BENTHIC ASSEMBLAGE STRUCTURE, AND THE FEEDING BIOLOGY OF SIXTEEN MACROINVERTEBRATE TAXA FROM THE BUFFALO RIVER, EASTERN CAPE, SOUTH AFRICA.

THESIS

Submitted in fulfilment of the requirements for the degree
DOCTOR OF PHILOSOPHY
in the Faculty of Science, Rhodes University, Grahamstown

by

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DECLARATION

In accordance with the regulations for the award of the degree of Doctor of Philosophy I declare that the work presented in this thesis is my own original research. I have used data on the physico-chemical variables at each of the sites in the Buffalo River that were collected as part of the Buffalo River Programme by Dr. J.H. O'Keeffe, Mr. R.W. Palmer and myself. Assistance with sample processing and statistical procedures have been acknowledged elsewhere. Neither the whole, nor any part of the thesis, has been, is being, or will be submitted for a higher degree from any other university.

Parts of Chapters 3, 4, and 6 have been accepted for publication.

PALMER, C.G., J.H. O'KEEFFE, AND A.R. PALMER. In press. Are macroinvertebrate species assemblages associated with particular biotopes in the Buffalo River, southern Africa? Journal of the North American Benthological Society 10(4). Publication date: November 1991.

PALMER, C.G. AND J.H. O'KEEFFE. In press. Feeding patterns of four macroinvertebrate taxa in the headwaters of the Buffalo River, eastern Cape. Hydrobiologia. Publication date: January 1992.

ABSTRACT

The River Continuum Concept (RCC) (Vannote et al. 1980) attempted to provide a unifying theory of river function. The Functional Feeding Group (FFG) concept (Cummins 1973, 1974) became a major component of the RCC. The FFG concept provides testable hypotheses about the changes in proportions of FFGs along a downstream gradient in a river, in response to the changing nature of food resources. The following short-comings of the FFG concept have been identified: 1) the variability of macroinvertebrate feeding, 2) problems with gut analysis as a method for assigning taxa to FFGs, and 3) inconsistent criteria defining FFGs.

The objective of this study was to investigate the macroinvertebrate fauna of the Buffalo River in order to assess the applicability of aspects of the RCC and the FFG concept. The specific aims of the study were: 1) to describe the distribution of macroinvertebrate assemblages in the Buffalo River; 2) to clarify aspects of the FFG concept listed above; 3) to establish whether selected taxa could be assigned to FFGs; 4) to assess whether the proportions of different FFGs in successive reaches of a southern African river conformed to the predictions of the RCC; and 5) to test whether a functional classification is a useful alternative to a taxonomic classification.

Macroinvertebrates were collected seasonally from a variety of biotopes at three sites, one each in the upper, middle and lower reaches. Riffles were sampled in summer at 16 sites. Over 100 taxa were identified and an hierarchical classification was prepared using two-way indicator species analysis. Invertebrate assemblages in the narrow headwater stream were taxonomically distinct from those of the middle/lower reaches and were not positively associated with subjectively identified biotopes. Biotopes were characterised by distinct assemblages in the wider middle/lower reaches. Sixteen abundant taxa whose feeding had not been previously investigated were selected for feeding studies, four from the headwaters and 12 from the middle/lower reaches. Methods used included gut content analysis, behavioural

observations, food choice experiments and morphological studies using scanning electron microscopy.

Three aspects of the functional feeding group concept were clarified. 1) Dietary variability was assessed using gut contents as an index of diet. The gut contents of both early (small) and late (large) instar larvae of all 16 taxa collected from different sites and biotopes, and in different seasons were compared using a multifactor analysis of variance. For all taxa the most consistently significant differences in gut contents were between large and small larvae. These were due to differences in the amount of material in the gut and in varying amounts of rarer dietary items. Dietary variability did not prevent taxa from being assigned to FFGs. 2) Gut content analysis satisfactorily provided basic information about the feeding biology of taxa but proved to be an inadequate single method for positively assigning taxa to FFGs. 3) Before taxa could be assigned to FFGs the definitions for some FFG categories had to be described clearly. It is suggested that the term shredder be based on the observation of shredding and a predominance of leaf fragments in the foregut. The presence of algae was not diagnostic of scrapers and a morphological basis is suggested. A morphological basis for the brusher FFG is described for the first time.

