

# Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics?

MIKE DOBSON,\* ADIEL MAGANA,† JUDE M. MATHOOKO† and FIDENSIO K. NDEGWA†

\*Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Manchester, U.K.

†Department of Zoology, Egerton University, Njoro, Kenya

## SUMMARY

1. The relationship between coarse particulate organic matter (CPOM) standing stock and benthic macroinvertebrate assemblages in Kenyan highland streams was determined by sampling seven sites on three rivers (2000–2700 m a.s.l.). Taxa recorded were allocated to functional feeding groups using published literature, mouthpart analysis and examination of gut contents. Patterns were compared with five structurally similar streams in three areas of Europe (south-west France, south-east England, north-east England).
2. Number of individuals and proportion of detritivores in Kenyan streams were equivalent to, or greater than, those in European sites. Shredders were, however, almost completely absent from Kenyan sites, despite high standing stocks of CPOM. Shredders were abundant in all European sites.
3. The phenomenon of low shredder abundance has been observed in other tropical streams in south-east Asia and Central and South America but, in contrast to these regions, the African rivers studied were devoid of shrimps or fish which may occupy the shredding niche elsewhere.
4. These preliminary data suggest that shredder-mediated detritus processing, which is a key functional component of streams in the North Temperate Zone, does not operate in East African streams. There are three possible reasons for this. The first is that tropical African rivers are functionally different to those in temperate regions. This could be because of enhanced microbial activity replacing shredder activity at high temperatures. Alternatively, it could be a result of low palatability of detrital inputs from dominant riparian trees in the region. The second and third are methodological: that our allocation to functional feeding groups is incorrect, and that our sampling methods missed a potentially key shredding taxon – the freshwater crab *Potamonautes* sp.

*Keywords:* benthos, coarse particulate organic matter (CPOM), East Africa, freshwater crab, macroinvertebrate

## Introduction

The activity of shredding detritivores is considered to be one of the dominant determinants of the rate at which allochthonous detritus is processed in small streams. The evidence for this has, however, derived

almost exclusively from streams in North America and Europe, and its relevance to other regions of the world has been questioned (e.g. Winterbourn, Rounick & Cowie, 1981; Marchant *et al.*, 1985). A large body of evidence gathered in recent years from a range of sites in the tropics has further cast doubt on its universal applicability. For example, benthic samples collected in Hong Kong (Dudgeon, 1989), New Guinea (Yule, 1996) and Central America (Pringle & Ramírez, 1998) contained very few taxa from groups that dominate the shredding detritivore guild in the

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Correspondence: Mike Dobson, Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Chester St., Manchester, M1 5GD, U.K.

E-mail: m.dobson@mmu.ac.uk

north temperate zone – Plecoptera, case-building Trichoptera, Tipulidae (Diptera) and Gammaridae (Amphipoda). Leaf pack colonisation studies in Brazil (Walker, 1987), Costa Rica (Rosemond, Pringle & Ramírez, 1998) and Hong Kong (Dudgeon & Wu, 1999) have likewise revealed few shredding taxa among the colonists, although Benstead (1996), also working in Costa Rica, recorded high densities of shredders, albeit of only three taxa.

The tropical zone covers by far the largest land area of the world's climatic regions. Therefore, its apparently low shredder populations may demonstrate that shredder-mediated breakdown is an unusual feature of the north temperate zone, rather than a universal component of the litter breakdown mechanism. Irons *et al.* (1994) proposed microbial activity as an explanation for the paucity of shredders in the tropics. Microbial leaf litter breakdown, which is temperature mediated, is more rapid and therefore relatively more important in tropical than in temperate regions. This reduces the resource for shredders, which are therefore less abundant in the tropics. Alternatively, Irons *et al.* (1994) suggested that leaf litter shredding may be a feeding mechanism that has developed in very few orders of aquatic invertebrates, all of which are evolutionarily adapted to cool waters and therefore scarce in the tropics for purely physiological reasons. If, however, allochthonous detritus is abundant in tropical streams, then it is to be anticipated that at least some species of detritivores will be adapted to exploit it. There have been few studies of leaf litter inputs and standing stocks in tropical rivers (Larned, 2000), but terrestrial litter fall studies (e.g. Martínez-Yrizar & Sarukhán, 1990; Haase, 1999; Sundarapandian & Swamy, 1999) imply that total annual inputs should be equivalent to those in temperate forested zones.

Invertebrate response to detritus in rivers has been little studied in Africa, apart from the warm temperate and taxonomically distinct Cape region. Cape streams support high densities of plecopteran (King *et al.*, 1987) and amphipod (Stewart, 1992) shredders. Tropical Africa, in contrast, supports a river invertebrate fauna that has few shredder taxa: gammarid shrimps and limnephilid caddisflies are absent, while Plecoptera are represented only by the single predatory perlodid genus *Neoperla*. Its rivers are therefore potential sources of valuable evidence for the role of invertebrates in leaf litter dynamics, and the development of shredding as a feeding mechanism in

taxonomic groups other than those that dominate north temperate streams. Despite this, research on feeding relationships among tropical African river invertebrates is almost non-existent. Tumwesigye *et al.* (2000), working in Uganda, were the first to demonstrate the apparent paucity of shredder taxa in East Africa, but did not assess potential food resources in their study river.

