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Feeding patterns of four macroinvertebrate taxa in the headwaters of the Buffalo River, eastern Cape

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Abstract

Gut content analysis, field and laboratory observations, and food choice experiments were used to assign four abundant macroinvertebrate taxa in the headwaters of the Buffalo River, eastern Cape, to functional feeding groups. The mayfly *Adenophlebia auriculata* (Leptophlebiidae) was classified as a collector : brusher; while the caddisflies, *Dyschimus ensifer* (Pisuliidae) and *Goerodes caffrariae* (Lepidostomatidae), and stoneflies *Afronemoura* spp. (Notonemouridae) were classified as shredders. The effects of organism size, season and biotope on dietary composition were tested, with size accounting for most of the dietary variability within each taxon. Larger individuals consumed more material, larger items, and, in the case of *A. auriculata*, a wider variety of food-types. There was little variation in the feeding of the taxa in different seasons or biotopes. Shredders ingested mainly leaf fragments, and this, rather than the size of particles in the gut, is a more useful basis for the shredder designation. *A. auriculata* was the most opportunistic feeder, and items in its diet additional to fine detritus varied seasonally and in the various biotopes. Of the shredders, *Afronemoura* spp. and *D. ensifer* were more varied in their diet, augmenting the staple intake of leaf material with other items. *G. caffrariae* was the most specialised feeder, being exclusively a shredder, regardless of biotope or season. Despite criticisms of the applicability of the FFG concept in the literature, we conclude that these taxa can reasonably be accommodated in functional feeding classes, and that the results are useful in describing the functions performed by the organisms in the river. The relationship between feeding function and river process is emphasised: we suggest that collectors contribute primarily to organic particle retention, while shredders facilitate organic particle size reduction and mobilisation, and the enhancement of substrates for microbial colonisation. An emphasis on river function is a useful context within which to view the FFG concept.

Introduction

The introduction to Cummins' (1973) review remains the most cogent *raison d'etre* for an investigation of macroinvertebrate feeding, as it relates a fundamental understanding of feeding activities to processes in the river and consequently to decision making and management. One aim of the Functional Feeding Group (FFG) concept was the development of insights into the processes governing organic material cycling (Cummins & Merritt, 1984; Cummins & Klug, 1979; Merritt *et al.*, 1984). It was also hoped that a functional classification would circumvent some of the prob-

lems associated with inadequate taxonomic knowledge (Cummins, 1974; Anderson & Sedell, 1979).

Initially, FFG classification of macroinvertebrates was described primarily by the mechanism of feeding: and shredders, collectors, scrapers, and predators were recognised (Cummins, 1973). From this there developed an implied association with both the kind and size of food eaten: predators feeding on other consumers; scrapers eating attached algae; shredders ingesting CPOM (coarse particulate organic matter, > 1 mm); and collectors feeding on FPOM and UFPOM (fine, and ultrafine particulate organic matter, 50 μm–1 mm and 0.5–50 μm respectively). Cummins (1974), and Cummins & Klug (1979) suggested that the organic fragments were less nutritionally significant than the associated microbial biomass, drawing a 'cracker-peanut butter' analogy.

Although the feeding of relatively few macroinvertebrates has been investigated in detail, the Merritt & Cummins (1984) designation of FFG's are frequently used to assign species or even families to FFG's (Townsend *et al.*, 1983; Rader & Ward, 1987; Irons, 1988). We investigated the feeding of four macroinvertebrates from the headwaters of the Buffalo River, eastern Cape. We aimed to establish the degree of spatial, developmental, and seasonal variation in the composition of their gut contents, to see whether they could be assigned to FFG's as taxonomic entities. We asked the following questions:

1. What food did these taxa ingest?
2. How did diet vary with season, biotope, and larval size?
3. Were taxa feeding specialists or generalists?
4. Could taxa be assigned to FFG's, and would it be useful to do so?

A number of aspects of the FFG concept have been criticised, and a clear synthesis of these criticisms is provided by King *et al.* (1988). Problems with the FFG concept include: well documented changes in macroinvertebrate diet with life cycle stage, season and location (Cummins, 1973; Hawkins, 1985; Feminella & Stewart, 1986; Chessman, 1986; Irons, 1988); the ability of organisms to adopt different feeding mechanisms (McShaffrey & McCafferty, 1986); inconsistent correlation between FFG's and food availability (Irons, 1988; Barmuta, 1988); the limitations associated with the use of gut analysis data (Shepard & Minshall, 1984; Hawkins, 1985; Wallace *et al.*, 1987), and confusion in the literature between mechanism and food as a basis for classification. The results of this study are discussed in the context of these criticisms, and the applicability of the FFG concept is examined.

Study site and methods

Field collections

The Buffalo River (32° 43′ S, 27° 14′ E), eastern Cape, rises in the Amatole mountains from a sponge in mesotrophic grassy fynbos (Campbell, 1985), which soon gives way to dense forest. During the study period, January 1987 to March 1988, the stream flowed strongly in the spring and summer (20 ls^{-1}), but flow was reduced to a trickle in autumn (1 ls^{-1}), and in winter only a series of pools remained. The study site was located in Afro-montane indigenous forest, interspersed with patches of alien trees, such as a stand of oak (*Quercus robor* L.) just upstream of the site.

The headwater stream was sampled monthly, and on each occasion three replicate box samples (0.0929 m^2, mesh 80 μm) were collected in each of five biotopes: riffles (RIF), waterfall face (WF), leaf packs from riffles (LP), stony backwaters (BW), and sediments (SED). Organisms were sorted and counted using a subsampling technique described in Palmer & O'Keeffe (1990).

The macroinvertebrate assemblage comprised 49 taxa. (A total of 5258 individuals were collected, and voucher specimens are lodged with the Albany Museum, Grahamstown.) Four abundant taxa were selected for investigation: a leptophlebiid mayfly, *Adenophlebia auriculata* (Eaton) (672 larvae collected), a lepidostomatid caddisfly, *Goerodes caffrariae* (Barnard) (219 individuals collected), a pisuliid caddisfly, *Dyschimus ensifer*

Barnard (214 larvae collected), and a group of stonefly larvae (268 collected) which could not be distinguished to species. The stoneflies all belonged to the family Notonemouridae, and may have been *Afronemoura amatolae* (Balinsky) and/or *A. spinulata* (Balinsky), as adults of these species were collected from the site.

Feeding studies

Three lines of investigation were followed:

1. Observation
A. auriculata larvae were observed feeding in the laboratory using an adapted binocular microscope, with the objective lens at right angles to the aquarium. Recording the behavioural repertoire was initiated by placing three larvae, distinguishable on the basis of size, in each of three aquaria (25 × 25 × 100 mm). A small stone, a leaf, a twig and 2 ml loose detritus from the stream were included, and observations were made in a constant temperature room (15 °C), under daylight conditions, continuously for 12 hours. Each larva was watched for 5 minutes every hour, and its behaviour was recorded every 30 s during that time. The range of behaviour was corroborated as being 'normal' by watching larvae in quiet backwaters of the stream, using goggles and snorkel. The other taxa were too cryptic in their behaviour to observe feeding.