All 16 taxa were assigned to FFGs. Three headwater taxa were shredders (Goerodes caffrariae (Lepidostomatidae), Dyschimus ensifer (Pisulidae), Afronemoura spp. (Notonemouridae)) and one was a collector:brusher (Adenophlebia auriculata (Leptophlebiidae)). These results were consistent with RCC predictions. All 12 of the taxa from the middle/lower reaches were filterers or collectors and this result was also consistent with RCC predictions. The Hydropsychidae, Cheumtopsyche afra and Macrostemum capense, were passive net filterers; Neurocaenis reticulatus (Tricorythidae) was a passive setal filterer; Caenidae sp. B and Pseudocloeon maculosum (Baetidae) were active filterers; Caenidae sp. A, and the Baetidae, Baetis harrisoni, Centroptilum excisum and Cloeon africanum, were collector:gatherers; the Leptophlebiidae, Choroterpes elegans and

Choroterpes nigrescens, were collector:brushers; and Afronurus harrisoni (Heptageniidae) was a scraper. Gut content analyses alone were insufficient to assign taxa to FFGs, but when augmented by morphological and/or behavioural data, taxa could be assigned to FFGs with confidence. In all cases the FFG designation referred to the most frequent style of feeding. N. reticulatus, A. harrisoni and A. auriculata were particularly flexible in their feeding behaviour.

A functional classification of macroinvertebrates in the Buffalo River was compared with a taxonomic classification. In both cases similar groups were identified, but their taxonomic and functional descriptions yielded different information. It is suggested that functional and taxonomic classifications should be viewed as complementary rather than alternative options.

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DEDICATION

To my grandfather, Herbert Tamplin Long,
who first showed me the wonder of the
night skies, walked with me in the veld,
and allowed me to collect grubs from the
garden manure.

PREFACE

Shoes, Ships, Sealing Wax .....and Rivers

"I do not know much about gods; but I think that the river
Is a strong brown god - sullen, untamed and intractable,
Patient to some degree, at first recognised as a frontier;
Useful untrustworthy, as a conveyer of commerce,
Then only a problem confronting the builders of bridges.
The problem once solved, the brown god is almost forgotten
By the dwellers in cities - ever, however, implacable,
Keeping his seasons and rages, destroyer, reminder
Of what men choose to forget. Unhonoured, unpropitiated
By worshipers of the machine, but waiting, watching and
waiting..."

T.S. Eliot "The Dry Salvages" from Four Quartets

Eliot reflects two aspects of man's interaction with rivers. Rivers are Gods, sacred and mystical, featuring powerfully in many of the great myths and religions. The Ganges River is a god; the Nile is home to sacred Egyptian Gods; Achilles was rendered invincible by immersion in the River Styx which is the great divide between life and the underworld; John the Baptist preached repentance, with immersion in the River Jordan symbolizing forgiveness and a new life; and Christ began his teaching after just such

a rite of passage. Closer to home, the amaXhosa, who were among the earliest inhabitants of the Buffalo River valley, traditionally believed rivers to be the home of "the people of the river" - the mischievious abantu bomlamba, which bear an astonishing resemblance to the mermaids of western mythology (Mahola 1990). In contrast to mystical reverence is the pragmatic view that rivers may be useful, conveyors of commerce, and their usefulness is controlled by the builders of bridges and dams. The God is demystified, tamed, tied and exploited.

