad diversity of streams, estimates expected daily gross primary production (GPP, $\text{mg C m}^{-2} \text{d}^{-1}$) using Chl *a* biomass ($\text{mg Chl } a \text{ m}^{-2}$) and stream temperature ($^{\circ}\text{C}$). We assumed that net primary production (NPP) constituted 50% of GPP (Likens 1975). We converted estimates of NPP ($\text{mg C m}^{-2} \text{d}^{-1}$) to AFDM using the mean %C ($13 \pm 5\%$; mean \pm standard deviation) of isolated algal samples collected throughout the study (see *Stable Isotope Analysis and Trophic Basis of Invertebrate Production* below). Primary production was assumed to be zero from December to March due to snow and ice cover over the stream. Although this approach has obvious shortcomings compared to direct measurements of primary production, we believe it provides a better estimate of autochthonous resource availability than algal biomass alone. Importantly, this analysis provided an estimate of temporal patterns of NPP that we could compare to patterns of

invertebrate production and trophic support.

Macroinvertebrate Abundance, 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 (>1mm) and fine fractions (<1mm >250µm) using nested metal sieves. Invertebrates were manually removed from both fractions using a dissecting microscope (15x magnification). Samples were sub-sampled ($1/2 - 1/16$) when necessary using a Folsom plankton splitter (Wildlife Supply Company, FL, USA) or were placed in a known volume of water, suspended in a modified Imhoff cone (Wards Natural Science, Rochester, New York, USA) with forced air and subsampled by volume with a wide-mouthed plastic syringe. We identified individuals to the lowest possible taxonomic division, generally genus, and assigned taxa to functional feeding groups (FFG; 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 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 individuals directly measured on that date. We determined biomass of individuals 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 AFDM m⁻² y⁻¹) and daily (mg AFDM 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 all other taxa, we estimated production using an empirical model that predicts growth rate based on size frequency data of taxa in West Blacktail Creek with easily identifiable cohorts (as in McCutchan and Lewis 2002):

$$g = 0.0107 (\pm 0.003) - 0.0019 (\pm 0.0018) m + 0.0193 (\pm 0.0004) \bar{T};$$

$$r^2 = 0.40; p < 0.001 \tag{1}$$

where g is the instantaneous growth rate (d^{-1} , mean \pm SE), m is individual mass in AFDM (mg) and \bar{T} is the mean stream temperature ($^{\circ}C$) for a given interval.

The taxa used to determine Equation 1 represented approximately 30% of the annual production of the invertebrate community. For taxa with production estimates $< 100 \text{ mg AFDM m}^{-2} \text{ y}^{-1}$ we applied a production:biomass ratio (P:B) of 5 to biomass estimates.

We calculated 95% confidence intervals (CI) of mean interval abundance, biomass, and production using bootstrap analysis as described in Benke and Huryn (2006). Briefly, size-specific abundance data from replicate samples on each date were randomly resampled with replacement 1,000 times to generate vectors of mean abundance and biomass. To generate vectors of interval production, each of the biomass estimates was multiplied by size-specific growth rates (Equation 1) and the time interval between sampling dates. We summed production vectors across all taxa and time intervals to generate a vector of

annual production estimates. Annual production was estimated on a per square meter basis.

Stable Isotope Analysis and Trophic Basis of Invertebrate Production

We measured natural abundance stable C and N isotope ratios of dominant invertebrate taxa, epilithic algae, and leaf litter on a monthly basis throughout the study. Dominant invertebrate taxa were collected with a kick net (1mm 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, homogenized, and lipids and bicarbonates 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (units are ‰, Peterson and Fry 1987). Subsamples of leaf litter from litter traps were dried, homogenized, weighed, and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and %C. Epilithic diatoms were isolated from bulk epilithon samples 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 isotopic analysis as described above. All samples were analyzed at University of California-Davis with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

The proportional contribution of allochthonous and autochthonous organic matter to the production of invertebrates was determined using a Bayesian

mixing model approach, Stable Isotope Analysis in R (SIAR, Parnell et al. 2010). Briefly, 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 the proportions sum to 1, while still treating each source input as independent. 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 (see Koch and Phillips 2002), and unidentified sources of variation (i.e., physiological variation or unidentified minor dietary sources; Parnell et al. 2010). In our study, proportional contributions of allochthonous and autochthonous resources were estimated using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the dominant taxa sampled on each date and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of epilithic algae and litter from the previous sampling date. This assumes that tissue turnover time was similar to our sampling interval time. This assumption is not perfect, but we believe it is more realistic than applying isotope ratios of food resources collected on the same sampling date which would not yet be incorporated into consumer tissues. On average, taxa included in isotope samples represented >60% of total interval production (range 61-81%). For the remaining taxa, we applied mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from taxa in similar functional feeding groups (e.g., collector-gatherers, scrapers, shredders).

We used bootstrap analysis, as described above, to estimate the mean and 95% confidence intervals of the trophic basis of production for each taxon over a given interval. For each taxon, we randomly resampled from vectors of

interval secondary production and resource contribution distributions estimated by SIAR. The product of these vectors yielded a third vector that represented the amount of production attributed to allochthonous or autochthonous material during a given time interval. Total contributions of allochthonous and autochthonous resources to interval secondary production were estimated by multiplying the resource contributions and interval production values for each taxon. Annual trophic support was calculated by summing across all intervals.

Statistical Analyses

We performed all statistical analyses in Program R (R Development Core Team, 2011). Figures were created in SigmaPlot (version 12; Systat Software Inc. CA, USA).

Results

Inputs and Availability of Allochthonous and Autochthonous Resources

Daily stream discharge and temperature varied seasonally and were characteristic of a snowmelt driven temperate system. Stream discharge ranged from 24 to 2,900 l/s. Minimum discharge occurred in January, and peak discharge coincided with snow melt in May. Mean daily stream temperature ranged from near 0°C throughout the months of December to March up to ~15°C in August (Figure 2).

Daily inputs of particulate allochthonous detritus were overwhelmingly

dominated by willow litter (>90% willow leaves and catkins). Inputs occurred from mid-August to mid-November, with peak litter input during October (Figure 3). Inputs of particulate detritus from December to July were negligible. Annual litter inputs were $187,099 \text{ mg m}^2 \text{ y}^{-1}$ (95% confidence interval (CI); 121,987 – 252,212).

Benthic organic matter standing stock roughly followed patterns of litter inputs (Figure 4), with the highest values occurring shortly after pulsed litter inputs in November. Mean CPOM standing stock ranged from $1,810 \text{ mg AFDM m}^{-2}$ to $15,970 \text{ mg AFDM m}^{-2}$ throughout the year, but varied widely among samples (Figure 4). Fine particulate organic matter standing stock was nearly always lower in biomass than CPOM, with mean values ranging from 1,233 to $7,320 \text{ mg AFDM m}^{-2}$ (Figure 5). Reduced standing stock of CPOM and FPOM occurred after peak discharge (i.e., in July 2009), suggesting that snowmelt flushed a large amount of allochthonous detritus downstream.

Epilithic Chl *a* concentration and NPP exhibited a bimodal temporal pattern with peak concentrations in early fall and spring (Figures 6 and 7). The peak Chl *a* concentration in the fall was greater than the highest values observed in spring. Although modeled estimates of NPP roughly mirrored patterns in Chl *a*, reduced stream temperatures also affected NPP leading to an earlier peak in stream primary production relative to Chl *a*.

