

Interaction of water temperature and shredders on leaf litter breakdown: a comparison of streams in Canada and Norway

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Abstract Litter decomposition in running water sometimes proceeds faster in small, cool tributaries than in warm, wide rivers because stenothermal, leaf-shredding invertebrates are more abundant in the cool streams. Evidence from eastern Canada suggests that the cold-stenothermal stonefly *Leuctra* has a disproportionate influence on rapid mass loss in upstream reaches of soft-water river systems, but is not replaced by an effective, warm-water shredder downstream. To test the generality of this observation, we compared litter decomposition rates in upstream (second or third order) and downstream (fourth or fifth order) reaches of a medium-size river system in Nova Scotia (Canada) and three river systems in Nordland (Norway). In all river systems, mass loss of nitrogen-rich speckled alder (*Alnus incana*) leaves and nitrogen-poor red maple (*Acer rubrum*) leaves proceeded faster at the upstream site only if water temperature there was significantly cooler than downstream. Decomposition rates in all systems were strongly correlated with abundance of *Leuctra*, and to a lesser extent the caddisfly *Lepidostoma*. The distribution of *Leuctra* seems to be driven primarily by water temperature,

with a strong peak of abundance at 14°C, but may also be influenced by competition from other shredding species.

Keywords Litter decomposition · Streams · Temperature · Shredders · *Leuctra* · Decay rates

Introduction

Riparian vegetation constitutes an important source of external energy for freshwater river systems (Minshall et al., 1985; Webster & Benfield, 1986; Tank et al., 2010). The dynamics of terrestrial litter decomposition in rivers are well documented, and emphasize the terrestrial contribution to the total energy budget of flowing waters (Petersen & Cummins, 1974; Bärlocher, 1985; Webster & Benfield, 1986; Boulton & Boon, 1991; Graça et al., 2001). The proportion of the river energy budget which constitutes terrestrial litter depends on the size of the river, usually decreasing with increasing order (Vannote et al., 1980). In wide, sun-warmed rivers, endogenous primary production may be sufficient to supply the majority of the energy requirement, reducing the dependence on terrestrial litter. In small, shaded streams, however, poor sunlight penetration and cold temperatures limit primary production (Hill et al., 1995, 2001) and terrestrial litter becomes an essential source of energy (Minshall et al., 1985; Tank et al., 2010).

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During litter decomposition, mass can be lost in three ways: leaching of soluble material by flowing water, microbial metabolism, and feeding and maceration by leaf-shredding invertebrates (Webster & Benfield, 1986; Graça et al., 2001; Hieber & Gessner, 2002). The three stages do not occur in strict succession, although leaching usually begins as soon as the litter is immersed (Gessner et al., 1999). Bacteria and fungi secrete exoenzymes into the leaf tissue, breaking down structural components and increasing the palatability of the litter. The addition of microbial biomass to the tissue increases the nutritive value of the litter, making it more attractive to invertebrates (Bärlocher, 1985; Graça et al., 1993; Stockley et al., 1998; Graça & Cressa, 2010). Invertebrates (shredders) contribute to mass loss by either directly consuming the tissue or by fragmenting the leaves (Chauvet et al. 1993; Dangles et al., 2001).

Decomposition rate of a particular litter type should vary with water temperature, all else being equal, because metabolic rates of aquatic hyphomycete fungi and bacteria increase with increasing temperature (Rajashekar & Kaveriappa, 2000; Fernandes et al., 2009; Dang et al., 2009; Ferreira & Chauvet, 2011a, b; Boyero et al., 2011). Consequently, litter tends to decompose more quickly in warmer seasons than cold seasons at any given site (Chergui & Pattee, 1993; Stockley et al., 1998; Graça et al., 2001; Bergfur, 2007), and at sites with warmer water within a river system compared with sites with cooler water (Benfield et al., 1979; Webster & Benfield, 1986; Stockley et al., 1998; Imberger et al., 2008).

Nevertheless, several studies have reported more rapid rates of litter decomposition in cold, headwater streams than in large, warm rivers (Minshall et al., 1983; Collier & Winterbourn, 1986; Chauvet et al., 1993; Baldy et al., 1995; MacDonald & Taylor, 2008), despite the presumably more rapid microbial metabolism in the rivers. This reversed pattern of temperature response has been attributed to the effect of shredding invertebrates, which tend to be more numerous in cool tributaries, where leaf litter is abundant, than in larger rivers (Baldy et al., 1995; Minshall et al., 1983; Collier & Winterbourn, 1986). Many common insect shredders are members of the orders Plecoptera and Trichoptera, which are largely restricted to cool-water habitats (Wiggins & Mackay, 1978).