It seems these disparate views have increasingly been compartmentalised. Ferrar et al. (1988) list a series of river functions and associated uses, including domestic, industrial and agricultural water supply, recreation, fisheries, and conservation, but they do not mention any symbolic or magical role. Even the pragmatic uses are compartmentalised. In South Africa the Kruger National Park (KNP) is sacrosanct, a national symbol of successful conservation. The Witwatersrand is the national repository of gold, and the driving centre of industry and economic wealth. The two have never been integrated. During the last decade, industrial development on the Witwatersrand has increasingly caused acid rain and pollution in the eastern Transvaal; the vast population supported in this industrial heartland produces prodigeous quantities of sewage; and there is increasing pressure to supply water to the burgeoning rural communities between the Witwatersrand and the KNP. The rivers which flow through the KNP rise in the industrialised highveld, and flow through rural Black homelands (Walmsley and Davies 1991). Increasing upstream abstraction has transformed several of these formerly perennial rivers into seasonal systems. The remaining unimpounded perennial river, the Sabie, is now threatened by impoundment (Allanson et al. 1990). The functioning of the KNP as an intact ecosystem is jeopardised by the deterioration of its rivers.

Rivers are longitudinal systems which cross man-made boundaries. Perhaps the gift from the brown river God, to man, in the late 20th Century, is to force him to think holistically. In order to maintain the KNP as a valuable tourist resource and as wild country of enormous aesthetic, spiritual and conservation value, the need for industrial and agricultural development must be integrated with a conservation ethic. This is only the first step. It is easy to see the KNP as a natural ecosystem worthy of conservation, it is less easy to realise that the sustainable use of all rivers, even just for water supply, is dependent on their healthy ecological functioning. This is not a new idea, the necessity of considering the river and its catchment as a single entity was argued eloquently by Hynes (1975).

The two faces of Eliot's river god wait and brood. The aspect of wrath and destruction was obvious in the unbelievable devastation wreaked on the wilderness area in the Umfolozi Game Reserve when the Umfolozi River came down in flood after cyclone Demoina in 1985. The alternative is a dawning understanding of holism, an acceptance of the concept that man is an integral part of the earth and that to survive he must acknowledge this, and accommodate the consequent complexity of decision-making.

The research which forms the basis of this thesis was undertaken in the Buffalo River catchment. The research plan and methods were developed within a framework of hypothesis testing, but at all times the work was fuelled by my intense love of the place, and fascination with the animals I investigated. It is impossible to ascribe a quantitative importance to the phenomenological basis of this study. It is enough to say that at all stages it was essential to visit the river: to sit on a round mid-stream stone with my feet in the water, watching a swirling,

tumbling riffle; to see the red-flashed underwing of a loerie disappear into the green forest or watch the jewelled flight of a malachite kingfisher; to swim between high rocks in green water; to lie with my face in the water, watching mayflies brushing fine detritus off leaves; or to sit at the bottom of the waterfall in an enchanted world of moss, fern, forest and falling white water. This is another aspect of holism. It will quickly disappear in the pages that follow, but the spirit of the river itself, and my love of it, has sustained this research.

"But the river is another matter. It is an image of water already in movement, finding its own way through great ravines, carrying all over cataract and rapid and through conditions of external danger, to emerge intact and triumphant for union with the sea out of which it rose as a vapour at the beginning. It succeeds in doing so only because it finds its own way without shortcuts, straight lines, or disregard of any physical impediments but in full acknowledgement of the reality of all that surrounds it, implying that the longest way round is the shortest, and only safe way to the sea. As a result,...water represents the nourishment that comes from above for life on earth, where it is transformed into an element which leads the heart of men to the soul locked within the body, reflecting there a light that is enclosed in the dark. Above all, the water which the river conducts so untiringly to the sea itself,....is a master image for what is abysmal in life."

