

Extreme seasonality of litter breakdown in an arctic spring-fed stream is driven by shredder phenology, not temperature

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SUMMARY

1. Using degree-days to calculate ‘temperature-corrected’ breakdown rates is a useful approach for comparing litter breakdown across sites with different thermal regimes. We used an alternative approach to investigate the importance of temperature by quantifying seasonal patterns in litter breakdown in an arctic spring-fed stream (Ivishak Spring, North Slope, Alaska) that experiences extreme seasonality in light availability and energy inputs while fluctuations in water temperature are relatively small.

2. We incubated mesh bags of senesced *Salix alaxensis* litter in Ivishak Spring for successive c. 30-day periods for 2 years. During our study, water temperature was very stable [5.7 ± 0.03 °C (daily mean ± 1 SE), range 3.7–7.8 °C]. Discharge was only slightly more variable (mean 112 ± 1 L s⁻¹, range 66–206 L s⁻¹), with lowest values occurring in late winter.

Dissolved nutrient concentrations were low (52 – 133 $\mu\text{g L}^{-1}$ NO₃⁻ – N, <1 – 3 $\mu\text{g L}^{-1}$ NH₄⁺ – N, <1 – 6 $\mu\text{g L}^{-1}$ soluble reactive phosphorus) and also showed evidence of seasonality (i.e. highest values in winter).

3. Litter breakdown rates were sharply seasonal, ranging from <0.01 day⁻¹ in mid-summer to >0.05 day⁻¹ in mid-winter. Invertebrate assemblage structure in litter bags showed pronounced seasonal cyclicity; total invertebrate biomass peaked in summer. Biomass of two dominant shredders (the nemourid stonefly *Zapada haysi* and the limnephilid caddisfly *Ecclisomyia conspersa*) showed the opposite trend, however, with mid-winter peaks in both population biomass and cohort growth rates that closely matched those we observed in litter mass loss.

4. Water temperature appeared to have negligible influence on litter breakdown rates in our study. Seasonal shifts in nutrient uptake may have increased rates of microbial activity in winter. The processing of litter inputs in Ivishak Spring, however, appeared to be most tightly coupled to shredder phenology. Our results demonstrate that extreme seasonality in the processing of allochthonous detritus can occur even in the absence of substantial temperature variation, driven by the activity of shredder taxa that have evolved to take advantage of pulsed organic matter inputs.

Keywords: Alaska, decomposition, litter processing, *Salix*, *Zapada*

Introduction

The metabolism of most rivers and streams is dominated by the respiration of carbon fixed outside

their ecosystem boundaries (Webster & Meyer, 1997). One particularly well-studied component of this heterotrophy is the breakdown of terrestrial leaf litter (Petersen & Cummins, 1974; Anderson & Sedell, 1979;

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Cummins *et al.*, 1989). Although much of the organic carbon contained in leaf litter that enters a stream is converted to CO₂ via biological processing, the rate of this process depends on a number of important abiotic variables (e.g. temperature, pH, dissolved nutrients). Of these, temperature is particularly significant as a driver of metabolic rate (Enquist *et al.*, 2003), and many studies have demonstrated a temperature effect on litter breakdown rate (Kaushik & Hynes, 1971; Suberkropp & Klug, 1976; Webster & Benfield, 1986; Irons *et al.*, 1994).

One approach to investigating the relative importance of temperature in controlling the breakdown of terrestrial leaf litter is the use of degree-days to calculate normalised per-degree breakdown rates (Webster & Benfield, 1986). Using degree-days allows the comparison of 'temperature-corrected' litter breakdown rates across sites with different thermal regimes. Such comparisons show that correcting for temperature can reveal considerable variation in breakdown rates along natural temperature gradients, suggesting that factors other than temperature have a critical effect on spatial and temporal patterns in litter breakdown (Irons *et al.*, 1994; Rowe *et al.*, 1996; Boyero *et al.*, 2011). For example, Irons *et al.* (1994) showed that per-degree breakdown rates in a cold, high-latitude stream in Alaska, U.S.A., were markedly higher than those at two much warmer sites at low- and mid-latitudes, attributing the faster processing in the cold stream to higher activity of shredding invertebrates. More recently, Boyero *et al.* (2011) also reported that per-degree breakdown rates increased with latitude across 22 stream sites but only in coarse-mesh litter bags that allowed shredder access.

Temperature-corrected comparisons of litter breakdown at sites that differ in temperature regime have been useful in attempts to isolate the effect of temperature but are not the only approach. One alternative involves following temporal patterns in breakdown at single sites that experience relatively stable temperature regimes, such as spring-fed streams. At such sites, breakdown rates should remain relatively constant through time if temperature is the dominant driver of breakdown. Spring-fed streams in the Arctic may be particularly well suited for such studies. Their temperature is often remarkably stable, despite steep annual gradients in air temperature. Moreover, seasonal changes in day-length at high latitudes mean that carbon inputs from

net primary production show extreme annual cycles in these systems, while respiration of all organisms can potentially be maintained at relatively constant rates by stable temperature. Primary production and respiration can consequently be temporally uncoupled, potentially leading to energetic shortfalls for poikilothermic consumers during the long arctic winter. Such dynamics might be expected to drive seasonal patterns in the breakdown of allochthonous carbon inputs, making arctic spring-streams compelling model systems for examining the relative effects of temperature and other factors in controlling breakdown of terrestrial litter.

