

Resource dynamics and detritivore production in an acid stream

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SUMMARY

1. Life history patterns and production of eight shredder-detritivore species were studied in relation to the detritus dynamics of a small acidic stream in England. Mean annual detritus inputs (direct and lateral sources combined) were approximately $400 \text{ g m}^{-2} \text{ year}^{-1}$ and showed significant seasonal and annual variation.

2. Detritus standing stock did not increase significantly during times of high input, reflecting low retention efficiency. However, the mean detritus standing stock was relatively large (108 g m^{-2}) reflecting a slow decomposition rate typical of acid streams.

3. Four species were univoltine with highly synchronous patterns of emergence and recruitment (*Leuctra inermis*, *Leuctra hippopus*, *Capnia vidua* and *Amphinemura sulcicollis*). Two species were univoltine with extended patterns of emergence and recruitment (*Nemoura cinerea*, *Potamophylax cingulatus*). *Leuctra nigra* was apparently semivoltine, while *Protonemura meyeri* showed two successive cohorts in the second year of the study, suggesting either bivoltinism or cohort splitting.

3. Secondary production of the dominant shredders was $1.67 \text{ g m}^{-2} \text{ year}^{-1}$ in 1997 and $1.99 \text{ g m}^{-2} \text{ year}^{-1}$ in 1998, which is low compared with other small European streams. This was probably because of an impoverished invertebrate community and poor food quality associated with acid conditions. Food availability probably did not account for the low production as the detritus standing stock far exceeded the estimated shredder ingestion of $42\text{--}50 \text{ g m}^{-2} \text{ year}^{-1}$.

4. Despite low overall shredder production, species-specific production was high, possibly because of competitive release in this species-poor acid stream. Periods of high production and growth showed no relationship with detritus availability but were closely related to life history.

Keywords: caddisfly, detritus dynamics, life histories, secondary production, stonefly

Introduction

Temperate, wooded, stream ecosystems are useful models for investigating secondary production, as their primary energy resource derives from

allochthonous inputs of detritus from terrestrial catchment vegetation, with dynamics that are relatively easy to determine (Webster & Meyer, 1997; Webster *et al.*, 1999). Furthermore, the dominant inhabitants are generally aquatic insects with clear life cycles and discrete generations. There is a large literature on the life history and secondary production of aquatic insects, which often dominate the detritivore feeding guild in such systems, and on the dynamics of detritus inputs and retention in streams

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(e.g. Benke *et al.*, 1988; Webster & Meyer, 1997; Webster *et al.*, 1999; Huryn & Wallace, 2000). However, only a few studies, such as that by Wallace *et al.* (1999) have attempted to combine these two approaches to determine the 'trophic basis of production' (i.e. reporting secondary production as a function of the food source production) for various guilds or taxonomic groups, despite repeated calls for such studies to understand better the bioenergetics of stream ecosystems (e.g. Benke & Wallace, 1980, 1997; Benke *et al.*, 1988; Hall, Likens & Malcolm, 2001).

Acid streams in Europe and North America generally show lower macroinvertebrate diversity and abundance than similar non-acid streams (Harriman & Morrison, 1982; Otto & Svensson, 1983; Giberson & Mackay, 1991). Similarly, invertebrate production in acid streams is often reduced in comparison to similar streams with higher pH (e.g. Krueger & Waters, 1983; Griffith & Perry, 1994; Krno, 1998). Despite this, certain components of the fauna, such as stoneflies (Plecoptera), can be very abundant in acid streams (Harriman & Morrison, 1982; Townsend, Hildrew & Francis, 1983; Griffith, Perry & Perry, 1994), and their production can be similar to or higher than that in non-acid streams (Griffith, Perry & Perry, 1993; Krno, 1998). This observation is somewhat paradoxical, in that the nutritional quality of detritus is low in acid streams because the low pH reduces the 'conditioning' influence of microorganisms (Groom & Hildrew, 1989; Griffith & Perry, 1994). However, poor food quality may be compensated by the large standing stock of detritus present on the streambed throughout the year in most acid streams, a consequence of reduced decomposition rates (Otto & Svensson, 1983; Hildrew *et al.*, 1984a). This idea is supported by evidence that detritivores may be food-limited in headwater streams that are not physically retentive (Dobson & Hildrew, 1992) and that seasonal low points or experimental reductions in detritus availability may constrain secondary production (Richardson, 1991; Wallace *et al.*, 1999). In addition, the high abundance of certain detritivore taxa in small acid streams may reflect a competitive release in the taxonomically impoverished community (Hildrew, Townsend & Francis, 1984b).

This study concentrated on shredder taxa, those feeding upon coarse particulate organic matter (CPOM: material >1 mm in size) for at least some part of their larval development. The aim was to

characterise the life cycles of the dominant shredders in a small wooded stream and to compare their secondary production to the availability of instream detritus, their main food resource.

Methods

Study site

Stake Clough is a permanently acid (annual pH range 3.5–5.0), second order stream in the Derbyshire Peak District of England (53°15'N, 1°59'W). The stream flows through peat moorland before entering mixed woodland dominated by oak (*Quercus robur* L.) and European larch (*Larix decidua* L.). Directly upstream of the study reach, the channel consisted of a series of deep pools and woody debris accumulations where a large amount of organic matter was retained. The study reach itself had no pools or woody debris, had a mean width of 1.8 m, a slope of 4.35% and an unstable substrata consisting of shale and flat stones. Discharge in Stake Clough was very variable, but fluctuated closely with rainfall (J. L. Pretty, unpublished data). In the absence of a continuous measuring station, rainfall measured at an Environment Agency weather station 1 km from the site was used as an indicator of discharge.

