

Macroinvertebrate community structure and altitudinal changes in the upper reaches of a warm temperate southern African river

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SUMMARY

1. The Buffalo River rises 1200 m above sea level, drops 600 m in the first 7 km, and a further 100 m in the next 30 river kilometres. Macroinvertebrates were sampled, and environmental variables measured monthly in 1987, at four sites along this part of the river.
2. Flow at the headwater site (1120 m a.s.l., 1 km from the source) was seasonal, though pools remained and subterranean flow was continuous. Twelve macroinvertebrate taxa were found exclusively at this site, where conductivity, pH and nutrient concentrations were low.
3. Flow at the foothill site (530 m a.s.l., 7 km from the source) was perennial. The invertebrate community, although distinct from that at downstream sites, lacked the unique taxa of the headwater site. Conductivity, pH and nutrient concentrations were higher.
4. The two sites downstream of the foothills (450 m a.s.l., 18 km from the source, and 410 m a.s.l., 31 km from the source), had similar invertebrate communities. Conductivity, pH and nutrient concentrations were higher than at the upper sites.
5. Community structure changed most between the headwater and foothill sites. This paralleled changes in river steepness rather than changes in measured physicochemical variables.

Introduction

Investigations of macroinvertebrate species composition in streams, and the influence of environmental variables on community structure, have frequently concentrated on the effects of water quality variables (Wright *et al.*, 1984; Furse *et al.*, 1984; Marchant, Mitchell & Norris, 1984; Faith, 1990; Rundle & Hildrew, 1990). During the past two decades, concepts of the structure and function of stream ecosystems developed vigorously (e.g. Vannote *et al.*, 1980), and macroinvertebrate distribution was primarily related to the organic energy base, as well as to habitat or biotope preferences (Culp & Davies, 1982; Cushing

et al., 1983; Hawkins, 1984; Bott *et al.*, 1985; Wallace, 1988). The role of slope and elevation has been mentioned (Sheldon, 1985; Marchant *et al.*, 1985; Devan & Mucina, 1986; Ormerod & Edwards, 1987; Benke & Meyer, 1988; Gladden & Smock, 1990), but not as explicitly emphasized as, for example, in vegetation ecology, where elevation has long been recognized as a surrogate for a range of environmental gradients which strongly influence vegetation composition (Austin, Cunningham & Good, 1983; Druitt, Enright & Ogden, 1990; Parker, 1991; Palmer & van Staden, 1992). The recognition of variables for which steepness and altitude are surrogates in aquatic ecosystems, is implicit in the long-standing recognition of the

importance of factors such as temperature and current speed (Hynes, 1970). More recently, Statzner, Gore & Resh (1988) have emphasized the importance of hydraulic variables such as shear stress, which are correlated with changes in steepness and altitude.

An intensive study of the ecology of the Buffalo River, eastern Cape, South Africa was conducted from 1986 to 1988, the initial aim being to evaluate the downstream effects of four impoundments (Palmer & O'Keeffe, 1989, 1990a,b; O'Keeffe *et al.*, 1990). In 1987 the study was extended to include a site in the headwaters of the river (Palmer, O'Keeffe & Palmer, 1991).

In the Buffalo River, the most obvious feature of benthic community structure was the unique species composition at the headwater site (1 km from the source), which differed even from the foothill site, a mere 6 km downstream, and still above the first impoundment (Palmer, 1991). Species composition continued to change along the next 23 km, but remained largely constant in the lower reaches (30–125 km from the source).

In contrast to streams at high latitudes and altitudes (Prowse, 1994; Scrimgeour *et al.*, 1994), which are subject to the physical effects of ice scouring, and

extreme temperatures, the Buffalo River is a warm temperate stream rising at a modest altitude (1200 m). Nevertheless, the sharpest changes in community structure were associated with the steepest part of the altitudinal gradient. We describe changes in community structure along the first 30 km of the river, together with concurrent changes in a range of physicochemical variables.