2. Experimentation
D. ensifer and the *Afronemoura* spp. were offered weighed leaf discs, to confirm that they were primarily shredders. *A. auriculata* was offered different types, and different sizes of food, and *D. ensifer* was offered different types of food. *G. caffrariae* were too scarce to be included in these experiments.

a) Food choice The food choice experiments were based on the null hypothesis that animals would move randomly, and that there would be an equal chance of finding any animal in any particular chamber (Shepard & Minshall, 1984). A second null hypothesis was that a feeding animal would be equally likely to be ingesting any of the available foods. All food choice experiments were conducted in a constant environment room at 15 °C (winter maximum, summer minimum stream temperature). This was cool enough to prevent the rapid emergence which occurred above 20 °C, but warm enough to allow feeding, growth and eventual emergence. In each aquarium, half the water was replaced with bore-hole water each day, and an aerator was placed centrally in a neutral area containing no food.

A. auriculata larvae were offered a choice of four of the most commonly available food sources in the stream: i) loose fine detritus; ii) a Rodophyte alga, *Batrachospermum* sp.; iii) leaf litter (indigenous); and iv) small rocks with surface organic layers. These were collected from the stream and placed in aquaria (Fig. 1a). Five replicate aquaria were set up to ensure that factors other than food were not affecting the distribution of the larvae in the aquaria. After a 48 hour laboratory acclimation period, twenty five larvae were

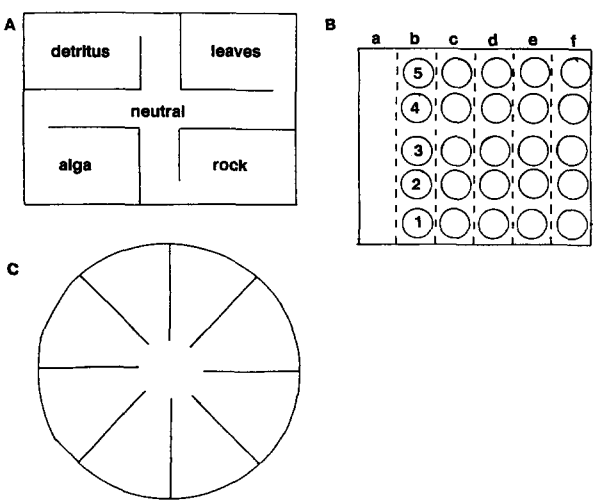

Fig. 1. Diagrams of food choice experiment aquaria: a) *A. auriculata* was given a choice of 4 food types: detritus, algae, stream rocks with organic layers, or stream collected indigenous leaves; b) *A. auriculata* was given a choice of 5 food particle sizes (A–F = gauze separated compartments; 1 = 80–250 μm, 2 = 250–500 μm, 3 = 500–850 μm, 4 = 850–4000 μm, 5 = >4000 μm); and c) *D. ensifer* was given a choice of the same 4 food types as *A. auriculata*, with each type in two of the compartments.

introduced to the neutral area of each aquarium. Aquaria were monitored at 09h00, 12h00, and 15h00 each day for 6 days. On the nights following days 5 and 6 nocturnal observations were made at 18h00, 21h00 and 24h00. The location of each larva in the aquarium, and whether or not it was feeding was noted.

Leaf packs in the stream were always dominated by non-indigenous oak leaves, though indigenous leaves were relatively more common in summer leaf packs. Irons *et al.* (1988) report macroinvertebrate preferences for leaves from particular species, so it was important to use a single leaf species when investigating particle size choice. When the experiments were conducted, oak leaves were virtually the only ones in the stream. They were collected from the stream, and dried at 60 °C for 24 hours, so they could be crushed and sieved. This resulted in fragments of uniform, known size from which the animals could choose. Fragments in the following five size classes were soaked for 48 hours in stream water to rehydrate: 80–250 μm, 250–500 μm; 500–1000 μm; 1–4 mm, >4 mm. The sizes were chosen on the basis of Minshall's (1988) scale ranking of organic matter in streams. Soaked fragments were placed sequentially in petri dishes in an aquarium, with five replicate sets each in a compartment separated from the others by gauze (Fig. 1b). A single aquarium was used so that the water was a uniform quality. The aerator was placed in an end compartment with no food so the current did not mix the different size particles, and oxygen levels were checked for uniformity in each compartment daily using an oxygen meter. After a 48 hour laboratory acclimation period, twenty *A. auriculata* larvae were introduced into each compartment of the aquarium. Their feeding behaviour, and location in each compartment were monitored at 09h00, 12h00 and 15h00, for 4 days. On nights 3 and 4 observations were also made at 18h00, 21h00 and 24h00.

Food choice by *D. ensifer* larvae were tested using 5 circular, white trays with eight compartments (300 mm diameter/30 mm depth, Fig. 1c). The four food types offered to *A. auriculata* were used. Each food type was placed in two of the compartments, and the sequence of foods was chosen randomly, differing in each replicate (Shepard & Minshall, 1984; Rosillon, 1988). Laboratory acclimated animals were introduced in the neutral area of each tray, and the presence of larvae in the various food compartments was recorded on seven occasions over two days. Other *D. ensifer* larvae were starved for 48 hours before being introduced, and their position was monitored once after 20 minutes.

For all the food choice experiments, the numbers present in each compartment, and the numbers feeding at the last observation were totalled for the five replicates, and a Chi-squared test was used to see if the number of feeding events on any of the foods was preferential, or if the distribution of larvae in the food compartments differed from uniform. The null hypothesis was that the proportion of larvae located in each area of the aquarium would be equal. (H_0: $p1 = p2 = p3 = p4 = p5$ where p is the proportion and 1–5 are the possible food compartments.) If the null hypothesis was rejected ($p < 0.05$) the Chi-squared test was repeated for the preferred food type (for example: p(leaves) expected against p(leaves) observed). The level of significance for these Chi-squared tests was reduced by dividing the nominal level of significance by the number of individual Chi-squared tests performed, to ensure that the overall level of significance was not higher than 5% ($p < 0.01$) (Miller, 1981). Where the proportion of larvae present in a compartment, or feeding on a food, was significantly more than expected, they were assumed to have shown a preference for the food type.

b) Leaf discs *Dyschimus ensifer* larvae, and the *Afronemoura* spp. were often collected from leaf packs in the stream, so 23 caddisfly, and 50 stonefly larvae were placed in two flat white trays (300 mm diameter/30 mm depth) with 25, and 20 pre-weighed, damp dried, oak leaf discs (20 mm diameter) respectively. As a control, fifteen leaf discs were placed in an aerated dish, with no animals. All leaf discs were removed, blotted dry, weighed, and returned, each week for four weeks to investigate possible shredding activities.

