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Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, eastern Cape, South Africa. I. Dietary variability

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SUMMARY

1. The question of whether the diets of twelve abundant macroinvertebrate taxa from the middle and lower reaches of the Buffalo River (eastern Cape, South Africa) were too variable to allow them to be assigned to functional feeding groups (FFGs) was addressed.
2. Spatial, temporal and developmental variations in diet were assessed. Foregut content analysis was used as an index to compare diets.
3. Foregut contents were compared from early (small) and late (large) instar larvae collected from riffles at thirteen sites in summer, and from riffles, stony backwaters and sediments at four of these sites in spring, summer, autumn and winter, in 1987.
4. For all individuals of all taxa, fine amorphous detritus (0.5–250 μm), was the most common dietary item. Differences in diet followed a similar pattern for all taxa. The most frequent differences in dietary content were between large and small larvae. The foreguts of large larvae contained more material, and a wider variety of rare items than small larvae. Neither species nor FFGs could be distinguished on the basis of foregut contents.
5. Two dietary types were recognized. The eight mayfly larvae were fine detritivores, having ingested fine detritus almost exclusively. In contrast, the two hydropsychid caddisfly larvae had ingested a mixed diet; their gut contents included chitinous invertebrate remains and other items as well as fine detritus.
6. Intra-specific dietary variability was not so great as to prevent these taxa from being assigned to FFGs. On the contrary, inter-specific dietary content was so similar that gut content analysis could not provide a positive basis upon which to identify FFGs.

Introduction

Although it is common practice to assign benthic taxa to functional feeding groups (FFGs) such as shredders, filterers, gatherers, brushers and scrapers, the use and usefulness of the FFG concept has been criticized (Lake *et al.*, 1985; Winterbourn, Hildrew & Box, 1985; Barmuta, 1988; King *et al.*, 1988). An area of concern has been that stream macroinvertebrates are such opportunistic generalists (Coffman, Cummins & Wuycheck, 1971), and have such flexible feeding behaviour (De Moor, 1988; McShaffrey & McCafferty, 1986, 1990) that it is meaningless to assign any species to a FFG. Both King *et al.* (1988) and Minshall (1988)

quote studies in which the feeding style and/or diet of benthic species changes at different life history stages and/or in different locations.

We have previously described results that showed that dietary variability in early and late instar larvae, collected seasonally from different biotopes, was not so great as to prevent four taxa from the headwaters of the Buffalo River being assigned to FFGs (Palmer & O'Keeffe, 1992). In the case of the shredder FFG, the presence of a predominance of leaf fragments in the gut was an important distinguishing feature. Macroinvertebrate assemblage composition, and patterns of distribution in the headwaters of the Buffalo River are considerably different from the middle and lower reaches (Palmer, O'Keeffe & Palmer, 1991). The question we consider here is whether dietary variability is too great to allow species from the middle and lower reaches of the Buffalo River to be assigned to FFGs as taxonomic entities.

Twelve numerically abundant macroinvertebrate species from the middle and lower reaches of the Buffalo River were selected for study: four baetid mayflies, *Baetis harrisoni* Barnard, *Pseudocloeon maculosum* Crass, *Cloeon africanum* Esben-Petersen and *Centroptilum excisum* Barnard; two leptophlebiid mayflies, *Choroterpes elegans* Barnard and *Choroterpes nigrescens* Barnard; a heptageniid mayfly, *Afronurus harrisoni* Barnard; a tricorythid mayfly, *Neurocaenis reticulata* Barnard; two caenid mayflies, Caenidae sp. A and sp. B; and two hydropsychid caddisflies *Cheumatopsyche afra* (Mosely) and *Macrostemum capense* (Walker). Gut content analysis is used as an index to compare the diets of individuals collected at different places and times.

Study area

The total area drained by the Buffalo River is approximately 1353 km^2 and the underlying geology consists primarily of easily erodable Beaufort Series mudstones and sandstones, intersected by more resistant dolerite intrusions (Mountain, 1962). The river is a fourth-order stream (*sensu* Strahler, 1974, at a scale of 1:250 000) by the time it drains into the sea at East London (32°20'S, 27°45'E), 140 km from its source (Fig. 1).

The river rises in the Amatole Mountains, at an altitude of 1300 m, from a wetland in mesotrophic grassy fynbos, which soon gives way to near pristine closed canopy Eastern Forest and Thicket (Campbell B.M., 1985). The headwater stream has a steep gradient of about 200 m km^{-1} for 6 km, before it flows into Maden dam, the first of two small impoundments in the foothills of the mountains (specifications of all four impoundments on the river are given by Palmer & O'Keeffe (1989)). Site 1, just above Maden dam, is faunistically distinct from the headwater stream (Palmer *et al.*, 1991), and Sites 1–13 are described as the middle/lower reaches of the river (Fig. 1).