Macroinvertebrate Abundance,
Biomass, and Secondary Production

Approximately 30 invertebrate taxa (22 families) were collected during the study. Total invertebrate biomass averaged 1,477 mg AFDM m⁻² (95% CI; 1,359 – 1,608), over 50% of which was attributed to four dominant taxa (Elmidae, Chironomidae, *Cinygmula* spp., *Classenia* spp.; Table 1). Mean annual production was estimated to be 7,598 mg AFDM m⁻² y⁻¹ (95% CI; 6,979 – 8,258, Table 1).

Invertebrate biomass and production varied through time and had contrasting patterns. Biomass was lowest in July (416 mg AFDM m⁻²; 95% CI; 295 - 538) and highest in November (2,521 mg AFDM m⁻²; 95% CI; 1,933 – 3,110, Figure 8). Daily production ranged from 8.2 mg AFDM m⁻² d⁻¹ in January (95% CI; 6.8 - 9.8) to 44.8 mg AFDM m⁻² d⁻¹ in August (95% CI; 37.0 - 53.5, Figure 9). High daily invertebrate production coincided with warm temperatures and high primary production during August through October. Elmidae was consistently the most productive taxon, representing between 20% and 40% of total invertebrate production during all intervals. Consequently, patterns of interval production closely followed production of Elmidae; production of elmids described most of the variation in interval secondary production (simple linear regression; $r^2 = 0.85$, $p < 0.001$). Relatively few other taxa dominated production, including *Cinygmula* spp., *Serratella* spp., *Sweltsa* spp., and Chironomidae, which combined represented ~20-40% of interval secondary production.

Stable Isotope Analysis and Trophic Basis of Secondary Production

Stable C and N isotope values of allochthonous detritus both were not statistically different among samples taken throughout the year (ANOVA, $p > 0.05$). Therefore, we combined litter isotope values from all dates for our analysis. Willow litter was consistently more depleted in ^{13}C relative to diatoms, while $\delta^{15}\text{N}$ signatures were similar for most dates. Conversely, patterns of algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed wide variation throughout the time (Figure 10). Mean algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranged from -26.43 to -13.37 and -0.39 and 6.43, respectively. $\delta^{13}\text{C}$ values of algae were significantly higher than those of litter on all sampling dates (Tukey HSD pair-wise comparison, $p < 0.001$).

Invertebrate trophic support roughly followed patterns of autochthonous production (cf. Figures 7 and 9). Autochthonous organic matter supported 58% of annual secondary production, while 42% was attributed to allochthonous detritus. Daily production attributed to allochthonous organic matter ranged from 19.1 mg AFDM $\text{m}^{-2} \text{d}^{-1}$ (95% CI 15.8 to 22.9) in August to 4.2 mg AFDM $\text{m}^{-2} \text{d}^{-1}$ (95% CI 3.4 to 5.0) in January. However, the proportion of the total interval production supported by allochthonous organic matter was greater in January (50%) relative to August (42%, Figure 9). Allochthonous organic matter supported between 25% (September) and 67% (May) of interval production (Figure 9) and was lowest during months of high NPP and highest during periods of low NPP (Figure 6) and relatively high BOM stocks (Figures 4 and 5).

The most productive taxa displayed varying degrees of trophic omnivory and little evidence for resource specialization. Trophic support of the most productive taxon, Elmidae, varied between near complete support by algae (89%) to dominance by litter (59%). This pattern tracked availability of basal resources, with highest support from autochthonous algae in August, coinciding with peak NPP. Other productive taxa showed more consistent reliance on allochthonous organic matter throughout the study. For example, allochthonous detritus supported $\geq 40\%$ of production of *Drunella doddsi*, *Cinygmula* spp., *Serratella* spp., and Chironomidae during all intervals. For a few taxa, allochthonous organic matter supported the majority of interval production. Approximately 75% of production of *Cinygmula* spp. and *Serratella* spp. was attributed to allochthonous organic matter during April. Trophic support of less productive taxa showed similar patterns of resource omnivory throughout the year.

Discussion

Inputs of allochthonous leaf litter have long been recognized as an important basal resource for consumers in many stream ecosystems, often greatly exceeding autochthonous production (Fisher and Likens 1973, Webster and Meyer 1997, 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, Brito et al. 2006). Our detailed temporal analysis

revealed strong variation in the relative importance of allochthonous and autochthonous resources to stream consumers, with much of the variation likely driven by the interaction of temperature and resource quality. Our results suggest that widely differing resources from spatially distinct habitats can serve complimentary, but dissimilar roles in fueling aquatic food webs in seasonally variable stream ecosystems of the northern Rockies.

Even as ecologists continue to accumulate evidence on the ubiquity of resource subsidies across ecosystems, it remains unclear whether the response of consumers to resources subsidies should be similar across ecosystems (Vanni et al. 2004). Recent focus has shifted to understanding context dependency of the response of recipient food webs to resources subsidies (Marczak et al. 2007, Anderson et al. 2008, Holt 2008). For example, characteristics of the donor and recipient ecosystems, such as, perimeter:surface area ratio (Polis and Hurd 1996), productivity (Polis et al. 1997), and the trophic position where resource subsidies enter the food web (Huxel et al. 2002), may modulate the response of recipient consumers. In a recent meta-analysis, Marczak et al. (2007) found that increases in the density or biomass of subsidies relative to autochthonous resources had a positive relationship with effect size, as measured by the ratio of recipient consumer density or biomass between high- and low-subsidy scenarios. In our study, the relative availability of terrestrial detritus versus autochthonous production was largely influenced by seasonal patterns of primary production. Although standing stock of terrestrial detritus was relatively similar through the year, periods of low temperatures and ice cover greatly reduced production of

benthic algae, increasing the relative abundance of allochthonous resources. Terrestrial litter supported the majority (55 – 67%) of production of invertebrate consumers during these periods, demonstrating that resource dynamics within the recipient ecosystem play a crucial role in determining when resources subsidies will be most important for consumers.

Inputs of terrestrial detritus may stabilize food webs in stream ecosystems by increasing resource diversity and alleviating volatile fluctuations in autochthonous resource availability. However, the response of recipient food webs to resource subsidies is dependent on the ability of consumers to effectively utilize allochthonous resources. Stream consumers have multiple strategies for utilizing pulses of allochthonous resources, including evolved life histories that coincide with high subsidy abundance (Cummins et al. 1989); i.e., shredders and terrestrial litter fall), generalist feeding strategies (Mihuc 1997; i.e., trophic omnivory), and ontogenetic diet shifts (Hawkins 1990; e.g., shift from primary consumer to predator between early and late instars of *Drunella* spp.). Each of these strategies increases the diversity of trophic interactions in the food web, and allows consumers to partition resources in time and space. Increased diversity in trophic interactions may weaken many consumer-resource linkages, theoretically increasing food web stability (McCann et al. 1998, Huxel et al. 2002). Wetzel (1995) suggested that detritus may also stabilize ecosystem functions, such as secondary production, because of its relatively slow and constant metabolism in comparison to widely fluctuating dynamics of algae and algal-based food webs. In our study, allochthonous detritus was persistently

available during fluctuations in NPP, providing a key subsidy to consumers during periods of autochthonous resource scarcity. Consumers switched from reliance on autochthonous resources to allochthonous litter during periods of low algal production, demonstrating the importance of subsidies to stream consumers. These patterns support the role of allochthonous resources in stabilizing food webs in these streams.