Laurens van der Post (1976)
Jung and the Story of our Time

CHAPTER 1
INTRODUCTION

1.1 Water Resources in South Africa

South Africa is an arid country. Although it shares a mean annual precipitation of 500 mm with Australia and Canada, the mean annual run-off as a proportion of precipitation in Canada is 65.7%, whereas in the two southern hemisphere land masses it is considerably lower: 9.8% for Australia and 8.6% for South Africa (Alexander 1985). In addition, precipitation and run-off are extremely variable. Average values for the coefficient of variation (a comparative method for assessing relative variability) for both South Africa and Australia (0.7) are more than three times higher than European values (0.2) (Alexander 1985, Braune 1985). The stochastic hydrology has implications for riverine species, which might be expected to be resilient, and to have flexible, unsynchronised life histories (Allanson et al. 1990); and for managers, who have responded to the erratic nature of run-off by impounding rivers to stabilize water supply to users (Department of Water Affairs 1986, Walmsley and Davies 1991). Currently, in South Africa, most of the economically and geographically viable impoundment sites have been developed. Centres for industrial development, like the Witwatersrand, are distant from the largest impoundments such as the H F Verwoerd and P K le Roux dams on the Orange River. As a result, water is relocated via a number of inter-basin transfer schemes, with little cognizance taken of the ecological consequences to either the donor, or the recipient systems (Petijean and Davies 1988). Water is a limited resource in an otherwise resource rich sub-continent. An ever increasing demand for water, and the scarcity of further suitable dam sites, means that proposed sites for new impoundments are often in ecologically sensitive areas, with impounded

waters threatening to flood places of high aesthetic and conservation value, and to interrupt processes such as fish migration and spawning.

Ecologists are increasingly being consulted during the planning stages of development. The quality of their response can be impaired by both the paucity of existing data on the processes which constitute healthy river function, and by the time constraints of developers, which may preclude even short term pre-impoundment studies. It is not possible to conserve rivers in isolated reserves, so river conservation has to include both the maintenance of ecosystem function and the utilization of the resource (O'Keeffe 1989). In the face of increased agricultural and industrial development in catchments, and the consequences of pollution and erosion, the aim of conserving biotic diversity of rivers actually reduces to one of conserving the quantity and quality of water (O'Keeffe et al. 1989). The need to maintain flows in South African rivers for environmental reasons has been recognised in the last decade (Roberts 1981, 1983, O'Keeffe et al. 1989, Ferrar 1989, Walmsley and Davies 1991, Bruwer in press) and the necessity to manage water resources for the maintenance of ecological functioning has been acknowledged (Department of Water Affairs 1991). A response to the crisis of water management requires co-operation between researchers and developers, together with relevant fundamental research, a commitment to communicate results to managers, and a concept of habitat and ecosystem conservation (Siegfried and Davies 1982).

In southern Africa, much river research has been descriptive (Allanson et al. 1990). Invertebrate fauna, microflora, and/or water chemistry have been used to characterise river zones, but there have been few attempts to elucidate underlying ecological processes. Research in the northern hemisphere, particularly in the

USA, has provided theoretical concepts of river structure and function. One of these unifying concepts is the River Continuum Concept (RCC) (Vannote et al. 1980).

1.2 The River Continuum Concept (RCC)

In the early nineteen seventies one focus in stream ecology concerned the calculation of energy budgets, and tracing the cycling and transport of organic material (Fisher and Likens 1972, 1973, Fisher 1977). It was recognised that processes in streams were inextricable from, and a reflection of, catchment processes (Hynes 1975). From this developed an understanding that the aquatic environment of streams could not be viewed in isolation, as it reflected processes which occurred in the catchment. In the following decade the results of this research direction led to the development of the RCC.