In its upper middle reaches (Sites 1–5) the river flows through agricultural lands. Land use in the relic flood plain upstream of King William's Town (Sites 6 and 7) is intensive market gardening, and water quality deteriorates because of fertilizer-rich

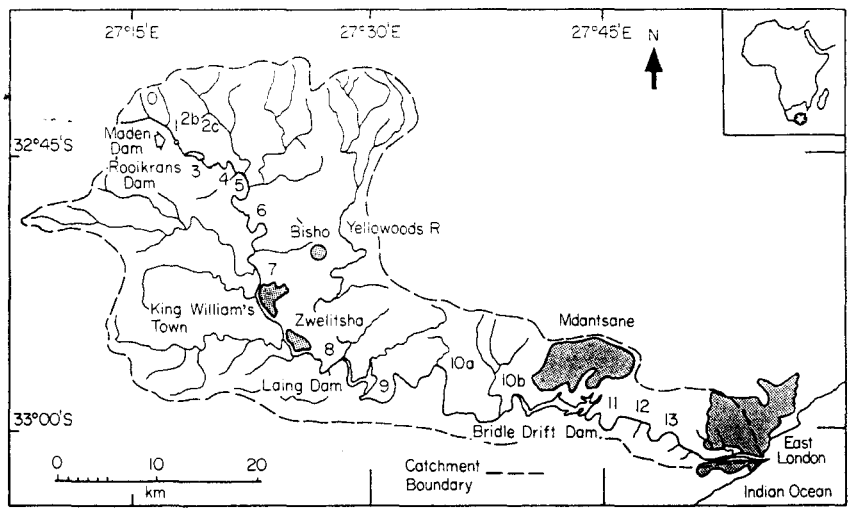

Fig. 1 A map of the Buffalo River catchment, eastern Cape, showing the location of the four impoundments and of the sixteen sampling sites (0–13) (from Palmer and O'Keeffe, 1990a). Sample site numbers used in the Buffalo River Programme have been retained to facilitate cross referencing.

agricultural run-off carrying suspended solids and nutrients such as nitrates (Palmer & O'Keeffe, 1990a). Below Site 7, the river flows through the urban/industrial area of King William's Town/Zwelitsha and the water quality is seriously impaired as the river carries treated sewage and industrial effluent. Site 7 and particularly Site 8 are heavily polluted, with the river becoming 'a liability rather than a resource' (Allanson *et al.*, 1990). Laing dam, which supplies water to Zwelitsha, and intermittently to King William's Town, is downstream of Site 8, and receives eutrophic mineralized water. Laing dam acts as a large settling pond, and nutrient levels downstream of the dam are considerably reduced (O'Keeffe, 1989; Palmer & O'Keeffe, 1990a).

Below Laing reservoir catchment use is mainly extensive agriculture, and erosion rather than fertilizer-rich runoff is the major problem (Sites 9, 10a and 10b) (Palmer & O'Keeffe, 1990a). The last and largest impoundment is Bridle Drift, which is situated in the lower reaches of the river and receives the overspill from Laing dam (Fig. 1). The river looks very attractive in these lower reaches and flows between steeply incised valley slopes, covered in *Euphorbia* spp.-dominated Succulent Thicket (Site 12). However, water quality in the river deteriorates because of sewage effluent from Mdantsane (Site 13, Fig. 1).

Materials and Methods

Field sampling and gut content analysis

The benthic macroinvertebrate fauna was sampled from Sites 1 to 13 (Fig. 1) seasonally in 1987: summer (February), autumn (May), winter (August) and spring (November). At each site, three replicate box samples (0.09 m^2, net mesh 80 μm) were collected from riffles, and at Sites 1, 6 and 12 stony backwaters, marginal vegetation, and sediments were also sampled. Sampling, sorting and identification methods have been described (Palmer *et al.*, 1991).

In order to assess spatial, temporal and developmental dietary variability, large (late instar) and small (early instar) larvae from all twelve species were selected. In the case of the baetid mayflies, very early instar larvae could not be positively identified to species, so the 'small' larvae dissected were the smallest that could be identified positively. Both head capsule width and body length were measured, and there was no overlap in size between larvae termed 'small' and those termed 'large'. Three large and three small individuals were separately dissected, and slides made of the individual gut contents. These sets of replicate slides were prepared from larvae collected from each site, season, and biotope combination wherever possible (species were absent from some biotopes and in some seasons).

Eleven categories of ingested food were recognized: amorphous detritus in the size ranges (1) 0.5–50 μm (UFPOM), (2) 50–250 μm (FPOMa) and (3) 250 μm–1 mm (FPOMb); (4) fungi; (5) unicellular algae; (6) diatoms; (7) filamentous algae; (8) leaf fragments; (9) pollen; (10) invertebrate remains; (11) inorganic silt. The areal method of gut content analysis first described by Coffman *et al.* (1971) was used in the manner described by Palmer & O'Keeffe (1992). In all instances the term 'diet' has been used synonymously with gut contents. Counted food items from the foregut may not constitute the entire diet but they have been used in this study as an index of dietary content.

Data analysis

Analysis of variance (ANOVA) procedures were applied to the gut content measures. The ANOVA procedure assumes equality of variance, but Bartlett's test (Sokal & Rohlf, 1969) revealed that the raw data did not conform to this requirement. The area values for each food type were calculated as a proportion of the total area of one field of vision and then transformed (arcsin) (*sensu* Rader & Ward, 1987; Becker 1990) before dietary comparisons were made. In all these comparisons, food type was treated as an explanatory factor (rather than a dependent factor) for the arcsin transformed proportions of the total microscope fields occupied by each food type. This procedure is suboptimal in that it does not adequately take into account the relationships that exist between particle size (area) and the counts of area covered. However, it does give an insight into the dominating features of dietary composition and variability in the data.