This paper presents data from highland streams in Kenya, collected with the aim of investigating the ecological role of detritivorous invertebrates and the potential importance of detritus as a food resource. It is, to our knowledge, the first study in tropical Africa that specifically addresses these questions. The data were compared with equivalent collections made in rivers subject to a wide range of conditions from three regions of Europe. This comparison, at the functional feeding group level, allowed us to assess the degree of functional difference between rivers on the two continents.

## Methods

### *Kenyan study sites*

The study was carried out in the central highland region of Kenya. Rainfall in this region is normally bimodal, with rainy seasons in October–December and March–May, although the March–May rains had failed during the study year. Average daily temperatures at 2000 m altitude range from around 15 °C in July to 26 °C in January.

Samples were taken from seven sites on three rivers (Table 1). In all sites, the immediate riparian area was thickly wooded and the river was generally heavily shaded, but the adjacent land use ranged from undisturbed wilderness to intensive human activity.

Four sample sites were along the Naro Moru River, a tributary of the Ewaso Nyiro, which drains the western slopes of Mt Kenya. Discharge data for this river are provided by Mathooko (1998b); its annual discharge is bimodal, with peaks of around 2 ms<sup>-1</sup> coinciding with the periods of high rainfall. During July, discharge is normally at an annual low of around 0.8 ms<sup>-1</sup>, although the drought during the study period meant that it was no more than half of this at the time of sampling. Percival's Bridge (PB: 0°10'S, 37°10'E) is in Mt Kenya National Park, approximately 300 m below the altitude of the tree line; there is very

**Table 1** Summary physical data for Kenyan the sample sites. All readings other than altitude were taken on the sample date

Site	Percival's bridge	Karandi bridge	Nanyuki road	Naro Moru lodge	Burguret up-stream	Burguret down-stream	Njoro
Date sampled	3 July 1999	3 July 1999	4 July 1999	4 July 1999	4 July 1999	4 July 1999	11 July 1999
Altitude (m a.s.l.)	2700	2300	2100	2035	2100	2100	2220
Temp (°C), plus time at which measured	7.5 (15:00)	12.3 (16:30)	15.1 (10:00)	15.9 (11:30)	14.2 (08:00)	14.5 (08:30)	15.0 (14:00)
Width (m)	2.60	6.48	7.59	9.95	6.57	8.20	2.0
Maximum depth (cm)	20	31	23	26	49	24	32
Water velocity (ms <sup>-1</sup> )	0.31	0.20	0.20	0.17	0.30	0.42	0.54
Conductivity (µS cm <sup>-1</sup> )	25.5	41.7	113.6	116.5	98.4	104.4	286
pH (approx.)	6	6	6.5–7	6–6.5	6–7	7	8
Substrate	Rocky	Pebbles, fine sand	Gravel, pebbles	Fine silt, pebbles, sand	Pebbles, boulders	Gravel, pebbles, boulders	Fine silt, bedrock
Canopy cover (%)	90	50	10	85	40	80	60

little human activity at this point and the banks are heavily vegetated with bamboo (*Arundinaria alpina* K. Schum.). Karandi Bridge (KB: 0°11'S, 37°07'E) is below the limit of the National Park but in a heavily wooded area with little grazing and no cultivation; vegetation is dominated by *Podocarpus gracilior* Pilger and cypress (*Cupressus* sp.). Nanyuki Road (NR: 0°09'S, 37°01'E) is in an area of moderate human activity, with grazing and patchy cultivation; the river channel at the sample point was partially open, with *Syzygium guineense* (Willd.) and *P. gracilior* as the dominant trees, along with *Vernonia* sp. and *Doryalis* sp. Naro Moru Lodge (LO: 0°10'S, 37°01'E) is in the grounds of a tourist hotel, adjacent to formal lawns on the left bank and thick scrub on the right bank, but is completely overshadowed with *S. guineense* and *P. gracilior*; this is the site of previous intensive research (e.g. Mathooko, 1994, 1998b).

The Burguret River, another tributary of the Ewaso Nyiro draining the western slope of Mt Kenya to the north of the Naro Moru River, was sampled at two adjacent sites next to the Nanyuki Road (0°07'S, 37°02'E) and within 200 m of each other. At both sites, *S. guineense*, *P. gracilior*, *Vangueria* sp., *Maytenus* sp. and *Ficus* sp. dominated. The upper site (BU, upstream of the road) was partially open, adjacent to scrub and cultivated fields, but relatively inaccessible to livestock. The lower site (BL, downstream of the road) was completely shaded but was heavily used as a livestock-watering site.

The seventh site (NJ: 0°22'S, 36°56'E) was on the Njoro River, which drains the Mau Ridge south-west of Nakuru and flows into Lake Nakuru. This site is

adjacent to the Egerton University campus and approximately 300 m downstream of a stretch heavily used for water collection and laundry; the study site itself was, however, wooded with *Syzygium cordatum* (Hochst. Ex Krauss) and *Dombeya goetzenii* (K. Schum), with nearby cultivation on each side. A 2-km stretch of the Njoro River has been the subject of intensive ongoing research (e.g. Mathooko, 1995; Mathooko, M'Erimba & Leichtfried, 2000).