Study area and methods

General descriptions of the Buffalo River appear in papers referred to in the Introduction. In the present study only the first 31 km of the river were considered (Fig. 1). Over this distance there was an elevation change of 780 m, whereas over the following 210 km the change was only a further 410 m (Fig. 2). The Buffalo River rises in the Amatole Mountains, at an elevation of 1200 m, from a grassy wetland, which soon gave way to near-pristine closed-canopy, Afro-montane forest (Site 0, 1120 m a.s.l., Fig. 1). The headwater stream had a steep gradient of about 200 m km^{-1} for 7 km, dropping 600 m between Sites 0 and 1. Site 1, the foothill site, was just above Maden Dam, the first of four impoundments (specifications

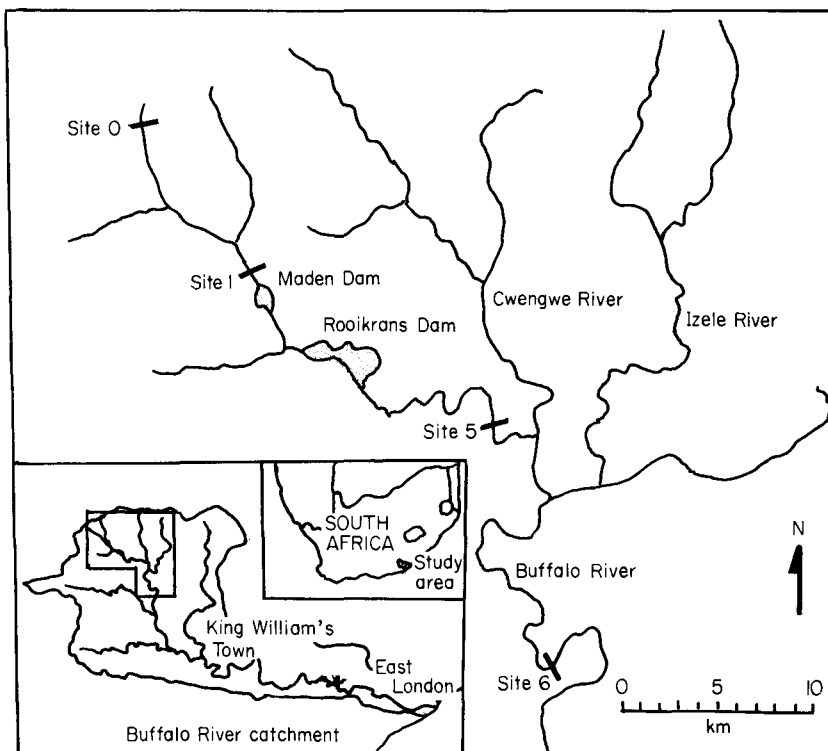


Fig. 1 Map of the upper catchment of the Buffalo River, eastern Cape, South Africa. The sample site numbers are not sequential, as sites were selected from sixteen sampled in a more extensive study. The same site numbering has been retained in all publications concerning the Buffalo River, to facilitate cross referencing.

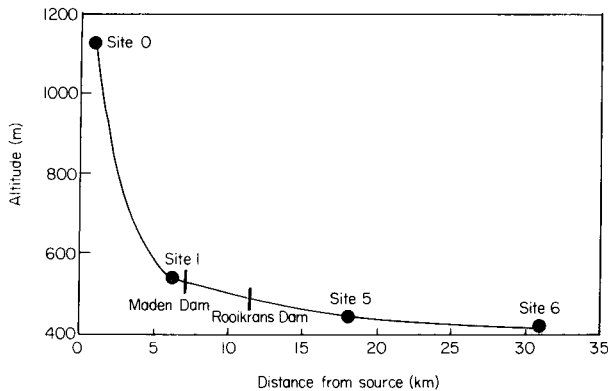


Fig. 2 Altitudinal profile of the upper Buffalo River showing the position of the sampling sites and impoundments.

of the impoundments are given in Palmer & O'Keeffe, 1990a). Rooikrans Dam is 5 km downstream of Maden Dam. In its upper middle reaches (Sites 2b–5) the river flowed through agricultural land. Land use in the relic flood plains upstream of Kingwilliam's Town (Sites 6 and 7) was intensive market gardening, and water quality was affected by fertilizer-rich, agricultural runoff. Site 6 was 180 m lower than Site 1, at the beginning of the lower middle reaches of the river.

The river was sampled approximately monthly (April 1986–April 1988) at sixteen sites; details of methods, and the physicochemical characteristics of the sites are given by O'Keeffe *et al.* (1990) and Palmer & O'Keeffe (1989, 1990a–c). Since the aim of the present study was to evaluate the role of altitude and slope in structuring the macroinvertebrate community, Sites 0, 1, 5 and 6 were selected from among the other sites. They span the distance over which the elevation gradient changed from steep to shallow. Sites 0 and 1 were upstream of any dams, whereas Site 5 was 6.5 km below Rooikrans Dam, beyond the reset distance of most factors (Palmer & O'Keeffe, 1989, 1990a). Data from Sites 2, 3 and 4 are not considered in this paper as they reflect the downstream effects of Maden and Rooikrans Dams. Sites further downstream beyond Site 6 were not considered as they were complicated by deteriorating water quality, and two large impoundments (Palmer & O'Keeffe, 1989, 1990a).