Leaf shredding is generally attributed to a guild or functional group of invertebrates (Vannote et al., 1980), rather than a single genus or species. However, in small river systems of Nova Scotia, Canada, MacDonald & Taylor (2008) attributed rapid decomposition in headwater streams compared with main-stem rivers to the stenothermal, leaf-shredding stonefly *Leuctra*, which is numerically dominant in cool streams but absent in warm rivers. Further work (B. Taylor, unpublished report, 2013) showed that *Leuctra* is the only shredding invertebrate in these systems whose distribution is determined primarily by temperature, rather than litter type or stream order. Hence, the rate of a fundamental ecosystem process in these river systems appears to be strongly influenced by a single insect genus, whose distribution creates an inverse relationship between water temperature and decomposition rate. Previous observations of single taxa dominating the decomposition process have mostly involved amphipods (Dangles & Guérol, 2001; Tiegs et al. 2009), which do not occur in soft-water rivers of eastern Canada, or highly disturbed ecosystems (Whiles et al., 1993) in which the insect fauna was pauperate (but see Benstead & Huryn, 2011).

These observations on the importance of stenothermal shredders generally, and *Leuctra* in particular, on decomposition in cool water may apply to other circumboreal rivers, but have not been tested outside Nova Scotia. Therefore, the present study tests the generality of MacDonald & Taylor's (2008) results by comparing litter decomposition in rivers of Nova Scotia and Norway. First, we followed decomposition of red maple and speckled alder leaf litter at two sites on a Nova Scotia river system to confirm findings by MacDonald & Taylor (2008). Next, we followed decomposition in three Norwegian river systems to determine if relatively faster litter decomposition in cold water could be detected there. In all four rivers we predicted that: (1) decomposition would proceed faster at the cool, upstream site compared with the warm, downstream section of the main stem; (2) the faster upstream decomposition would be accompanied by larger populations of *Leuctra* colonizing the litter and (3) the distribution of *Leuctra* would be determined by water temperature and not by location along the river continuum or litter type.

Materials and methods

Decomposition rates were compared in four small river systems: one in northern Nova Scotia, Canada (South River) and three in Nordland, Norway (Sandjordelva, Futelva and Børelva). All four systems drain forest and farmland with drainage basins ranging from 70 to 110 km². An upstream site and a downstream site were selected on each system. The upstream site was a narrow second or third order tributary, with partial or complete canopy cover from riparian forest; the South River upstream site was >10 m wide, but the three Norwegian streams were 4–6 m wide (Table 1). The downstream site was a fourth- or fifth-order section of the main stem, often near the mouth, with a channel width >10 m, sufficient to prevent effective riparian shading of the water. Sites were chosen based on physical characteristics which were expected to create a temperature difference between upstream and downstream, but glacial runoff into two Norwegian rivers mitigated downstream temperature increases to <0.5°C (Table 1). The third Norwegian river displayed a temperature gradient similar to that in South River. The experiment thus included two systems with a temperature gradient (South, Børelva), and two without (Sandjordelva, Futelva).

South River drains into St. George's Bay on the northeast coast of mainland Nova Scotia, Canada (Fig. 1). Land use in the basin is mostly short rotation, mixed Acadian forest, intermittent with pastures and clear cuts. Water is soft at the upstream site and hard at the downstream site (Table 1) due to an intrusion of calcareous rock, but pH is circumneutral throughout. The current upstream is fast, running over a mixture of sand, gravel, rock and bedrock. The current downstream is slower, over a bottom of silt, sand and cobble. MacDonald & Taylor (2008) describe the system in more detail.

Of the three Norwegian systems, the Sandjordelva and Futelva are adjacent, while the Børelva system drains into neighbouring Elvefjorden (Fig. 2). Although the Sandjordelva and the Futelva systems run parallel, the Sandjordelva drains into Soløyvatnet Lake, while the Futelva diverts directly into Saltfjorden. The Norwegian watersheds encompass mature mixed forest, with birch (*Betula pubescens* L.) often dominating the riparian zone. The downstream section of the Futelva system runs through a rural

neighbourhood, where much of the riparian vegetation has been removed. The water in these rivers is alkaline. Average current velocities range from 0.3 to 0.6 m/s. Bottom material is rock, gravel and cobble at upstream sites but ranges from sand and gravel to rock and bedrock downstream.

Litter decomposition was estimated using the litter bag method. Red maple (*Acer rubrum* L.) and speckled alder (*Alnus incana* (L.) Moench) leaves were collected from riparian forests in Nova Scotia at leaf fall the previous year and air dried. These species were chosen to be consistent with previous studies; very similar species in these genera grow in Norway. Two gram portions of each species were weighed to the nearest 0.01 g and humidified for 24 h to reduce brittleness. The leaves were placed in 15 × 15 cm bags with a mesh size of either 2.5 mm (coarse) or 250 µm (fine). The coarse mesh bags were sewn closed loosely, allowing larger invertebrates access to the leaves from one end. The fine mesh bags were sewn shut tightly using a sewing machine. The narrow stitch and fine mesh prevented benthic invertebrates from reaching the leaves, except for a few, early-instar chironomids.

Maple and alder leaves in coarse mesh bags were placed upstream and downstream in all four river systems. Maple and alder leaves in fine mesh bags were also placed upstream and downstream in South River. In Norway, only alder was also placed in fine mesh bags, and only in Børelva and Futelva river systems. Eighteen leaf packs of each type (alder or maple leaves in fine or coarse mesh bags) were placed in early June 2006 (Nova Scotia) or 2008 (Norway) at the upstream and downstream sites on each river, allowing for six collections of three replicates each. Each litter bag was pinned to the sediment using a 15-cm metal peg and anchored with a rock on one corner. The different types of leaf packs were placed randomly in rows of 10–15 across the channel.