Sampling

Throughout the study (December 1996 to December 1998), inputs of organic matter into the stream were monitored using two kinds of traps (vertical and lateral) near the stream edge on both banks. Vertical traps consisted of perforated plastic nets with an aperture of 0.05 m² fixed to posts 0.8 m high and collected inputs from direct litterfall. Lateral traps consisted of plastic trays (0.25 × 0.25 m) set into the river bank and covered with a plastic mesh 'tent' to prevent inputs other than the bankside movement of litter towards the stream. Twelve vertical and 12 lateral traps were placed along a 30 m stretch of stream and emptied weekly for the duration of the study. The contents of each trap were dried at 70 °C for 48 h and separated into four fractions: broadleaves, conifer needles, wood/bark and miscellaneous material (seeds, lichen etc.). Each fraction was weighed, burned in a muffle furnace at 550 °C for 3 h and re-weighed to obtain an ash-free dry mass

(AFDM). The mesh size for vertical and lateral traps was (<1 mm) but inputs of fine material were negligible and were not recorded. Because of a large difference in bank slope, lateral inputs were calculated separately for each bank and combined to give a total lateral input.

In addition to vertical and lateral inputs, mesh traps were positioned at the top and bottom of the study reach to monitor instream input and output of coarse detritus. Traps were emptied weekly and the catch was separated into woody and non-woody material before sub-samples were dried and ashed in the manner described above. Each trap (0.4 × 0.25 m) was secured in the stream's thalweg with steel poles and made from strong plastic netting (3 mm mesh). Initial trials showed that finer mesh traps quickly became clogged and inefficient, while a 3 mm mesh allowed sufficient throughflow of water for the traps to function throughout the collection period. Damage to traps was unavoidable during flash floods and instream transport is certainly underestimated, however, such inefficiencies were consistent between the traps allowing the net effect (input minus output) of instream transport to be assessed. Because of practical difficulties at the start of the study and the loss of traps during floods, data for instream transport are presented for 1998 only.

Benthic samples were collected at approximately monthly intervals using a Surber sampler (area 0.0625 m²; mesh size 250 µm). Five random samples were collected on each sample date from a 30 m stretch, then either preserved in 4% formalin or returned to the laboratory for immediate live sorting of benthic macroinvertebrates. Invertebrates were preserved in methanol and identified to species with the exception of chironomids and other dipteran larvae, which were identified to family.

Detritus from each Surber sample was separated into coarse and fine material by passing through a 1 mm mesh sieve. The coarse fraction of each sample was further elutriated to separate organic material from the mineral particles. Woody material (sticks and twigs <20 mm diameter; material larger than this was omitted from the analysis) was separated from the non-woody component of the sample, producing three detritus fractions from each sample; woody material, coarse material (>1 mm) and fine material (<1 mm). Each fraction was oven dried and ashed in the manner described above.

Adult flight was monitored using a single Malaise trap 2 m away from the stream edge between February 1997 and July 1998. The trap was emptied weekly and stoneflies and caddisflies were identified using the keys of Hynes (1984) and Macan (1973), respectively.

Life history and production

Life histories were evaluated for all shredder taxa that were sufficiently abundant for analysis by plotting size-frequency histograms and following the cohorts from recruitment to emergence. The length of each larva was measured to the nearest 0.1 mm using an ocular micrometer in a dissecting microscope. Data were then plotted as a frequency distribution showing size class distribution over time. Adult flight periods of common species were determined using data from the Malaise trap. While the Malaise trap provided information on the entire flight period and not just the emergence period, emergence was assumed to have coincided with at least the start of the flight periods.

Secondary productivity was estimated for the dominant shredder taxa using two different methods. The size-frequency method (including the CPI correction for the cohort production interval; Benke, 1984) was used to calculate production for all taxa, whilst the instantaneous growth rate (IGR) method (Benke, 1984) was only used for taxa where cohorts could be reliably determined and where there was not too much overlap of size classes. Body mass was estimated using length-dry mass regressions given by Brittain (1983); Meyer (1989) and Burgherr & Meyer (1997).

Ingestion rates for the shredder taxa were estimated using the equation given by Benke & Wallace (1980) and Lugthart & Wallace (1992):

$$I = \frac{P}{AE + NPE} \quad (1)$$

where *I*, ingestion; *P*, production; *AE*, assimilation efficiency; and *NPE*, net production efficiency. Reported values for assimilation efficiency for aquatic detritivores range from 5 to 25%, but most are near 10% (Benke & Wallace, 1980; Lugthart & Wallace, 1992; Hall *et al.*, 2001), so the value of 10% was used in this study. Values for net production efficiency for detritus consumption in the literature are reported to be near 40% (Lugthart & Wallace, 1992; Hall *et al.*, 2001), so this value was used.

Data analysis

Temporal variations in detritus input and standing stock were assessed using two-way ANOVA (\log_{10} transformed data) with 'month' and 'year' as factors to determine seasonal and inter-annual differences. Where data could not be normalised with log transformation Kruskal–Wallace tests were used instead. Detritus standing stock was compared with the monthly detritus input using Spearman's rank correlation.

Macroinvertebrate abundance (all taxa combined and shredder taxa only) was analysed using two-way ANOVA in the manner described above. In addition, invertebrate abundance was related to detritus standing stock and rainfall (the amount of rain 7, 14 and 30 days prior to each sampling date) using Spearman's rank correlation. The same procedure was repeated for the total biomass (mg m^{-2}) of shredder taxa.

Production and growth rates were evaluated for each interval for those species where interval-production could be determined by the IGR method (when cohorts did not overlap). Daily rates were calculated by dividing the production for the interval by the number of days in the interval. This enabled daily and monthly production rates for each interval

to be compared with monthly estimates of detritus input and standing stock using Spearman's rank correlation.