On each sampling occasion, three separate replicate samples (Chutter & Noble, 1966) were collected from riffles, at each of the sites. Samples were collected using a netted (80 μ m mesh) box sampler (0.09 m²;

Merritt, Cummins & Resh, 1984). In the laboratory, samples were washed through a 1 mm mesh net, into an 80 μ m mesh net. The retained macroinvertebrates were either counted totally, or if numbers were high (>500), counted using a subsampling method based on that of Allanson & Kerrich (1961), and described in detail by Palmer & O'Keeffe (1990c). Invertebrates were identified to species where possible (e.g. most Ephemeroptera, Trichoptera and Simuliidae), and otherwise to as fine a level as possible (e.g. Coleoptera to family, Oligochaeta to class and Nematoda to phylum). Voucher specimens and sorted samples are lodged with the national collection of freshwater invertebrates at the Albany Museum, Grahamstown, South Africa.

Taxonomic composition data from January to December 1987 are reported, since Site 0 was sampled over that period. Mean summer (December, January, February) and mean winter (June, July, August) values for four of the fifteen environmental variables which were measured over the entire sampling period are provided for each site (Table 1). These variables were selected from the larger data set as examples of patterns of variable change with downstream distance. Conductivity exemplifies the pattern of all the individual major ions sampled (magnesium, potassium, sodium, chloride, calcium, aluminium and fluoride); all increased in concentration downstream, but the range of concentrations, and their variability, also increased downstream. Phosphate concentrations like those of nitrate, nitrite and ammonia, were extremely variable. Temperature was the most seasonally distinct variable, and pH the only variable to show the greatest rate of change between Sites 0 and 1. All fifteen variables were related to species composition in the ordination procedure.

Absolute numbers of animals per sample were standardized by conversion to relative abundance scores. These were ordinated, and related to physicochemical variables using canonical correspondence analysis (CCA; ter Braak, 1988).

Results

In this study, data from the upper section of the Buffalo River were selected in an attempt to clarify the role of altitude and slope in structuring the benthic assemblage. More comprehensive descriptions of

faunal associations are reported in Palmer *et al.* (1991) and Palmer (1991). The most obvious feature of all analyses of faunal structure was the distinctive nature of the assemblage at Site 0. Greater changes in species composition occurred between Sites 0 and 1, which are separated by the steepest altitudinal change (Fig. 2), than between any other adjacent sites, despite there being no impoundment between these sites. Of the physicochemical variables measured, only pH showed the greatest rate of change between Sites 0 and 1 (Table 1). However, at the time of sampling, our primary focus was on the downstream effects of dams, and the role of habitat, season and physicochemistry on species composition. The steep part of the altitudinal gradient was not sampled, neither were the hydraulic characteristics recorded. Altitudinal data could not be included in the CCA because samples collected from the four sites in different months would all have provided the same altitudinal information. The role of altitudinal change therefore has to be inferred, and cannot be demonstrated by correlation.

It is possible to relate species composition at Sites 0, 1, 5 and 6 to physicochemical gradients (Fig. 3). CCA shows that Site 0 is separated from Site 1, 5 and 6 along axis 1, and that along this axis pH is the factor most strongly correlated with species composition. Along axis 2, where Sites 1, 5 and 6 are distinguished (although less strongly), sodium ions and total dissolved salts are most strongly correlated.

Site 1 is separated from Sites 5 and 6 by a steeper altitudinal gradient than occurs down the rest of the river, but also by two impoundments and changes in

physicochemistry (Palmer & O'Keeffe, 1990a). The marked distinction of Site 0 shown in Fig. 3 masks any differentiation of the other sites. CCA was also applied to data from Sites 1, 5 and 6, excluding Site 0 samples (Fig. 4); the separation of Site 1 from Sites 5 and 6 again paralleled the elevation gradient, and was correlated with pH.