Dietary compositions of large and small larvae from the different sites, biotopes and seasons were compared using ANOVA (Becker, 1990). Initially a comparison was made between the replicate data sets from three larvae of the same size that were

collected under the same conditions of biotope, site or season. Two-way ANOVA without interaction was used to establish the degree of dietary variability within the three replicates. Of the 219 sets of three replicate gut contents slides, 208 showed no significant difference ($P > 0.05$) in dietary composition. The eleven sets in which there was a difference consisted of one set each from eleven different species. Each set of replicates was therefore assumed to collectively represent the range of food items consumed by one of the twelve species under the conditions prevailing at the time of sample collection. Subsequently, sets of replicate foregut content slides were compared for differences in diet. Comparisons were made between the gut contents of large and small larvae, and between larvae collected from various sites, seasons and biotopes (three-way ANOVA with interaction of food type, the replicates, and either size, site, season or biotope).

It is theoretically possible to construct an ANOVA table that would make all these comparisons simultaneously. However, many of the species were absent from some of the biotopes or sites, and in one or more of the seasons. The ANOVA procedures available were unable to tolerate the extent to which the available data set was unbalanced and a stratified ANOVA procedure was followed. Separate three-way ANOVAs were calculated to compare gut content composition. Firstly, sets of replicate slides from three large and three small larvae were compared for size-related differences under each of the site, season and biotope conditions. Then, gut contents slides from large larvae collected from different sites, then seasons, then biotopes, were compared. The same procedure was followed for small larvae.

Food type was fitted as an explanatory factor, in the presence of other factors. If no interaction of food type with other factors was discerned, we inferred that the proportions of food types consumed were practically constant across the levels of the other factors. If interaction was discerned, we inferred that proportions of food type were affected by these factors, and have reported these relationships. Some information is lost by being unable to perform complete four-way and five-way ANOVAs, because of the patterns of species presence and absence, but major features of interest are revealed in the described procedure.

Most ANOVA procedures were performed using multifactor ANOVA (Anonymous, 1989). Very large ANOVAs, such as those comparing the dietary composition of species from several sites, were performed using BMDP2V (Dixon *et al.*, 1985).

Results

Gut content analysis revealed that fine, amorphous detritus (UFPOM 0.5–50 μm and FPOM 50–250 μm) was the most abundant material in the foreguts of all mayfly and small caddisfly larvae (Fig. 2). Large caddisfly larvae had also ingested UFPOM and FPOM as major dietary items, but were characterized by a mixed diet, including leaf fragments, diatoms and, particularly, abundant invertebrate remains (Fig. 2). Fine inorganic silt particles regularly constituted a small proportion of all the foregut contents. Fig. 2 provides typical examples of the gut contents of each of the species collected seasonally and from different sites and biotopes (Palmer, 1991).

For all species, significant differences in gut contents were most frequent between large and small larvae (Table 1). These differences followed a pattern of larger individuals, unsurprisingly, having ingested more material at the time of collection (higher area counts were recorded), and a wider range of items than small individuals. Differences in the gut contents of animals collected from different sites and seasons (Tables 2 and 3) were more common between large larvae, and were usually attributable to variation in the proportions of rarer food items, such as diatoms, algal filaments, leaf fragments and fungal hyphae. Only five of the species were collected from more than one biotope: *C. africanum* was collected from stony backwaters and marginal vegetation, and *C. excisum*, *A. harrisoni*, *C. elegans*, and Caenidae sp. A were collected from riffles and stony backwaters. In no case was there a significant difference in the gut contents of larvae collected from different biotopes from the same site and season (Palmer, 1991).

Significant differences in the composition of the gut contents followed a pattern: larger animals had more material in their foreguts and had ingested a wider variety of food items than small animals. Variation in the consumption of the less common food items contributed to the detection by the ANOVA of significant differences in the dietary composition of animals from different locations and in different seasons. The inclusion of rare items in the diet con-