Results

Detritus dynamics

Annual detritus inputs (vertical and lateral inputs combined) ranged from about 375 to 425 $\text{g m}^{-2} \text{ year}^{-1}$ ash free dry mass (Table 1a). Detritus input was strongly seasonal (two-way ANOVA, lateral: $F_{10} = 49.33$; $P < 0.001$; vertical: $F_{10} = 601.1$; $P < 0.001$; Fig. 1a) with October and November representing approximately 70% of the annual input in both years. In addition to the large seasonal variation, there were also significant inter-annual differences (two-way ANOVA, lateral: $F_{10} = 63.18$; $P < 0.001$; vertical: $F_{10} = 35.9$; $P < 0.001$; Fig. 1a), with greater input in 1997 than in 1998 (Table 1a). Inputs were dominated by vertical sources, with lateral (bankside) sources becoming important only during periods of low vertical input. Broadleaf litter was most important in the lateral inputs, whereas needle litter (mainly deciduous larch) contributed relatively more to the vertical inputs (Table 1a), reflecting the dominance of larch trees at the study site.

Table 1 Detritus dynamics at Stake Clough. (a) Total annual lateral and vertical inputs (1997 and 1998) and net instream transport calculated as input-export/stream area (1998 only); range indicates the minimum and maximum monthly input. (b) Mean annual detritus standing stock; SE reflects variation among sampling dates.

	Lateral input (g m^{-1} AFDM)		Vertical input (g m^{-2} AFDM)		Net instream transport (g m^{-2} AFDM)
	1997	1998	1997	1998	
(a) Detritus inputs/outputs					
Broadleaf	35.9 (0.2–10.4)	20.9 (0.1–5.1)	128.1 (0–91.2)	102.2 (0–50.5)	
Needle	15.2 (0.3–4.7)	14.4 (0.3–4.4)	159.1 (0.8–79.3)	157.8 (0.2–73.1)	
Miscellaneous	2.9 (0.1–0.9)	2.1 (0.1–0.4)	75.5 (1.2–18.6)	41.6 (0–7.2)	
Wood	3.7 (0.1–0.8)	10.8 (0–0.8)	24.3 (0.4–7.1)	26.6 (0.3–13.8)	–29
Total non-woody	54.0 (1.0–12.1)	37.4 (0.6–8.1)	362.7 (2.1–177.5)	301.6 (0.2–87.5)	–130
Total detritus	57.7 (1.1–12.4)	48.2 (0.8–8.6)	387.0 (5.0–178.0)	328.2 (0.9–88.9)	–159
Standing stock (g m^{-2} AFDM)					
		1997			1998
(b) Detritus standing stock					
CPOM		56.6 ± 9.4			72.3 ± 8.3
FPOM		24.3 ± 2.6			40.2 ± 3.2
Wood		13.8 ± 5.0			8.8 ± 2.2
Total		94.8 ± 11.5			121.4 ± 11.8

CPOM, coarse particulate organic matter (>1 mm); FPOM, fine particulate organic matter (<1 mm).

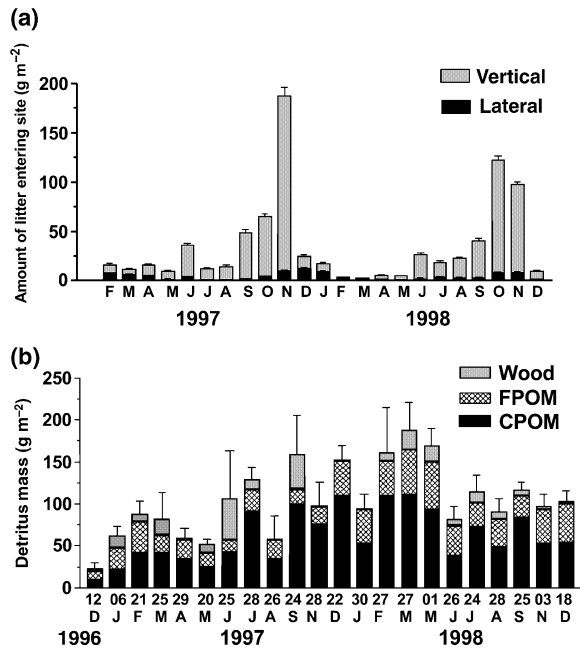


Fig. 1 (a) Monthly detritus inputs (g m^{-2}) during the study period. Heavy shading represents lateral inputs while light shading represents vertical inputs. Error bars represent variation among replicate traps, not temporal variability within each month. (b) Detritus standing stock (g m^{-2}) recorded on invertebrate collection dates + 1 SE. Coarse particulate organic matter (CPOM) material >1 mm; fine particulate organic matter (FPOM) material <1 mm in size.

Instream transport of detritus (in 1998) was highly variable and was greatest during the autumn/winter period. While the absolute amount of detritus in transit was difficult to quantify because of trap damage during spates, the net impact (i.e. input minus output) of instream transport was assessed. The instream output was considerably higher than the instream inputs, resulting in a net loss of 159 g m^{-2} over the study reach (Table 1a). This indicated that a large proportion of the detritus entering the study reach was derived from the local vertical and lateral inputs rather than transport from upstream regions. In addition, the large instream output suggests that much of the detritus entering the study reach from direct and lateral sources was not retained on the streambed.

In contrast to the detritus inputs, the detritus standing stock did not vary significantly throughout the year [Kruskal–Wallace (KW) statistic = 27.0, $P = 0.46$] or between years [Mann–Whitney U -test (U -statistic) = 38.0, $P = 0.06$]. Detritus standing

stock ranged from about 25 to 175 g m^{-2} on each sample date (average 108 g m^{-2}) and did not appear to decline during periods of extremely low input (Fig. 1b). CPOM made up about 60% of the total detritus standing stock in both years (Table 1b). On average, over the 2-year study, detritus standing stock (per m^2) represented approximately 27% of the total detritus input from vertical and lateral sources.