3. Gut analysis

Individuals from all four taxa, collected in spring (April), summer (February), autumn (May), and winter (August) were used for gut analysis. Three replicate slides of gut contents were prepared from late instar (large) and early instar (small) larvae collected in each biotope, in each season, wherever possible.

Head capsule width and body length (excluding cerci) were measured (Table 1). One large, and one small individual was dissected for each slide, except in the case of *A. auriculata*, where two small individuals were used. The foregut contents were dispersed in distilled water, mixed using a Fisons's 'Whirlimixer' and filtered through a 0.45 Millipore filter. This was cleared with immersion oil, and 10 fields at 400 × magnification were viewed and enumerated for each slide (Gray & Ward, 1979; Rader & Ward, 1987). Thirteen food categories were recognised: amorphous detritus in the size ranges: 1) 0.5–50 μm (UFPOM); 2) 50–250 μm (FPOMa); 3) 250 μm–1 mm (FPOMb); 4) fungi; 5) sestonic diatoms; 6) benthic diatoms; 7) multicellular algae; 8) vascular plant material, 0.5–50 μm (VP.UFPOM); 9) vascular plant material, 50–250 μm (VP.FPOMa); 10) vascular plant material, 250 μm–1 mm (VP.FPOMb); 11) pollen; 12) invertebrate remains; and 13) silt. For every field viewed, the area covered by each of the 13 categories of food was counted using a gridded occular micrometer (Coffman *et al.*, 1971; Cummins, 1973; Hawkins, 1985).

Dietary composition was compared using a multifactor ANOVA. ANOVA assumes equality of variance, but Bartletts test revealed that the raw data did not conform to this. Skewness in the distribution of errors tends to produce too many significant results in f tests, and for the binomial proportions, the arcsin of the square root of p is needed to stabilise the variance more effectively (Snedecor & Cochran, 1967). The area values were therefore transformed (arcsin) (*sensu* Rader & Ward, 1987) before dietary comparisons were made.

The data included 75 sets with 3 complete replicates, but 25 sets were incomplete as there were insufficient animals to make three replicate slides. Differences in dietary composition within each set of three replicates was tested (two-way ANOVA without interaction, with food type and sample as the two factors). Once it was established that these replicates were not significantly different (for 69 sets $p > 0.05$, for 6 sets $p > 0.01$), it was accepted that each slide comprised the same 'population' of gut contents. In these instances, 30 fields were counted from the one or two slides available. The more conventional technique of estimating the missing values by using the mean of the existing values in the ANOVA cell was also performed, but it was felt that counts of extra fields from the existing slides gave a better reflection of the dietary range of the animals (S. Radloff, pers. comm.). These repeated count data were included to enable a balanced ANOVA design. Three-way ANOVA with interaction was

Table 1. The size range, and number of individuals used to determine gut contents.

Taxon	Size	Head width (mm)	Body length (mm)	Numbers
Adenophlebia	small	0.95–2.00	3.50–9.15	42
auriculata	large	2.35–2.80	12.00–20.70	25
Dyschimus	small	0.30–0.65	2.35–5.20	21
ensifer	large	0.80–1.40	7.10–17.70	24
Goerodes	small	0.40–0.50	1.90–2.85	25
caffrariae	large	0.65–0.95	3.80–6.50	24
Afronemoura	small	0.45–0.80	2.35–3.95	39
spp.	large	0.95–1.10	4.75–6.30	25

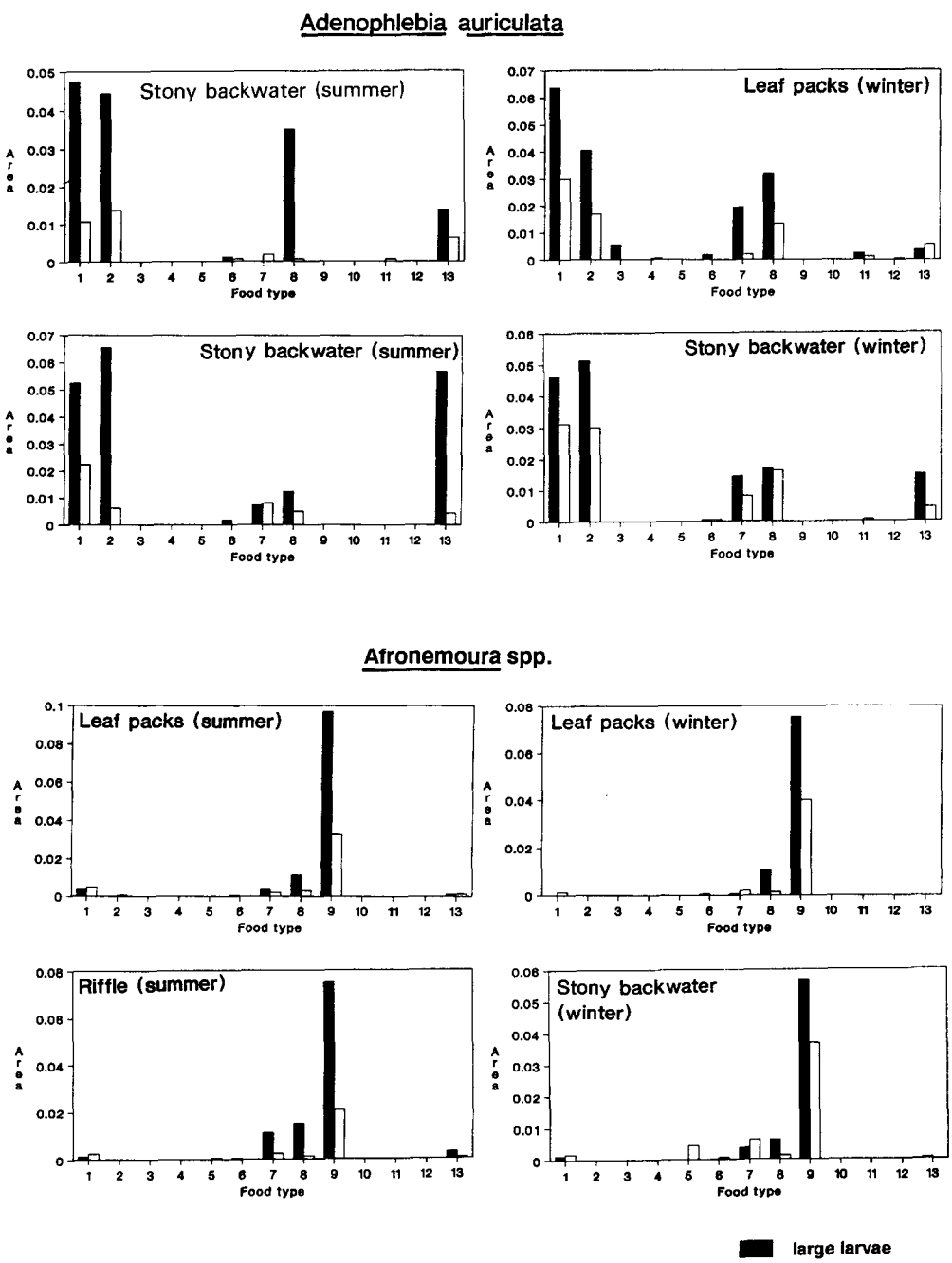

Fig. 2. Typical examples of the gut contents of *Adenophlebia auriculata*, *Dyschimus ensifer*, *Goerodes caffrariae* and the Plecoptera are shown. Large (shaded) and small (unshaded) animals collected from summer and winter stony backwater and leaf pack biotopes were selected, as they illustrate the trends described in the text. The area value given is the mean area covered in 10 microscope fields (400 ×) by each food type for the 3 replicate gut contents slides. 1 = detritus (0.5–50 μm), 2 = detritus