In this paper, we document temporal patterns in the breakdown of terrestrial leaf litter in a spring-fed stream in arctic Alaska that experiences extreme seasonality in light-energy inputs while showing a remarkably stable temperature regime. We use our data to examine the relative importance of different biotic and abiotic factors in controlling the processing of carbon subsidies in this stream ecosystem. In particular, we ask the question: under conditions of extreme seasonality but greatly reduced temporal variation in water temperatures, what factors might drive seasonal dynamics in the utilisation and breakdown of allochthonous organic matter?

Methods

Study site

Fieldwork for this study was conducted in Ivishak Spring, a first-order spring-fed tributary of the Ivishak River located in the Arctic National Wildlife Refuge on Alaska's North Slope, U.S.A. (69.02433°N, 147.71803°W, 441 m a.s.l.). The spring discharges on a steep talus slope before forming a discrete channel that flows for 275 m to its confluence with an adjacent rain-fed stream. Water temperature is a constant 7.3 °C at the spring source, while discharge is very stable compared with rain-fed streams of the region (Parker & Huryn, 2006). The stream channel is composed primarily of riffles and runs, with few pools (mean depth = 12 cm). The substratum is a cobble/gravel mix and covered by a high biomass of bryophytes [c. 80 g ash-free dry mass (AFDM) m⁻²]. Riparian vegetation is typical of North Slope spring-fed streams, consisting of willows (*Salix* spp., 1–2 m high) and a grove of balsam poplar (*Populus balsamifera*

L., c. 10 m high) along one bank. Mean benthic litter storage is low, however (<3 g AFDM m⁻²; A.D. Huryn & J.P. Benstead, unpubl. data). Ivishak Spring supports a relatively diverse invertebrate assemblage (c. 25 spp.), mostly composed of grazers and predators supported by algal production (Parker & Huryn, 2006). Northern Dolly Varden char (*Salvelinus malma malma* Walbaum) is the only fish species recorded at the site.

Physicochemical conditions

Water samples for NH₄⁺ - N, NO₃⁻ - N and soluble reactive phosphorus (SRP) analysis were collected at 10- to 20-m intervals along the stream ($n = 15$) each month (except June and December) between May 2007 and August 2009. Ammonium concentrations were measured using the orthophthaldialdehyde fluorometric method [Holmes *et al.*, 1999 as modified by Taylor *et al.* (2007)], NO₃⁻ - N was quantified using ion chromatography (Dionex ICS 2000 Ion Chromatograph, Dionex Corp., Sunnyvale, CA, U.S.A.; APHA, 1998) and SRP concentrations were measured using the ascorbic acid method (Murphy & Riley, 1962). Water temperature and stage height were measured every 5 min at the end of the reach using an Onset U20-001-01 water-level logger (Onset Computer Corp., Pocasset, MA, U.S.A.). The discharge record was subsequently estimated using a stage-discharge relationship ($n = 16$, $r^2 = 0.65$) based on discharge measurements made using steady-state rhodamine WT releases (Webster & Valett, 2006).

Litter breakdown rate and macro-invertebrate colonisation

We assessed seasonal changes in detritus processing rate by conducting successive monthly (c. 30 days) incubations of a standardised litter species. On each visit to the study site, ten litter bags (nylon pecan bags, mesh size 8 × 3 mm) containing weighed 5 g ± 0.1 g of air-dried willow [*Salix alaxensis* (Andersson) Coville] litter were anchored along a single riffle using tent stakes. Litter bags were collected and replaced with identical bags on the subsequent visit (typically c. 30 days later). Once transported to the laboratory, contents of litter bags were placed into a container of water and whole leaves and identifiable litter fragments were removed by hand. The water and

remaining material were then passed through a 250-µm mesh sieve. Macro-invertebrates retained on the sieve were preserved in 4% formaldehyde. Litter fragments were dried (72 h at 55 °C) and weighed. Subsamples of litter were subsequently ashed at 500 °C for ≥1 h to obtain estimates of AFDM loss over time. Breakdown rates (k coefficients) were calculated using linear regression of log_e-transformed per cent mass loss data plotted against time in days (k , day⁻¹) and degree-days (k_{dd} , dd⁻¹) for each monthly deployment (Webster & Benfield, 1986). Calculation of k coefficients assumes that the mass loss rates followed an exponential pattern (Petersen & Cummins, 1974).

Macro-invertebrates were identified to the lowest practical taxonomic level (chironomids to subfamily and other insects to genus or species; Merritt, Cummins & Berg, 2008). Functional feeding groups were assigned based on the study by Parker & Huryn (2006). Biomass was estimated using family-level length-mass relationships (Benke *et al.*, 1999). Mean individual dry mass (DM, derived using published, family-level length-weight relationships; Benke *et al.*, 1999) was estimated for larvae of major shredding taxa on each sampling date. These data were used to produce seasonal patterns of growth and potential resource demand for each identifiable cohort of dominant shredder taxa.