Abundance patterns

The macroinvertebrate community was typical of acid streams and was dominated by stoneflies (44% of total numbers) and Chironomidae (47%), with the remaining taxa comprising mainly Trichoptera, *Dicranota* and Naididae (Table 2). Total invertebrate abundance varied through the year with no obvious seasonal patterns (Fig. 2a). In contrast to the total invertebrate assemblage, stonefly abundance showed a clear pattern for increase in late summer to a peak in January/February, followed by a gradual decline in spring (Fig. 2b). To some extent, declines in the benthic abundance (Fig. 2) corresponded to flash floods associated with high rainfall, particularly in October to November 1997, February to March 1998 (Fig. 3). However, life history patterns (i.e. recruitment and emergence) drove most of the observed changes in abundance and there were no significant relationships between invertebrate abundance and detritus standing stock or rainfall (Spearman's rank correlation $P > 0.05$ in all cases).

Life History patterns of numerically dominant shredders

One caddisfly and seven species of stonefly found in Stake Clough were abundant enough for life history analysis. *Nemurella pictetii*, *Brachyptera risi* and *Siphonoperla torrentium* were present but were rare and could not be evaluated (Table 2). Six of the species clearly had univoltine life cycles (*Potamophylax cingulatus*, *Leuctra inermis*, *L. hippopus*, *Capnia vidua*, *Nemoura cinerea*, and *Amphinemura sulcicollis*; Fig. 4). Growth patterns and life history timing differed among species (Fig. 4; Table 3), but in general, most of the growth occurred during the autumn or winter. Most of the univoltine species were highly synchronous, but *P. cingulatus* and

Table 2 Macroinvertebrate assemblage in Stake Clough

Species	Feeding guild	Relative abundance over study period (%)
Plecoptera		
<i>Leuctra hippopus</i> (Kempny)*	Shredder	14.16
<i>L. inermis</i> Kempny*	Shredder	6.36
<i>L. nigra</i> (Olivier)*	Shredder	1.97
<i>Nemoura cinerea</i> (Retzius)*	Shredder	15.36
<i>Amphinemura sulcicollis</i> (Stephens)*	Shredder	3.08
<i>Protonemura meyeri</i> (Pictet)*	Shredder	1.01
<i>Nemurella pictetii</i> (Klapalek)	Shredder	0.05
<i>Capnia vidua</i> Klapalek*	Shredder	2.18
<i>Brachyptera risi</i> (Morton)	Shredder	0.05
<i>Siphonoperla torrentium</i> (Pictet)	Predator	0.01
Trichoptera		
<i>Potamophylax cingulatus</i> (Stephens)*	Shredder	0.52
<i>Drusus annulatus</i> Stephens	Scraper	1.28
<i>Plectonemia conspersa</i> (Curtis)	Predator	1.83
Megaloptera		
<i>Sialis fuliginosa</i> Pictet	Predator	0.05
Coleoptera		
<i>Agabus didymus</i> (Olivier)	Predator	0.17
Diptera: Chironomidae		
Diamesinae	Scraper/collector	47.51
Tanypodinae	Predator	0.03
Diptera: Tipulidae		
<i>Dicranota</i> spp.	Predator	2.46
Limoniinae	Predator	0.23
Diptera: others		
Simuliidae	Collector/filterer	0.29
Empididae	Predator	0.52
Oligochaeta		
Naididae	Collector	0.81

*Shredder species were abundant enough for the analysis of life histories and production. Feeding guilds are based on those reported in the literature. Shredders are capable of consuming large fragments of leaf material for at least some part of their larval development.

N. cinerea showed a pattern of extended recruitment and emergence and *N. cinerea* and *L. hippopus* showed a wide variation in size classes on most sample dates. The life cycle of *Leuctra nigra* was not very clear, but was apparently semivoltine with at least some larvae having a 2-year life cycle. *Protonemura meyeri* was scarce during the first year of the study but showed two successive cohorts in the second year of the study.

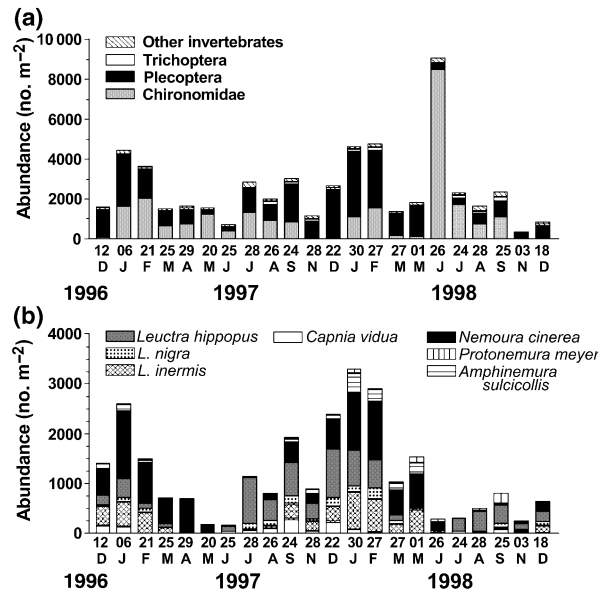


Fig. 2 Abundance of benthic macroinvertebrates (a) total macroinvertebrate abundance (no. m⁻²). (b) stonefly abundance (no. m⁻²).

Secondary production of dominant shredders

Estimates of secondary production were similar for the two methods but, where the two could be compared directly, the size-frequency method gave consistently higher values than the IGR method, even when the cohort production interval was calculated (Table 4). The divergence was greatest in species showing the greatest variation in size on most sample dates, for example, *N. cinerea* and *L. hippopus*. To ensure consistency, comparisons of species-specific production were made using the size-frequency method only, because the IGR method could not be used to calculate production for all species.