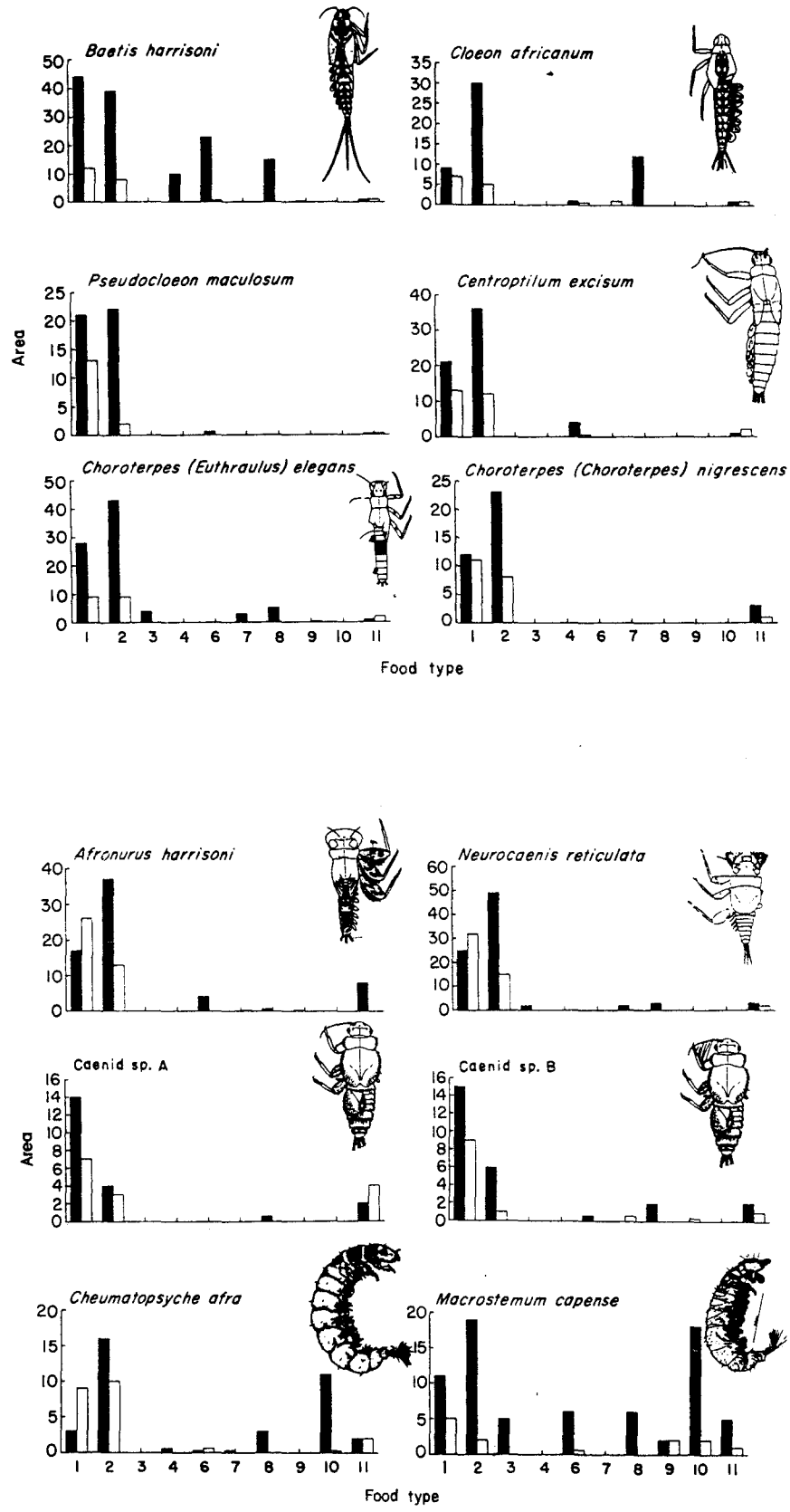

Fig. 2 Typical examples of the gut contents of large (▨) and small (□) larvae of the twelve selected species from the middle/lower reaches of the Buffalo River. The complete set of gut content data is given in Palmer (1991). The area value given (mm^2) is the mean area covered in ten microscope fields (400×) by each food type for three replicate gut contents slides. 1, Detritus (0.5–50 μm); 2, detritus (50–250 μm); 3, detritus (250 μm–1 mm); 4, fungi; 5, planktonic algae (never found); 6, diatoms; 7, filamentous algae; 8, leaf fragments; 9, pollen; 10, invertebrate remains; 11, inorganic silt. (Drawings from Barnard (1932), Crass (1947), Scott (1983), and Barber (acknowledged).)

Table 1 Size comparisons. The gut contents of large larvae are compared with those of small larvae. Separate large *v* small comparisons of larvae collected from different sites, seasons and biotopes were made. Gut contents of the larvae of twelve species from the middle/lower reaches were compared using a three-way ANOVA with interaction. Each significant ($P < 0.05$) interaction is indicated by an x (interaction is explained in the text). Significant differences in dietary composition are indicated. ** $P < 0.01$, * $P < 0.05$. Seasons: Sp, spring; Su, summer; A, autumn; W, winter. Biotopes: RIF, riffle; BW, stony backwater; MVO, marginal vegetation (out of current)

Baetidae					Leptophlebiidae					Hydropsychidae				
Baetis harrisoni					*Choroterpes elgans*					*Macrostemum capense*				
Site 1	Su	RIF	*	x	Site 5	Su	RIF	**		Site 1	Su	RIF	**	x
Site 2c	Su	RIF	*		Site 6	Su	RIF	**		Site 5	Su	RIF	**	
Site 3	Su	RIF		x		A	RIF	**	x	Site 6	A	RIF	**	x
Site 6	Su	RIF		x			BW	**	x		W	RIF	**	x
	A	RIF	**	x		W	BW	**	x		Sp	RIF	*	
	Sp	RIF	**	x	Site 7	Su	RIF	**	x	Site 7	Su	RIF		
Site 7	Su	RIF	**	x	Site 10a	Su	RIF	**	x	Site 11	Su	RIF	*	
Site 8	Su	RIF	**	x	Site 10b	Su	RIF	*	x	Site 12	Su	RIF	**	x
Site 10a	Su	RIF			Site 12	Su	RIF	**	x		A	RIF	*	
Site 11	Su	RIF	**	x		A	RIF				W	RIF	**	
Site 12	Su	RIF		x		W	RIF	**	x	Site 13	Su	RIF	**	x
	A	RIF	*		Site 13	Su	RIF	**	x	*Cheumatopsyche afra*				
	Sp	RIF			*Choroterpes nigrescens*					Site 1	Su	RIF	**	
Site 13	Su	RIF		x	Site 6	A	BW	*		Site 5	Su	RIF	**	x
Pseudocloeon maculosum						W	BW	**		Site 6	A	RIF	**	x
Site 12	Su	RIF	**	x							W	RIF		
	A	RIF			Caenidae						Sp	RIF	**	x
	W	RIF	**	x	Caenidae sp. A					Site 7	Su	RIF	**	x
	Sp	RIF			Site 5	Su	RIF			Site 11	Su	RIF	**	
Site 13	Su	RIF	**	x	Site 6	Su	RIF			Site 12	Su	RIF		x
Cloeon africanum						W	BW				A	RIF	**	x
Site 6	Su	BW			Site 7	Su	RIF				W	RIF	**	x
		MVO	*	x	Site 8	Su	RIF				Sp	RIF	**	
	A	BW	*		Site 10a	Su	RIF			Site 13	Su	RIF	**	
	Sp	BW	**	x	Site 12	Su	BW		x					
Site 12	Su	BW				A	BW							
		MVO		x	Site 13	Su	RIF							
	A	BW	*	x	Caenidae sp. B									
	W	BW			Site 12	Su	RIF							
	Sp	BW				A	RIF							
Centroptilum excisum						W	RIF	*	x					
Site 6	A	BW	**	x										
Site 12	W	BW			Tricorythidae									
	Sp	BW		x	*Neurocaenis reticulata*									
					Site 5	Su	RIF	**	x					
Heptageniidae					Site 6	A	RIF	*						
Afronurus harrisoni						W	RIF	**						
Site 1	Su	RIF	**	x	Site 7	Su	RIF	**						
Site 2c	Su	RIF	**	x	Site 11	Su	RIF	**	x					
Site 6	A	BW			Site 12	Su	RIF	**	x					
Site 10a	Su	RIF	**	x		A	RIF	**	x					
Site 12	Su	RIF	**	x		W	RIF	**	x					
		BW	**	x		Sp	RIF	**	x					
	A	RIF	**	x	Site 13	Su	RIF	**	x					
		BW												
	W	RIF	*											
		BW	**	x										
Site 13	Sp	RIF	**											