Statistical analysis

Seasonal shifts in the composition of the litter bag assemblage were analysed using four multivariate techniques: ordination, seriation, analysis of similarities and similarity percentages, using the MDS, RELATE, ANOSIM and SIMPER routines, respectively, in PRIMER (Version 6, Plymouth Marine Labs, Plymouth, U.K.; see Clarke & Warwick, 2001). First, we generated a dissimilarity matrix by comparing log_e-transformed taxon biomass data between every pair of dates. Between-date compositional similarities were computed using the Bray-Curtis coefficient (Bray & Curtis, 1957), which, compared with several commonly used dissimilarity coefficients, has been shown to have the most robust relationship with ecological distance (Faith, Minchin & Belbin, 1987). We then used the ordination technique of non-metric multidimensional scaling to provide a graphical summary of the relationships in the similarity matrix (Clarke & Warwick, 2001).

Seasonality in the structure of the invertebrate assemblage was tested using the RELATE routine in PRIMER by comparing the biomass similarity matrix against a model matrix of distances between ordinal sampling dates. The two matrices were compared using Spearman's rank correlation coefficient and tested statistically via permutation of the biomass matrix ($n = 999$ simulations; Clarke & Warwick, 2001). We further examined seasonal patterns in litter invertebrate assemblage structure by separating samples into summer (15 March–14 September) and winter (15 September–14 March) periods. Significant separation in assemblage structure between the two seasons was first confirmed using the ANOSIM routine in PRIMER. The two seasons were then compared using the SIMPER routine in PRIMER, which calculates the percentage contribution (Di) of each invertebrate taxon to the overall dissimilarity between the two groups. The SIMPER routine also calculates the ratio of the mean Di for all sample pairs between seasons to the standard deviation of Di , which is a measure of the consistency with which each taxon discriminates assemblages between seasons. The SIMPER analysis was run using \log_e -transformed taxon biomass data from all replicates (i.e. litter bags) for each date.

Finally, litter breakdown rates were regressed against water temperature, $\text{NO}_3^- - \text{N}$, $\text{NH}_4^+ - \text{N}$ and SRP concentrations and the mean cohort growth rates of major shredder taxa. Either mean k or k_{dd} coefficient was used in the regressions, as appropriate.

Results

Physical and chemical conditions

The water temperature of Ivishak Spring *c.* 240 m below the spring's source (30 m downstream of the litter incubation site) was very stable (mean ± 1 SE daily temperature 5.7 ± 0.03 °C, range 3.7–7.8 °C), despite air temperatures that ranged from –38 to 23 °C (Fig. 1a). Discharge was slightly more variable (mean 112 ± 1 L s^{-1} , range 66–206 L s^{-1}), with lowest values occurring in late winter and highest discharge in late summer (Fig. 1a). Dissolved nutrient concentrations were generally low ($52\text{--}133$ $\mu\text{g L}^{-1}$ $\text{NO}_3^- - \text{N}$, $<1\text{--}3$ $\mu\text{g L}^{-1}$ $\text{NH}_4^+ - \text{N}$, $<1\text{--}6$ $\mu\text{g L}^{-1}$ SRP). Concentrations of $\text{NH}_4^+ - \text{N}$ and SRP were often at or below detection limits, making seasonal cycles difficult to

discern (Fig. 1b). A seasonal cycle was evident in concentrations of $\text{NO}_3^- - \text{N}$, however, with values in winter months up to 80 $\mu\text{g L}^{-1}$ higher than those in summer (Fig. 1b).

Seasonal pattern in litter breakdown rate

Mass loss rates of *Salix* litter showed a strong seasonal pattern, peaking in winter and reaching minima during summer months (Fig. 2). The range in breakdown rates (k coefficients, day^{-1}) was large, with typical values spanning from *c.* 0.01 day^{-1} during the spring and summer months of April–July to >0.05 day^{-1} during November of both winters (Fig. 2). The highest breakdown rates during 2007 occurred from 4 September (0.024 day^{-1}) to 20 November 2007 (0.052 day^{-1}), after which breakdown rates rapidly declined. A similar pattern was observed in 2008, with an increase from 4 September (0.015 day^{-1}) to 23 January (0.05 day^{-1}), followed by a rapid decline. Breakdown rates were consistently low (*c.* 0.01 day^{-1}) from 2 March to 4 September 2008. When normalised for temperature using degree-days >0 °C, the seasonal pattern remained, with values of k_{dd} ranging from 0.001 dd^{-1} (28 May–4 July 2009) to 0.01 dd^{-1} (17 October–20 November 2008).

Seasonal patterns in macro-invertebrate colonisation of litter

Summer and winter dates showed a high degree of separation in assemblage structure (ANOSIM, $R = 0.33$, $P = 0.003$; Fig. 3). A non-metric multidimensional scaling ordination of the assemblage biomass data had a relatively low stress value of 0.1 (Fig. 3), indicating that the plot was an acceptable two-dimensional representation of the multivariate distances between dates in the similarity matrix (Clarke & Warwick, 2001). Further analysis of seasonal patterns indicated that the invertebrate assemblage in litter bags had a statistically significant cycle in structure over the 2 years of the study (RELATE, Spearman's $\rho = 0.54$, $P = 0.001$). Simple separation of the invertebrate data into summer and winter periods, followed by SIMPER analysis, identified dominant taxa responsible for driving seasonal differences in assemblage structure. A total of seven taxa contributed $\geq 5\%$ towards the overall dissimilarity between summer and winter periods (SIMPER,