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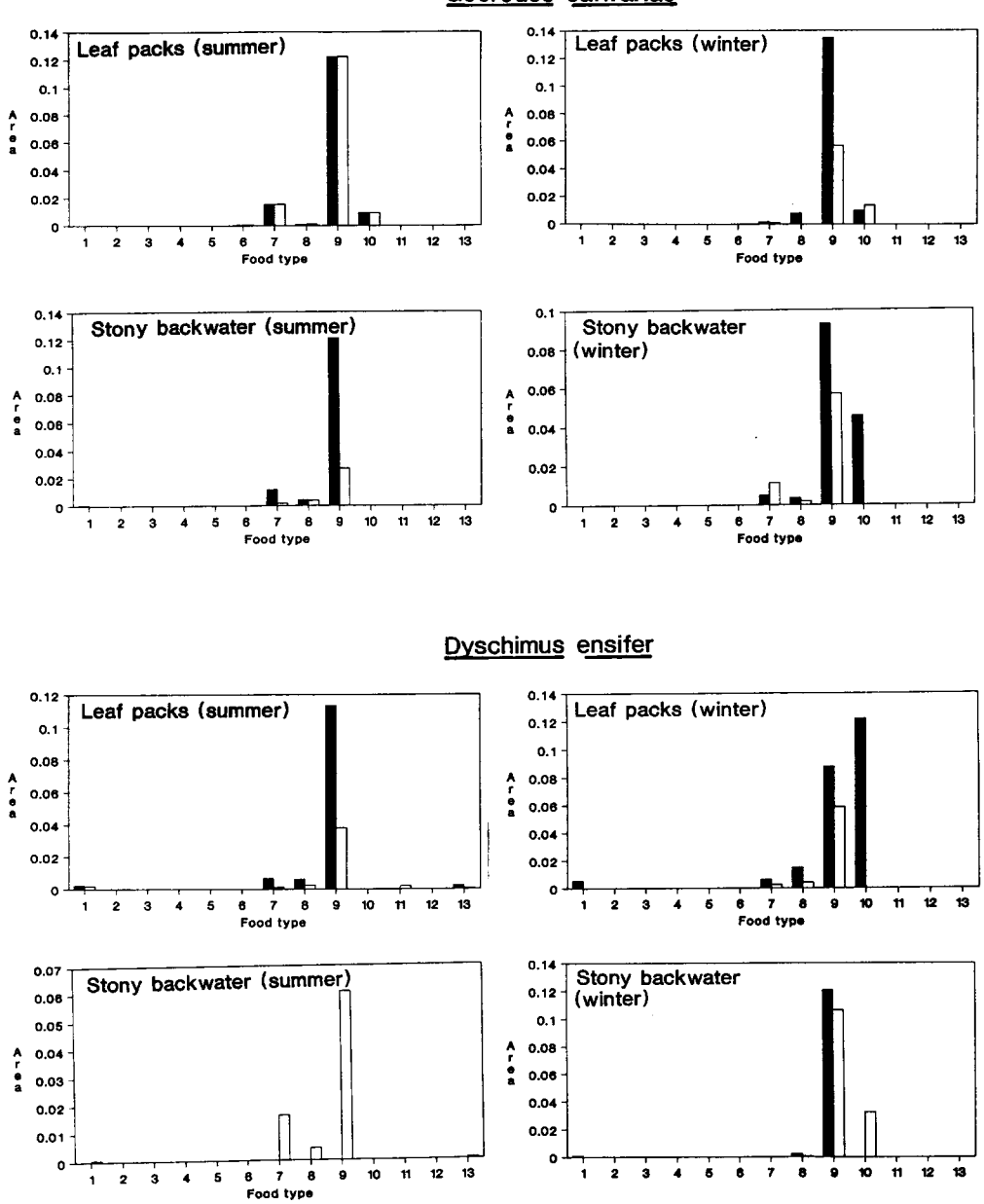

(50–250 μm), 3 = detritus (250 μm–1 mm), 4 = fungi, 5 = planktonic diatoms, 6 = benthic diatoms, 7 = filamentous algae, 8 = vascular plant fragments (0–50 μm), 9 = vascular plant fragments (50–250 μm), 10 = vascular plant fragments (250 μm–1 mm), 11 = pollen, 12 = invertebrate remains, 13 = silt.

used to assess dietary differences associated with size, biotope and season.

All 232 samples (excluding double counts) were classified on the basis of their dietary composition using TWINSPAN (Hill, 1979).

Results

Analyses of variance of food types found in the foreguts of the four taxa revealed that there were most frequently differences between large and small individuals. *A. auriculata* and *D. ensifer* feeding in different seasons and biotopes showed some variation in their gut contents, which was not the case for *G. caffrariae* and *Afronemoura* spp. The ANOVA design has generated a set of tables where larval size, biotope, and seasonal effects on dietary composition are considered separately (Tables 3, 4 and 5). While this does not analyse the combined interactions of these factors as a 4-way ANOVA would, the raw data for each taxon (eg. Fig. 2), revealed basically similar dietary composition regardless of season and biotope. The frequent differences between large and small larvae were mainly, and unsurprisingly, attributable to the greater amount of material ingested by the larger individuals.

The range of food types in the foreguts of all individuals from each taxon was basically the same (Fig. 2). Such differences as there were (eg. seasonal and biotope differences in *A. auriculata* and *D. ensifer*), reflected variations in the amounts and proportions of some of the less common food types. The ANOVA has recognised such variations as significant differences, but they are of limited biological significance, and have been given little weight in our conclusions.

Where there are significant differences in gut contents, the ANOVA indicates whether there is interaction between dietary composition and the factor under consideration, whether size, biotope, or season. Where there is no interaction, the same food types had been ingested, and their relative proportions were not significantly different, but the amount of food ingested was different. Where there is interaction between food and size, biotope or season, the same food types may have been ingested, but the relative proportions were significantly different, and the total amount of food ingested may or may not have been different.