#### Data collection

Each site was visited on one occasion, during which all physicochemical parameters were recorded (Table 1). Water velocity was estimated using a flotation method, while canopy cover was estimated by eye. Ten benthic samples were taken from each site using a modified Hess sampler (area 0.0285 m<sup>2</sup>; mesh size 80 µm). Samples were taken from randomly chosen points over a 10-m stretch of each site and preserved in the field using 4% formalin.

The standing stock of forest floor detritus was estimated by taking 10 detritus samples from the ground, using a cylindrical sampler (area 0.0483 m<sup>2</sup>). Five samples were taken from each bank, 1 m apart and no more than 1 m from the river bank. Within each sample, detritus lying above the soil surface was collected.

In the laboratory, aquatic detritus was separated from benthic samples, cleaned of sediment and divided into dead wood (DW), coarse particulate organic matter (CPOM: particle diameter > 1 mm) and fine particulate organic matter (FPOM: particle

diameter < 1 mm). Terrestrial detritus was similarly sorted and then all detritus was dried at 60 °C for 48 h, following which CPOM components were identified to species wherever possible and all detrital fractions were weighed.

Invertebrates in benthic samples were separated into morphologically distinguishable groups and enumerated. Morphological groups were identified as far as possible, using unpublished keys in the possession of Egerton University and appropriate taxonomic works for the region; keys for European families were also used, in association with taxonomic lists of species known to be present in Kenya (e.g. Johanson, 1992; Mathooko, 1998a).

Feeding behaviours are almost unknown for East African macroinvertebrates, but morphological groups ('morphotaxa') were allocated to probable functional feeding groups by analysis of mouthparts and comparison with closely related north temperate taxa; such comparisons were made using functional feeding group information in Tachet, Bornaud & Richoux (1980). Selected individuals of common taxa were subjected to examination of gut contents. Animals were placed onto a microscope slide, their heads removed with a scalpel and the contents of the foregut carefully squeezed into a drop of water; they were then examined under a microscope for identifiable particles.

#### European sites

Invertebrate and CPOM data from Kenyan sites were compared with equivalent information from five rivers in three regions of Europe. The Oreval (43°23'N, 2°6'E) in the Montagne Noire, south-west France, is a circumneutral stream, 2–3 m wide, flowing through woodland dominated by beech (*Fagus sylvatica* L.) and alder [*Alnus glutinosa* (L) Gaertn.]. Its river bed is dominated by pebbles and boulders, with some gravel. Marsh Green (51°04'N, 0°05'E) and Broadstone Stream (51°04'N, 0°03'E) are situated in the Ashdown Forest of south-east England. Broadstone is an acid stream, 1–2 m wide, running through dense broadleaved woodland dominated by birch (*Betula* sp.), alder and oak (*Quercus robur* L.); the river bed is covered by a layer of leaf litter up to 10 cm deep. Marsh Green is a circumneutral stream, 5 m wide, running through open pasture but with riparian alder; its river bed is pebble and gravel. Archer Cleugh (55°15'N, 2°36'W) and Steep Sike (55°11'N,

2°36'W) are circumneutral streams situated in Kielder Forest, north-east England. Archer Cleugh, 3–5 m wide, runs through a mature spruce [*Picea abies* (L.) Karsten; *P. sitchensis* (Bong.) Carrière] plantation; its bed is dominated by pebbles and boulders. Steep Sike, 1–3 m wide, runs through riparian alder and pasture; its bed is dominated by pebbles and sand.

The data used for comparison with Kenyan sites were derived from samples taken in previous studies. All were collected from random points in reference river stretches, using a Surber sampler (area 0.0625 m<sup>2</sup>, mesh size 250 µm) and preserved in the field using 70% alcohol (Ashdown Forest) or 4% formalin (Oreval, Kielder Forest). Invertebrates were identified and enumerated and CPOM was dried at 60 °C for 48 h and weighed. Oreval data, derived from the study described by Dobson (1994) and further unpublished research, were collected in April, August and October 1991 (12 Surber samples each). Ashdown Forest data, derived from the study described by Dobson & Hildrew (1992), were collected in November 1987; February, May and November 1988; and May and November 1989 (14 samples each). Kielder Forest data, from the study described by Pretty (2000) and Pretty & Dobson (2000), were collected every 2 months from April 1997 to April 1999 (five samples each).

#### Analysis

To allow direct comparison among samples, all data were adjusted to values per m<sup>2</sup>. All invertebrates sorted from Kenyan samples were >250 µm diameter, so samples are comparable, despite being collected using different mesh sizes in the two regions. Statistical analyses were carried out using Systat® Version 9.

For statistical comparisons, data were pooled into two regions: Kenya and Europe. Because Kenyan data were derived from a single season, they were compared with European data from different seasons, to determine whether they lay within the European ranges of the parameters recorded. Kenyan values for mass of CPOM and invertebrate density were therefore compared with European data from two dates per site, these being the dates on which mean values of the parameters under comparison were at their highest and lowest recorded levels, respectively. Total invertebrate density was compared by means of a

*t*-test, following  $\log_{10}$  transformation to fit a normal distribution. The CPOM mass, which could not be made to fit a normal distribution, was compared by means of a Mann–Whitney *U*-test.