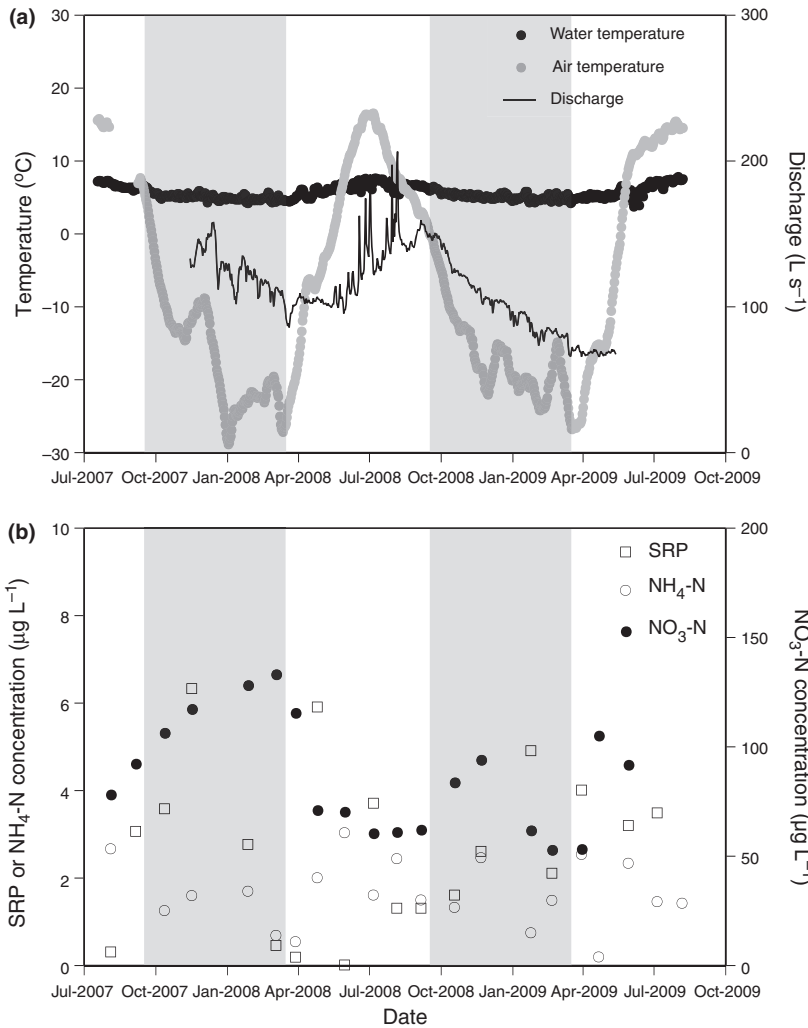


Fig. 1 (a) Mean daily air temperature, water temperature and discharge in Ivishak Spring, Alaska, from July 2007 to August 2009. Water temperature and discharge were recorded at the downstream end of the study reach, c. 240 m below the spring source and 30 m downstream from the litter incubation site. Air temperature data are smoothed (30-day running average). (b) Mean ambient concentrations of soluble reactive phosphorus (SRP), NH_4^+ - N and NO_3^- - N in Ivishak Spring, Alaska, from July 2007 to August 2009. Shaded areas indicate 'winter' months (September 15–March 14), as used in the multivariate analysis of community structure (see text).

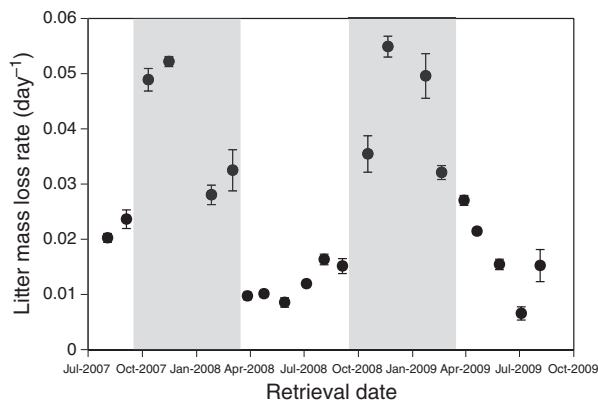


Fig. 2 Mean mass loss rates (± 1 SE) of *Salix alaxensis* litter in Ivishak Spring, Alaska, from July 2007 to August 2009. Shaded areas indicate 'winter' months (September 15–March 14), as used in the multivariate analysis of community structure (see text).

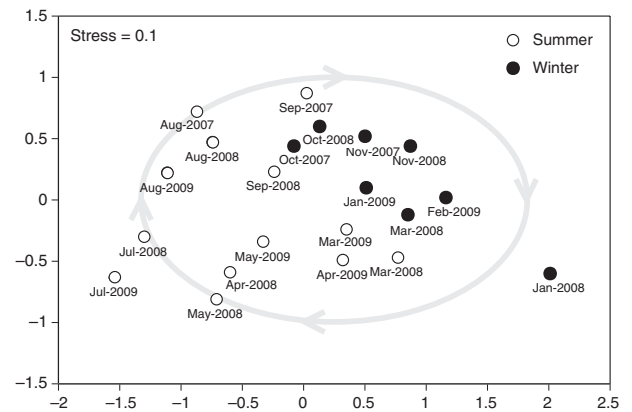


Fig. 3 Non-metric multidimensional scaling ordination plot of $\log_e(x + 1)$ -transformed invertebrate biomass data from litter bags retrieved from Ivishak Spring, Alaska, from July 2007 to August 2009. Biomass was averaged across all litter bags on each date ($n = 10$ on most dates). Grey arrow indicates the direction of the statistically significant seasonal cyclicity in the community data (RELATE test, $P = 0.001$).