Adenophlebia auriculata

Observations

A. auriculata, the most versatile feeder, was most often observed brushing in both the stream and laboratory. Other feeding activities included, collecting: the use of palps to scoop up larger detrital fragments such as the oak fragments (500–1000 μm), and nibbling: observed when larvae ingested *Batrachospermum* sp. algae by feeding a strand into their mouth and nibbling the end. Three larvae were kept in a small aquarium with only leaves for several weeks. Faecal detritus was removed, and water replaced with fresh, filtered water daily. The larvae survived, and the surface layer of leaf cells was removed. This was not the case in control samples of leaves with no larvae. The abrasion to the leaves was not considered sufficient to constitute shredding, and was probably the result of continuous brushing.

Watching *A. auriculata* larvae at intervals over 12 hours revealed that the one larva which moulted while being observed did not feed during the 12 hours prior to ecdysis; that the most common feeding behaviour was brushing; that brushing cycles lasted from 0.5 to 5 minutes: and that each cycle typically involved a sequence of reversing rapidly, then brushing forward, reversing again, etc. The most common behaviour when not brushing, was a motionless stance with the gills pulsating. Other activities included shifting position, grooming, defecating, swimming and interacting with other larvae by making contact with antennae, legs and cerci.

Food choice

Larvae ingested all the food types and sizes offered experimentally, and may be classified as generalists, but they more often brushed the surface of substrates than any other feeding activity (Table 2).

Table 2. A Chi-squared test was used detect preferential feeding on any of the foods, or preferential presence of larvae in any of the food compartments. The null hypothesis was that the proportion of larvae located in each area of the aquarium would be equal. If the null hypothesis was rejected (**$p < 0.01$, *$p < 0.05$) the Chi-squared test was repeated for the preferred food type (for example: p (leaves) expected against p (leaves) observed). The level of significance for these Chi-squared tests was reduced by dividing the nominal level of significance by the number of individual Chi-squared tests performed (*$p < 0.01$, **$p < 0.001$). Where the proportion of larvae present in a compartment, or feeding on a food, was significantly more than expected, they were assumed to have shown a preference for the food type.

Adenophlebia auriculata

ai) Choice of food types, presence in a compartment recorded:

	Detritus	Leaves	Algae	Rocks	Neutral
f (obs)	12	17	17	18	36

Chi-square 17.1 4 d.f. Sig. **

aii) Preferred food compartment (neutral) proportions:

	Neutral	Balance
f (obs)	36	64

Chi-square 16 1 d.f. Sig. **

bi) Choice of food types, feeding events recorded:

	Detritus	Leaves	Algae	Rocks	Neutral
f (obs)	2	1	1	1	7

Chi-square 11.333 4 d.f. Sig. *

bii) Preferred food compartment (neutral) proportions:

	Neutral	Balance
f (obs)	6	6

Chi-square 6.75 1 d.f. Sig. **

ci) Choice of food sizes/style, presence in a compartment recorded:

	80–250	250–500	500–800	800–1000	>4000	Brushing
f (obs)	3	4	4	4	7	80

Chi-square 280.706 5 d.f. Sig. **

cii) Preferred food size/style (brushing) proportions:

	Brushing	Balance
f (obs)	80	22

Chi-square 280.165 1 d.f. Sig. **

di) Choice of food sizes/style, feeding events recorded:

	80–250	250–500	500–800	800–1000	>4000	Brushing
f (obs)	2	4	3	4	7	46

Chi-square 134.909 5 d.f. Sig. **

dii) Preferred food size/style (brushing) proportions:

	Brushing	Balance
f (obs)	46	20

Chi-square 133.636 1 d.f. Sig. **

Dyschimus ensifer

ai) Choice of food types, presence in a compartment recorded:

	Detritus	Leaves	Algae	Rocks	Neutral
f (obs)	4	28	2	13	3

Chi-square 48.2 4 d.f. Sig. **

aii) Preferred food compartment (leaves) proportions:

	Leaves	Balance
f (obs)	28	22

Chi-square 40.5 1 d.f. Sig. **

bi) Choice of food types by starved larvae, presence in compartments:

	Detritus	Leaves	Algae	Rocks	Neutral
f (obs)	5	25	3	9	8

Chi-square 30.4 4 d.f. Sig. **

bii) Preferred food compartment (leaves) proportions:

	Leaves	Balance
f (obs)	25	25

Chi-square 28.125 1 d.f. Sig. **

Gut analysis

The 67 *A. auriculata* larvae which were dissected had ingested mainly fine detritus (UFPOM, FPOMa, VP.FPOMa) with some filamentous algae (Fig. 2).

The gut contents of small individuals comprised only fine detritus, whereas larger larvae ingested more material, and included a wider variety of food (Fig. 2, Table 3). There were significant variations in the gut contents of larvae from different seasons and biotopes (Tables 4 & 5). These were due to different proportions of the less frequent dietary components such as pollen, fungi, invertebrate remains and larger leaf fragments. Any leaf fragments ingested would have been brushed up rather than shredded and are simply a part of the fine detritus which is the major food source of this species.

On this basis, *A. auriculata* would be classified as an opportunistic collector:brusher (*sensu* McShaffrey & McCafferty, 1988); with size playing a more important role than biotope or season in dietary variation.

Goerodes caffrariae

G. caffrariae (49 dissected) was the most specialised feeder, with leaf fragments (VP.UFPOM and VP.FPOMa) almost exclusively filling the foregut (Fig. 2). Larger animals had chewed off and ingested bigger pieces (VP.FPOMb) (Table 3), but there were no variations with biotope or season (Tables 4 & 5). Shredding by Lepidostomatidae is well documented (Anderson & Grafius, 1975; Anderson *et al.*, 1979; Grafius & Anderson, 1979; 1980), and this study confirms that *G. caffrariae* is a shredder.

Dyschimus ensifer

Observations and leaf discs

D. ensifer were observed feeding on the surfaces of leaves, and 23 larvae reduced the mean leaf disc mass of 25 oak discs by 52.8% over a period of 4 weeks, with a mean rate of consumption of 18 mg animal^{-1} week^{-1} (Fig. 3). Frass and faecal fragments produced were in the 50–250 μm size range, a size reduction of two orders of mag-

Table 3. Size comparisons: In each season and biotope the dietary composition of large and small larvae of *A. auriculata*, *G. caffrariae*, *D. ensifer* and *Afronemoura* spp. was compared using a 3-way ANOVA with interaction $^{**}p < 0.01$, $^{*}p < 0.05$, × -interaction. Interactions indicate that the relative proportions of the various food items in the diet are significantly different.