Temperature can play an important role in determining metabolic demands of invertebrate consumers. Growth rates of poikilothermic invertebrates generally increase with temperature (within tolerance boundaries; Brown et al. 2004), requiring high acquisition of nutrients that make up the machinery (e.g., phosphorus-rich RNA) and building blocks (e.g., nitrogen-rich proteins) of new tissue (Sterner and Elser 2002). Because invertebrates are relatively homeostatic with regard to their body nutrient content (Persson et al. 2010a), high amounts of nutrients in food are required during times of rapid growth. Growth rates of invertebrate consumers varied greatly during our study with >50% of annual production occurring over three months from August to October, coinciding with relatively high temperatures and NPP. Algae are often considered a higher quality resource (i.e., higher nutrient content) than leaf litter and other detrital resources (Cross et al. 2003). The abundance of high quality autochthonous resources in summer and early fall likely reduced stoichiometric constraints on invertebrate consumer growth during periods of high temperatures. While the availability of high quality resources are important at elevated temperatures, low temperatures and reduced growth rates may make

consumers less susceptible to limitation by essential nutrients such as nitrogen and phosphorus (Persson et al. 2010b). During colder months, the availability of high quality resources may not be as critical, as temperature likely limits the growth rates of consumers and ingested resources are largely dedicated to fueling basal metabolism instead of new tissue.

Relatively few taxa dominated annual invertebrate production, and these taxa represented key 'gate keepers' of energy flow through the stream food web. This pattern is similar to that observed in other studies of community production, highlighting the important linkages between species and ecosystem processes (e.g., Lawton and Jones 1995, Hall et al. 2001, Hall et al. 2006). Elmidae was consistently the most productive taxon and contributed to a large proportion of community biomass (Figure 8) and production (Table 1) throughout the year. This pattern was most pronounced during periods of high primary production (e.g., August and September), when the highest proportion of invertebrate production was attributed to Elmidae. Isotope analysis suggested that Elmidae, which are considered to exhibit a wide range of feeding strategies, might preferentially select high quality algal resources when they are available; $\delta^{13}\text{C}$ values were very close to algae during months of high NPP. We do not know how many species are included in this taxonomic group, and this could explain the large discrepancy in production between Elmidae and other taxa. Although examining this taxon at a finer taxonomic resolution may have helped elucidate specific patterns of energy flow, it is clear that this group plays a large role in regulating energy flow through the West Blacktail Deer Creek food web. The

quantification of energy flows is important for understanding the dynamics and structure of food webs and the presence of few quantitatively dominant pathways of energy flow may have implications for community interactions such as competition and predation (Benke 1993, Polis 1994, Benke and Wallace 1997).

Patterns in C and N stable isotope ratios differed between allochthonous and autochthonous organic matter in our study. Stable isotope ratios of allochthonous litter were fairly constant throughout the study, as has been shown in previous research (McCutchan and Lewis 2001). Atmospheric C is relatively homogeneous and temporally stable, which may explain the narrow variation in carbon isotope ratios of terrestrial plants (Rounick and Winterbourn 1986). However, stable isotope ratios of algae were much more temporally variable. This pattern was likely due to the variable sources and concentrations of dissolved inorganic C and N relative to metabolic demands of aquatic algae. For example, the supply rate of CO₂ relative to photosynthetic demands may play a large role in carbon isotope fractionation by algae (Finlay et al. 1999). Physicochemical characteristics of the aquatic environment such as water velocity (Finlay et al. 1999), light, nutrient levels, and stage of epilithon development (Hill et al. 2008) interact to determine carbon isotope ratios of algae by influencing boundary layer thickness and rates of algal production. We saw a general pattern of enrichment (less negative) in $\delta^{13}\text{C}$ values of diatoms from summer (August) to autumn (October), however this pattern was quite variable. Hill et al. (2008) reported enrichment in ^{13}C with increased light levels, which may partially explain the above enrichment in algal C isotope signatures, as light

availability to the stream likely increased following litter fall. Spring snowmelt likely caused the low and highly variable $\delta^{13}\text{C}$ values of diatoms we observed in May and June. The increased water velocity and reduced primary production associated with snowmelt likely affected the availability of inorganic carbon relative to demand, influencing the discrimination of carbon isotopes by stream algae.

Controls of ^{15}N signatures in algae are less understood because of the complexity of the N cycle and the in-stream and watershed-scale processes controlling the $\delta^{15}\text{N}$ of dissolved inorganic nitrogen. We observed large $\delta^{15}\text{N}$ enrichment during spring snowmelt, contrasting with multiple previous studies in which snowmelt led to depleted ^{15}N (McCutchan and Lewis 2001, Burns and Kendall 2002). These conflicting patterns may be related to different processes influencing the inorganic N pool during snowmelt. It is possible that the enrichment we observed was attributed to the flushing of ammonium from upstream wetlands during snowmelt. However, additional research is needed to understand ultimate controls on algal isotope signatures. Importantly, the wide variation in algal isotope values measured during our study demonstrates that isotopic food webs analysis may be greatly improved by sampling available food resources often and on a timescale relevant to seasonal patterns of consumer growth rates (McCutchan and Lewis 2001).

Riparian plant communities within Yellowstone National Park (YNP) have experienced large changes since the park's inception (Wagner 2006), likely altering terrestrial-aquatic linkages and consumer-resource interactions in stream

food webs. Communities of willow have received much attention because willow often dominates riparian communities of western North America (Amlin and Rood 2002). For much of the past century, willow communities have seen appreciable declines in distribution and recruitment within YNP (Chadde and Kay 1991). Recently, however, many riparian willow communities within YNP have experienced a trend of increasing growth and spatial extent (Beyer et al. 2007); although it is unclear whether this pattern is consistent across the landscape (Smith et al. 2003). A range of both top-down and bottom-up factors have been cited to explain the variability in willow growth across Yellowstone National Park (National Research Council 2002). Wolf reintroduction in 1995 restored a natural predator that directly and indirectly influenced populations of herbivores such as elk (White and Garrott 2005, Creel and Christianson 2009). Multiple authors have suggested that the balance between resource acquisition and predation risk may cause elk to select relatively safe riparian areas, thereby releasing areas from herbivory where predation risk is higher (Ripple and Beschta 2004, Fortin et al. 2005). Much less research has focused on bottom-up factors to explain patterns in willow regeneration (but see Tercek et al. 2010). However, Bilyeu et al. (2008) found that water availability may constrain willow growth even in the absence of browsing. Clearly, a combination of both top-down and bottom-up factors contribute to patterns of willow growth across the landscape. Though our study was focused on a single stream that has experienced large increases in riparian willow, it provides a baseline on which to assess the impacts of future changes in riparian vegetation for stream ecosystems in YNP and the northern

Rockies.

Our findings document the importance of both autochthonous and allochthonous resources for stream food webs in northern temperate environments. High quality resources were important in supporting invertebrate production, during the abbreviated periods of relatively high temperatures and consumer growth rates. Input of allochthonous resources, dominated by willow leaf litter, supported consumers during periods of slow growth and scarcity in autochthonous resources. These findings highlight the role of the environmental template in recipient stream ecosystems in determining the relative importance of resource subsidies throughout the year.

Table 1. Mean and 95% confidence intervals of annual abundance (N, individuals m⁻²), biomass (mg AFDM m⁻²), secondary production (mg AFDM m⁻² y⁻¹), Production:Biomass ratios (P/B, y⁻¹), and percent contribution from allochthonous and autochthonous resources of macroinvertebrate taxa in West Blacktail Deer Creek, Wyoming, USA.