Table 1 Mean biomass (mg AFDM liter bag⁻¹) of the invertebrate taxa that contributed $\geq 5\%$ to the overall dissimilarity between summer and winter litter bag communities. Di is the % contribution of each taxon to the overall dissimilarity between the two seasons; $Di/SD(Di)$ is the ratio of the mean Di for all sample pairs between seasons to the standard deviation of Di and is a measure of the importance of each taxon in discriminating communities between seasons

Taxon	FFG	Summer Biomass	Winter Biomass	Summer versus Winter	
				% Di	$Di/SD(Di)$
'Summer' taxa					
Orthocladiinae	Collector-gatherer	5.1	0.3	12.65	1.47
<i>Baetis</i> sp.	Collector-gatherer	16.1	6.0	12.13	1.29
<i>Isoperla petersoni</i>	Predator	44.6	23.3	11.17	0.98
Diamesinae	Collector-gatherer	1.0	0.2	5.37	0.95
'Winter' taxa					
<i>Ecclisomyia conspersa</i>	Shredder	2.7	5.6	13.14	1.35
<i>Zapada haysi</i>	Shredder	5.6	15.9	10.93	1.42
<i>Ephemerella</i> sp.	Grazer	0.5	1.3	7.16	1.03

FFG, functional feeding group.

Table 1). Four of these showed their highest biomass in summer; all were either collector-gatherers or predators (Table 1). The remaining three taxa showed their highest biomass in winter. Two of these 'winter' taxa are the dominant shredding invertebrates in Ivishak Spring (Parker & Huryn, 2006): the nemourid stonefly *Zapada haysi* (Ricker) and the limnephilid caddisfly *Ecclisomyia conspersa* Banks. Both taxa are omnivorous with leaf detritus composing a substantial component of their gut contents (Parker & Huryn, 2006). Other taxa recorded from litter bags included the following: Turbellaria, Oligochaeta, Hydrachnidia, *Cinygmula* sp. (Ephemeroptera), Tanytarsini (Chironomidae), *Pericoma* sp. (Psychodidae), *Prosimulium* sp. (Simuliidae), *Tipula* sp. (Tipulidae), *Chelifera* sp., *Oreogeton* sp. (Empididae), *Limnophora* sp. (Muscidae) and Ostracoda.

Mean total invertebrate biomass in litter bags varied tenfold over the 2 years of study, with peaks of >200 mg AFDM bag⁻¹ in summer and minima of $c. 20$ mg AFDM bag⁻¹ in winter (Fig. 4a). As indicated in the SIMPER analysis, biomass of the two dominant shredders (*Z. haysi* and *E. conspersa*) showed the opposite seasonal pattern, with peaks in winter (Fig. 4b).

Patterns of individual growth by dominant shredder taxa

Zapada haysi followed a semivoltine life cycle in Ivishak Spring, with early instar larvae first appearing in October and requiring $c. 20$ months for growth and development; emergence of adults occurred in May. As a consequence, three cohorts of *Z. haysi* larvae were present during the study. The first cohort (adults

emerged in May 2008) showed a major increase in larval biomass from 4 August 2007 (0.64 ± 0.03 mg DM ind.⁻¹, mean \pm SE, $n = 275$) to 2 March 2008 (1.20 ± 0.05 mg DM ind.⁻¹, $n = 94$; Fig. 5a). Larvae of the second cohort (adults emerged in May 2009) showed a comparable increase in biomass from 28 May 2008 (0.13 ± 0.005 mg DM ind.⁻¹, $n = 98$) to 16 February 2009 (1.42 ± 0.03 mg DM ind.⁻¹, $n = 122$; Fig. 5a). Larvae of the third cohort (adults emerged in 2010) attained a mass of 0.47 ± 0.03 mg DM ind.⁻¹ ($n = 89$) by 4 August 2009 (Fig. 5a).

Ecclisomyia conspersa in Ivishak Spring followed a univoltine life cycle, with first instar larvae appearing in late July and adults emerging from late May to June. Growth was relatively continuous except for a short, apparent quiescent period during winter (Fig. 5b). Two cohorts were sampled during the study. The first cohort (adults emerging in May 2008) showed rapid growth from 4 August 2007 (0.23 ± 0.02 mg DM ind.⁻¹, $n = 43$) to 25 April 2008 (2.81 ± 0.16 mg DM ind.⁻¹, $n = 76$). The second cohort (adults emerging in May 2009) showed rapid growth from 4 August 2008 (0.15 ± 0.04 mg DM ind.⁻¹, $n = 30$) to 29 March 2009 (1.77 ± 0.06 mg DM ind.⁻¹, $n = 173$).