Every week for 6 weeks, three litter bags of each type were removed from the water, sealed in plastic bags with some stream water and transported to the laboratory on ice. Litter bags were stored at 4°C and processed within 48 h. Leaves were removed from the bags, washed on a 500-µm sieve to remove silt and invertebrates, dried at 70°C for 48 h and weighed to determine dry mass remaining. Ten additional leaf samples were weighed and oven dried to calculate an air-dry to oven-dry conversion factor for each species (maple = 0.936, alder = 0.929).

Table 1 Physical and chemical characteristics of one Nova Scotian and three Norwegian river systems used in this study

System	Site	Latitude/ longitude	Wetted width (m)	Bankfull width (m)	Depth (cm)	Velocity (m/s)	pH (units)	Temperature (°C)
South	Upstream	N45°26'54"	6.9	12.8	23.4	0.6	7.3	17.0
		W61°55'04"	(0.5)	(2.3)	(5.3)	(0.2)	(0.6)	(1.6)
	Downstream	N45°33'38"	22.6	44.6	21.2	0.4	6.7	19.6
		W61°54'13"	(4.3)	(1.1)	(1.9)	(0.1)	(0.3)	(2.1)
Sandjordelva	Upstream	N67°20'11"	3.0	4.1	13.5	0.6	7.9	12.2
		E14°38'13"	(0.2)	(0.1)	(4.7)	(0.2)	(0.1)	(2.1)
	Downstream	N67°19'15"	5.7	9.8	22.1	0.3	8.0	12.5
		E14°37'44"	(0.6)	(1.0)	(6.5)	(0.1)	(0.2)	(2.1)
Futelva	Upstream	N67°19'22"	3.3	5.6	9.7	0.3	7.8	13.8
		E14°39'18"	(1.0)	(1.1)	(1.8)	(0.1)	(0.1)	(2.0)
	Downstream	N67°18'10"	6.8	8.3	15.3	0.3	7.7	14.0
		E14°37'36"	(0.7)	(1.1)	(8.3)	(0.1)	(0.1)	(1.8)
Børelva	Upstream	N67°10'51"	2.7	6.7	9.7	0.5	7.1	10.1
		E14°45'07"	(0.4)	(0.6)	(1.6)	(0.1)	(0.3)	(1.4)
	Downstream	N67°10'49"	13.3	15.2	17.5	0.5	7.8	13.3
		E14°44'46"	(0.9)	(1.1)	(10.1)	(0.2)	(0.3)	(2.1)

Data are means and standard deviations (in parentheses); $n = 3$ for wetted width and bankfull width, $n = 15$ – 24 for depth. Values for pH are means of weekly observations ($n = 6$). Velocity was recorded with three replicates weekly ($n = 18$). Temperature values are means of half-hourly thermistor records over 6 weeks ($n = 2,016$)

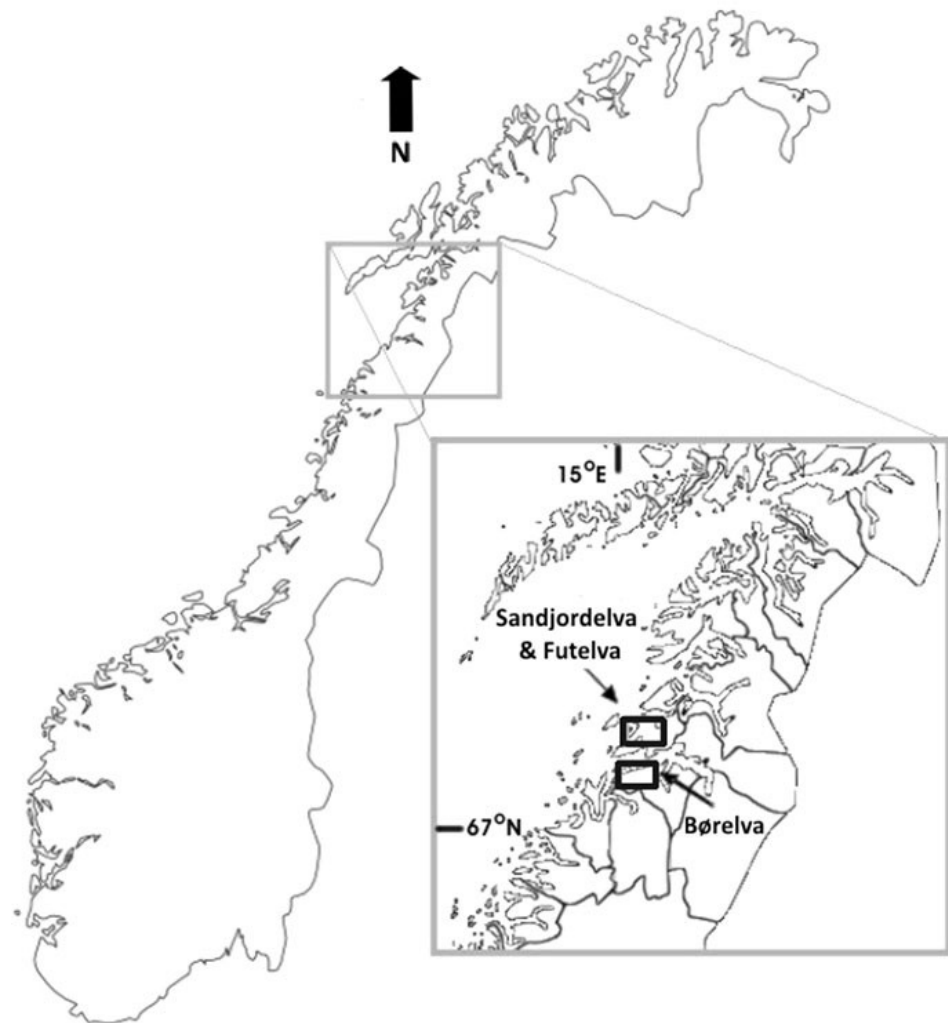
Fig. 1 Study region in northern Nova Scotia, Canada