Table 2 Site comparisons. The gut contents of the larvae of twelve macroinvertebrate species from the middle/lower reaches collected in one site were compared with those of larvae collected from one or more different sites (given in brackets). In each three-way ANOVA with interaction, the gut contents of one species, of one size, collected in one biotope, in one season, but from two or more sites were compared. Each significant ($P < 0.05$) interaction is indicated by an x (interaction is explained in the text). Significant differences in dietary composition are indicated: ** $P < 0.01$, * $P < 0.05$. Seasons: Sp, spring; Su, summer; A, autumn; W, winter. Biotopes: RIF, riffle; BW, stony backwater; MVO, marginal vegetation (out of current). Sizes: L, large; S, small

Baetidae				
Baetis harrisoni				
Su	RIF	L (Sites 1, 2c, 3, 6, 7, 8, 10a, 11, 12, 13)	**	x
		S (Sites 1, 2c, 3, 6, 7, 8, 10a, 11, 12, 13)	**	
Pseudocloeon maculosum				
Su	RIF	L (Sites 12, 13)		
		S (Sites 12, 13)		x
Cloeon africanum				
Su	BW	L (Sites 6, 12)		
		S (Sites 6, 12)		
	MVO	L (Sites 6, 12)		x
		S (Sites 6, 12)		
A	BW	L (Sites 6, 12)		
		S (Sites 6, 12)		
W	BW	L (Sites 6, 12)		
		S (Sites 6, 12)		
Sp	BW	L (Sites 6, 12)		
Centroptilum excisum				
Sp	BW	S (Sites 6, 12)		
Heptageniidae				
Afronurus harrisoni				
Su	RIF	L (Sites 1, 2c, 5, 10a, 12, 13)	**	x
		S (Sites 1, 2c, 5, 10a, 12, 13)		x
Leptophlebiidae				
Choroterpes elegans				
Su	RIF	L (Sites 5, 6, 7, 10a, 12, 13)	**	x
		S (Sites 5, 6, 7, 10a, 12, 13)		x
Caenidae				
Caenidae sp.A				
Su	RIF	L (Sites 5, 6, 7, 8, 10a, 12, 13)		
		S (Sites 5, 6, 7, 8, 10a, 12, 13)		
Caenidae sp.B				
Su	RIF	L (Site 12, 13)		
Tricorythidae				
Neurocaenis reticulata				
Su	RIF	L (Sites 2b, 5, 7, 11, 12, 13)		
		S (Sites 2b, 5, 7, 11, 12, 13)		
Hydropsychidae				
Macrostemum capense				
Su	RIF	L (Site 1, 5, 7, 11, 12, 13)	**	
		S (Site 1, 5, 7, 11, 12, 13)	**	
Cheumatopsyche afra				
Su	RIF	L (Site 1, 5, 7, 11, 12, 13)	**	x
		S (Site 1, 5, 7, 11, 12, 13)	**	x

tributed to dietary variability, but was insufficient to warrant the recognition of different diets. Therefore, dietary variability did not prevent species from being assigned to FFGs, but gut content analysis results alone did not enable species to be assigned to FFGs.

Baetis harrisoni (Baetidae) was the most abundant and widely distributed mayfly in the Buffalo River. Larvae were collected from riffles where they were always observed on the surfaces of rocks and stones. In the summer of 1987, large and small individuals were collected from Sites 1, 2c, 3, 6, 7, 8, 10a, 11, 12 and 13, and in autumn and spring from Sites 6 and 12. Larvae were absent in winter. A total of eighty-four individuals were dissected, and in all cases small detrital fragments (UFPOM and FPOMa) and silt were the most common components of the gut contents (Fig. 2). Diatoms, filamentous algal fragments, leaf fragments and pollen grains were occasional dietary components, more common in large than in small individuals. Small individuals had also generally ingested a higher proportion of the smallest detrital particles. These differences between large and small individuals are reflected in Table 1, which shows a significant difference between large and small individuals in more than half of the comparisons made. An interaction was found between food and size (Table 1), which means that not only was there a difference in the area covered by each of the food types, but there was also a difference in the relative proportions of the different foods.