Potential factors controlling seasonal pattern of litter breakdown

Temperature showed only a weak relationship with the seasonal pattern of litter breakdown rate ($r^2 = 0.14$, $P = 0.09$, d.f. = 20). Rather than showing a positive relationship with breakdown rate, the apparent relationship was negative. Not surprisingly, the normalisation of breakdown rate using degree-days

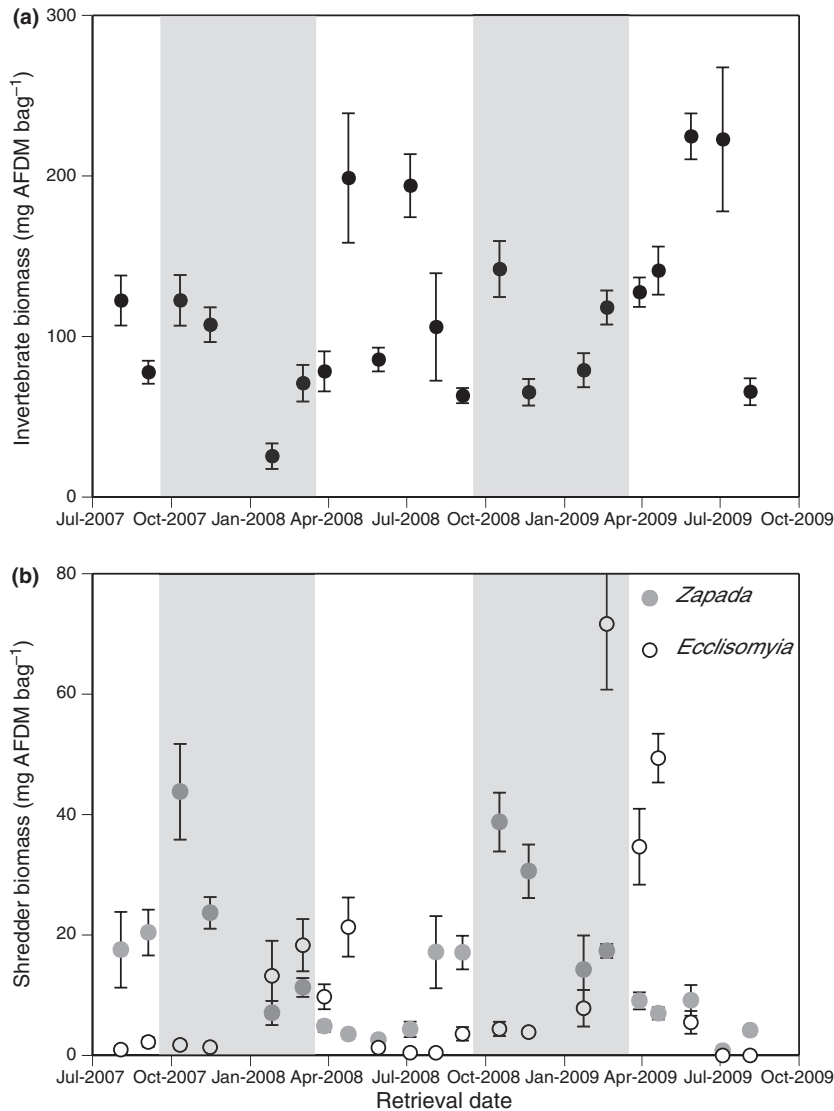


Fig. 4 (a) Mean total invertebrate biomass (± 1 SE) and (b) mean biomass (± 1 SE) of the two dominant shredder taxa (*Zapada haysi* and *Ecclisomyia conspersa*) in litter bags retrieved from Ivishak Spring, Alaska, from July 2007 to August 2009. Shaded areas indicate 'winter' months (September 15–March 14), as used in the multivariate analysis of community structure (see text).

($dd^{-1} > 0$ °C) had little effect on the seasonal pattern of breakdown (see Fig. 5).

Seasonal patterns of nutrient concentration similarly showed only weak relationships with litter breakdown rate (k_{dd}). Of the three macronutrients we assessed, only $NO_3^- - N$ showed an apparent relationship. The relationship was highly significant for the first year of the study, from 3 August 2007 to 17 October 2008 ($r^2 = 0.53$, $P = 0.005$, d.f. = 12, power model). When data from 20 November 2008 to 28 May 2009 were included, however, the relationship was no longer significant.

Patterns of potential energetic demand by larvae of *Z. haysi* were closely related to litter breakdown rates (k_{dd}). The first cohort of *Z. haysi* (emerged in May 2008) showed a significant relationship between its

period of maximum growth (c. 4 August–2 March 2008) and k_{dd} ($r^2 = 0.72$, $P = 0.03$, d.f. = 6, exponential model). The second cohort of *Z. haysi* (emerged in May 2009) showed an even stronger relationship between the seasonal pattern of maximum larval growth (c. 28 May 2008–16 February 2009) and litter breakdown ($r^2 = 0.95$, $P < 0.0001$, d.f. = 7, exponential relationship). Seasonal patterns of growth of *E. conspersa* showed no significant relationship with litter breakdown rates.

Discussion

Our serial incubations of leaf litter in a spring-fed arctic stream revealed a pronounced seasonal cycle in the rate of litter processing under conditions of