A. auriculata				
Spring	riffles	:	**	×
	stony backwaters	:	**	×
	leaf packs	:	**	×
Summer	riffles	:	*	
	stony backwaters	:	**	×
	leaf packs	:	**	×
Autumn	stony backwaters	:	**	×
	leaf packs	:		×
	sediments	:	**	×
Winter	stony backwaters	:	**	
	leaf packs	:	**	×
G. caffrariae				
Spring	leaf packs	:	*	
Summer	riffles	:	**	×
	stony backwaters	:	*	
	leaf packs	:	*	×
	sediments	:	**	×
Autumn	stony backwaters	:	**	×
	leaf packs	:		×
Winter	stony backwaters	:		×
	leaf packs	:	**	×
D. ensifer				
Summer	riffles	:		×
	leaf packs	:	**	×
Autumn	stony backwaters	:	**	×
	leaf packs	:	**	×
	sediments	:	**	×
Winter	stony backwaters	:	**	×
	leaf packs	:	**	×
Afronemoura spp.				
Spring	riffles	:		×
	leaf packs	:		
Summer	riffles	:	**	×
	leaf packs	:	*	×
Autumn	leaf packs	:	**	×
Winter	stony backwaters	:		
	leaf packs	:		
	waterfall	:		×

Table 4. Biotope comparisons: The dietary composition of large and small *A. auriculata, G. caffrariae, D. ensifer* and *Afronemoura* spp. larvae in different seasons, collected from various biotopes (given in brackets) was compared, using a 3-way ANOVA with interaction, $^{**}p < 0.01$, $^{*}p < 0.05$, × -interaction. Interactions indicate that the relative proportions of the various food items in the diet are significantly different.

A. auriculata				
Spring	large larvae	(riffles, stony backwaters, leaf packs, sediments):	**	×
	small larvae	(riffles, stony backwaters, leaf packs) :	**	×
Summer	large larvae	(riffles, stony backwaters) :	**	×
	small larvae	(riffles, stony backwaters, leaf packs) :	**	×
Autumn	large larvae	(stony backwaters, leaf packs, sediments, pool) :	**	×
	small larvae	(stony backwaters, leaf packs, sediments) :	**	×
Winter	large larvae	(stony backwaters, leaf packs, pool) :	**	×
	small larvae	(stony backwaters, leaf packs) :		
G. caffrariae				
Spring	large larvae	(stony backwaters, leaf packs) :		×
Summer	large larvae	(riffles, stony backwaters, leaf packs, sediments):		
	small larvae	(riffles, stony backwaters, leaf packs, sediments):		
Autumn	large larvae	(stony backwaters, leaf packs) :		
	small larvae	(stony backwaters, leaf packs) :		
Winter	large larvae	(stony backwaters, leaf packs) :		
	small larvae	(stony backwaters, leaf packs) :		
D. ensifer				
Spring	large larvae	(leaf packs, sediments) :		
Summer	large larvae	(riffles, leaf packs)	**	×
	small larvae	(riffles, stony backwaters, leaf packs, sediments):		
Autumn	large larvae	(stony backwaters, leaf packs, sediments) :		
	small larvae	(stony backwaters, leaf packs, sediments) :	**	×
Winter	large larvae	(Stony backwaters, leaf packs) :	**	×
	small larvae	(Stony backwaters, leaf packs) :	**	×
Afronemoura spp.				
Spring	large larvae	(riffles, leaf packs) :		
	small larvae	(riffles, leaf packs) :	*	×
Summer	large larvae	(riffles, leaf packs) :		
	small larvae	(riffles, leaf packs) :		
Autumn	large larvae	(stony backwaters, leaf packs, waterfall) :	**	×
	small larvae	(sediments, leaf packs, waterfall) :		×
Winter	large larvae	(stony backwaters, leaf packs, waterfall) :		
	small larvae	(stony backwaters, leaf packs, waterfall) :		

nitude. *D. ensifer* tended to wear away the surface of leaf discs evenly.

Food choice

D. ensifer larvae showed a significant preference for chambers containing leaves (Table 2). Larvae observed over several days also congregated in compartments with rocks, which could indicate a need for shelter, or negative phototropism, rather than a feeding preference. During the day in the stream, *D. ensifer* could often be found under stones.

Gut analysis

The foregut contents of *D. ensifer* larvae (45 dissected) comprised a wider variety of foods than *G. caffrariae*, but were still dominated by leaf fragments (Fig. 2).

Large larvae had chewed off and ingested proportionally more of the larger leaf fragments

Table 5. Seasonal comparisons: The dietary composition of large and small *A. auriculata, G. caffrariae, D. ensifer* and *Afronemoura* spp. larvae, collected from various biotopes, was compared in different seasons (shown in brackets) using a 3-way ANOVA, $^{**}p < 0.01$), $^{*}p < 0.05$, × -interaction. Interactions indicate that the relative proportions of the various food item in the diet are significantly different.

A. auriculata				
Large larvae,	riffles (spring, summer)	:	**	×
Small larvae,	riffles (spring, summer)	:		
Large larvae,	stony backwaters (spring, summer, autumn, winter):		**	×
Small larvae,	stony backwaters (spring, summer, autumn, winter):		**	×
Large larvae,	leaf packs (spring, autumn, winter)	:	**	×
Small larvae,	leaf packs (spring, summer, autumn, winter)	:	**	×
Large larvae,	sediments (spring, autumn)	:		
Large larvae,	pool (autumn, winter)	:	*	
G. caffrariae				
Large larvae,	stony backwaters (spring, summer, autumn, winter):			×
Small larvae,	stony backwaters (summer, autumn, winter)	:		
Large larvae,	leaf packs (spring, summer, autumn, winter)	:		
Small larvae,	leaf packs (spring, summer, autumn, winter)	:		
D. ensifer				
Large larvae,	stony backwaters (summer, autumn, winter)	:	**	×
Small larvae,	stony backwaters (summer, autumn, winter)	:	**	×
Large larvae,	leaf packs (spring, summer, autumn, winter)	:	**	×
Small larvae,	leaf packs (spring, summer, autumn, winter)	:		
Large larvae,	sediments (spring, summer, autumn)	:		
Small larvae,	sediments (spring, summer, winter)	:		×
Afronemoura spp.				
Large larvae,	stony backwaters (autumn, winter)	:	*	
Large larvae,	leaf packs (spring, summer, autumn, winter)	:	*	
Small larvae,	leaf packs (spring, summer, autumn, winter)	:		
Small larvae,	sediments (summer, autumn)	:		×
Large larvae,	waterfall (autumn, winter)	:		×
Small larvae,	waterfall (autumn, winter)	:		×

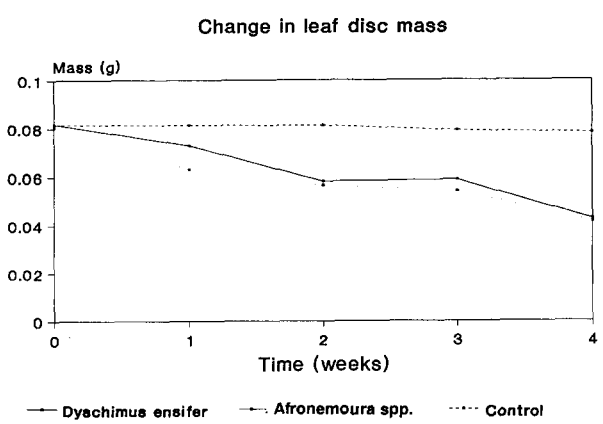

Fig. 3. Shredding activity: change in mean leaf disc mass over time. (vertical bars – 95% confidence limits).