All invertebrates retained on the 500- μ m sieve during washing of the leaves were preserved in 70% ethanol and later identified to the lowest practical level, usually genus, using published keys (Peckarsky et al., 1990; Stewart & Stark, 1993; Knopp & Cormier, 1997; Wiggins, 2000; Tachet et al., 2006).

Invertebrates were classified into functional feeding groups according to Merritt et al. (2008) and information in the literature. Facultative shredder genera (e.g. *Paraleptophlebia*) were considered shredders.

Water temperature was recorded at 30-min intervals over the 6 weeks of the decomposition experiment

Fig. 2 Study region in Nordland, northern Norway



using Optic “Stowaway” thermistors (Onset Corporation, Bourne, MA, USA), placed near the bank in shaded pools at each site. Temperature readings, accurate to $\pm 0.2^\circ\text{C}$, were later converted to daily means. Temperatures were compared between upstream and downstream using a two-way ANOVA, with site (upstream or downstream) nested within river system.

Leaf mass data were fitted to negative exponential curves of the form $M_t = M_o \times e^{-kt}$, where M = percent mass remaining and t = time. Linear regressions on ln-transformed mass remaining data yielded estimates of decomposition rates (k , day^{-1}). Values of k were compared between sites (upstream and downstream) and litter types using ANCOVA. Mass remaining at the end of the 42-day experiment was also compared (ANOVA) to corroborate decomposition rate comparisons. Regressions were also calculated on (ln-transformed) percent mass remaining against

cumulative heat units (degree-days), to remove the effect of temperature on breakdown rates. Cumulative heat units for each collection date were calculated by summing daily mean temperatures from the thermistors. Regressions of mass remaining against cumulative heat units determine if the difference in decomposition rate is temperature-dependent (Benstead & Huryn, 2011). Shredder populations were compared between sites using two-way ANOVA with a repeated measures design. Spearman’s rank correlation was used to find associations among (strongly non-normal) distributions of shredders in the litter bags and decomposition rates.

Results

In 2006, the shaded upstream site in South River remained consistently 3°C cooler than the downstream

site ($P < 0.01$, $n = 43$). This difference was smaller than the 7°C reported by MacDonald & Taylor (2008) in the same system the previous year, as a result of a cool summer. Mass remaining in coarse mesh bags at the end of the 6-week experiment in South River was significantly lower upstream than downstream for both litter types ($P < 0.01$, $n = 18$). The difference was more pronounced for alder litter, which showed 45% mass remaining upstream and 65% mass remaining downstream after 42 days. Litter mass loss in coarse mesh bags followed an exponential model of decay ($P < 0.01$ for all regressions). Decomposition rates (k) in coarse mesh bags were significantly higher at the upstream than at the downstream site ($P < 0.05$) (Fig. 3). Maple leaves decomposed more quickly than alder leaves ($P < 0.01$), so mass remaining was consistently higher for alder than for maple both upstream and downstream ($P < 0.01$, $n = 18$).

At the upstream site, remaining mass of litter for both litter types was higher in fine mesh bags than in coarse mesh bags (Tukey's test, $P < 0.05$, $n = 12$). Downstream, mass remaining was equal between coarse mesh and fine mesh bags ($P > 0.10$). Data from fine mesh bags fit an exponential model of

decomposition, though less effectively for alder leaves at the downstream site ($r^2 = 0.50$). Upstream, decomposition rates in coarse mesh bags were double those in fine mesh bags, a highly significant difference ($P < 0.01$) (Fig. 3). The rate of decomposition for both litter types was equal between fine and coarse mesh bags at the downstream site ($P > 0.10$), suggesting that shredder influence was minimal there. Interestingly, decomposition rates in fine mesh bags did not differ between upstream and downstream sites ($P > 0.10$), despite the warmer downstream temperatures. Substituting cumulative heat units for time in regressions of mass loss produced identical patterns among sites and litter types (not shown).