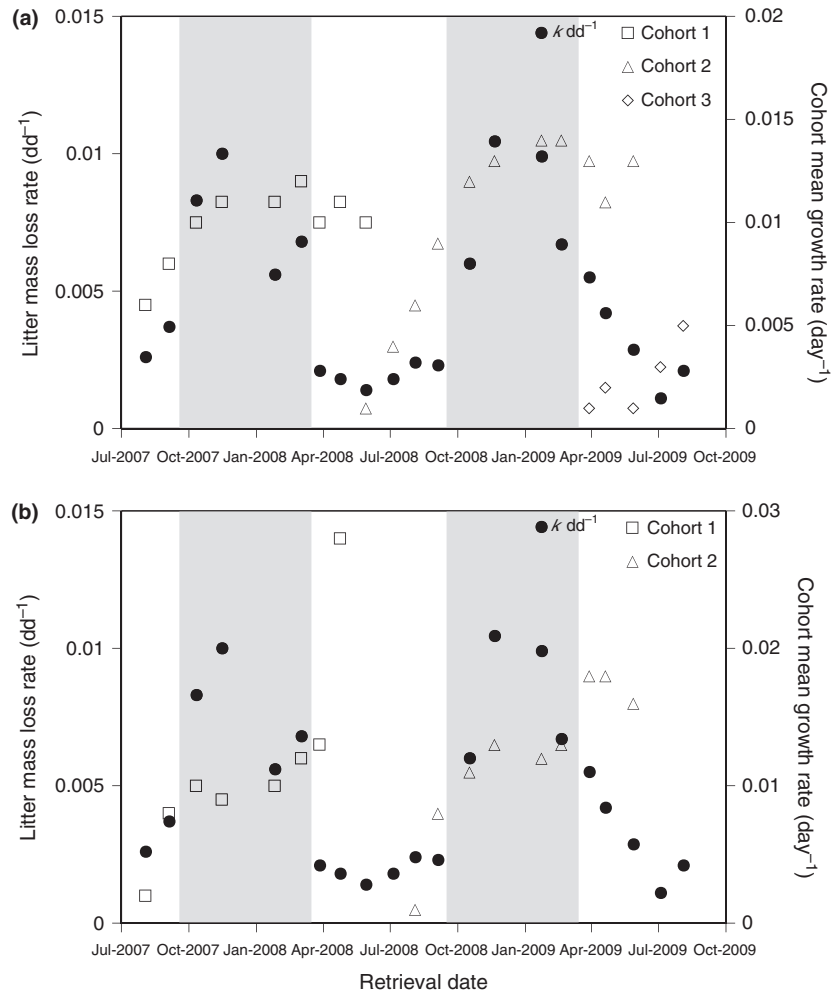


Fig. 5 Temperature-corrected litter mass loss rates (k per degree-day or dd^{-1}) of *Salix alaxensis* litter relative to mean instantaneous growth rates of successive cohorts of the two dominant shredders (a) *Zapada haysi* and (b) *Ecclisomyia conspersa* in Ivishak Spring, Alaska, from July 2007 to August 2009. Shaded areas indicate 'winter' months (September 15–March 14), as used in the multivariate analysis of community structure (see text).

marked stability in water temperatures (i.e. <4 °C annual variation). Maximal rates of litter breakdown occurred during winter temperature minima and were surprisingly high for an arctic stream ($>0.05 \text{ day}^{-1}$), although not without precedent. Similar rates have been reported in a central Alaska stream, albeit only for alder (*Alnus* sp.), a high-nitrogen litter species that is typically processed rapidly (Cowan *et al.*, 1983). Surprisingly, the breakdown rates we measured for *S. alaxensis* were most similar to those reported for the same species incubated in a Costa Rican stream (0.062 day^{-1} , mean water temperature 26 °C) in a latitudinal study of litter decomposition that included boreal, temperate and tropical streams (Irons *et al.*, 1994). The winter breakdown rate measured for *S. alaxensis* litter in an interior Alaska stream in the same study was only 0.016 day^{-1} . The cycle in litter breakdown we observed was matched by a similar annual cycle in the

structure of the invertebrate assemblage that colonised litter bags, as well as in the concentration of $\text{NO}_3^- - \text{N}$, the dominant pool of dissolved inorganic nitrogen in the stream. Our results indicate that temperature was less important for controlling litter breakdown rate than the relative activity of the biotic community responsible for organic matter breakdown.

Our study involved successively estimating breakdown rates over relatively short intervals for more than two annual cycles. As a thermally stable stream embedded in an intensely seasonal environment, conducting such a study in Ivishak Spring offered a unique alternative to the degree-day approach for examining the effect of temperature on organic matter processing. Under conditions of dominant control by temperature, temperature-corrected (i.e. per-degree day) breakdown rates of litter are expected to be similar regardless of thermal regime (Webster &

Benfield, 1986; Irons *et al.*, 1994). Similarly, we hypothesised that litter breakdown rates in thermally stable Ivishak Spring would show constancy through the year, if temperature was of overwhelming importance in controlling the rate of litter breakdown. This null hypothesis was roundly rejected by our results.

Although our serial incubations allowed the fine-scale tracking of temporal patterns in litter breakdown rate, the study design also had some drawbacks. First, no studies have employed a similar design, so we were unable to compare our results with analogous serial data collected from other geographic regions or from streams with different thermal regimes. Second, our single collection date for each interval meant that we had to assume exponential breakdown for our calculations of standard breakdown coefficients (k values; Petersen & Cummins, 1974). However, assumption of other breakdown models (e.g. linear mass loss) would not have changed the pattern of extreme seasonality in litter breakdown that we found at Ivishak Spring. Calculating k values also facilitated comparison with other studies in the literature. The last drawback of our single collection date for each data interval was that the condition of litter remaining at the end of each *c.* 30-day period varied greatly with season, from largely intact in summer to completely skeletonised by shredder feeding in the winter. Such large seasonal contrasts complicated any attempt to tease apart the relative role of microbes versus shredders in litter breakdown over time (e.g. by partitioning the breakdown attributed to the two groups; see Hieber & Gessner, 2002). For example, our plans to use ergosterol as a proxy for microbial biomass were abandoned because of high mass loss during winter months. Similarly, estimation of shredder consumption rates was complicated by low litter mass (and correspondingly low invertebrate biomass) at retrieval, caused by winter peaks in shredder consumption.