A central theme in the RCC was a description of the nature of sequential structural and functional changes from the headwaters to the lower reaches of rivers. The concept included predictions concerning patterns of organic matter input, generation and transformation (Cummins 1979, Naiman and Sedell 1980, Hawkins and Sedell 1981, Culp and Davies 1982, Minshall et al. 1982, Minshall et al. 1983, Merritt et al. 1984a, Statzner and Higler 1985). Headwater reaches were envisaged as being narrow and shallow, with a steep slope, and typically with a canopy above the stream shading the water. Autochthonous production would therefore be low, but allocthonous input in the form of fallen leaves would be high. Headwaters were therefore thought to be heterotrophic. The middle reaches were seen as being wider, with a lower gradient and with relatively clear water. The lack of shading would allow periphyton growth, which would contribute to autochthonous production and the system would become autotrophic. The RCC predicted that the lower reaches would become heterotrophic due to

turbidity causing light limited primary production. Fine particulate organic matter (FPOM), imported from upstream, was envisaged as the primary organic energy base.

Transport and cycling of organic particles could be caused by either biotic or physical processes, and Cummins (1973) suggested that the feeding activities of aquatic invertebrates were an important component of biotically mediated organic material cycling. This led of the inclusion of the Functional Feeding Group (FFG) concept into the RCC.

1.3 The Functional Feeding Group Concept

The Functional Feeding Group concept was developed over the last two decades (Cummins 1973, 1974, 1975, 1979, 1988, Cummins and Klug 1979, Minshall et al. 1983, Merritt and Cummins 1984, Cummins and Wilzbach 1985, Cummins et al. 1989). Based on research into the feeding biology of aquatic invertebrates the FFG concept provided functional categories to which organisms could be assigned. It aimed to link the origin and fate of organic matter in streams to the feeding of macroinvertebrates, emphasising the role played by feeding activities in the mediation of stream processes. The concept was also developed as a response to the difficulties of identifying aquatic macroinvertebrates to species level: "As long as the species is assumed to be the basic ecological unit, ... the perpetually incomplete state of our taxonomic knowledge will constitute a major constraint for the development of ecological theory." (Cummins, 1974).

The objective of the FFG concept (Cummins 1973, 1974) was to provide categories which could potentially enhance an understanding of ecological processes in streams, and obviate the need to identify organisms to species

level. The recognition that most macroinvertebrates in streams were generalist omnivores (Coffman et al. 1971), led Cummins (1973, 1974) to try to base the initial FFG categories on the mechanism of feeding, which was more likely to provide an insight into functional roles than dietary content. Morphological adaptation was seen as reflecting mechanism. For example, taxa with filtering or scraping mouthparts were expected to be structurally restricted to feeding on a particular resource: suspended organic particles in the case of filterers, and attached periphyton in the case of scrapers.

The following functional groups were identified:

predators - feeding on other consumers;

scrapers - eating periphyton, which was assumed to include algae;

shredders - dealing with CPOM (coarse particulate organic matter, >1mm);

collectors - feeding on deposited UFPOM and FPOM (ultra-fine and fine particulate organic matter, 0.5-50µm and 50µm-1mm, respectively); and

filterers - feeding on suspended UFPOM and FPOM (Cummins 1973, 1974).

McShaffrey and McCafferty (1988) modified this classification, distinguishing between active and passive filterers, adding the category 'brusher', and relating FFGs to the hydraulic distribution of organic particles.

The FFG concept was incorporated into the RCC, which predicted a sequence of downstream changes in the proportions of functional groups (Cummins 1979). The RCC suggested that shredders would be the most abundant headwater functional group, as they would make use of coarse organic matter in the form of fallen leaves. Limited primary production would limit the numbers of scrapers, but collectors would also be abundant, utilising fine organic particles generated by either mechanical abrasion or the activities of shredders. The

middle reaches were expected to be dominated by collectors and scrapers. The scrapers could make use of abundant periphyton growing in the unshaded, clear water. Collectors, a large component of the middle/lower reaches fauna, could feed on fine particles generated by upstream processes. Collectors would dominate the turbid, slower flowing lower reaches with their abundant FPOM resources. Predators would be evenly distributed down the river. The FFG composition of the macroinvertebrate assemblage was expected to provide an insight into the processes occurring in the stream which could not be provided by a description of the taxonomic composition.