All three Norwegian river systems were cooler than the Canadian sites, ranging from 10 to 14°C (Table 1). Only the Børelva system maintained a significant temperature difference between sites, with downstream remaining 3°C warmer than upstream ($P < 0.01$, $n = 45$). Despite minimal riparian shading at downstream sites of Sandjordelva and Futelva, glacial runoff prevented effective warming of the water, resulting in both upstream and downstream sites remaining cold (Table 1). Across all three rivers, mass loss from maple leaf litter, but not alder, in coarse mesh bags was marginally faster upstream than downstream ($P = 0.055$, $n = 54$), although the difference is substantial when expressed in terms of heat units ($P = 0.0015$). There was also a highly significant difference in mass loss rate in coarse mesh bags among river systems ($P < 0.001$); mass loss for both litter types was relatively faster in Futelva and substantially slower in Sandjordelva (Fig. 4). Analysis of final mass remaining reveals the same differences among river systems ($P < 0.001$, $n = 32$) and lower mass remaining upstream than downstream for maple ($P = 0.016$, $n = 18$), but not for alder.

As in Nova Scotia rivers, final mass remaining in coarse mesh bags in the Børelva system was lower upstream than downstream for both litter types ($P < 0.01$, $n = 36$), despite the warmer downstream temperature. Mass loss data fit an exponential model of decay, although data were variable (Fig. 4). Calculated k values confirmed that decomposition in coarse mesh bags proceeded faster at the cold, upstream site ($P < 0.01$). Maple leaves decomposed twice as fast as alder both upstream and downstream ($P < 0.01$). When cumulative heat units were substituted for time in mass loss regressions, k values remained higher at

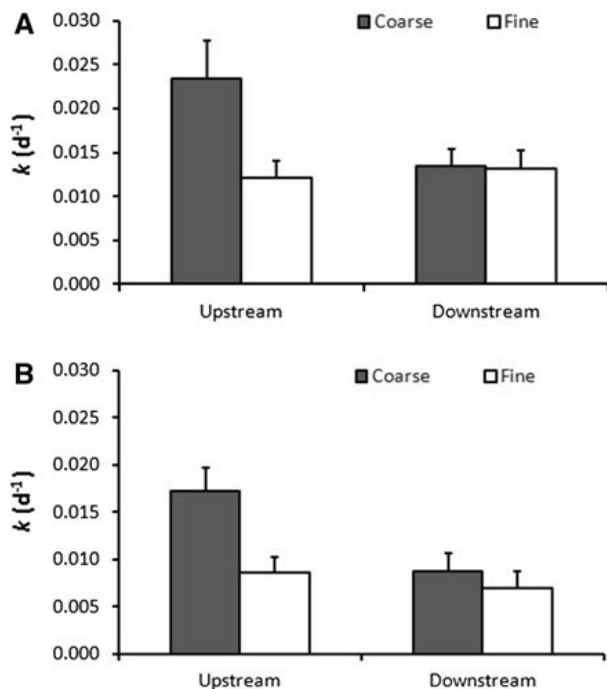


Fig. 3 Exponential decomposition rates (k) of **A** maple and **B** alder leaf litter in coarse mesh litter bags (including shredders) and in fine mesh litter bags (excluding shredders) in South River, Nova Scotia. Error bars are standard errors

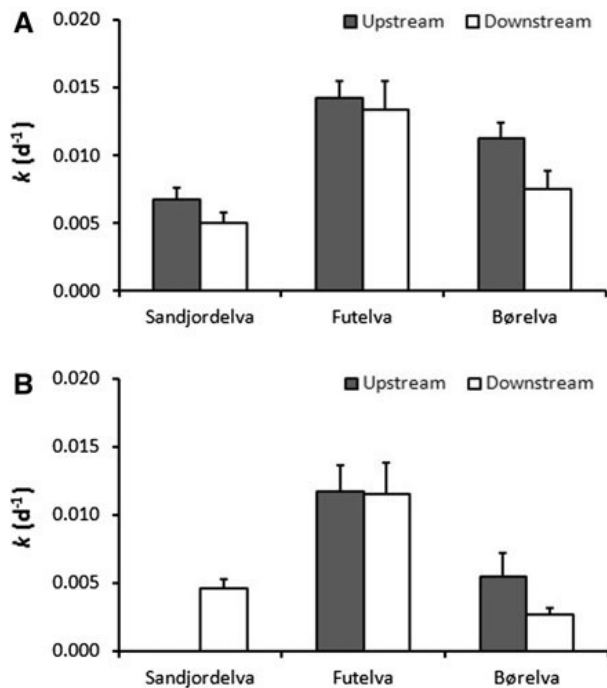


Fig. 4 Exponential decomposition rates (k) of **A** maple and **B** alder leaf litter in coarse mesh bags in three river systems in northern Norway. *Error bars* are standard errors. Mass loss from alder litter in upstream Sandjordelva was too slow to fit to an exponential model

the upstream site ($P < 0.05$) by a factor of 2.0 for maple and 2.7 for alder (Fig. 5). In contrast, mass loss from alder litter in fine mesh bags was so slow that measurable decomposition was not observed in downstream Børelva. The rate in fine mesh bags upstream ($k = 0.0016 \text{ day}^{-1}$, $r^2 = 0.27$, $P < 0.05$, $n = 18$) was barely 30% of the rate in coarse mesh bags (0.0054 day^{-1}).