Taxon	N	B	P	P/B	% Allo.	% Auto
Elmidae	960 (796-1129)	428 (360-500)	2623 (2608-2640)	6.13 (5.64-6.60)	33	67
<i>Cynigmul</i> a spp.	253 (190-325)	142 (108-179)	790 (784-796)	5.58 (5.19-6.00)	54	46
<i>Serratella</i> spp.	252 (198-313)	85 (61-111)	459 (455-464)	5.40 (5.04-5.81)	56	44
Chironomidae	1145 (868-1462)	166 (126-210)	455 (450-460)	2.75 (2.00-3.60)	47	53
<i>Sweltsa</i> spp.	211 (156-271)	66 (47-91)	420 (415-426)	6.31 (5.49-7.22)	55	45
<i>Acentrella</i> spp.	753 (565-943)	51 (40-62)	361 (258-264)	7.06 (6.66-7.44)	51	49
<i>Drunella doddsi</i>	71 (55-88)	58 (41-76)	295 (293-298)	5.09 (4.74-5.46)	57	43
Elmidae ⁺	50 (41-59)	38 (37-39)	261 (259-263)	6.80 (6.36-7.19)	36	64
Rhyacophilidae	55 (41-72)	70 (46-97)	213 (211-215)	3.08 (2.47-3.84)	49	51
<i>Epeorus</i> spp.	314 (227-405)	27 (18-36)	196 (194-199)	7.21 (6.56-7.86)	47	53
<i>Baetis</i> spp.	276 (203-365)	26 (20-34)	190 (188-192)	7.26 (6.68-7.85)	50	50
<i>Classenia</i> spp.	13 (8-19)	108 (45-187)	188 (185-191)	1.94 (.90-3.95)	48	52
<i>Ephemeralla</i> spp.	80 (58-105)	31 (22-40)	175 (173-176)	5.61 (5.13-6.07)	56	44
Perlodidae	30 (17-46)	15 (9-23)	110 (108-112)	7.16 (6.36-8.02)	62	38
<i>Barbaetis</i> spp.	86 (59-115)	13 (7-21)	103 (101-105)	7.75 (6.26-8.81)	46	54
Leptophlebiidae	193 (135-262)	15 (11-19)	75 (55-97)	5*	48	52
Simuliidae	115 (62-172)	11 (8-18)	52 (24-89)	5*	43	57
<i>Zapada</i> spp.	75 (45-108)	15 (8-23)	75 (42-116)	5*	41	59
<i>Ameletus</i> spp.	35 (16-62)	10 (6-15)	51 (30-77)	5*	47	53
Hydropsychidae	10 (5-16)	31 (15-50)	155 (77-249)	5*	43	57
<i>Pericoma</i> spp.	159 (124-197)	8 (6-11)	41 (31-54)	5*	57	43
<i>Drunella</i> spp.	16 (10-24)	9 (6-13)	46 (28-67)	5*	55	45
<i>Rhithrogena</i> spp.	30 (16-46)	7 (5-10)	36 (23-51)	5*	52	48
Tipulidae	10 (6-15)	18 (10-28)	92 (50-139)	5*	60	40
<i>Suwallia</i> spp.	25 (16-35)	5 (4-7)	26 (18-34)	5*	63	37
<i>Brachycentrus</i> spp.	91 (69-116)	4 (3-6)	20 (14-28)	5*	51	49
Glossosomatidae	7 (4-12)	8 (3-15)	40 (16-73)	5*	42	58
Other	117 (91-146)	10 (8-12)	48 (38-59)			
Sum all taxa	5434 (5021-5876)	1477 (1359-1608)	7598 (6979-8258)	5.14	42	58

Annual P:B of 5 assumed for these taxa

Aquatic adult life stages

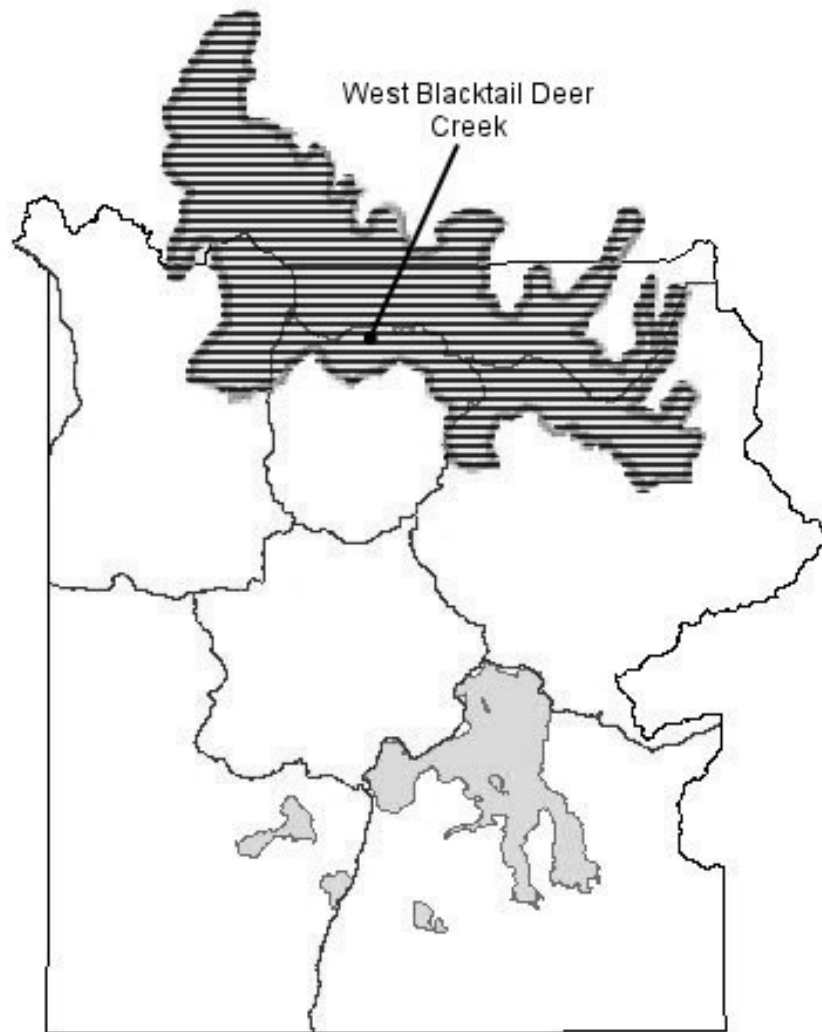


Figure 1. Map of Yellowstone National Park showing West Blacktail Deer Creek Wyoming, USA. The lined region represents the wintering range of the northern elk herd.