(Fig. 2), which contributed to the detection of differences in the gut contents of large and small larvae (Table 3). Seasonal and biotope differences could be ascribed to differing proportions of filamentous algae in the gut (Fig. 2 and Tables 4 & 5).

Although less exclusive than *G. caffrariae*, the gut contents, choice experiments, and laboratory feeding experiments indicate that *D. ensifer* is a shredder.

Afronemoura spp.

Observations and leaf discs

It was difficult to observe the larvae feeding as they fed on the underside of the leaves. In contrast to *D. ensifer*, the stoneflies skeletonised one part of a leaf disc at a time rather than nibbling the whole surface, and 50 stoneflies reduced the mean mass of 20 oak leaf discs by 51.1% over a 4 week period (Fig. 3). The mean rate of consumption was 8 mg animal^{-1} week^{-1}.

Gut analysis

Afronemoura spp. (64 dissected) are also shredders (Fig. 2), differing from the caddisflies in that their gut contents contained a wider variety of material, which may be a reflection of the presence of more than one species. There were no consistent differences in gut content composition between large and small individuals (Table 3) though some of the small individuals had ingested more detritus than leaf fragments. There were also few detectable differences either seasonally or in different biotopes, both of which might have indicated specific differences. The predominance of vascular plant fragments in the gut (Fig. 2), and feeding behaviour in the laboratory (Fig. 3), indicate that the *Afronemoura* spp. are members of the shredder guild.

Classification on the basis of diet

In an attempt to achieve an objective functional classification, a TWINSPAN analysis was used to develop hierarchical groupings of all the gut contents' samples. The classification is based on food type presence, absence and predominance (Fig. 4).

At level 1 gut content samples with UFPOM, FPOMa, silt and some diatoms (Group I) were distinguished from samples with no FPOMa, less UFPOM and silt, and very few diatoms (Group II). Group I comprised all the *A. auriculata* samples, and a few small *Afronemoura* spp. samples. The balance of the stonefly samples, and all the *D. ensifer* and *G. caffrariae* samples remained in Group II (Fig. 4).

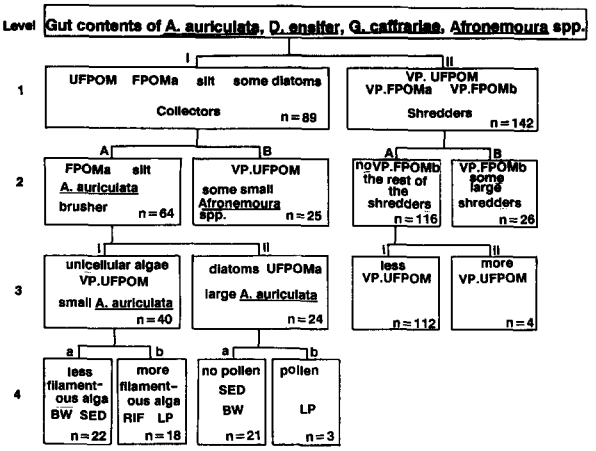

Fig. 4. An hierarchical classification of the gut contents of four macroinvertebrate taxa: the result of a TWINSPAN classification. (VP.UFPOM = vascular plant fragments (0.5–50 μm) VP.FPOMa = vascular plant fragments (50–250 μm); VP.FPOMb = vascular plant fragments (250 μm–1 mm); UFPOM = detritus (0.5–50 μm); RIF = riffle; BW = stoney backwater; SED = sediments; LP = leaf pack.

Group I

At level 2, the *A. auriculata* samples (Group IA) were distinguished from the small *Afronemoura* spp. samples (Group IB). Group IA was characterised by the predominance of FPOMa and silt, with fungi, pollen and invertebrate remains present, and very little VP.UFPOM. Group IB samples contained little FPOMa and silt, no fungi, pollen or invertebrate remains and were dominated by VP.UFPOM (Fig. 4).

At level 3, Group IAi samples were distinguished by the presence of unicellular algae and VP.UFPOM, fewer FPOMa and diatoms, and the absence of FPOMb. In Group IAii samples, FPOMb was present, while sestonic algae and VP.UFPOM were absent. Diatoms and UFPOM were more common than in Group IAi. the majority of Group IAi samples comprised small *A. auriculata* individuals, while Group IAii were mainly large individuals (Fig. 4).

At level 4, small *A. auriculata* (Group IAia) samples, from depositional, BW and SED biotopes, were distinguished from leaf pack samples (Group IAib) because they contained less filamentous algae. Large *A. auriculata*

(Group IAiia) samples, from depositional, BW and SED, biotopes were separated from erosional SIC and LP samples (Group IAiib) because of the absence of pollen, FPOMb and invertebrate remains (Fig. 4).

Group II

At level 2, the presence/absence of VP.FPOMb was the distinguishing feature. The gut contents of only the largest *G. caffrariae* and *D. ensifer* contained VP.FPOMb (Group IB), all the rest of *G. caffrariae*, *D. ensifer* and *Afronemoura* spp. samples did not (Group IA) (Fig. 4).

At level 3, a large set of samples, Group IIAi, was distinguished from a smaller set, Group IIAii, because the latter contained more VP.UFPOM (Fig. 4). These dietary distinctions could not be linked to taxon, organism size, biotope or season.

Discussion

Dietary composition and variability

We were able to answer the basic questions posed in the introduction concerning the feeding of four macroinvertebrates from the headwaters of the Buffalo River: 1) Ingestion: *A. auriculata* ingested mainly fine detritus, and *G. caffrariae*, *D. ensifer* and the *Afronemoura* spp. shredded leaves, ingesting leaf fragments. 2) Dietary variability: In all four taxa diet varied with size, though most of this variation was simply in the amount of material ingested. Some small stoneflies differed from large ones in the predominance of fine detritus, and absence of leaf fragments in the gut. *A. auriculata* and *D. ensifer* ingested varying amounts of rare dietary items in different seasons and biotopes, whereas *G. caffrariae*, and the *Afronemoura* spp. showed no such differences. 3) Dietary specialisation: *A. auriculata* was a generalist, feeding on the widest range of food, using a variety of behavioural feeding techniques. The other three taxa could be ranked, with *G. caffrariae* being the most specialised, feeding exclusively on leaves, and the *Afronemoura* spp. the least specialised, including varying amounts of fine detritus and periphyton in their diet.

The fourth question concerned the assigning of the taxa to FFG's. One of the major concerns about the applicability of the FFG concept identified by King *et al.* (1988) is that spatial, developmental and temporal dietary variability precludes the realistic assigning of macroinvertebrate taxa to FFG's. This was not the case in this study. *A. auriculata* was identified as a collector: brusher, while *G. caffrariae*, *D. ensifer* and the *Afronemoura* spp. were classified as shredders. Some of the small stonefly larvae had ingested mainly fine detritus, and could have been classified as collectors, but most had also included leaf material in their diet. Chessman (1986) recorded Plecoptera which included surface detritus in their diets. In all four taxa the most consistent dietary differences were between early and late instar individuals. All the results confirm Hawkins' (1985) findings that although size does influence diet, it does so in a specific way, with larger organisms ingesting larger particles, and usually a wider range of food. The variation associated with different seasons and biotopes reflects the degree of opportunism within each taxon, as found by Irons (1988) in a group of subarctic caddisflies.