Although assessing the relative role of microbes and invertebrate shredders was confounded by our study design, some inferences can be made about the potential importance of these two groups in controlling the seasonality in litter breakdown at Ivishak Spring. We observed marked shifts in concentrations of $\text{NO}_3^- - \text{N}$, with concentrations during winter months often $80 \mu\text{g L}^{-1}$ higher than those in the summer. These seasonal swings in $\text{NO}_3^- - \text{N}$ concentration were very likely linked to the seasonal cycle in

primary production in the spring, itself driven by the pronounced seasonal cycle in daylength at the site (A.D. Huryn & J.P. Benstead, unpubl. data). Winter increases in $\text{NO}_3^- - \text{N}$ availability for heterotrophic microbes could potentially have increased their activity on incubated litter, especially given the N-limited status of Ivishak Spring (A.D. Huryn & J.P. Benstead, unpubl. data). For example, addition of dissolved nitrogen and phosphorus increased breakdown rate of *Salix* litter in a tundra stream close to Ivishak Spring on the North Slope of Alaska (Benstead *et al.*, 2005), and many other studies have demonstrated the stimulatory effect of nutrients on litter breakdown (e.g. Gulis & Suberkropp, 2003; Suberkropp *et al.*, 2010).

Any nutrient-induced increase in microbial activity during winter months likely would have interacted with the seasonal changes we observed in invertebrate assemblage structure. The entire invertebrate assemblage in litter bags displayed a statistically significant pattern of seasonal cyclicity. Of particular relevance to organic matter processing, we observed a much higher biomass of shredders within litter bags in winter. These increases were driven by the life history phenology of two key shredder taxa: *Z. haysi* and *E. conspersa*. We could not calculate meaningful consumption rates by shredders because high rates of litter processing in the winter left little substrate for colonisation by the retrieval date. However, maximum rates of mass loss coincided with peak periods of growth for cohorts of these two shredder taxa. This was particularly true of *Z. haysi*, and it is probable that this species played the most significant role in litter mass loss over the winter period in Ivishak Spring. While *E. conspersa* was found in litter bags and probably contributed to litter breakdown, relationships between its cohort growth rates and litter mass loss were much weaker than those for *Z. haysi*. The diet of *E. conspersa* is also broader than that of *Z. haysi*, encompassing algae and invertebrate prey in addition to litter (Parker & Huryn, 2006).

The phenology of shredder taxa has been implicated in the control of litter breakdown rates in other studies, particularly those from high-latitude streams (Haapala, Muotka & Markkola, 2001). For example, fast breakdown of three litter species was attributed to shredder feeding in a central Alaska stream that reached temperatures as low as 0°C during the winter months (Cowan *et al.*, 1983). Studies from cold

streams at high altitudes have also highlighted the dominant role of shredder phenology in controlling litter breakdown. Litter consumption by winter stoneflies, including *Zapada* spp., drove high breakdown rates in a Rocky Mountain stream in Colorado, U.S.A. (Short & Ward, 1981). Similarly, Mutch & Davies (1984) found that rapid breakdown rates ($>0.02 \text{ day}^{-1}$) in another Rocky Mountain stream were driven largely by consumption by *Zapada columbiana* (Clas-sen) nymphs. Our results from Ivishak Spring consequently reinforce the important role of the phenology of key shredder taxa in driving seasonal litter break-down dynamics.

In conclusion, we found significant seasonal variation in breakdown rate of litter in a spring-fed stream in arctic Alaska that has a very stable thermal regime. Winter breakdown rates of litter were surprisingly high for such a high-latitude system. However, our data complement mounting evidence for a strong positive relationship between latitude and shredder activity (Irons *et al.*, 1994; Boyero *et al.*, 2011). In the absence of analogous data sets describing serial incubations from other streams, our results beg some interesting questions. Are large seasonal shifts in litter breakdown rate the norm for mid- to high-latitude stream ecosystems, with highest rates in the winter driven by shredder phenology and a consequently small role played by temperature? More studies with a serial incubation design will provide answers. Similarly, how much temporal variation in breakdown rate would be expected in the stable temperature regimes that are relatively common for streams at tropical latitudes? Many tropical streams are embedded in terrestrial ecosystems that experience little seasonality. In marked contrast to Ivishak Spring, we would predict that the stable temperature of tropical streams be accompanied by little evidence for temporal patterns in litter breakdown driven by phenology or other seasonal factors related to the stream catchment (see Wolda & Flowers, 1985; Jackson & Sweeney, 1995). Indeed, it is likely that terrestrial seasonality becomes an increasingly important driver of stream ecosystem processes as latitude increases. Our finding of pronounced seasonal variation in litter breakdown rate, even in the face of relative stability in water temperature, attests to the primacy of catchment-level processes in driving the structure and function of stream ecosystems, including the evolution of

shredder phenology and the processing of terrestrial organic matter (Ross, 1963; Hynes, 1975; Valett *et al.*, 2008). In contrast, water temperature appears to play a minor role relative to the key seasonal cycles of organic matter input and consumer life history.

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