1.4 Objective and Aims of this study

The overall objective of this thesis was to investigate the macroinvertebrate fauna of the Buffalo River in order to assess the applicability of aspects of the RCC and the FFG concept. Prior to this study there were insufficient data concerning the feeding biology of most South African aquatic invertebrates for them to be classified into FFGs. It was consequently not possible to establish whether the changes in FFG proportions predicted by the RCC applied to a river in this southern hemisphere sub-continent; or to assess the usefulness of a functional classification of the invertebrates in enhancing an understanding of river processes. The obvious questions to be asked were therefore: 1) What is the distribution of macrobenthic taxa in a selected river? 2) To which FFGs do they belong? 3)How do FFG proportions change down the river? and 4) Do these changes conform to the predictions of the RCC?

However, some of these questions were intractable. It was not possible, for example, to assign all the macroinvertebrate taxa in the Buffalo River to FFGs. It was inappropriate to use North American FFG designations (Merritt and Cummins 1984) for related southern African

taxa (King et al. 1988). Additionally, aspects of the usage of the FFG concept had been criticised (King et al. 1988). Therefore the aims of the study were: 1) to describe the macroinvertebrate assemblage structure of the Buffalo River; 2) to clarify the ambiguous definitions of some FFGs; 3) to establish whether taxa selected for feeding studies could be assigned to FFGs; 4) if so, to attempt to assess whether the FFG proportions in successive reaches of the Buffalo River conformed to the predictions of the RCC; and 5) to test whether a functional classification is a useful alternative to a taxonomic classification, as suggested by Cummins (1974).

1.5 Community Concept in the RCC

Since the objective was to assess the applicability of the RCC predictions concerning sequential changes in FFG proportions, it is appropriate to consider the concept of community presented in the RCC.

Two alternative concepts of community structure have influenced research in stream ecology: the "community-unit" and "individualistic" concepts. They arose respectively from the work of Clements (1916) and Gleason (1926, 1939), and their relative usefulness was debated by Whittaker (1962). In the community unit approach species were thought to interact closely, with the presence of one being dependent on the presence of others. Because the same species interact, a community would be characterised by a particular species composition and the boundaries of distribution of those species would coincide (Shipley and Keddy 1987). At its most extreme the concept of a biotically mediated community led to the idea of the community as a "super organism". In the individualistic approach communities were viewed as the sum of groups of species, each of which responded individually to environmental gradients

(Whittaker 1956, 1967). Shipley and Keddy (1987) traced the development of the debate as to which concept of communities was more accurate, and described four alternative predictions of species distributions along environmental gradients.

The RCC, by including the term "continuum" in its title suggested a conceptual association with the continuum, or gradient-based individualistic concept. However, the RCC depicted stream communities as tightly organised biotically mediated "units", whose species composition changed sequentially along a downstream axis, following shifts in the nature of available organic matter, with downstream assemblages capitalising on inefficient processing upstream. The "community unit" nature of the RCC was recognised and rejected by Lake and Barmuta (1986).

The RCC was developed in the seasonally predictable northern hemisphere and when the concept was criticised, its applicability to stochastic southern hemisphere rivers was particularly questioned. Winterbourn et al. (1981) considered that the RCC provided an inadequate conceptual model for the understanding of New Zealand streams. The RCC is deterministic in nature, and Winterbourn et al. (1981) noted that New Zealand streams were stochastic and abiotically driven, by nature poorly retentive, and subject to unpredictable flooding. Successful organisms were therefore likely to be opportunistic generalists, with poorly synchronised life histories and the paucity of shredders was considered a consequence of the lack of CPOM retention. In response to these criticisms Barmuta and Lake (1982) noted the utility of two aspects of the RCC: a standardized description of the organic energy base in streams (Naiman and Sedell 1980), and the FFG classification (Cummins 1973, 1974). Winterbourn (1982) remained unconvinced of the practical likelihood of standardized methods, and

reiterated the importance of distinguishing between the highly structured, biotically mediated stream processes hypothesised by the RCC, and the stochastic, unpredictable and therefore individualistic nature of the processes driving New Zealand streams. Lake et al. (1985) concluded that "longitudinal community structure of Australian benthos is more complicated than Northern Hemisphere-oriented deterministic models suppose".