The diets of large and small *B. harrisoni* larvae collected from different sites were significantly different (Table 2). Unpublished gut content data from animals collected from all sites in all seasons (Palmer, 1991) showed that *B. harrisoni* larvae ingested a much wider range of food types at Site 1 than at any of the other sites. The only seasonal differences in gut contents (Table 3) were in large animals from Site 6, where, in spring, larvae had ingested a similarly wide range of food, including large numbers of diatoms. Both site and seasonal differences were attributable to variations in the relative amounts of the rarer dietary items.

Larvae of another riffle dweller, *Pseudocloeon maculosum* (Baetidae), were found in large numbers, but were restricted in distribution to Sites 12 and 13. At Site 12, large and small larvae were collected in all

Table 3 Seasonal comparisons. The gut contents of the larvae of twelve macroinvertebrate species from the middle/lower reaches collected in one season were compared with those of larvae collected from one or more different seasons (given in brackets). In each three-way ANOVA with interaction, the gut contents of one species, of one size, collected in one biotope, but from two or more seasons were compared. Each significant ($P < 0.05$) interaction is indicated by an x (interaction is explained in the text). Significant differences in dietary composition are indicated: ** $P < 0.01$, * $P < 0.05$. Seasons: Sp, spring; Su, summer; A, autumn; W, winter. Biotopes: RIF, riffle; BW, stony backwaters. Sizes: L, large; S, small

Baetidae			
Baetis harrisoni			
RIF	L Site 6 (Su, A, Sp)	**	x
	S 6 (Su, A, Sp)		
	L Site 12 (Su, A, Sp)		x
	S 12 (Su, A, Sp)		x
Pseudocloeon maculosum			
RIF	L Site 12 (Su, A, W, Sp)	*	x
	S Site 12 (Su, A, W, Sp)	*	x
Cloeon africanum			
BW	L Site 12 (Su, A, W, Sp)		
	12 (Su, A, W, Sp)		
BW	S Site 6 (Su, A)		
	12 (Su, A, W, Sp)		
Centroptilum excisum			
BW	L Site 12 (W, Sp)		
BW	S Site 6 (A, W)		
	12 (W, Sp)		
RIF	L Site 12 (W, Sp)	*	x
Heptageniidae			
Afonurus harrisoni			
BW	L Site 12 (Su, A, W)	**	x
	Site 6 (Su, A, W)		x
RIF	L Site 12 (A, W)	*	
RIF	S Site 12 (A, W)		
Leptophlebiidae			
Choroterpes elegans			
RIF	L Site 6 (Su, A)	**	
	12 (Su, A, W, Sp)	**	x
RIF	S Site 6 (Su, A)		
	12 (Su, A, W)		
BW	L Site 6 (A, W)		
	S Site 6 (A, W)		
Caenidae			
Caenidae sp.A			
BW	L Site 12 (Su, A)		
	S Site 12 (Su, A)		
Caenidae sp.B			
RIF	L Site 12 (Su, A, W, Sp)		x
	S Site 12 (Su, A, W)	*	x
Tricorythidae			
Neurocaenis reticulata			
RIF	L Site 6 (A, W, Sp)		
	12 (A, W, Sp)		
RIF	S Site 6 (A, W, Sp)		
	12 (A, W, Sp)		
Hydropsychidae			
Macrostenum capense			
RIF	L Site 6 (A, W, Sp)	*	x
	12 (Su, A, W)	**	
RIF	S Site 6 (A, W, Sp)		
	12 (Su, A, W, Sp)		
Cheumatopsyche afra			
RIF	L Site 6 (A, W, Sp)		
	12 (A, W, Sp)		x
RIF	S Site 6 (A, W, Sp)	**	
	12 (A, W, Sp)		

seasons. Thirty individuals were dissected, and their gut contents comprised predominantly UFPOM, FPOMa and silt (Fig. 2). These three dietary items constituted 99% of the total area of gut content slides counted for all the individuals dissected. Diatoms and leaf fragments formed rare additions to this basic diet.

There were no clear spatial or temporal differences in the proportions and amounts of ingested food, although there was evidence of size-related differences (Table 1), with smaller animals having less food in the foregut and proportionally less of the larger detrital fragments than large larvae (Fig. 2). The diets of large and small larvae at Sites 12 and 13 were the same (Table 2), but seasonally gut content composition was significantly different (Table 3).

Cloeon africanum (Baetidae) larvae were found exclusively in depositional biotopes—stony backwaters and the marginal vegetation fringing these backwaters. These biotopes were only sampled at Sites 1, 6 and 12, and *C. africanum* was found at both Sites 6 and 12. A total of fifty-seven individuals were dissected and UFPOM and FPOMa constituted 83% of the total area of gut content slides counted for all the individuals dissected. Diatoms, filamentous algae, leaf fragments, and silt made up the balance (Fig. 2).