Overall shredder production was greater in 1998 than in 1997, at 1.99 and 1.67 g m⁻² year⁻¹ dry mass, respectively (Table 4). Among the stoneflies, *L. hippopus* and *N. cinerea* dominated production in both years, although *P. meyeri* was also important in 1998. *Potamophylax cingulatus* showed relatively high production despite low abundance because of its large size at maturity. Production for individual taxa varied annually; *P. cingulatus*, *L. inermis*, *P. meyeri*, and *A. sulcicollis* showed higher absolute and relative (to the total) production rates in 1998 than 1997, whereas *L. hippopus*, *L. nigra*, *C. vidua*,

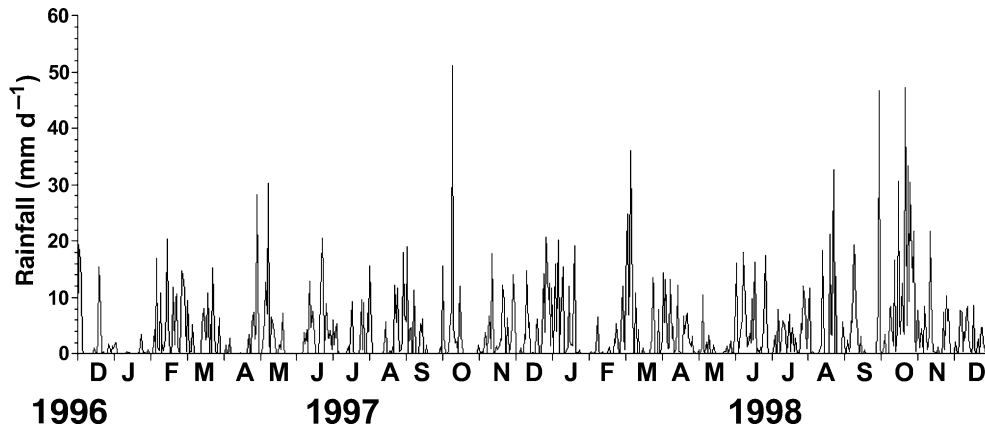


Fig. 3 Daily rainfall (mm) over the study period from a rain gauge located approximately 1 km from the site.

and *N. cinerea* were more important in 1997 than in 1998.

It was possible to determine production between sampling intervals for non-overlapping cohorts that could be followed through time. Interval-specific production rates for these taxa varied among species and tended to be related to life history timing. Highest production rates occurred during the midpoints of the cohorts for most species (Fig. 5).

Interactions between shredder production and detritus dynamics

Detritus standing stock and shredder production were higher in 1998 than in 1997, despite slightly (although not significantly) higher detritus inputs in 1997. Similarly, relationships between shredder production and detritus were weak. The periods of highest shredder production or growth showed little relationship with detritus for most taxa. No relationships were found between detritus input and production (Spearman's rank correlation; $P > 0.05$), but production was weakly related to detritus standing stock for *L. hippopus* (Spearman's rank correlation; $r_s = 0.48$, $P = 0.03$).

Based on an assimilation efficiency of 10% and a net production efficiency of 40%, shredder ingestion was estimated to be 42 and 50 $\text{g m}^{-2} \text{ year}^{-1}$ in 1997 and 1998, respectively. These estimates suggest that the dominant shredders consumed approximately 10% of the detritus that entered the study reach, and was considerably lower than the mean annual detritus standing stock of 108 g m^{-2} .

Discussion

The amount of detritus on the streambed showed no significant or consistent seasonal pattern despite highly seasonal inputs (approximately 70% of annual input between September to the end of October). This is not unusual in high-gradient streams susceptible to flash floods, where seasonal peaks in detritus input can be readily washed downstream (Maridet *et al.*, 1995; González & Pozo, 1996). The net instream transport was negative, reflecting a net export of detritus from the reach of 159 $\text{g m}^{-2} \text{ year}^{-1}$. The downstream loss of coarse detritus represents a major proportion of the annual detritus input, far outweighing the estimated 42–50 $\text{g m}^{-2} \text{ year}^{-1}$ consumed by the shredder community. Furthermore, the instream export of detritus represents a large potential food resource that is unavailable to the benthic invertebrate community, and highlights the importance of detritus retention in the energetics of small woodland streams (Webster & Meyer, 1997; Webster *et al.*, 1999).

Despite a poor relationship between input and standing stock, the average detritus standing stock was high (mean 108 g m^{-2}). Retention efficiency is related to the structural and hydrological characteristics of a stream (Snaddon, Stewart & Davies, 1992). The study reach at Stake Clough was characterised by the flashy nature of its discharge, an unstable streambed and a lack of retention features such as woody debris. Therefore, it is possible that the high detritus standing stock was related to low decomposition rates associated with acid conditions and a