Percentage of invertebrate individuals that could be allocated to detritivorous functional feeding groups was compared, each Kenyan site acting as a single replicate while two replicates were used from each European site, corresponding to dates when the percentage allocated to the feeding group of interest was at its highest and its lowest. Comparisons were made using Mann–Whitney *U*-test; this comparison was carried out for detritivores (shredders and collector-gatherers combined) and for shredders alone. The correlation between detritivore and shredder abundance and CPOM standing stock in Kenyan sites was determined.

## Results

The Kenyan sites all had a high biomass of benthic organic matter, derived from a variety of plant species; DW was also common on the stream bed at all sites (Table 2). The diversity of CPOM sources normally mirrored that of the riparian vegetation at each site and was therefore high in all sites except Percival's Bridge (Table 2). Total mass of CPOM did not differ between regions (Mann–Whitney:  $P = 0.195$ ), although it was generally higher in Kenyan sites than in all but the highly retentive Broadstone Stream (Fig. 1).

The taxa recorded from the Kenyan streams are listed in Table 3, along with their functional feeding group allocations. All Kenyan sites were dominated by Ephemeroptera, mainly Baetidae, Caenidae and Heptageniidae. Chironomidae, Scirtidae and Elmidae were also very common in some sites, and the Njoro River supported high densities of Oligochaeta. Morphotaxon richness underestimates the true species richness of the Kenyan sites. For example, at least three species of *Baetis* (s.l.)-type Baetidae are found at Naro Moru Lodge (Mathooko, 1998b), although taxonomic revision of this family in Africa is currently in a state of flux, making precise identification premature at this stage. Despite this very conservative estimate of taxon richness, however, the Kenyan streams were similar to the European sites in this respect (Table 4).

In most cases, functional groups inferred from mouthpart or gut contents analysis were equivalent

**Table 2** Organic matter recorded from the river bed and riparian zone at each site. Standing stocks are given as mean (SE), in  $\text{gm}^{-2}$ . All other figures are percentages of the total. DW = dead wood; FPOM = fine particulate organic matter

	Aquatic	Terrestrial
<b>(a) Percival's Bridge (PB)</b>		
Standing stock	113.8 (56.5)	422.7 (56.2)
DW (%)	51.7	15.4
<i>Arundinaria</i> (%)	29.3	63.9
Other leaves (%)	0.3	1.0
FPOM (%)	18.6	19.6
<b>(b) Karandi Bridge (KB)</b>		
Standing stock	78.1 (20.5)	565.6 (49.5)
DW (%)	26.2	44.3
<i>Trichocladus</i> (%)	31.9	9.2
<i>Podocarpus</i> (%)	7.1	2.4
<i>Eucalyptus</i> (%)	1.5	2.8
<i>Rubus</i> (%)	0.9	–
<i>Maesa</i> (%)	–	1.6
Other leaves (%)	13.1	14.7
FPOM (%)	19.3	25.0
<b>(c) Nanyuki Road (NR)</b>		
Standing stock	119.4 (38.6)	307.1 (70.9)
DW (%)	40.5	30.7
<i>Grevillea</i> (%)	12.8	–
<i>Podocarpus</i> (%)	9.2	–
<i>Albizia</i> (%)	4.5	2.7
<i>Eucalyptus</i> (%)	2.1	–
<i>Syzygium</i> (%)	1.9	–
<i>Triumfetta</i> (%)	–	26.0
Other leaves (%)	29.0	18.8
FPOM (%)	–	21.9
<b>(d) Lodge (LO)</b>		
Standing stock	68.5 (18.0)	645.4 (108.3)
Wood (%)	36.5	14.1
<i>Syzygium</i> (%)	24.7	14.2
<i>Podocarpus</i> (%)	22.8	27.5
Other leaves (%)	5.9	13.1
FPOM (%)	10.2	31.2
<b>(e) Burguret River (upper) (BU)</b>		
Standing stock	153.4 (66.6)	263.1 (40.5)
DW (%)	35.5	6.6
<i>Triumfetta</i> (%)	23.3	–
<i>Syzygium</i> (%)	6.3	4.1
<i>Grevillea</i> (%)	5.9	–
<i>Podocarpus</i> (%)	0.2	–
<i>Ficus</i> (%)	–	38.1
<i>Juniperus</i> (%)	–	11.3
Other leaves (%)	16.1	9.1
FPOM (%)	11.8	30.8
<b>(f) Burguret River (lower) (BL)</b>		
Standing stock	281.1 (106.0)	622.1 (89.1)
DW (%)	49.0	25.8
<i>Ficus</i> (%)	19.0	–
<i>Syzygium</i> (%)	5.0	5.8
<i>Albizia</i> (%)	0.2	2.3
<i>Podocarpus</i> (%)	0.1	–

Table 2 (Continued)