Mass loss data from coarse mesh bags in both Futelva and Sandjordelva systems, where no temperature difference was observed, fit the exponential model of decomposition well, except for alder leaves in upstream Sandjordelva, which showed no evident mass loss (Fig. 4). Decomposition rates of maple or alder litter in coarse mesh bags in both the Sandjordelva and Futelva systems did not differ between upstream and downstream ($P > 0.10$), a trend maintained when cumulative heat units were substituted for time (Figs. 4, 5). Final mass remaining did not differ for maple litter (Tukey's Test, $P > 0.05$) in these two rivers, but was significantly greater upstream for alder litter ($P < 0.05$), reflecting the negligible loss in upstream Sandjordelva.

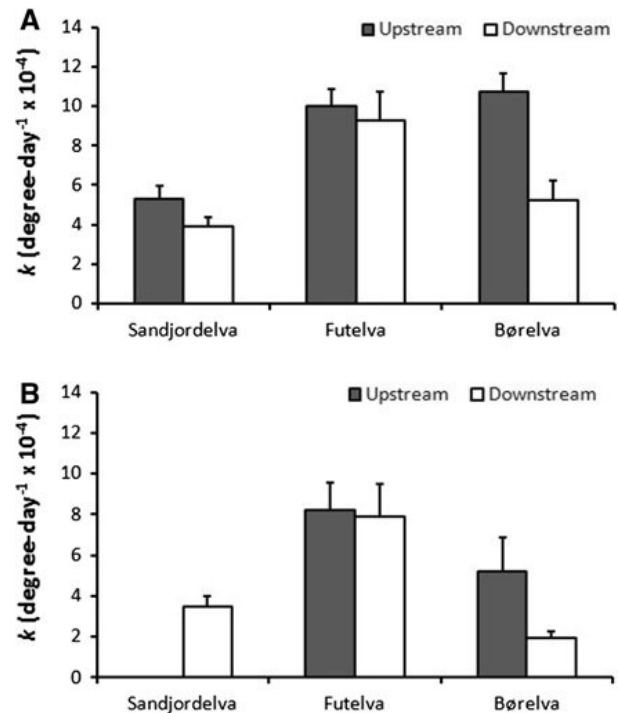


Fig. 5 Exponential decomposition rates (k) based on cumulative heat units (degree-days) of **A** maple and **B** alder leaf litter in coarse mesh bags in three river systems in northern Norway. *Error bars* are standard errors. Mass loss from alder litter in upstream Sandjordelva was too slow to fit to an exponential model

When alder litter in Futelva was confined in fine mesh bags to exclude shredders, the downstream data showed no significant mass loss over time; mass loss upstream was barely detectable ($k = 0.00068 \text{ day}^{-1}$, $r^2 = 0.18$, $P = 0.083$, $n = 18$) and only 6% of the rate in coarse mesh bags (0.012 day^{-1}). In both Futelva and Børelva systems, alder litter in fine mesh bags retained $> 90\%$ of original mass after 42 days in the water.

There were significantly more shredders on coarse mesh litter bags of either litter type upstream in South River than downstream ($P < 0.01$, $n = 36$) (Tables 2, 3). The caddisfly *Lepidostoma* was the dominant shredder downstream ($1.0\text{--}1.6 \text{ bag}^{-1}$); the mayfly *Paraleptophlebia* was also present, but only on alder litter (1.1 bag^{-1}). In contrast, shredder abundance was high upstream on both litter types, and heavily dominated by the stonefly *Leuctra* ($15\text{--}19 \text{ bag}^{-1}$). *Paraleptophlebia* and, to a lesser extent, *Lepidostoma* were also present (Tables 2, 3). *Paraleptophlebia* did not occur in Norway.

Shredder populations were negligible on both litter types in the Børelva system and did not differ between upstream and downstream ($P > 0.10$, $n = 36$) (Tables 2, 3). Total invertebrate communities were heavily dominated by Chironomidae (37–85%), some of which may have been shredders. *Leuctra* was the most abundant shredder upstream (0.5 bag^{-1}), amounting to 18 individuals on both litter types over 6 weeks. Shredding invertebrates at the downstream site were even scarcer, with the dominant stonefly *Taeniopteryx* amounting to seven individuals in maple and five in alder litter bags over 6 weeks. *Lepidostoma* was not found in the Børelva system.

Shredder abundance was also low in both the Futelva and the Sandjordelva systems, compared with South River, Nova Scotia (Tables 2, 3). *Taeniopteryx* was the dominant shredder on maple and alder litter at both upstream and downstream sites on the Sandjordelva system ($0.7\text{--}1.8 \text{ bag}^{-1}$). *Leuctra* was also present both upstream and downstream, but in more modest numbers (up to 1.1 bag^{-1}) and showed no preference for either litter type ($P > 0.10$, $n = 36$). *Lepidostoma* was not found in the Sandjordelva system. Shredder densities on both litter types in the Futelva system were higher upstream than downstream ($P < 0.05$), attributable to relatively large *Taeniopteryx* and *Lepidostoma* populations upstream.