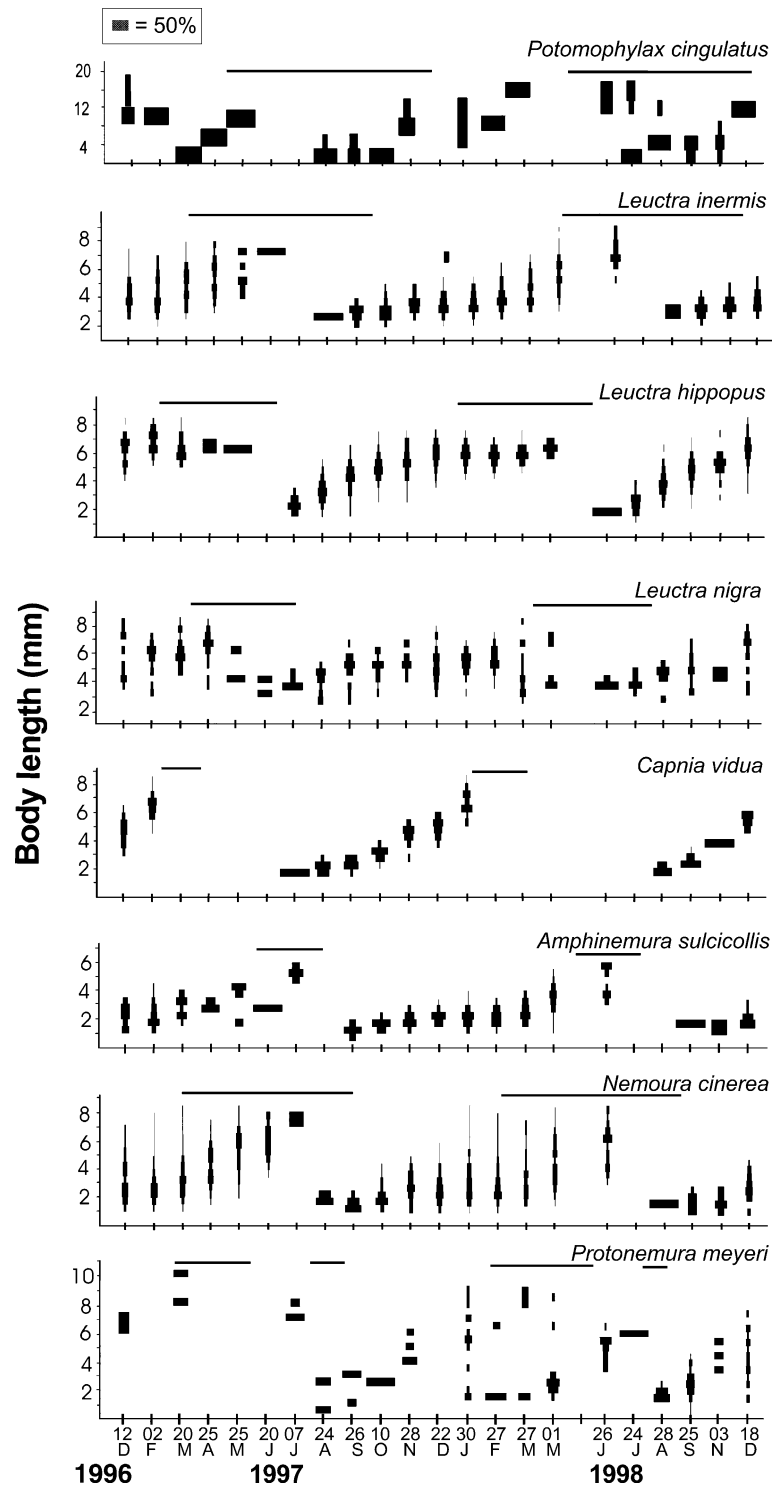


Fig. 4 Life history patterns (growth and flight periods) for the abundant shredder taxa. The width of each bar is relative to the number of individuals in the population at that time. Flight periods are indicated by the line at the top of each chart, based on Malaise trap data (February 97 to July 98). *x*-Axes show sampling dates.

low overall ingestion rate by the detritivores, rather than high retention efficiency of the detritus entering the study reach. Furthermore, if the stream had a high retention efficiency, it is more likely there would have

been a positive relationship between inputs and standing stock that is apparent in many highly retentive streams (e.g. Iversen, Thorup & Skriver, 1982; Abelho & Graça, 1998).

Table 3 Life history summary of dominant shredders in Stake Clough, December 1996 to December 1998

Taxon	Life-cycle type	Estimated recruitment period	Adult flight period	Growth summary	Per cent of total shredder abundance	Per cent of total shredder biomass	Per cent of total shredder production
<i>Potamophylax cingulatus</i>	Univoltine Non-synchronous	Sept–Mar	Jul–Sept	Relatively slow growth in all seasons	1.0	31.9	16.3
<i>Leuctra inermis</i>	Univoltine Synchronous	Aug–Oct	Mar–Oct	Slow through autumn, rapid in March/April	18.1	4.6	6.1
<i>L. hippopus</i>	Univoltine Synchronous	Jul–Aug	Jan–Jun	Rapid through July to November, then slow through the winter	26.5	29.1	35.8
<i>L. nigra</i>	Possibly semivoltine Synchronous	Jun (?)–Sept	Apr–Jul	Slow growth; recruitment in June of year 1 to emergence in spring of year 2	5.4	2.7	1.9
<i>Capnia vidua</i>	Univoltine Synchronous	Jul–Aug	Feb–Apr	Rapid growth through the winter and early emergence	5.0	3.4	5.3
<i>Amphinemura sulcicollis</i>	Univoltine Synchronous	Sept–Oct	Jun–Jul	Slow growth through the autumn, then rapid growth in spring	6.7	1.5	2.8
<i>Nemoura cinerea</i>	Univoltine Non-synchronous	Aug–Mar	Mar–Sept	Relatively rapid growth regardless of season; extended egg hatching and emergence	35.2	22.3	22.4
<i>Protonemura meyeri</i>	Possibly bivoltine or cohort splitting Synchronous	Aug–Sept, Jan–Mar	Mar–Jun, Aug	Rapid growth in all seasons	2.2	4.5	9.4

Table 4 Secondary productivity values calculated for dominant shredders in Stake Clough, December 1996 to December 1998