	Aquatic	Terrestrial
<i>Juniperus</i> (%)	–	11.3
Other leaves (%)	21.9	7.8
FPOM (%)	4.8	58.3
(g) Njoro River (NJ)		
Standing stock	217.3 (75.4)	1250.0 (268.1)
DW (%)	42.2	21.7
<i>Syzygium</i> (%)	16.5	30.2
<i>Dombeya</i> (%)	2.5	–
<i>Rhus</i> (%)	2.2	0.7
<i>Ipomea</i> (%)	–	0.7
<i>Eucalyptus</i> (%)	–	0.6
Other leaves (%)	7.4	3.2
FPOM (%)	29.2	43.0

to those in the literature. An exception was the baetid *Acanthiops*, an African endemic that was assumed to be a shredder on the strength of one individual whose foregut contained only large pieces of leaf litter (up to 1 mm diameter); four other specimens examined all had empty guts. *Baetis*-type mayflies are generally allocated to the grazer-scraper functional feeding group (but see Winterbourn, Hildrew & Box, 1985); examination of gut contents of several Kenyan individuals, however, revealed FPOM to be the dominant food source during the collection period.

Densities of invertebrates were significantly higher in Kenyan streams than in European streams ( $t_{166} = 5.26$ ;  $P < 0.001$ ), although highest densities for

most European sites were within the range recorded from Kenyan sites (Fig. 2). Detritivore proportions did not differ among regions (Mann–Whitney:  $P = 0.152$ ), but shredder proportions were significantly lower in Kenyan than European sites (Mann–Whitney:  $P = 0.002$ ). Indeed, shredder proportions were very low in all Kenyan sites except Percival's Bridge, and shredders were apparently completely absent from samples taken in the Njoro River (Fig. 3). Kenyan shredders, where present, were generally small-bodied (<7 mm long), with the exception of crabs (*Potamonautes* sp.) in Karandi Bridge and large Tipulinae in Percival's Bridge. Among European sites, Marsh Green and Oreval supported shredder proportions close to the low values recorded from Kenya, but only in spring and early summer when their detrital standing stocks were very low. In three of the Kenyan sites, numbers of detritivores correlated positively with mass of CPOM, but only two of these sites showed a correlation between CPOM mass and number of shredders (Table 5).

## Discussion

This study demonstrates some important similarities between the regions under comparison, in that mass of CPOM and number of taxa in Kenya were within the ranges recorded from a heterogeneous range of European sites. Invertebrate densities were higher in Kenyan than European sites, and detritivores were

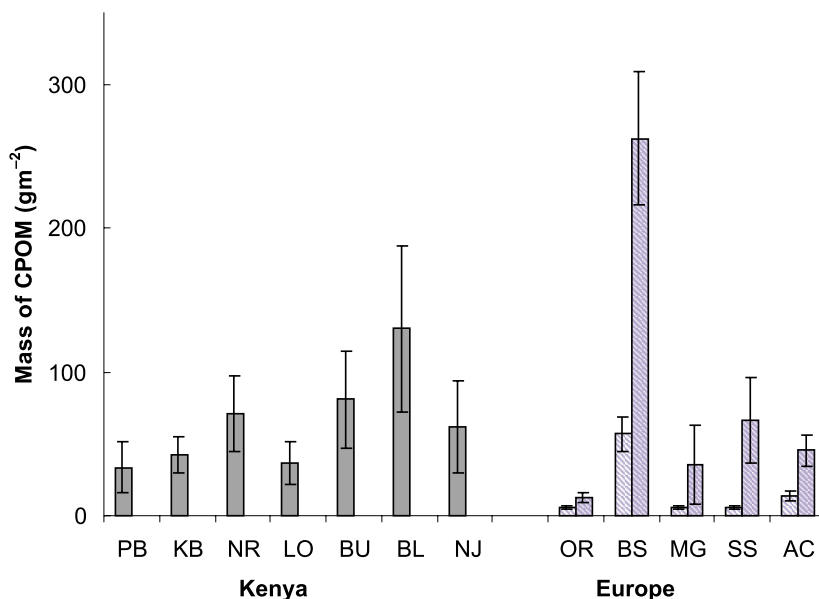


Fig. 1 Mass of CPOM ( $\text{gm}^{-2}$ ) in all sites. For Kenyan sites, mean mass recorded ( $\pm 1$  SE) is plotted. For European sites, the left hand bar of each pair shows mean mass ( $\pm 1$  SE) during the sample date when CPOM standing stocks were at their lowest, while the right hand bar shows mean mass ( $\pm 1$  SE) during the sample date when they were at their highest. Note that values for Kenyan sites differ from those in Table 2 because DW and FPOM have been excluded. See legend to Table 4 for site abbreviations.