The primary separation of Site 0, and the secondary distinction of Site 1 was also apparent in terms of presence and absence of taxa. Table 2 shows the percentage frequencies of taxa collected in riffle samples from Sites 0, 1, 5 and 6 in the summer of 1987. Twelve taxa occurred exclusively at Site 0, one at Site 1, three at Site 5 and four at Site 6. Riffles dried in the winter at Site 0, and the percentages of taxa collected from riffles in winter (Table 3) show four taxa unique to Site 1, five collected only from Site 5, and one exclusive to Site 6.

Discussion

In contrast to the cold water, high elevation streams described elsewhere in this issue, the upper Buffalo River is a warm temperate stream, which rises in coastal mountains at an elevation of 1200 m, and has a headwater temperature range of 8–17°C. Despite the lack of temperature and altitudinal extremes, major changes in the macroinvertebrate fauna occurred within the first 7 km, over an elevation drop of 600 m.

The riffle community at the headwater site (Site 0) was the most distinct of the four sites, as shown by the CCA ordination, and by the occurrence of twelve taxa that were only found at this site. Palmer (1991)

Table 1 Mean (\pm SE) summer (S) and winter (W) values for temperature, conductivity and phosphate concentration, and pH ranges for Sites 0, 1, 5 and 6

	Site no.							
	0		1		5		6	
	S	W	S	W	S	W	S	W
Conductivity (mS m ⁻¹)	3.3 (\pm 1.3)	4.9 (\pm 1.6)	6.2 (\pm 2.0)	10.8 (\pm 1.7)	9.9 (\pm 3.2)	14.6 (\pm 4.0)	26.4 (\pm 15.4)	57.9 (\pm 10.6)
pH	5.3–7.3	5.9–6.6	6.5–7.2	6.8–7.5	6.7–7.4	7.0–8.3	7.0–7.9	7.5–8.1
Temperature (°C)	15.6 (\pm 2.3)	8.8 (\pm 0.1)	16.4 (\pm 1.9)	9.2 (\pm 1.8)	22.0 (\pm 2.3)	11.2 (\pm 0.8)	22.8 (\pm 3.5)	12.8 (\pm 0.7)
Soluble reactive phosphate (mg l ⁻¹)	0.051 (\pm 0.04)	0.090 (\pm 0.009)	0.072 (\pm 0.05)	0.074 (\pm 0.05)	0.057 (\pm 0.02)	0.053 (\pm 0.06)	0.074 (\pm 0.02)	0.045 (\pm 0.07)