In a reassessment of the RCC from a northern hemisphere perspective Statzner and Higler (1985) focused on conceptual details concerning the characteristics and functioning of homeostatic mechanisms in streams. The nature of this criticism differed from southern hemisphere concerns which emphasised differences in the driving processes in streams. Concurrently, the RCC proponents synthesized the results of RCC-linked research, which confirmed their view that that holistic and interactive processes were of central importance to stream function (Minshall et al. 1985). In a review of progress in the understanding of the processing, transport and utilisation of organic matter in streams by micro-organisms and benthic invertebrates,Winterbourn (1986) acknowledged the contribution made by the RCC, particularly Cummins' (1974) conviction of the importance of process orientated research. However subsequent criticisms of the RCC have continued to question its 'Clementsian' nature. Hildrew and Townsend (1987) noted their skepticism of mechanisms of evolution operating at the community level as is implied in the RCC, where downstream assemblages were envisaged as being adapted to capitalise on trophic inefficiencies upstream.

Minshall (1988) suggested that differences in the perception of how rivers function may be a consequence of differences in the spatial and temporal scales at which investigations are conducted. He noted that differences in precipitation and run-off patterns create dramatically

different conditions, which may affect life history strategies, competitive interactions, and ecosystem structure and function, helping to explain why some investigators view the stream environment as stochastic while others see it as deterministic. In discussions concerning the functioning of southern African rivers O'Keeffe et al. (1989) and Allanson et al. (1990) maintained that the RCC still provides a useful paradigm within which to test hypotheses of stream function in southern Africa, although they expressed reservations as to whether the concept would prove to be applicable in this region.

1.6 Correlations and Causation

Macroinvertebrate distribution patterns in streams are complex, and two levels of hypothesis are useful (Shipley and Keddy 1987). At the first level, "hypotheses of pattern" result from the recognition of correlations, which may be followed by the establishment of causal relationships or "hypotheses of mechanism". The methods used in data collection and analysis determine which hypothesis level can be appropriately addressed. In river studies, benthic samples are usually collected at a range of sites, concurrently with physico-chemical data (Townsend et al. 1983, Cushing et al. 1983, Wright et al. 1983, 1984, Learner et al. 1983, Furse et al. 1984, Glazier and Gooch 1987, Marchant et al. 1984, Bunn et al. 1986, Ormerod 1987, Ormerod and Edwards 1987, Wade et al. 1989, Graca et al. 1989, Rutt et al. 1989, Rundle and Hildrew 1990, Marchant 1990, Boulton and Lake 1990). Macroinvertebrates are then identified to as fine a taxonomic level as possible, and the assemblage composition data are analysed using a range of numerical analyses, usually involving both ordination and classification procedures. These analyses provide clusters or associations of samples based on the presence, absence and relative abundance of the

constituent taxa, which can then be correlated with physico-chemical variables. At this stage of analysis nothing can be said about causal relationships between assemblage structure and environmental variables. This approach has been termed indirect gradient analysis (Gaugh 1982), and enables researchers to suggest "hypotheses of pattern" (Shipley and Keddy 1987). The next stage involves the testing of aspects of these correlational hypotheses using experimental procedures and/or direct gradient analysis (Gaugh 1982), with the goal of achieving "hypotheses of mechanism". Causal relationships elucidated in this way become "multiple working hypotheses" from which concepts can be developed (Shipley and Keddy 1987).