**Table 3** Taxa recorded from Kenyan sites, with allocation to functional feeding groups

	f.f. group	PB	KB	NR	LO	BU	BL	NJ
Planaria	Pre	<1	3	<1	8	1	3	3
Nematoda	Pre	<1			<1			
Oligochaeta – Lumbriculidae*	Col†	2	2	<1	2	<1	1	12
Ancylidae – <i>Ferrisia</i>	Gra†				3			<1
Sphaeriidae	Filt†	8	2					<1
Ostracoda	Pre				<1			1
Decapoda – <i>Potamonautes</i>	Shrt†		<1					
Acari	Pre							<1
Perlodidae – <i>Neoperla</i>	Pre†			2	<1	2	3	
Anisoptera	Pre†				<1			
Zygoptera – Protoneuridae	Pre†							1
Baetidae – <i>Baetis</i> s.l.*	Col†, ‡	12	13	8	35	7	17	3
Baetidae – <i>Acanthiops</i>	Shrt†, ‡	3				1	<1	
Caenidae*	Col	32	10	19	2	1	<1	21
Oligoneuridae – <i>Oligoneuriopsis</i>	Filt†, ‡					<1	1	
Heptageniidae – <i>Afronurus</i>	Gra†		11	5	9	20	11	
Leptophlebiidae – <i>Choroterpes</i> ( <i>Euthraulus</i> )	Col†, ‡	1	20	2	1	4	2	
Prosopistomatidae – <i>Prosopistoma</i>	Gra†		<1					
Tricorythidae – <i>Diceromyzon</i>	Filt†					<1		
Hydropsychidae	Fil	1	1	2	2	4	6	1
Lepidostomatidae	Shr	1		<1	<1	<1	<1	
Leptoceridae	Shr	4	<1		<1	<1	2	
Philopotamidae – <i>Chimarra</i>	Fil		<1	<1		1	<1	
Polycentropodidae	Pre							<1
Scirtidae*	Gra	30	2	1	3	3	4	
Elmidae*	Gra			4	3	10	12	1
Dytiscidae	Pre†	<1						
Gyrinidae	Pre	<1						
Tipulidae – Tipulinae*	Shr	3		<1	<1	<1		
Chironomidae – Tanytopodiinae	Pre	2	4	2	4			
Chironomidae – others*	Col	1	27	54	26	33	22	54
Simuliidae	Filt†	1	5	<1		15	15	
Ceratopogonidae								
<i>Culicoides</i> type	Pre			<1	<1	1	<1	3
<i>Atrichopogon</i> type	Col							<1
Athericidae	Pre					<1	<1	
Dixidae	Col	<1						

Taxa marked \* were separable into distinct morphological forms, presumed to represent different species. 'Chironomidae – others\*' includes Chironominae, Orthoclaadiinae and many very small individuals which were not identified further.

Allocation was by reference to literature and, where possible, †mouthpart analysis and ‡gut contents analysis. Figures refer to the approximate abundance of each taxon as a percentage of the total within each site. Col = collector-gatherer; Fil = filterer; Gra = grazer-scrafer; Pre = predator; Shr = shredder. PB = Percival's Bridge, KB = Karandi Bridge, NR = Nanyuki Road, LO = Naro Moru Lodge, BU = Upper Burguret River, BL = Lower Burguret River, NJ = Njoro River.

important functional components in both regions. These patterns therefore make the apparent paucity of shredders in Kenyan streams all the more remarkable. Shredders were important only in Percival's Bridge and, even there, numbers were low, albeit dominated by individually large tipulid larvae. Elsewhere, however, the shredder guild was generally represented by very low numbers of individuals, usually small in size. In this respect, data from the

streams sampled appear to support the evidence from studies in Latin America, South-east Asia and Uganda, cited earlier, that shredders are poorly represented in tropical streams.

The paucity of shredders is not the result of a shortage of CPOM, as all sites supported high biomass of detritus. Furthermore, terrestrial detritus measurements demonstrated a large and diverse potential source of lateral inputs, while high standing stocks of

**Table 4** Taxon richness in each site. The table shows total number of distinguishable taxa in each of the Kenyan sites, and the range in number of taxa recorded on each sample date from the European sites. The total area sampled on each occasion is given, to allow comparison of sampling effort

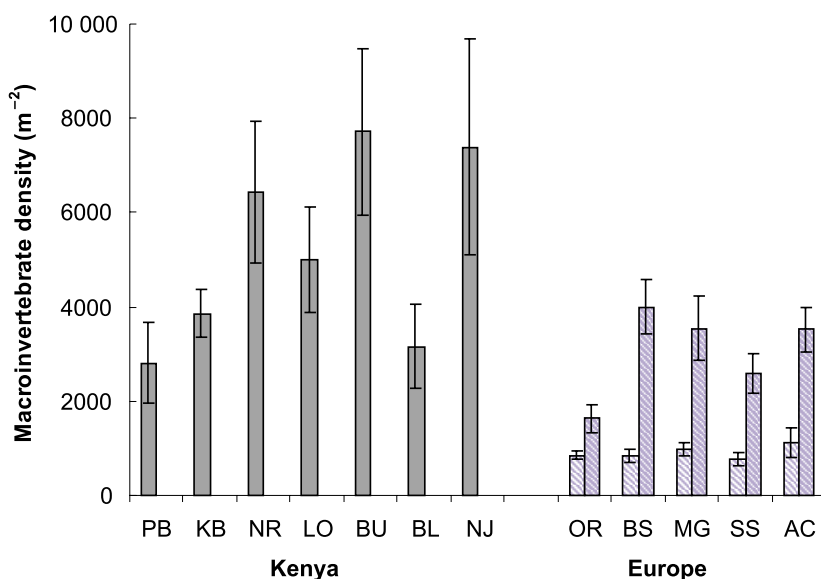
Region	Total area sampled (m <sup>2</sup> )	Site	Number of taxa
Kenya: Naro Moru River	0.285	KB	22
		PB	19
		NR	20
		LO	22
Kenya: Burguret River	0.285	BU	26
		BL	22
Kenya: Njoro River	0.285	NJ	19
Southern France	0.75	OR	21–33
South-east England	0.875	BS	14–23
		MG	14–23
		SS	17–25
North-east England	0.3125	SS	17–25
		AC	29–40