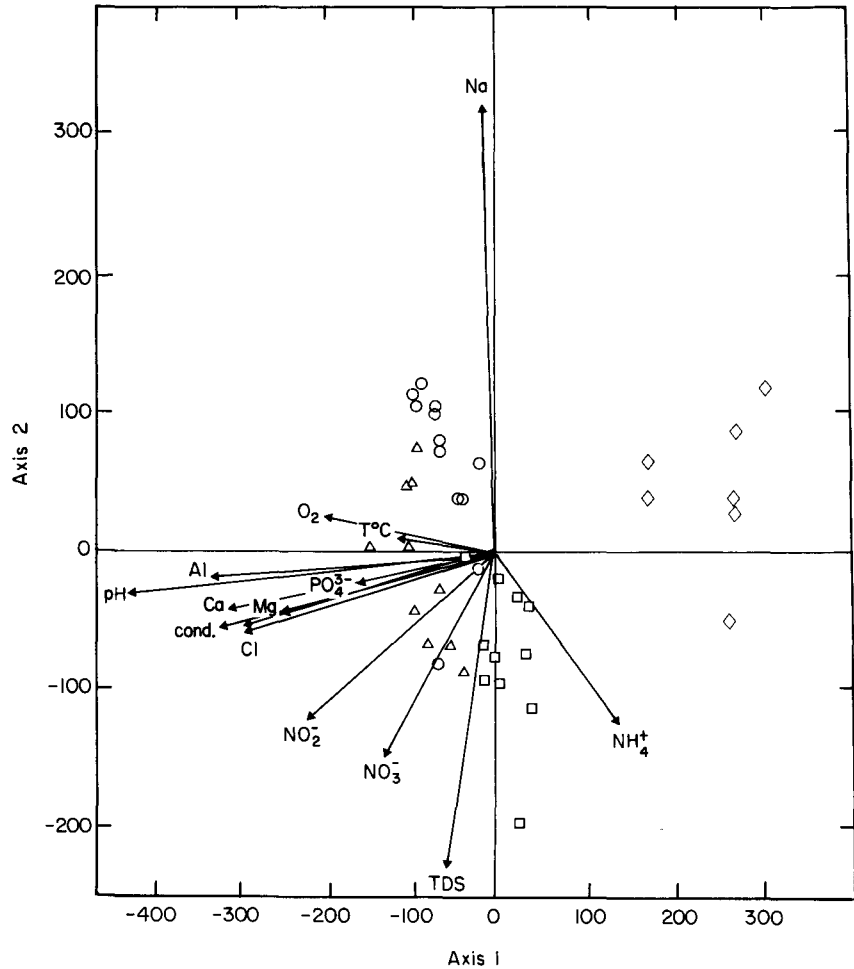


Fig. 3 Ordination diagram (Canonical Correspondence Analysis) showing the association of sets of three replicate samples collected monthly during 1987 from riffles in the Buffalo River at Sites 0 (\diamond), 1 (\square), 5 (\circ), and 6 (\triangle). Site 0 is separated from the other sites along axis 1, and Site 1 from Sites 5 and 6 along axis 2. The discrimination of sites based on faunal composition follows the altitudinal gradient, and is most strongly correlated with pH.

showed that Site 0 was faunally distinct from all others on the river, and that the degree of change in community composition between Sites 0 and 1 was not repeated elsewhere along the river. This indicated that environmental factors structuring the community at the top of the river were different from those at the foothills and downstream.

An important factor to consider is seasonality of flow. The data presented here were collected from riffles, and between May and October 1987 riffles were exposed, so that surface water was restricted to pools connected by groundwater flow. Several of the dominant species, such as the leptophlebiid *Adenophlebia auriculata*, were found in riffles and pools in summer, and survived in pools during winter. However, 500 m below Site 0 the stream was perennial, and provided a source of potential upstream colonists. Pool fauna were sampled at Sites 0, 1 and 6, throughout the year, and like the riffle

fauna in flowing conditions, species composition in pools at Site 0 was different from that at Site 1 (Palmer, 1991). Therefore, although the role of seasonality, and flow cessation, should not be discounted there is evidence that it does not adequately account for the degree of faunal change between Sites 0 and 1.

There has been considerable interest in factors affecting macroinvertebrate distribution in streams. Environmental variables commonly implicated have been physical factors such as: hydraulic conditions (Statzner *et al.*, 1988) and substrate composition (Rabeni & Minshall, 1977; Minshall & Minshall, 1977; Reice 1981); water chemistry (Faith, 1990; Rundle & Hildrew, 1990) particularly pH (Wade, Ormerod & Gee, 1989); salinity (Bunn & Davies, 1992); the consequences of increased nutrient loads (Haslam, 1990); water temperature (Vannote & Sweeney, 1980); availability and type of food (Hawkins, Murphy & Anderson, 1982; Winterbourn, 1982; Drake, 1984;