The dietary differences between large and small

individuals followed the pattern of small individuals having ingested proportionally more UFPOM than FPOMa, fewer rare items, and less food in total, but the differences were seldom significant at the 1% level (Table 1). In no case was there any significant difference in the diets of larvae from Site 6 compared with Site 12 (Table 2), or between those collected in different seasons (Table 3), or from stony backwaters compared with marginal vegetation biotopes (Palmer, 1991).

Centroptilum excisum (Baetidae) larvae were found in both riffle and stony backwater biotopes, at Sites 6 and 12, in all seasons. Larvae had ingested mainly UFPOM and FPOMa (85% of all food items counted), along with small amounts of silt, and occasional diatoms (Fig. 2). There were few dietary differences, although in one instance of size-related differences (Table 1), larger larvae had more diatoms in the foregut than small larvae. Large larvae collected in spring also contained more diatoms than those collected in winter (Table 3; Palmer, 1991). There were no discernible dietary differences between larvae collected from different sites (Table 2) and biotopes (Palmer, 1991).

Choroterpes elegans (Leptophlebiidae) was the most widely distributed leptophlebiid mayfly in the Buffalo River. It was collected in samples from Site 5 to Site 13, in both riffle and stony backwater biotopes, in all seasons. A total of seventy-eight larvae were dissected: UFPOM, FPOMa and silt comprised 90% of all the food items counted, and leaf fragments were the most common occasional items (Fig. 2). A significant difference in the amount and proportions of food ingested by large and small larvae was found consistently (Table 1). Large larvae had more food in their foreguts, and included occasional items more frequently. The significant differences in diet between large larvae from different sites (Table 2) and seasons (Table 3) were also attributable to variable amounts of the rarer dietary items. There were no such differences in the gut contents of small larvae (Tables 2 and 3), which contained only the three major categories of food — UFPOM, FPOMa and silt. No differences were found in the gut contents of either large or small larvae collected from different biotopes (Palmer, 1991).

Choroterpes nigrescens (Leptophlebiidae) was a rare member of the macroinvertebrate assemblage. It was included in this study because it was a leptophlebiid closely related to *C. elegans*, and was found exclusively in depositional backwater biotopes. Only fifteen larvae were dissected and UFPOM, FPOMa, silt and isolated diatoms were found in their guts (Fig. 2; Palmer, 1991). Differences in the foregut contents of large and small larvae (Table 1) could be ascribed to greater amounts of material in the former (Fig. 2). There were no seasonal differences in the gut contents (Table 3) and larvae were absent from summer samples.

Afronurus harrisoni (Heptageniidae) larvae were found between Sites 1 and 13, in both riffle and stony backwater biotopes. A total of seventy-two larvae were dissected, with UFPOM, FPOMa and silt comprising 84% of the food items counted (Fig. 2). Diatoms were the most common of the infrequent dietary items, which also included occasional fungal hyphae, leaf fragments and pollen grains (Fig. 2). *A. harrisoni* larvae had a higher proportion of diatoms in the foregut than the larvae of any other species dissected.

In most instances there was a significant difference in the proportions and amount of food in the foreguts of large and small larvae (Table 1). These differences followed a common trend: large individuals had more material and a wider variety of food items in the foregut, but still had essentially the same diet as small larvae. For the same reason there were significant differences in the diets of large larvae collected from different sites and in different seasons (Tables 2 and 3), whereas there were no such differences between small larvae. The diets of large and small larvae collected from riffles or stony backwaters did not differ significantly (Palmer, 1991).

Neurocaenis reticulata (Tricorythidae) larvae were collected from riffles between Sites 5 and 13. A total of sixty-six larvae were dissected. The most common dietary components were UFPOM, FPOMa and silt, with rarer inclusions of diatoms, leaf fragments and filamentous algal fragments (Fig. 2). There was a difference in the proportion and amounts of food ingested by large and small larvae (Table 1), but the gut contents of neither large nor small larvae collected from different sites or seasons differed significantly from one another (Tables 2 and 3).

Caenidae sp. A was one of two caenid mayflies which could not be identified to species. Larvae were collected from riffles and stony backwaters from Site 5 to Site 13. Their gut contents consisted

predominantly of UFPOM, FPOMa and silt, with occasional diatoms, algal filaments and leaf fragments (Fig. 2). Fifty-seven larvae were dissected and in no case was there a significant difference in the diets of animals of different size collected in different seasons, from various sites or biotopes (Tables 1–3).

Caenidae sp. B was less common (twenty-four individuals dissected) than sp. A. Larvae were only collected from riffles at Sites 12 and 13. The diet was very similar to that of Caenidae sp. A (Fig. 2). There were no significant differences in the foregut contents of larvae collected from different sites, and only a few seasonal differences (Tables 2 and 3).

Cheumatopsyche afra (Hydropsychidae) larvae were collected from riffles between Sites 1 and 13, in all seasons, and seventy-eight larvae were dissected. Large larvae had ingested a wide range of foods, whereas the gut contents of some of the small larvae were reminiscent of those of all the Ephemeroptera — filled mainly with UFPOM, FPOMa and silt. The gut contents of large larvae were characterized by a high proportion of leaf fragments and invertebrate remains (Fig. 2). These size differences were consistently significant (Table 1). There was a significant difference in the amounts and proportions of foods in the foreguts of both large and small larvae collected from different sites (Table 2), but not, in general, between those collected in different seasons (Table 3).