PB = Percival's Bridge, KB = Karandi Bridge, NR = Nanyuki Road, LO = Naro Moru Lodge, BU = Upper Burguret River, BL = Lower Burguret River, NJ = Njoro River, OR = Oreval, BS = Broadstone Stream, MG = Marsh Green, SS = Steep Sike, AC = Archers Cleugh.

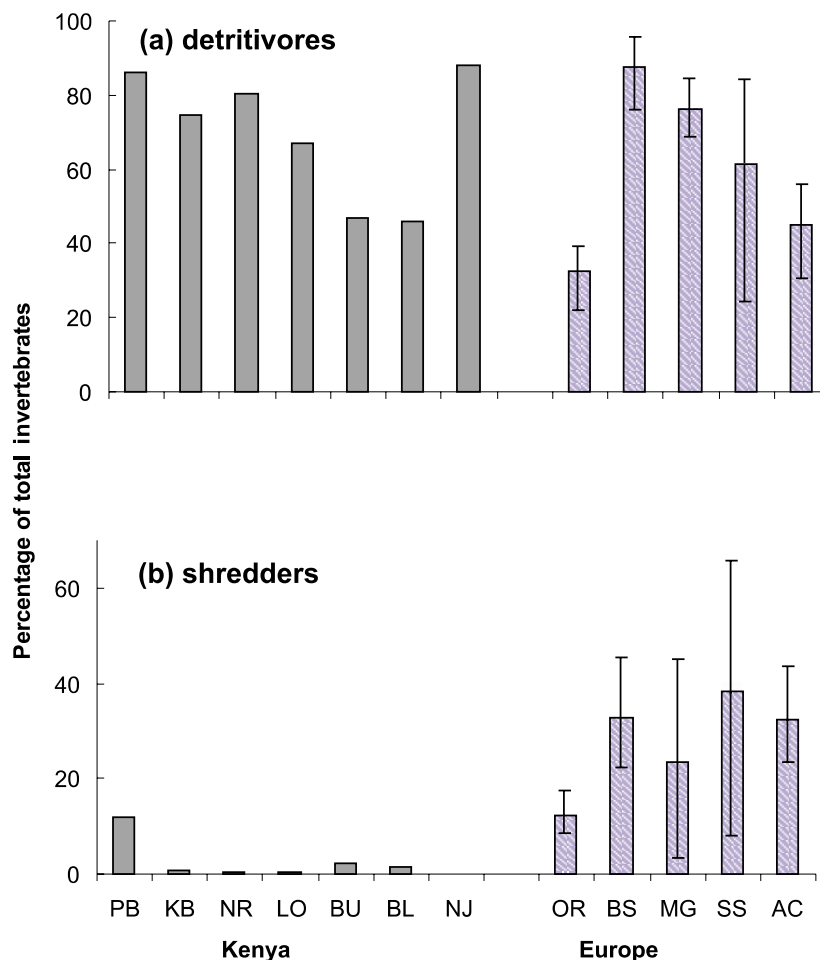
DW in the channels would imply efficient retention under moderate flows. The standing stock of CPOM in pools in the Njoro River site averages  $>700 \text{ g}^{-2}$  and, although highly variable, is never  $<20 \text{ g}^{-2}$  (Magana, 2000). This compares with a maximum recorded standing stock of  $260 \text{ g}^{-2}$  in the most retentive European site, and  $<10 \text{ g}^{-2}$  from several European sites during spring and summer. In contrast to European rivers, however, there is no distinct seasonality

observed in CPOM standing stocks in the Njoro River; inputs are continuous but standing stocks are determined by discharge (Magana, 2000). The high standing stocks in all the Kenyan sites were probably a reflection of the low flows being experienced in the region during the period of this study. The failure of the autumn rains meant that rivers had not been replenished; indeed the Njoro River, which is heavily dependent upon seasonal rains, ceased to flow several months after this study was completed. The Mount Kenya rivers were, however, less affected by this because the mountain has a major influence on local climate and receives rain on its higher slopes every day, although flows were rather lower than normal.