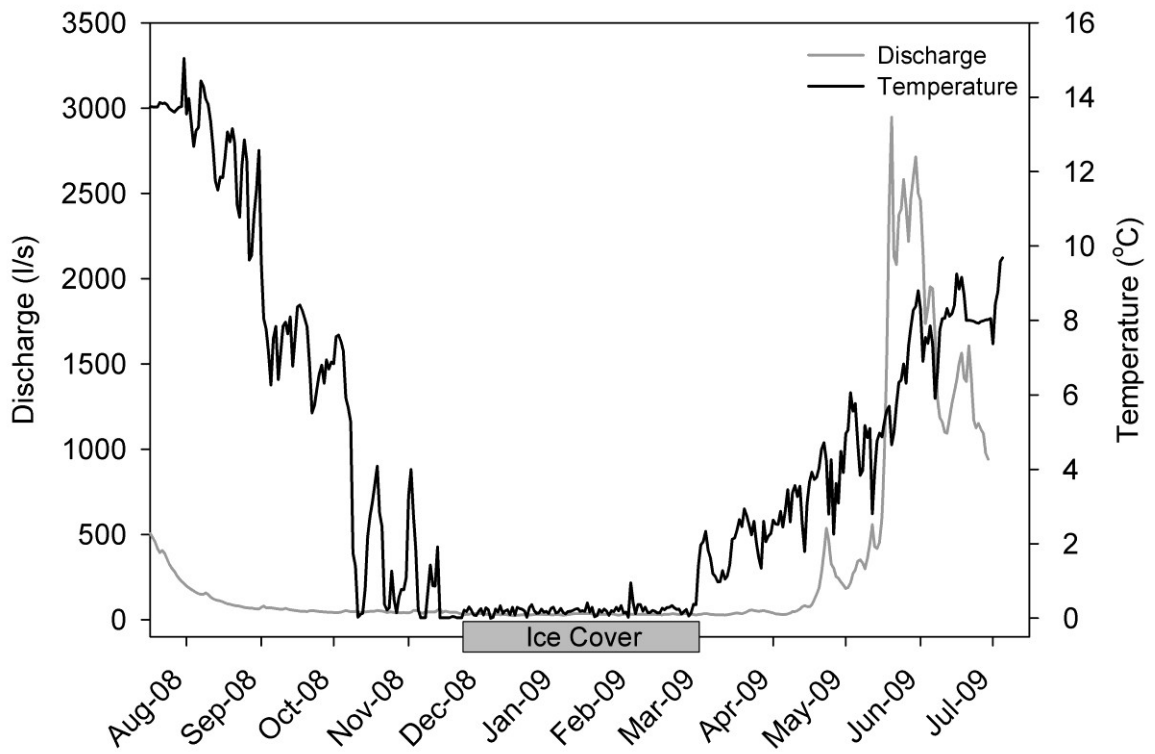


Figure 2. Temperature (°C) and stream discharge (l/s) profile of West Blacktail Deer Creek between July 2008 and July 2009.

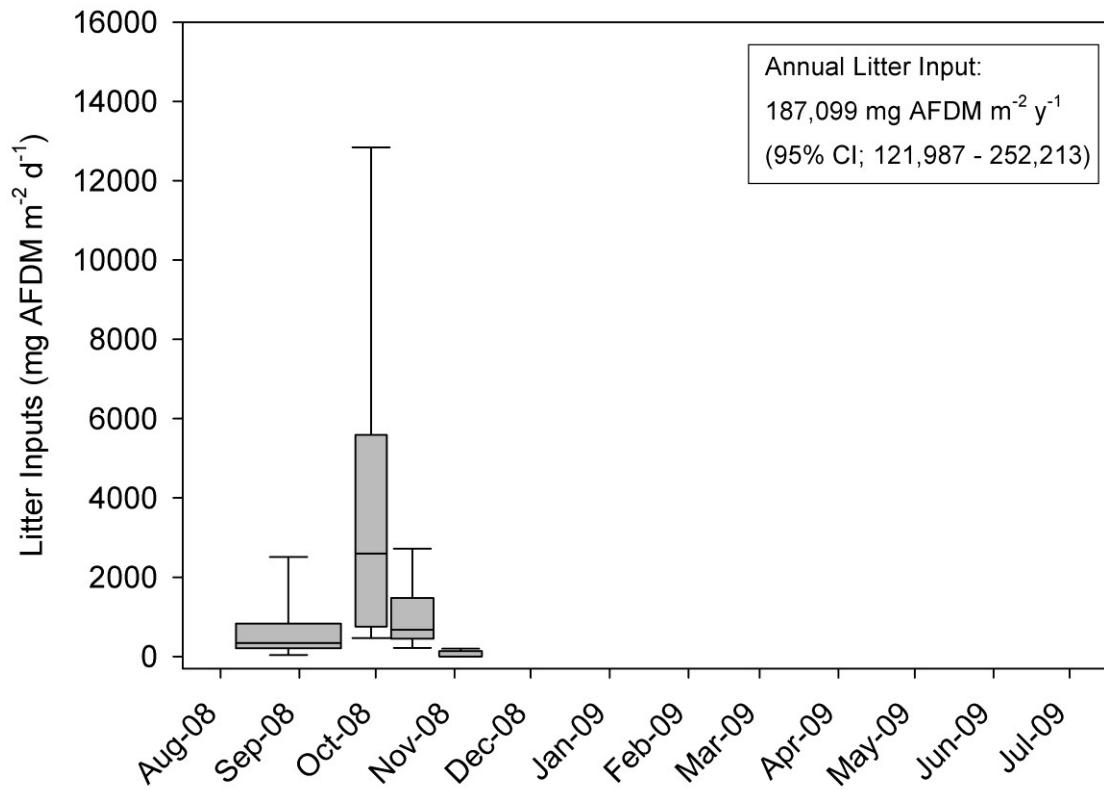


Figure 3. Daily leaf litter inputs (mg AFDM m⁻² d⁻¹) to West Blacktail Deer Creek from July 2008 to July 2009. Shaded boxes represent the median and 25% and 75% percentiles. Error bars show the 5% and 95% percentiles.

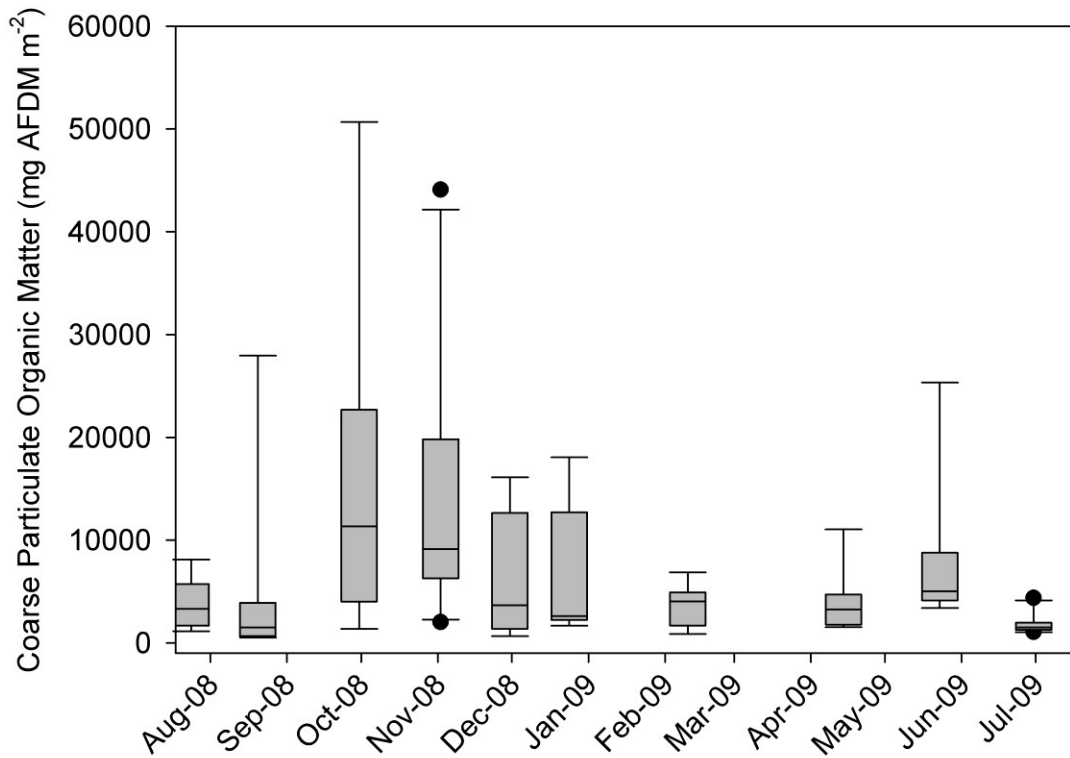


Figure 4. Standing stock of coarse particulate organic matter (mg AFDM m⁻²) on each sampling date during the study. Shaded boxes represent the median and 25% and 75% percentiles. Error bars show the 5% and 95% percentiles. Dots are observations which fall outside the 5% and 95% percentiles.