Leuctra was present in about equal abundance upstream and downstream (ANOVA, $P = 0.095$, $n = 72$) and did not show a preference for either litter type (Tables 2, 3).

Across the 16 decomposition estimates for both litter types in all four river systems, the total number of shredders in all coarse litter bags was significantly correlated with k ($r_s = 0.65$, $P < 0.01$), indicating the shredder contribution to mass loss. Among shredder genera, k was positively correlated with *Lepidostoma* ($r_s = 0.74$), *Leuctra* (0.59) and *Paraleptophlebia* (0.50). Oddly, k was negatively correlated with numbers of *Amphinemura* (-0.70). Rank correlations among shredder genera define three groups whose members are positively correlated with each other but negatively correlated with members of other groups: *Leuctra*, *Lepidostoma* and *Paraleptophlebia* (Group 1), *Nemoura* and *Taeniopteryx* (Group 2) and *Amphinemura* (Group 3). Of these three groups, only the sum of Group 1 members was significantly, positively correlated with k ($r_s = 0.80$, $P < 0.001$). If *Paraleptophlebia*, which occurred only in Nova Scotia, is omitted from Group 1, the correlation with k is identical. Hence, the combined number of *Leuctra* plus *Lepidostoma* was the best correlate with decomposition rate (Fig. 6). Correlations of shredders with k from heat units regressions showed identical results

Table 2 Mean numbers (± 1 SD) of leaf litter-shredding insects in maple leaf litter bags over the 6-week experiment ($n = 18$)

System	Site	<i>Leuctra</i>	<i>Taeniopteryx</i>	<i>Nemoura</i>	<i>Amphinemoura</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
South	Up	19.2 (15.1)	0	0	0	1.5 (2.8)	4.3 (4.0)
	Down	0	0	0	0	1.0 (0.7)	0
Sandjordelva	Up	0.1 (0.3)	1.8 (3.6)	0.4 (1.4)	0.5 (1.0)	0	0
	Down	0.6 (0.78)	1.1 (1.8)	0.3 (0.7)	0.4 (1.2)	0	0
Futelva	Up	2.3 (1.8)	5.3 (4.9)	1.8 (2.1)	0	3.4 (2.5)	0
	Down	1.6 (1.9)	0.3 (0.8)	1.3 (2.1)	0	1.9 (1.6)	0
Børelva	Up	0.5 1.0	0	0.5 (1.2)	0.1 (0.5)	0	0
	Down	0.3 0.5	1.2 (0.8)	0	0	0	0

Table 3 Mean numbers (± 1 SD) of leaf litter-shredding insects in alder leaf litter bags over the 6-week experiment ($n = 18$)

System	Site	<i>Leuctra</i>	<i>Taeniopteryx</i>	<i>Nemoura</i>	<i>Amphinemoura</i>	<i>Lepidostoma</i>	<i>Paraleptophlebia</i>
South	Up	15.0 (10.8)	0	0	0.1 (0.3)	1.6 (2.2)	3.1 (4.4)
	Down	0	0	0	0	1.6 (2.8)	1.1 (1.1)
Sandjordelva	Up	0.3 (0.7)	0.7 (1.2)	0	1.2 (1.7)	0	0
	Down	1.1 (1.3)	1.1 (1.7)	0.1 (0.3)	0.6 (0.8)	0	0
Futelva	Up	2.6 (3.3)	3.4 (4.2)	2.7 (3.7)	0	6.3 (4.5)	0
	Down	1.6 (1.7)	0	1.7 (2.1)	0	1.1 (1.1)	0
Børelva	Up	0.5 (1.2)	0.2 (0.5)	0.3 (1.2)	0.2 (0.4)	0	0
	Down	0	0.3 (0.6)	0	0.1 (0.3)	0	0

to those above except that absolute values were slightly lower.

Discussion

In general, the river systems examined in this study provide persuasive evidence to support our primary hypothesis: decomposition in cold, shaded tributaries occurs faster than in warm, medium-size rivers, but there is no difference if the sites are equally cold.

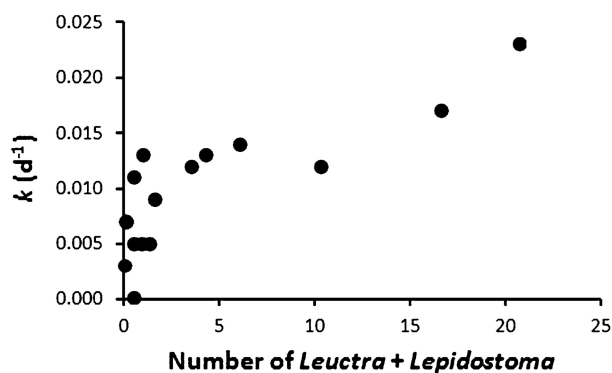


Fig. 6 Relationship between mean number of *Leuctra* and *Lepidostoma* in each litter bag ($n = 18$) and decomposition rate (k) of alder and maple leaf litter decomposing in rivers in Norway and Nova Scotia

Significant differences in decomposition rate arose even where mean temperatures differed by only a few degrees between upstream and downstream, suggesting that decomposition rates are strongly influenced by temperature, as has been observed elsewhere (Irons et al., 1994; Bergfur, 2007; Ferreira & Chauvet 2011a). Our findings from South River, Nova Scotia, were congruent with both a previous study on the same river (MacDonald & Taylor, 2008) and more recent work on small river systems nearby (B. Taylor, unpublished report 2013). Decomposition in other rivers in mainland Nova Scotia parallels that in South River, which makes South River a good model for comparisons between Nova Scotia and Norway.