Our implicit assumption so far is that shredders were rare despite high CPOM levels. An alternative perspective, however, is that CPOM levels are high because there are few shredders. Low shredder abundance means that leaf litter breakdown is mediated by microbial activity and physical attrition. During low flows, physical attrition is low and this, in turn, will limit microbial densities, which are dependent upon detritus being broken up and exposing a high surface area to optimise their activity. Low physical attrition and absence of shredding activity will therefore result in slow breakdown rates, allowing CPOM to persist for long periods. A further process influencing CPOM standing stocks may be the diversity of shredder species; Jonsson, Malmqvist & Hoffsten (2001; see also Jonsson & Malmqvist, 2000) present a compelling argument for the importance of multispecies shredder



**Fig. 2** Density of invertebrates ( $\text{m}^{-2}$ ) in all sites. For Kenyan sites, mean number recorded ( $\pm 1$  SE) is plotted. For European sites, the left hand bar of each pair shows mean number ( $\pm 1$  SE) during the sample date when densities were at their lowest, while the right hand bar shows mean number ( $\pm 1$  SE) during the sample date when they were at their highest. See legend to Table 4 for site abbreviations.



**Fig. 3** Percentage of total invertebrates recorded that were (a) detritivores and (b) shredders. For European sites, the bar represents the mean value based upon percentages calculated for each of the sampling dates separately, with error bars representing the minimum and maximum percentage recorded from each site. See legend to Table 4 for site abbreviations.

**Table 5** Summary of Pearson's product moment correlation coefficients comparing detritivore and shredder densities with CPOM biomass;  $n = 10$  in each case. See Table 4 for abbreviations

Site	Detritivores	Shredders
PB	0.777*	0.611
KB	-0.075	-0.485
NR	0.962***	0.830**
LO	0.605	-0.005
BU	0.673	0.251
BL	0.750*	0.913**
NJ	-0.059	-

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

assemblages in enhancing the efficiency of leaf litter breakdown. If different detritivore species within an assemblage contribute to detritus processing in different ways, then optimum efficiency at exploiting the resource may only be achieved in the presence of a species-rich shredder assemblage (Covich, 1999). The low diversity of shredders in the Kenyan rivers may

therefore reduce the efficiency of this guild at processing the entire detritus resource.

We speculate that there are three potential reasons for the paucity of shredders in our Kenyan samples. First, tropical streams may be genuinely different to north temperate streams in that they do not support shredders. Possible support for this suggestion comes from the data presented here: the only site in which shredders were apparently important was Percival's Bridge, which, being at high altitude, was the coldest. This lends support to the microbial activity hypothesis of Irons *et al.* (1994): at high altitudes, microorganisms no longer have the temperature advantage and detritus will therefore persist in the river long enough to support invertebrate detritivores. Investigations of detritus processing and shredder abundance across a range of altitudes would help to demonstrate the importance of this process. Actual differences between tropical and temperate regions are, however, likely to be more complex than simply a direct effect

of temperature. Lack of seasonality of leaf litter inputs, coupled with high variation in flow, reduces the predictability of the detrital food source in many tropical streams. Furthermore, whereas north temperate streams often support riparian trees with relatively labile leaf litter, such as alder and willow (*Salix* spp.), many of the common riparian trees in our study sites have waxy leaves that are probably refractory and require extended periods of conditioning.

Secondly, we may have allocated our specimens incorrectly. Published data on feeding mechanisms and diets of baetid mayflies would have led us to allocate *Acanthiops* to the grazer or collector-gatherer feeding guild. The Baetidae has, however, undergone radiation in Africa that is absent elsewhere, including, for example, predatory forms (Lugo-Ortiz & McCafferty, 1998). Therefore, feeding groups cannot be assumed to be the same as those of relatives in Europe. Among other groups, however, there is no evidence that allocations from the literature were incorrect; *Acanthiops* is morphologically very different to other baetid larvae, whereas other taxa collected do not show such major differences. Only a more detailed study of gut contents analysis and feeding preferences will, however, answer this criticism adequately.

Thirdly, our sampling strategy may have been inadequate to catch potentially important shredders. Pringle & Ramírez (1998) demonstrated that standard benthic sampling methods severely underestimated the abundance of several taxa that were probably important shredders in their Costa Rican site. By taking drift samples, they showed that numbers of atyid shrimps were very high in parts of their study river, despite not having been recorded to any great extent in benthic samples. An analogous situation may be operating in Kenyan rivers. Drift measurements and gut contents analysis of introduced rainbow trout (*Oncorhynchus mykiss* Walbaum) at Naro Moru Lodge revealed the same taxa, in similar proportions, to those caught in benthic samples (Mathooko, 1994, 1996); this demonstrates that, in one site at least, we were not missing taxa that drift measurements would have revealed. There is, however, a freshwater crab (*Potamonautes* sp.), which was only caught at Karandi Bridge by the formal sampling process, but which is abundant in the Njoro River (personal observation). Crabs are very dispersed on the river bed, reducing the probability of being caught by the sample method used. Furthermore, larger

individuals, which can exceed 50 mm, are probably able to move away when they sense the approach of the sampling device. The only specimens caught were small, with carapace width under 20 mm.

We believe that the reality is a combination of these three factors. First, Kenyan streams have more rapid microbial decomposition than European sites, but also there is the complication of low palatability leaf litter inputs. Secondly, until we have made more detailed studies of feeding preferences, some of our functional feeding group allocations must be considered tentative. Finally, the shredding guild is clearly not dominated by taxa that occupy it in the north temperate zone, but this does not mean that it is absent. Crabs do eat detritus and may be abundant enough to fill the shredder niche; an accurate indication of their densities would allow this prediction to be tested.

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