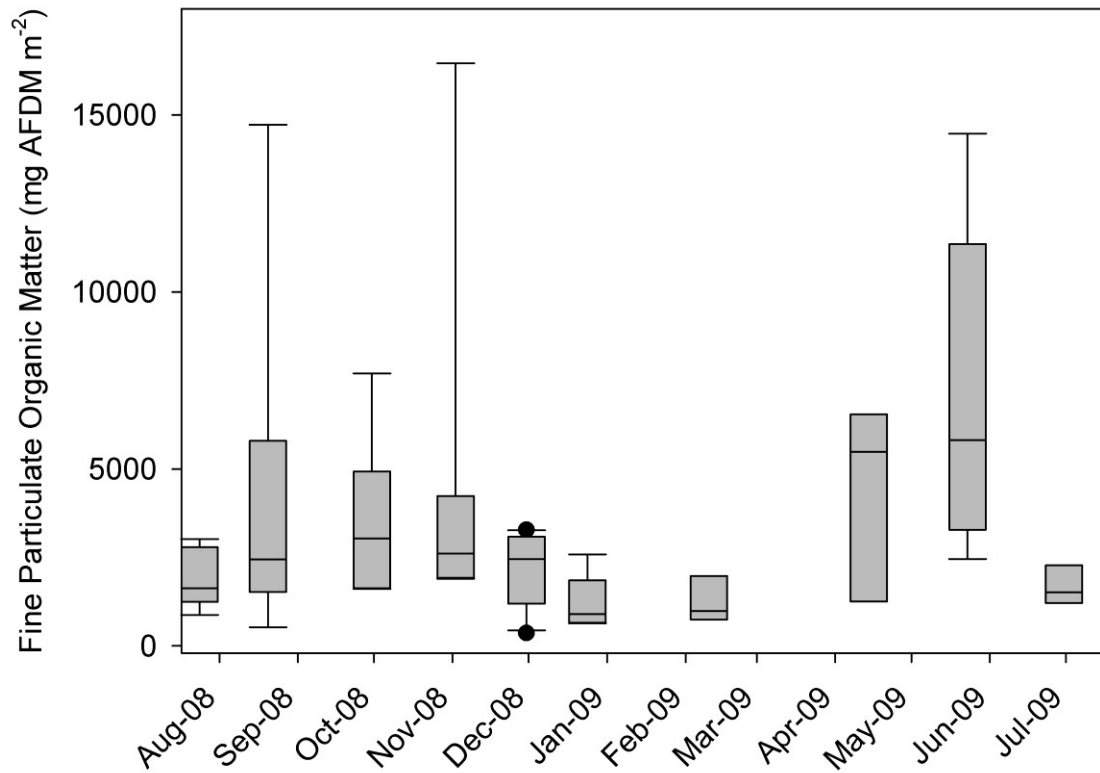


Figure 5. Standing stock of fine particulate organic matter (mg AFDM m⁻²) on each sampling date during the study. Shaded boxes represent the median and 25% and 75% percentiles. Error bars show the 5% and 95% percentiles. Dots are observations which fall outside the 5% and 95% percentiles.

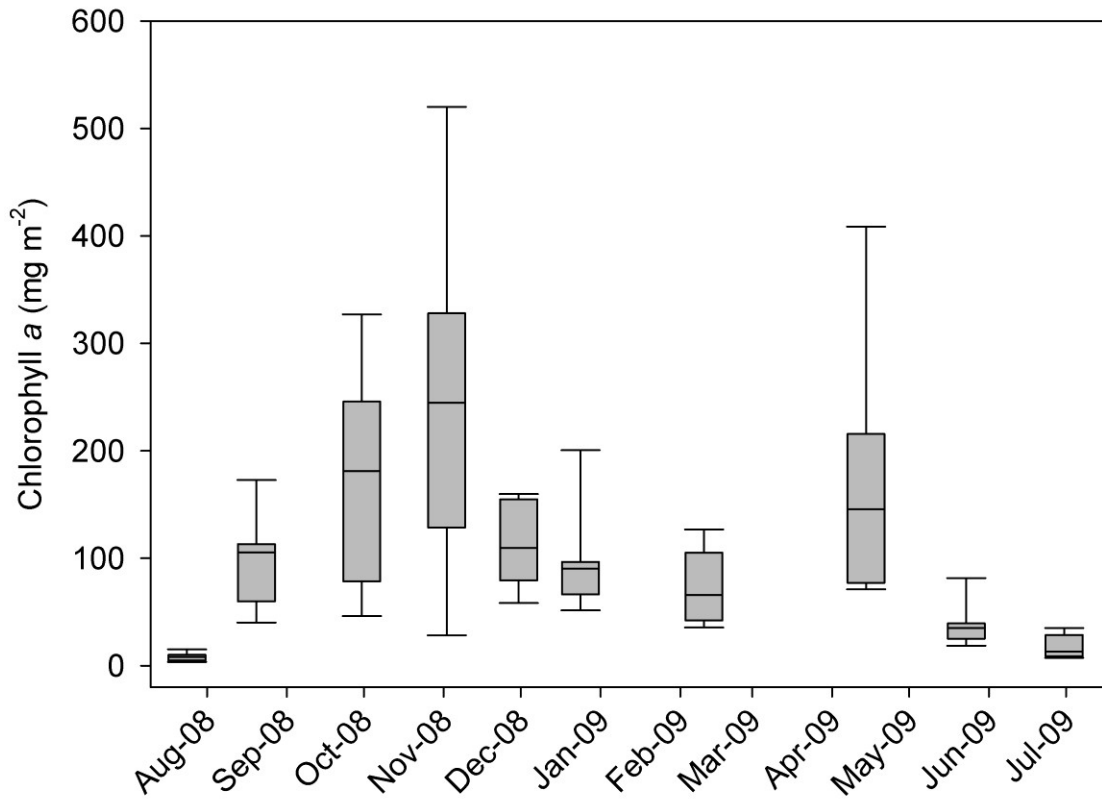


Figure 6. Benthic chlorophyll a standing stock (mg Chl a m⁻²) of epilithon on each sampling date during the study. Shaded boxes represent the median and 25% and 75% percentiles. Error bars show the 5% and 95% percentiles.