Gut analysis has been criticised when used on its own to investigate macroinvertebrate feeding (see King *et al.*, 1988). In this study it proved to be a useful tool in assigning taxa to FFG's. Foregut contents reflect the material an organism has ingested and not necessarily that which contributes to assimilation. On the basis that feeding behaviour contributes to the fitness of an organism (Calow, 1977; Cummins & Klug, 1979), Hawkins (1985) made the reasonable assumption that gut contents do reflect ingestion of assimilable food items. We have concentrated on whether the type of material ingested, and the manner of ingestion contributes to an understanding of processes in the stream. Together with behavioural and morphological data, gut content analysis can contribute to an understanding of invertebrate feeding (McShaffrey & McCafferty, 1988), and ecology (Chessman, 1986).

Functional classification

The FFG concept was also proffered as an alternative classification scheme for stream fauna (Cummins, 1974; Anderson & Seddell, 1979). The TWINSPAN analysis provides an hierarchical classification based on dietary composition, and is an attempt to achieve an objective classification of a component of the headwaters fauna on the basis of the size and type of food in the gut. The primary distinction (level 1, Fig. 4) was made between collectors (*A. auriculata* and some small *Afronemoura* spp.) and shredders (*G. caffrariae*, *D. ensifer* and most of the *Afronemoura* spp.). At subsequent levels, there was no connection between diet and existing descriptions of FFG's. However, the classification does indicate that size is an important secondary determinant of diet, with biotope influencing *A. auriculata* diet only at level 4, and not influencing the shredders at all. The presence or absence of algae in the gut was often a distinguishing feature in the groups differentiated by TWINSPAN (and the reason for differences revealed by the ANOVA). Periphyton has been shown to influence other species ecologically: its abundance affected the distribution of the caddisfly larva *Helicopsyche borealis* (Lamberti & Resh, 1983; Vaughn, 1986), and the inclusion of algae in the diet of the heptageniid *Stenonema vicarium* contributed significantly to its growth (Webb & Merritt, 1987).

It is interesting that the two groups distinguished at level 1 (Fig. 4), are more easily defined functionally than taxonomically, and that at no stage are the three shredder taxa distinguished by the TWINSPAN analysis. The inclusion of some small *Afronemoura* spp. in the collector group is an indication that although primarily shredders, fine detritus forms and important part of the diet of early instars. On a scale from generalised collector to specialised shredder the taxa would be: *A. auriculata*, *Afronemoura* spp., *D. ensifer* and *G. caffrariae*. We think such functional classifications are useful, despite Minshall's (1988) warning that 'valuable information can be lost by not maintaining the taxonomic integrity of the community' by 'collapsing the entire community in 3–6 composite categories (FFG's)'. Functional classifications do not replace taxonomy, they provide an opportunity to group organisms in such a way as to gain an insight into the functioning of the ecosystem.

Definitions of 'function'

The original FFG concept was envisioned as contributing to an understanding of stream processes (Vannote *et al.*, 1980). We suggest that the key aspect of the FFG concept is the term 'function'. Its meaning in the FFG concept has never been defined, and as a result, has been variously interpreted. McShaffrey & McCafferty (1986, 1988) have a mechanistic view of function. They use morphology and behavioural studies to elucidate how an animal feeds, and, together with gut analysis, to indicate the functional role of the species. They discuss their work in the context of the distribution of stream macroinvertebrates, since food is distributed in streams in response to flow characteristics (either suspended, loosely deposited, or tightly accreted), and animals will be found where they feed.

We have approached the term 'function' by asking the question: What are the functions in streams which the feeding activities of macroinvertebrates facilitate? This returns the FFG concept to the context of stream function and complements feeding research performed at an organismal level.

Stream functions facilitated by macroinvertebrate feeding include: alteration of organic particle size; retention or mobilisation of organic matter; mineralisation of organic matter; and preparation of substrates for microbial colonisation. Filterers convert UFPOM and FPOM to animal biomass and faeces, consequently increasing organic particle size, retaining organic matter, and providing substrates for microbial colonisation. Collectors, both feeding on, and excreting fine particles probably contribute mainly to retention and the enhancement of substrates for microbial activities. Shredders, by converting leaves to animal biomass, leaf skeletons, frass and faeces,

are involved in particle size reduction, the mobilisation of organic matter, and the enhancement of microbial colonisation.

One of the FFG debates which is clarified by this approach concerns the definition of the term 'shredder'. King *et al.* (1988) elaborate many of the inconsistencies surrounding this functional designation. In streams, shredders primarily reduce organic particle size by ingesting fallen leaves. They do not need to be defined in terms of the size of organic particle in their gut, nor is it important whether they rasp or skeletonise leaves. If one organism chews pieces off leaves and another rasps away the surface, the process of leaf shredding in the stream is still effected and the animal is a shredder. The predominance of leaf fragments of any size in the gut is a more valuable indication of shredding than particle size. It must be remembered that the size of particle in the gut does not necessarily bear any relation to the original size of the food item eaten. In this study, the case building caddisflies and the stoneflies are all classified as shredders, despite their different styles of shredding and varying degree to which leaves exclusively constitute their diet. Irons (1988) used presence of plant matter in the gut as being diagnostic of shredding, but also linked this to particle size. If a predominance of leaf fragments in the gut was used as a diagnostic feature of shredding, the confusion in the literature surrounding the 'shredder' definition on the bias of particle size could be avoided.

In the Buffalo River, the shredders *G. caffrariae*, *D. ensifer* and the *Afronemoura* spp. primarily perform the function of reducing leaf particle size, with the three taxa reducing dietary overlap by augmenting leaves with other organic material to a varying extent. Darrow & Holland (1989) have shown that hydropsychid caddis larvae increase the retention of leaves in the stream by using leaf material to build their retreats. This may also be true of the lepidostomatid and pisuliid caddis in this study, which use leaves to build their cases. Cummins & Klug (1979) emphasised the nutritional importance of the microbial component of organic detritus. The increased surface area provided by shredded leaf fragments, frass, and faeces is ideal for microbial colonisation, and the enriched detritus forms the food supply for collectors. The collector/brusher *A. auriculata*, feeding on exactly this food source, primarily performs the function of retaining fine particles. This process is aided by the physical retention of fine particles in leaf packs and backwaters.

The approach in this study of defining feeding variability, assigning species to FFG's, classifying the macroinvertebrate assemblage on the basis of ingested food, and recognising the facilitation of river function by macroinvertebrate feeding is being extended to the middle/lower reaches of the Buffalo River.

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