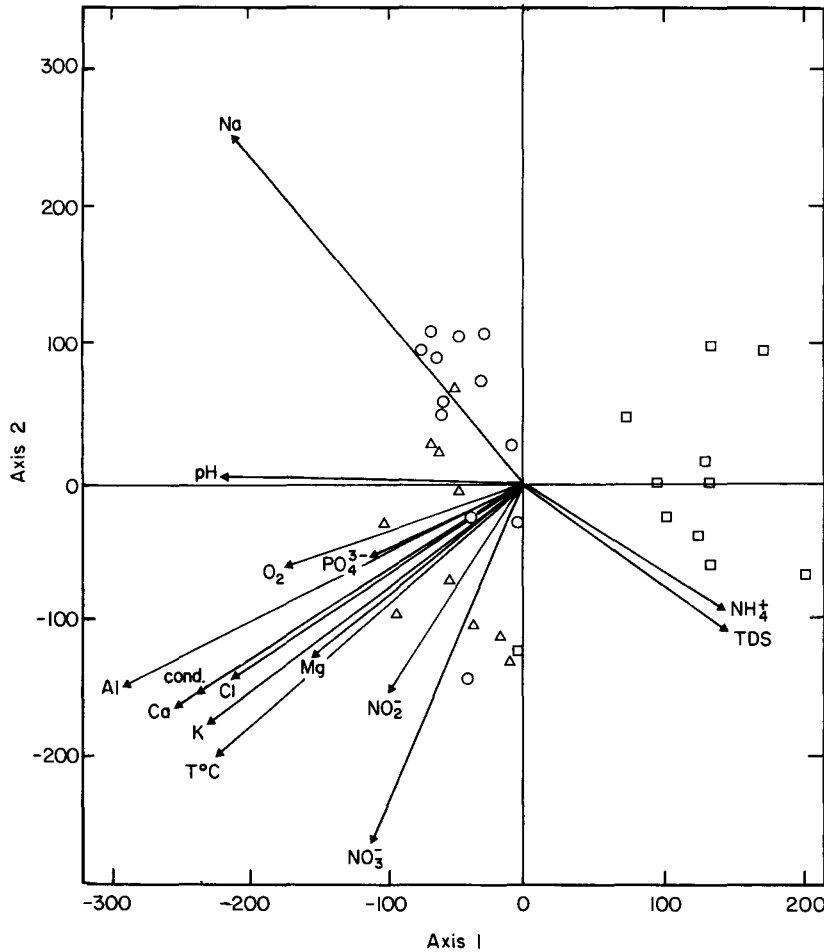


Fig. 4 Ordination diagram (Canonical Correspondence Analysis) showing the association of sets of three replicate samples, collected monthly during 1987, from riffles in the Buffalo River, at Sites 1 (\square), 5 (\circ), and 6 (\triangle). Site 0 is excluded from the ordination, and Site 1 is separated from Sites 5 and 6, along axis 1; pH is most closely correlated with axis 1.

Barmuta, 1988); and habitats (Cowie, 1985; McCulloch, 1986; Barmuta, 1989; Brussock & Brown, 1991). Each of these factors can be considered in relation to the faunal changes observed along the upper Buffalo River.

Hydraulic conditions

We restricted our comparison to macroinvertebrates from riffle habitats, which implies a fairly similar range of hydraulic conditions. Therefore it is unlikely that hydraulic differences accounted for the pronounced dissimilarity between communities at Sites 0 and 1.

Physicochemistry

Water chemistry gradients did not parallel the rate of

change in community composition between Sites 0 and 1, except for pH, which was also most strongly correlated with faunal composition in the ordination. Although it seems likely that pH is the most important physicochemical variable, it should be noted that the pH at Site 0 was generally slightly above 6, compared with 7–7.5 at the other three sites, although values up to 7.8 were recorded at Site 0. Major ion composition, exemplified by conductivity, changed by less than 5 mS m^{-1} over the first 7 km, and by at least 20 mS m^{-1} over the subsequent 24 km. Soluble reactive phosphate ($\text{PO}_4\text{-P}$) concentrations were highly variable, but the range at all four sites was comparable. Temperatures rose gradually down the river from a summer mean of 16°C at Site 0 to 23°C at Site 6, and from a winter mean of 9°C at Site 0 to 13°C at Site 6. Temperature changed less between Sites 0 and 1 than between Sites 1 and 5.

Table 2 Percentage composition and total numbers of macroinvertebrates collected in riffle samples from four sites in the upper Buffalo River during the summer of 1987 (November–April). (Species in order of descending abundance at Site 0; A, Arthropoda; C, Coleoptera; Co, Coelenterata; Cr, Crustacea; D, Diptera; E, Ephemeroptera; M, Mollusca; P, Plecoptera; Pl, Platyhelminthes; T, Trichoptera)