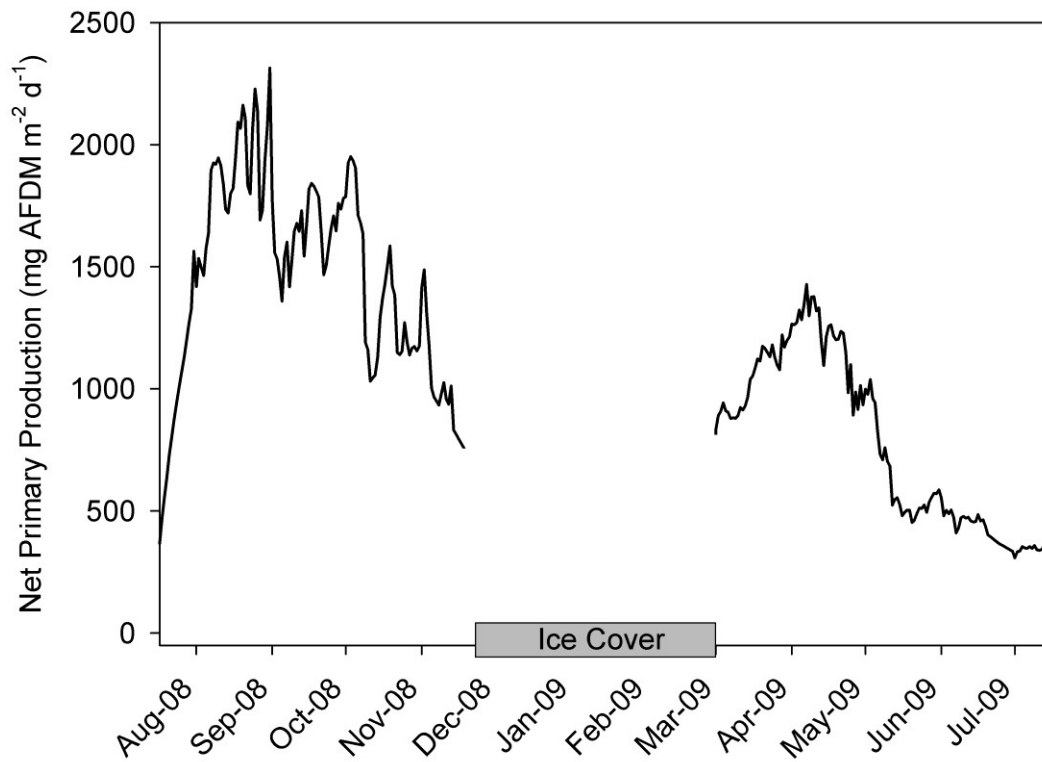


Figure 7. Daily net primary production (mg AFDM m⁻² d⁻¹) estimates derived from chlorophyll *a* (mg Chl *a* m⁻²) and stream temperature (°C) values (Morin et al. 1999).

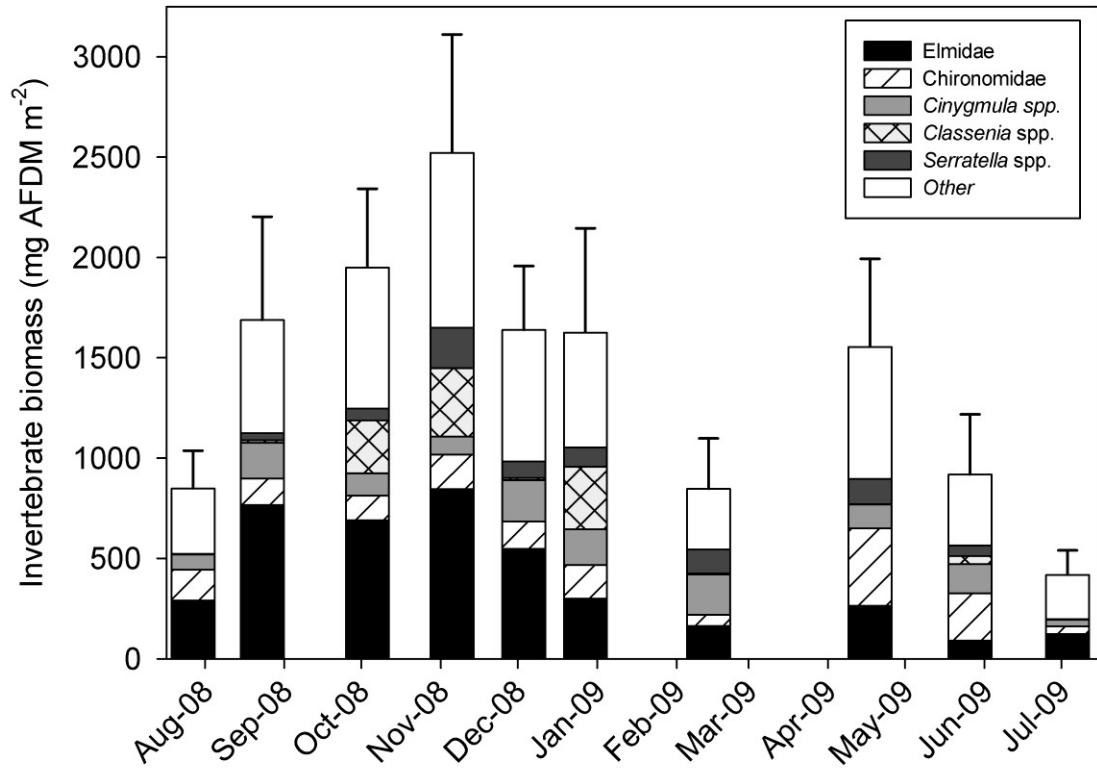


Figure 8. Total mean invertebrate biomass (mg AFDM m⁻²; +95% confidence interval) of the community, highlighting the most productive taxa.

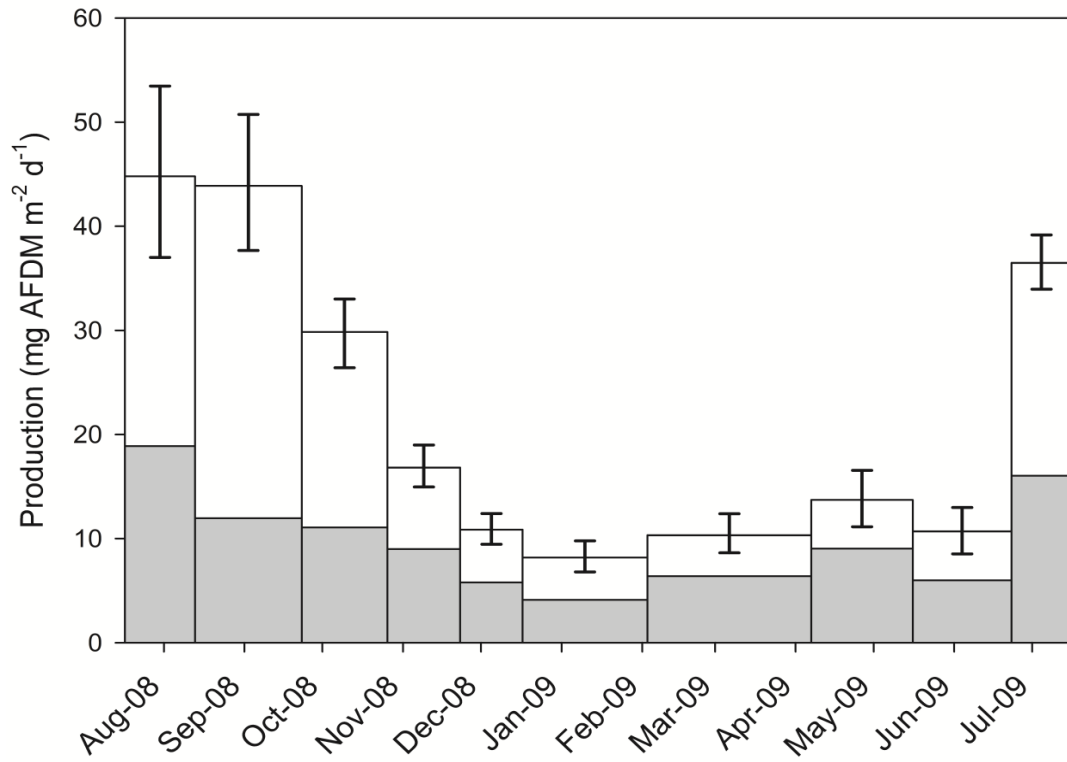


Figure 9. Daily production (mg AFDM m⁻² d⁻¹; mean ± 95% confidence interval) of stream invertebrate community. The amount portion of production supported by allochthonous organic matter is represented in the shaded region, while the white regions represent support from autochthonous resources.