Taxon	1997				1998				
	Production (g m ⁻² year ⁻¹)			Percentage of 1997 production	Production (g m ⁻² year ⁻¹)			Percentage of 1998 production	Cohort P/B
	IGR	S-F	Annual P/B		IGR	S-F	Annual P/B		
<i>P. cingulatus</i>	–	0.232	9.5	13.9	–	0.367	10.1	18.4	–
<i>L. inermis</i>	0.064	0.081	5.0	4.8	0.135	0.142	6.0	7.1	5.8
<i>L. hippopus</i>	0.560	0.678	5.0	40.5	0.501	0.635	5.5	31.9	5.0
<i>L. nigra</i>	–	0.036	2.9	2.2	–	0.033	2.9	1.7	–
<i>C. vidua</i>	0.113	0.125	6.6	7.5	0.063	0.068	6.5	3.4	5.2
<i>A. sulcicollis</i>	0.024	0.025	7.5	1.5	0.075	0.076	7.3	3.8	5.8
<i>N. cinerea</i>	0.303	0.433	4.4	25.9	0.284	0.388	4.1	19.5	4.0
<i>P. meyeri</i>	–	0.064	9.3	3.8	–	0.282	8.9	14.2	–
Total		1.674				1.991			

Production was calculated using the instantaneous growth rate method (IGR) where cohorts could be distinguished and with the size-frequency method (S-F) for all taxa. Production to mean biomass (P/B) was calculated from the size-frequency estimates. Cohort P/B was calculated directly where complete cohorts could be followed (Fig. 4).

Life histories of the main shredder taxa in Stake Clough generally followed the patterns reported in previous studies. Recruitment generally occurred in

late summer or early autumn, with the main periods of growth occurring in autumn or late winter for most taxa. *Leuctra inermis*, *L. hippopus*, *C. vidua* and

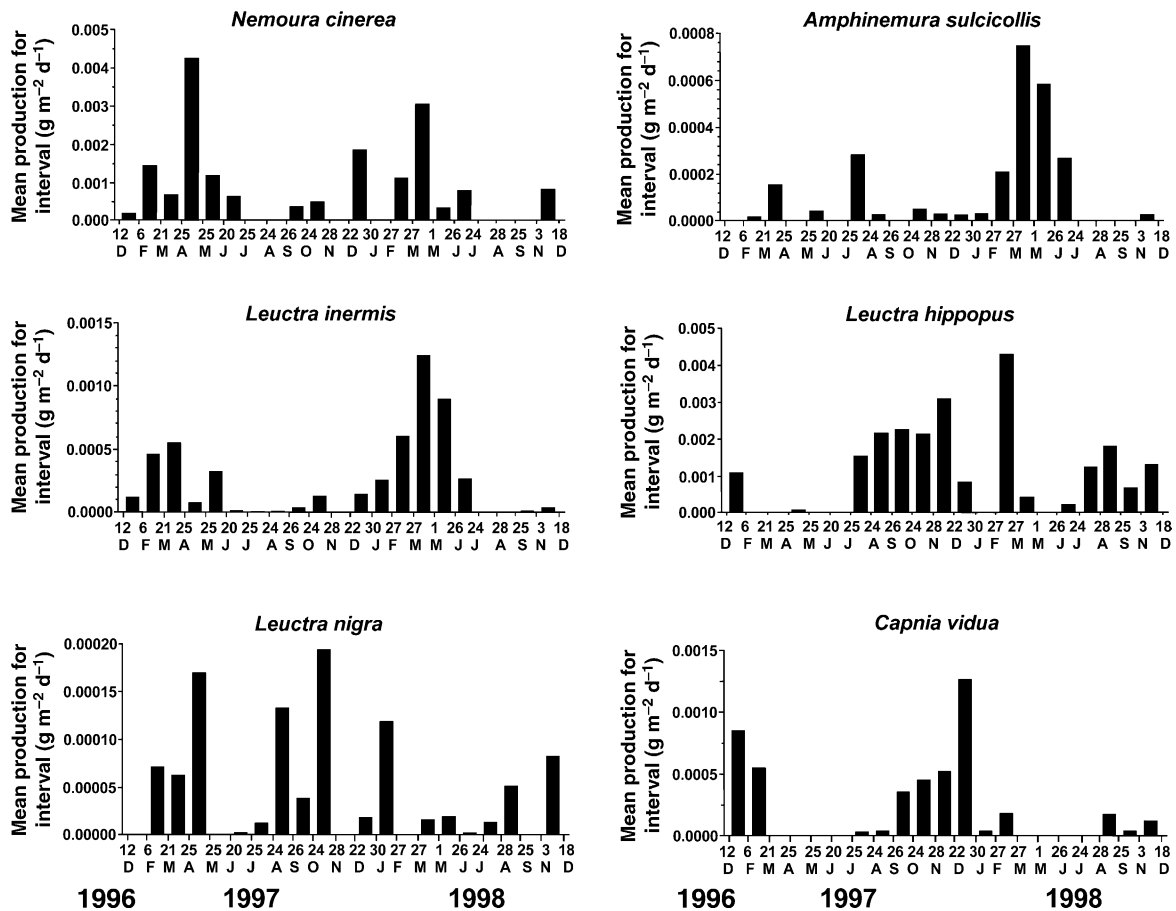


Fig. 5 Interval-specific production rates for the abundant shredder taxa. x-Axes show sampling dates.