Taxa		Site no.				Total numbers (m ²)
		0	1	5	6	
<i>Goerodes cafrariae</i>	T	100	0	0	0	363
<i>Dischymus ensifer</i>	T	100	0	0	0	240
Megaloptera		100	0	0	0	219
<i>Baetis capensis</i>	E	100	0	0	0	96
<i>Simulium dentulosum</i>	D	100	0	0	0	85
<i>Aulonogyryus</i> spp.	C	100	0	0	0	56
<i>Baetis monticola</i>	E	100	0	0	0	24
<i>Centroptilum sudafricanum</i>	E	100	0	0	0	32
<i>Cheumatopsyche maculata</i>	T	100	0	0	0	16
Hydracarina	A	100	0	0	0	16
Collembola		100	0	0	0	16
Hydrophilidae	T	100	0	0	0	16
<i>Castanophlebia calida</i>	E	94.8	5.2	0	0	1018
<i>Adenophlebia auriculata</i>	E	92.2	1.1	0	6.7	1838
Notonemourinae	P	87.8	12.2	0	0	1146
Nematoda		83.7	2.3	14.0	0	702
Tipulidae	D	60	40	0	0	80
Annelida		57.7	26.4	12.4	3.5	1415
Oligochaeta		45.5	3.0	40.6	10.9	4828
Orthocladiinae	D	29.3	0	54.7	16.0	1309
Chironominae	D	25.0	0	51.4	23.6	1206
Tanypodinae	D	21.4	0	57.3	21.3	426
Odonata		16.5	29.0	33.0	21.5	279
Ceratopogonidae	D	11.9	18.3	19.1	50.7	1695
<i>Gyrinus</i> spp.	C	11.6	0	68.4	20	414
<i>Baetis natalensis</i>	E	10	90	0	0	917
<i>Atherix</i> sp.	D	0.6	42.0	45.0	4.4	742
<i>Potomonautes</i> spp.	Cr	8.4	12.6	47.4	31.6	380
<i>Centroptilum parvum</i>	E	5.2	67.8	13.7	13.4	4392
<i>Cheumatopsyche thomasseti</i>	T	5.1	5.2	65.0	24.8	8079
Blephariceridae	D	4.6	95.4	0	0	1392
<i>Simulium nigrirarse</i>	D	3.1	3.8	25.4	67.7	66547
Ancylidae	M	1.8	66.9	27.6	3.7	2717
Elmidae	C	1.2	0.9	27.0	70.9	9553
Platyhelminthes		1.1	58.0	37.3	3.6	1387
<i>Cheumatopsyche afra</i>	T	1.1	33.6	28.3	37.0	10995
<i>Baetis harrisoni</i>	E	0.5	19.3	43.9	36.3	13436
Caenidae type A	E	0.4	0.9	85.0	13.7	7419
<i>Macrostemum capense</i>	T	0.3	1.1	37.6	61.0	21006
<i>Neurocaenis reticulata</i>	E	0.1	12.1	47.4	40.4	33416
<i>Simulium adersi</i>	D	0.03	1.7	0.9	97.3	61366
<i>Ecnomus</i> spp.	T	0	100	0	0	35
<i>Simulium vorax</i>	D	0	94.5	5.5	0	4687
Psephenidae	C	0	92.6	7.4	0	897
<i>Burnupia</i> sp.	M	0	40.5	22.6	36.9	19406
<i>Afronurus harrisoni</i>	E	0	36.8	15.9	47.3	1818
<i>Centroptiloides bifasciatum</i>	E	0	36.0	32.3	31.7	437
Turbellaria		0	14.0	31.0	55.0	8699
<i>Simulium medusaeforme</i>	D	0	6.1	38.9	55.0	17921
<i>Chimarra</i> spp.	T	0	4.1	95.9	0	9303
Tabanidae	D	0	4.0	43.4	52.6	396
<i>Choroterpes elegans</i>	E	0	0.2	76.5	23.2	15886
<i>Hydra</i> sp.	Co	0	0	100	0	260
Thaumaleidae	D	0	0	100	0	82
Caenid type B	E	0	0	100	0	38
<i>Pseudocloeon maculosum</i>	E	0	0	71.4	28.6	632
<i>Simulium dannosum</i>	D	0	0	12.1	87.9	1186
<i>Corbicula</i> spp.	M	0	0	0	100	2304
<i>Baetis glaucus</i>	E	0	0	0	100	203
<i>Centroptilum excisum</i>	E	0	0	0	100	54
Hemiptera		0	0	0	100	16