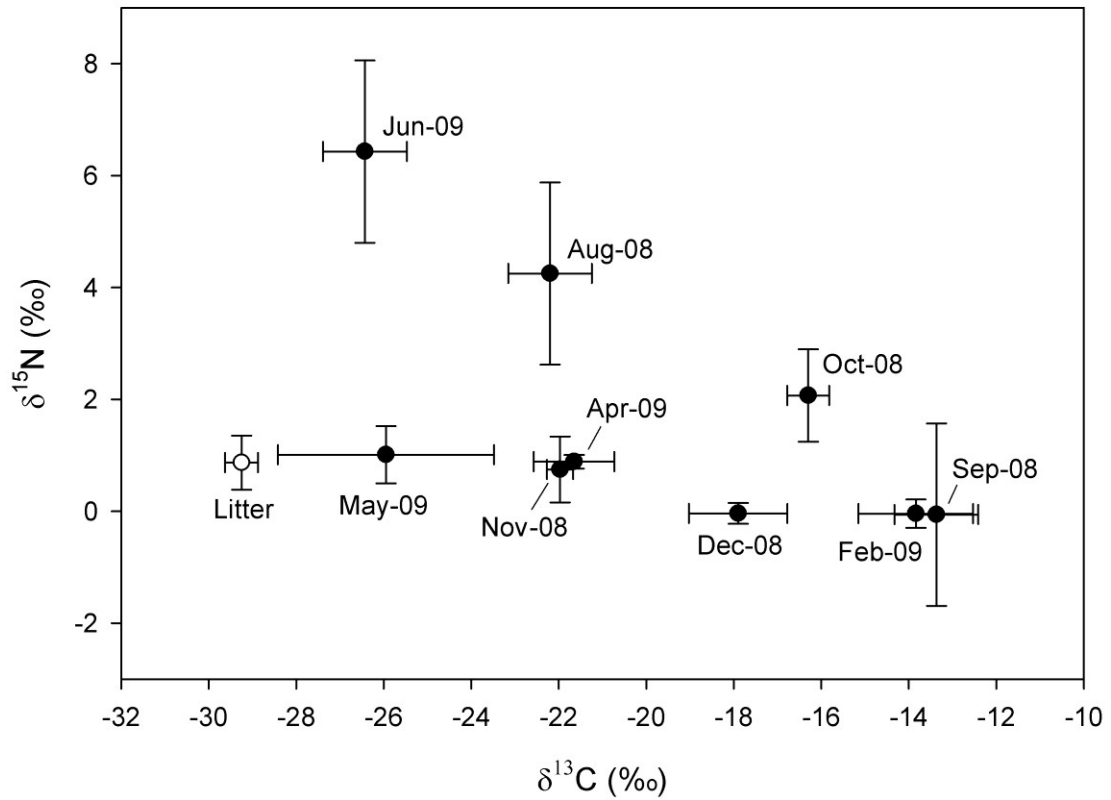


Figure 10. Stable isotope ratios of C and N of allochthonous and autochthonous resources on each date. The open circle represents the mean \pm standard deviation of leaf litter collected on all dates. Closed circles show the mean \pm standard deviation of diatoms on each sampling date.

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APPENDICES

APPENDIX A

MONTHLY TROPHIC SUPPORT OF MACROINVERTEBRATE TAXA

Taxon	Aug-08		Sep-08		Oct-08		Nov-08		Dec-08		Jan-09		Mar-09		May-09		Jun-09		Jul-09	
	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.	% Allo.	% Auto.
Elmidae	40	60	11	89	37	63	53	47	49	51	37	63	51	49	59	41	35	65	41	59
<i>Cynigmula</i> spp.	42	58	40	60	41	59	66	34	63	37	63	37	65	35	74	26	64	36	46	54
<i>Serratella</i> spp.	42	58	40	60	40	60	61	39	58	42	51	49	76	24	76	24	63	37	46	54
Chironomidae	43	57	40	60	48	52	63	37	65	35	52	48	62	38	62	38	56	44	45	55
<i>Sweltsa</i> spp.	52	48	45	55	52	48	64	36	63	37	70	30	76	24	66	34	43	57	47	53
<i>Acentrella</i> spp.	53	47	39	61	45	55	62	38	53	47	44	56	60	40	77	23	67	33	48	52
<i>Drunella doddsi</i>	60	40	40	60	47	53	62	38	43	57	50	50	62	38	71	29	45	55	67	33
Elmidae ⁺	40	60	15	85	34	66	53	47	50	50	35	65	51	49	57	43	37	63	39	61
Rhyacophilidae	52	48	40	60	52	48	63	37	46	54	51	49	58	42	67	33	52	48	46	54
<i>Epeorus</i> spp.	41	59	40	60	36	64	65	35	45	55	60	40	64	36	58	42	64	36	40	60
<i>Baetis</i> spp.	54	46	39	61	44	56	63	37	52	48	44	56	62	38	74	26	67	33	46	54
<i>Classenia</i> spp.	52	48	37	63	51	49	63	37	61	39	73	27	79	21	68	32	44	56	48	52
<i>Ephemerella</i> spp.	41	59	38	62	47	53	62	38	63	37	52	48	61	39	76	24	65	35	45	55
Perlodidae	50	50	45	55	48	52	63	37	63	37	70	30	78	22	66	34	43	57	48	52
<i>Barbaetis</i> spp.	42	58	40	60	49	51	60	40	53	47	43	57	61	39	77	23	68	32	47	53
Leptophlebiidae	44	56	41	59	48	52	61	39	63	37	54	46	47	53	45	55	62	38	46	54
Simuliidae	40	60	42	58	45	55	60	40	50	50	31	69	60	40	62	38	33	67	33	67
<i>Zapada</i> spp.	50	50	50	50	50	50	55	45	54	46	46	54	62	38	68	32	62	38	44	56
<i>Ameletus</i> spp.	42	58	40	60	49	51	61	39	62	38	51	49	62	38	75	25	64	36	46	54
Hydropsychidae	51	49	39	61	44	56	55	45	51	49	31	69	60	40	62	38	33	67	33	67
<i>Pericoma</i> spp.	43	57	40	60	49	51	62	38	63	37	53	47	63	37	75	25	63	37	47	53
<i>Drunella</i> spp.	59	41	40	60	47	53	62	38	43	57	50	50	60	40	71	29	45	55	67	33
<i>Rhithrogena</i> spp.	42	58	38	62	48	52	61	39	64	36	49	51	62	38	74	26	81	19	43	57
Tipulidae	50	50	45	55	55	45	55	45	46	54	34	66	60	40	68	32	61	39	43	57
<i>Suwallia</i> spp.	52	48	45	55	53	47	63	37	54	46	70	30	87	13	67	33	39	61	68	32
<i>Brachycentrus</i> spp.	42	58	40	60	48	52	61	39	62	38	51	49	62	38	72	28	52	48	46	54
Glossosomatidae	39	61	20	80	36	64	53	47	45	55	37	63	50	50	57	43	35	65	40	60
<i>Other</i>	42	58	39	61	47	53	62	38	62	38	51	49	60	40	76	24	65	35	45	55
All taxa	43	57	27	73	42	58	59	41	54	46	50	50	63	37	67	33	52	48	45	55