A. sulcicollis were clearly univoltine, with generally synchronous development as reported elsewhere (Elliott, 1967, 1987a, 1988; Svensson, 1977; Hynes, 1984; Petersen *et al.*, 1999). *Nemoura cinerea* was also univoltine, and the pattern of prolonged emergence and egg hatching was similar to that reported elsewhere (Hynes, 1984; Elliott, 1988; Krno, 1998), a result of the highly variable rates of egg development apparent in this species (Brittain & Lillehammer, 1987). *Leuctra nigra* has been variously reported to be semivoltine (Elliott, 1987b; Thomsen & Friberg, 2002) or univoltine (Krno, 1998), although Elliott (1987b) suggested that mortality was high for this species at temperatures that produce a 1-year cycle. In Stake Clough, *L. nigra* was apparently semivoltine, but the pattern was obscured by low capture success of small life stages. *Protonemura meyeri* was reported to be univoltine by Elliott (1967) but clearly showed two cohorts in the second year of the study, indicating either bivoltinism or cohort splitting that can arise through delayed hatching and different growth rates among *Protonemura* larvae (Marten & Zwick, 1989). *Potamophylax cingulatus* had a 1-year life cycle in Stake Clough, with a simple univoltine cycle similar to that reported by Sangpradub, Giller & O'Connor (1999). There was no evidence that life cycles were prolonged in Stake Clough because of low food quality, perhaps because the taxa present at this site are highly tolerant of acid conditions and, presumably, the associated reduction in detritus quality.

Total shredder production (approximated from the sum of production of the eight numerically dominant shredder species) was low relative to most other small European streams (Iversen, 1988; Krno, 1998; Friberg *et al.*, 2002; Meyer & Poepperl, 2003). Low secondary production is typical of acid streams as they generally have lower species richness and abundances compared with structurally similar non-acid streams (Krueger & Waters, 1983; Griffith *et al.*, 1994). The physicochemical conditions at Stake Clough would exclude acid sensitive taxa such as *Gammarus* spp. (Amphipoda), which can contribute greatly to secondary production in non-acid streams (e.g. Iversen, 1988; Dangles & Guérol, 2001; Friberg *et al.*, 2002). Furthermore, the paucity of large bodied shredders in Stake Clough may have contributed to the low shredder production because such organisms can contribute greatly to overall values of secondary production. For example, estimates of shredder pro-

duction can be dominated by the large bodied taxa like the dipteran larvae *Tipula* spp. (Krueger & Waters, 1983; Griffith *et al.*, 1994), while limnephilid caddisfly larvae may also have high production rates (Iversen, 1988; Friberg *et al.*, 2002). The relative importance of large bodied organisms is further demonstrated in this study where the limnephilid *P. cingulatus* had a high production rate despite its low abundance. In addition to large organisms, the importance of small-sized (body mass <10 µg dry weight) early instar insect larvae in contributing to total secondary production has been recently highlighted (Stead, Schmid-Araya & Hildrew, 2005). Such small larvae were overlooked in this study but would have certainly increased our estimates of secondary production. Chironomids accounted for >40% of the organisms captured during the study and because of their rapid life cycles potentially contribute greatly to community production. However, most non-Tanytopodinae chironomid taxa are scrapers of biofilm or collector detritivores, rather than shredders (Berg, 1995) so were unimportant in this context.

The low shredder production in Stake Clough could not be attributed to a quantitative limitation in food resources, despite the relatively small proportion of the annual input that was retained on the streambed. Shredder production was 1.67–1.99 g m⁻² year⁻¹ and estimated ingestion 42–50 g m⁻² year⁻¹, which, compared with a mean annual detritus standing stock of 108 g m⁻² year⁻¹ represents a large resource that was not exploited by the shredder taxa. Furthermore, there is now clear evidence that stoneflies in acid streams may graze upon the epilithic biofilm as well as consuming detritus (Ledger & Hildrew, 2000), so annual production may not be entirely associated with detritus in such streams. Stonefly production was more closely related to life history than to detritus inputs possibly because detritus standing stock did not vary significantly through the year, and the stoneflies only consumed a small proportion of the available detritus. Similarly, González & Graça (2003) found that temporal patterns in the production of *Sericostoma vittatum* (Limnephilidae) were related to its life history rather than detritus availability.

The estimated shredder ingestion was considerably lower than for an acid stream in southern England, where leaf litter ingestion from just two stonefly species (*N. pictetii* Klapalek and *L. nigra*) was estimated to exceed 80 g m⁻² year⁻¹ (Henderson,

Hildrew & Townsend, 1990). Detritus ingestion can vary dramatically with temperature, pH and leaf species (Groom & Hildrew, 1989; Henderson *et al.*, 1990; González & Graça, 2003) and it is likely that all three factors contributed to the difference between sites. Furthermore, rather than direct measurements, our estimation of ingestion was calculated using published assimilation and net production efficiencies. Some care should be taken when using literature values of assimilation efficiency and net production efficiency, when dealing with acid streams. Groom & Hildrew (1989) found that growth of *N. pictetii* was slower on acid-conditioned leaves than those conditioned in neutral water, suggesting that more food may be required for the same energetic gain in acid waters. Energy content of stoneflies reared in acid waters may also be lower than those in more neutral conditions (Raddum & Steigen, 1981). Therefore, the calculated ingestion rate of 42–50 g m⁻² year⁻¹ was almost certainly an underestimate, although this does not affect the general conclusion that food availability was not limiting in this stream.

In contrast to the overall shredder productivity, production rates for the individual shredder species found in Stake Clough were generally higher than had been reported elsewhere in the literature (e.g. Mortensen & Simonsen, 1983; Iversen, 1988; Krno, 1998; Friberg *et al.*, 2002). Production of individual taxa is difficult to compare in different studies, because production can vary dramatically from year to year and site-to-site, and different methods are used to calculate production. While acknowledging these problems, we suggest that the higher species-specific production rates reported here could be indicative of competitive release for acid tolerant species. In a study of detritivorous stoneflies from streams of differing species richness, Hildrew *et al.* (1984b) found evidence of density compensation and increases in niche width and niche overlap in species-poor streams. Such observations are consistent with theories of competitive release in acid streams, and it is likely that species-specific production rates may also be higher in taxonomically impoverished streams.

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