Macrostemum capense (Hydropsychidae), also a net spinner, resembled *C. afra* in the breadth of dietary items in the foregut (Fig. 2), and in the consistency of differences between the gut contents of large and small larvae (Table 1). Significant differences were found in the diets of large and small larvae collected from different sites. Dietary composition showed no discernible (multiple range test) downstream trend. The gut contents of large larvae collected from Sites 1 and 5 differed from those of larvae from all other sites and from each other. Larvae from Site 5 had ingested the widest variety of food, and those from Site 1 the narrowest, with the other sites within this range. The gut contents of small larvae collected from Site 7 were different from those found in larvae from other sites, and included an unusually large variety of items. Only large larvae showed seasonal differences in gut contents.

Discussion

The FFG concept (Cummins, 1973, 1974) described categories to which stream macroinvertebrates could be assigned on the basis of their trophic role in streams. Coffman *et al.* (1971) had indicated that unspecialized omnivory was common, and consequently FFG definitions were intended to emphasize morphological adaptations as indicators of feeding mechanisms. Although the FFG terms themselves were indicative of mechanism, the first definitions included information on the food ingested, and the original FFG descriptions (Cummins, 1973, 1974) implied that stream macroinvertebrates could quite readily be distinguished on the basis of diet. There was an emphasis on gut content analysis as the primary technique for investigating diet (e.g. Coffman *et al.*, 1971; Cummins, 1973), and generally the size and/or type of food ingested has been the basis on which taxa have been assigned to FFGs (King *et al.*, 1988).

The hope was also expressed (Cummins, 1974) that FFGs might provide an alternative to taxonomic classification. However, taxonomy has remained the basis for the recognition of stream macroinvertebrates, and taxa are regularly assigned to FFGs (e.g. Merritt & Cummins, 1984). In a somewhat tautological fashion the concern arose that the feeding of a taxon might be too variable to allow it to be placed in a single FFG.

In this investigation of dietary variability, the most obvious feature of the gut contents of the twelve species studied from the middle/lower reaches of the Buffalo River was their similarity. All twelve species had mainly the same material in their foreguts: fine, amorphous detritus. This result may reflect insufficient differentiation of components of fine detritus; it certainly indicates the inadequacy of gut content analysis as the sole basis for FFG designations.

The predominance of fine detritus in the gut contents of stream invertebrates is not uncommon. A study of Australian stonefly larvae reported that thirteen out of nineteen species had gut contents consisting of between 69% and 100% detritus (Sephton & Hynes, 1982). Fine detritus was similarly important in the diets of Australian oligoneuriid and siphlonurid mayflies (Campbell I.C., 1985), and in the diets of 127 macroinvertebrate taxa from two Victorian rivers (Chessman, 1986). Slides of gut

contents prepared from twenty-five New Zealand macroinvertebrate species contained mainly particles in the size range 0.45–75 μm (Winterbourn, 1982; Winterbourn, Cowie & Rounick, 1984). Examples of FPOM feeding are abundant from North American studies (Gilpin & Brusven, 1970; Koslucher & Minshall, 1973; Clifford, Hamilton & Killins, 1979; Gray & Ward, 1979; Hamilton & Clifford, 1983; Short, 1983; Hawkins, 1985; Wallace *et al.*, 1987; Rader & Ward, 1987, 1989; McShaffrey & McCafferty, 1990). In a southern African study, King *et al.* (1988) recorded the same pattern of FPOM predominating in the gut contents of macroinvertebrates from a western Cape, second-order stream.

Despite an overall dietary predominance of detritus, taxa in the studies mentioned above were assigned to FFGs. *Ameletoides* spp. were described as scrapers on the basis of the presence of algae in the gut and a mandibular scraping tooth (Campbell I.C., 1985). Taxa were also broadly described as scraper/collector gatherers (Gray & Ward, 1979; Hamilton & Clifford, 1983; Georgian & Wallace, 1983; Rader & Ward, 1987). Koslucher & Minshall (1973) simply described algal and detrital feeders as herbivores. Scrapers have therefore, on occasion, been recognized on the basis of a minor algal dietary component. More commonly, the FFG given has been broad and unspecific. For the FFGs scraper, collector, gatherer, brusher and filterer, which are the FFGs most common in the middle and lower reaches of rivers, fine detritus is the 'staple' food. Gut content analysis provides information on diet, but is unlikely to discriminate between these FFGs.

This was certainly the case for twelve macroinvertebrates from the middle/lower reaches of the Buffalo River. Consequently, on the basis of the gut content analysis results alone, it was only possible to identify two broad FFGs: (1) fine detritus microvores, which included all the mayfly species, and (2) mixed diet microvores, characterized by the inclusion of invertebrate remains in the diet, which included both the net spinning caddisfly species.

In this study, a comparison of foregut contents was used to assess dietary variability. Spatial, temporal, and developmental variability in diet was limited; in fact dietary content was so similar that different species were not distinguishable on the basis of foregut contents. The most obvious pattern of dietary variation was that larger animals had more material in the foregut, together with larger fragments, and a wider range of items. Significant variations in the gut contents of larvae from different sites and seasons resulted from the ingestion by large larvae of varying proportions of rarer food items (diatoms, filamentous algae, and leaf fragments).

Gut content analysis may not have enabled the positive recognition of FFGs, but it provided basic data on the feeding habits of these benthic taxa, and emphasized the importance of fine organic matter as an energy base in turbid river reaches (Palmer & O'Keeffe, 1990b). Positive FFG designations for these taxa on the basis of behavioural and morphological studies will be discussed in a subsequent paper (Palmer, O'Keeffe & Palmer, 1993).

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