Results from our study in the Børelva system, the only Norwegian river with a temperature difference between the upstream and the downstream sites, also support our first hypothesis, even though the temperature difference was small. On the Futelva and Sandjordelva systems, where water remained cold downstream, all four sites behaved like upstream sites in Nova Scotia. Hence, this experiment confirmed findings that decomposition rates respond to water temperature both directly (presumably by modulating metabolism of decomposers) and indirectly (through the distribution of invertebrate shredders), in rivers outside of Nova Scotia.

The present work compared shredder colonization of litter samples on the basis of numbers. Where organisms of diverse size are present, accuracy would be enhanced by using biovolume or biomass. Measuring biomass in this work was impractical because organisms were stored in alcohol pending identification. However, all the major shredders observed in these river systems were similarly small; in previous work, conclusions based on counts or biovolumes were identical.

MacDonald & Taylor (2008) suggest that the stenothermal stonefly *Leuctra* may be disproportionately responsible for rapid decomposition in cool streams of Nova Scotia. The current study confirms the role of *Leuctra* role in South River, and suggests that *Leuctra* may play a similar role in Norway. However, the caddisfly *Lepidostoma* also appears to have a stronger influence than other genera in Norway. The best model of spatial variations in decomposition rate includes densities of both insects. Thus our second hypothesis receives only qualified support.

In the Børelva system, however, where *Lepidostoma* did not occur, *Leuctra* was the only non-chironomid shredder that varied in accordance with decomposition rate. Although *Leuctra* populations were greater upstream in that river system, the total abundance was only 18 individuals, perhaps too few to account for a doubling of the rate of decomposition compared with that downstream. The shredder community at this site included Nemouridae and *Lepidostoma*, along with an unknown number of Chironomidae. The latter family, while individually small, was present in numbers an order of magnitude greater than the identified shredders upstream, on both litter types, yet was essentially absent downstream. The proportion of these organisms that were shredders is unknown. The possibility that the collective effect of many small chironomids contributed to the more rapid litter decay upstream cannot be discounted.

Previous work in Nova Scotia (B. Taylor, unpublished report 2013) suggests that litter type and site location may be more important than temperature in determining distribution of some shredding species (e.g., *Lepidostoma*). Our findings confirm this, with both *Lepidostoma* and *Taeniopteryx* preferring one litter type over the other and an upstream site over a downstream site, even when mean temperatures were equal at both sites. *Leuctra*, on the other hand, showed no preference for litter type or site location, if both

sites were at the same temperature, demonstrating the importance of water temperature to the distribution of this pivotal shredder.

Combining data from Nova Scotia and the present work, we obtain a distribution of *Leuctra* in litter bags with mean daily temperature. Density peaked near 14°C, with steep declines in abundance at temperatures above or below 14°C. The decrease above 14°C is expected, given that some *Leuctra* species are known to be stenothermal (Elliott, 1978), but the decrease below 14°C is surprising. *Leuctra* is considered a cold-water shredder and has been found active at water temperatures as cold as 5°C (Fjellheim, 1996; Paril et al., 2008). Since the decline in abundance around 14°C cannot be temperature-induced, another factor must be responsible. One possibility is competition with other shredders (*Taeniopteryx*, *Lepidostoma*, *Paraleptophlebia*, Nemourids).

If *Leuctra*'s distribution is further restricted by competition within its already limiting cold-water preference, then the future of this important shredder becomes uncertain in the face of climate change. Daufresne et al. (2004) and Heino et al. (2009) showed that in general, cold-water invertebrate species are negatively affected by warmer climate, while thermophilic species expand their geographical range to include more northern habitats. *Leuctra*, as a cold-water shredder with a very narrow temperature range, could be quickly removed from warmer streams. Since the streams would remain shaded, internal energy production would not provide an alternative energy source. Left without sufficient light for photosynthesis and without *Leuctra*'s efficient shredding ability, headwater stream communities could face an energy deficiency.

Conclusion

Experiments in Norway and Canada confirm that decomposition of leaf litter in temperate climates may proceed faster in cold, narrow tributaries than in warm, medium-size rivers. This difference in decomposition rate may be attributed to activity of stenothermal shredders, especially the *Leuctra* genus. Unlike other shredding species, the distribution of *Leuctra* is primarily driven by water temperature, with a distinct density peak around 14°C. Our data also suggest that *Leuctra* is forced into a narrow temperature range by

competition with other shredding species. *Leuctra*'s influence extends beyond Nova Scotia, although more research is required before its importance can be confirmed on a regional scale.

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