Taxa		Site no.			Total numbers (m ²)
		1	5	6	
<i>Simulium dentulosum</i>	D	100	0	0	1717
<i>Baetis natalensis</i>	E	100	0	0	406
Blephariceridae	D	100	0	0	197
Notonemourinae	P	100	0	0	91
<i>Chimarra</i> spp.	T	98.1	0	1.9	475
Psephenidae	C	83.5	16.5	0	304
<i>Afronurus harrisoni</i>	E	73.0	27.0	0	892
<i>Centroptilum parvum</i>	E	50.1	43.7	6.2	3321
<i>Potomonautes</i> spp.	G	60.0	50.0	0	32
<i>Atherix</i> sp.	D	43.6	20.8	35.6	477
Nematoda		40.3	53.2	6.5	248
<i>Simulium nigrirtarse</i>	D	21.0	27.0	52.0	6740
<i>Burnupia</i> sp.	M	18.9	18.5	62.6	10318
Elmidae	C	13.3	31.9	54.8	1506
Odonata		11.0	66.9	22.1	145
<i>Baetis harrisoni</i>	E	8.6	61.9	29.5	3437
<i>Corbicula</i> spp.	M	5.6	8.8	85.6	571
<i>Neurocaenis reticulata</i>	E	5.4	54.4	40.2	20422
<i>Cheumatopsyche afra</i>	T	5.1	26.2	68.7	5364
Tabanidae	D	4.9	31.7	63.4	328
Turbellaria		4.2	32.7	63.1	7681
<i>Macrostemum capense</i>	T	1.1	41.7	57.2	20333
Oligochaeta		0.8	84.5	14.7	2058
<i>Cheumatopsyche thomasseti</i>	T	0.8	59.4	39.8	2779
<i>Choroterpes elegans</i>	E	0.06	96.4	3.54	16218
<i>Simulium medusaeforme</i>	D	0	100	0	641
<i>Adenophlebia auriculata</i>	E	0	100	0	192
<i>Centroptilum excisum</i>	E	0	100	0	175
Empididae	D	0	100	0	105
Collembola		0	100	0	50
<i>Pseudocloeon maculosum</i>	E	0	94.7	5.3	2547
Caenidae type A	E	0	87.4	12.6	653
<i>Hydra</i> sp.	Co	0	50.0	50.0	100
Ceratopogonidae	D	0	34.9	65.1	301
<i>Gyrinus</i> spp.	C	0	28.8	71.2	626
<i>Simulium adersi</i>	D	0	8.0	92.0	2965
Thaumaleidae	D	0	0	100	180

Table 3 Percentage composition and total numbers of macroinvertebrates collected in riffle samples from three sites in the upper Buffalo River during the winter of 1987 (May–October). Site 0 is excluded as riffles were dry during winter. (Species in order of descending abundance at Site 1; A, Arthropoda; C, Coleoptera; Co, Coelenterata; Cr, Crustacea; D, Diptera; E, Ephemeroptera; M, Mollusca; P, Plecoptera; Pl, Platyhelminthes; T, Trichoptera)

Food availability

We have no quantitative data on the benthic food base (diatoms, filamentous algae, fungal–microbial biofilms) of the Buffalo River, but leaf packs were common at both Sites 0 and 5, although absent from Sites 1 and 6. Shredders were only found at Site 0 (Palmer & O’Keeffe, 1992). Their absence from Site 5 was apparently not because of a lack of leaf detritus. Suspended organic material increased between Sites 0 and 6, ranging from 1 to 5 mg l⁻¹ at Site 0, and from 0.1 to 11 mg l⁻¹ at Site 6 (Palmer & O’Keeffe, 1990b). The median ratio of coarse to fine suspended POM

was 1.6 at Site 0, 1.2 at Site 1, and 1.5 at Sites 5 and 6 (Palmer & O’Keeffe, 1990b). While the influence of food availability on distribution should not be ignored, available data provide no indication of a clear link between community structure and food availability.

Habitats

Another difference which distinguished Site 0 from the other sites was the scale of the habitats and river channel (Palmer *et al.*, 1991). The headwater stream was only 2.5 m broad, and habitats formed a mosaic of small patches. Physical conditions in these habitats

changed frequently because of variable discharge, whereas habitats at Site 1 formed larger discrete units and changes in discharge were more gradual and less frequent. Palmer *et al.* (1991) suggested that this difference of scale was a factor contributing to the presence of a distinct fauna at the headwater site.

The roles of seasonality and scale discussed above are speculative. The environmental gradient that most closely paralleled downstream changes in species and abundance was change in channel gradient (steepness). In terrestrial vegetation studies, elevation is recognized as a complex surrogate for local conditions of air temperature, incident radiation, evaporation and moisture availability (Austin, 1980). Similarly, steepness may be a surrogate for complex hydraulic and geomorphological channel characteristics (Statzner *et al.*, 1988). A correlation between faunal changes and steepness was inferred in this study by indirect gradient analysis (Whittaker, 1973; Gauch, 1982). Direct gradient analysis could be used to confirm the existence of such a relationship, but would require a number of additional sample sites between Sites 0 and 1.

Although factors which influence community structure may include pH, food availability and seasonality of flow, our results indicate that the rate of elevation change is an environmental descriptor which parallels the pattern of changes in the riffle-dwelling macrobenthos of the upper Buffalo River. This is of interest because the Buffalo River has relatively low altitude headwaters, and is a warm temperate stream, indicating that altitudinal gradients are not only important in high mountains and at high latitudes.

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