Water velocity and substratum are environmental features which influence the distribution of macroinvertebrates (Minshall and Minshall 1977, Rabeni and Minshall 1977, Hawkins 1984, Rutherford and Mackay 1984). Consequently stream habitats or biotopes have been described as either erosional or depositional because these categories are defined in terms of velocity and substratum characteristics (Merritt and Cummins 1984). Field experiments (Barmuta 1990) and investigations of complex hydraulics (Davis 1986, Statzner et al. 1988, Davis and Barmuta 1989, Jowett and Richardson 1990) have more closely identified the causal relationship between substratum, velocity and macroinvertebrate distribution. In this study, erosional and depositional biotopes were recognised, and were the basis of a stratified random sampling procedure (Southwood 1978). Ordination and classification were used to investigate the association of macroinvertebrate assemblages and species with a range of subjectively identified biotopes. The macroinvertebrate assemblage structure in the Buffalo River is described at the level of hypothesis of pattern.

1.7 Application of the FFG Concept

Once the aim of describing the assemblage structure had been achieved and feeding studies on selected taxa were initiated it became clear that the FFG concept was in disarray (King et al. 1988). The original theoretical criteria describing the basis upon which taxa should be assigned to FFGs were ambiguous. The concept had been widely applied using inconsistent criteria, rendering the debate on the applicability of the concept useless. It is not possible to debate, for example, the dominance of shredders in the headwaters of streams unless the term "shredder" has been applied consistently.

It also became clear that the assigning of taxa to FFGs on the basis of their taxonomic proximity to North American organisms, simply because extensive FFG designations exist for a wide range of North American taxa, was unacceptable (King et al. 1988). The most comprehensive documentation of macrobenthic FFGs is that of Merritt and Cummins (1984). It may be appropriate to apply these generic designations to North American species, since North American studies provided the original data. What must be viewed with real misgiving is the subsequent propensity for stream ecologists from other continents to apply these designations to "equivalent" taxa. In a study of macroinvertebrate assemblages in a second order stream in the western Cape of South Africa (King et al. 1988), taxa were assigned to FFGs both on the basis of gut content analysis and using FFG designations given for taxonomically related North American organisms by Merritt and Cummins (1984). Each method classified many of the species into different FFGs, highlighting the dangers of simply applying published FFG designations for related taxa, especially from geographically distant regions.

Recent Australian studies which assigned animals to FFGs

(e.g. Marchant et al. 1985, Doeg et al. 1989) referred extensively to feeding data on Australian species (Chessman 1986), but where the feeding biology of an organism was unknown use was made of the FFG designation given for a related taxon by Merritt and Cummins (1984). In an investigation of FFG responses to environmental gradients, Faith (1990) drew attention to the necessity for testing apparent relationships between FFG distribution and environmental gradients. However, the FFG designations on which his arguments were based, were those given by Marchant et al. (1985), 50% of which were derived from North American taxonomic analogues. This, together with the inconsistency of the definition of FFG detracts from the value of the work. In other Australian work, Barmuta (1988, 1989) used Merritt and Cummins' (1984) FFG designations more cautiously, referring to their descriptions of the mouthpart morphology expected for various FFGs, and combining this with an analysis of foregut contents and observations of feeding behaviour. Towns (1981), Lake and Doeg (1985) and Barmuta (1990) did not mention the basis upon which their taxa were assigned to FFGs so it was not possible to assess the validity of their conclusions concerning FGGs. Often the method used to assign FFGs was not given, and the definitions of FFGs given by Cummins (1973, 1974), and Hawkins and Sedell (1981) were simply cited.

It is worth recalling the warning that "uncritical use of the preliminary summaries of trophic relations published by Merritt and Cummins (1984) may do more to inhibit progress in stream ecology than to foster it " (Minshall 1988).

1.8 Clarification of the FFG Concept

Cummins (1973, 1974) aimed to define functional feeding groups in terms of the mechanism of feeding, but even in the original descriptions mention was made of the food

eaten by the various groups, and subsequently, food eaten was given as the basis for defining FFGs (Cummins 1988). There have been recent studies which concentrate on mouthpart morphology (Sephton and Hynes 1982), but most feeding studies have followed the trend of recognising the relationship between FFGs and the size and/or type of food ingested. This shift in emphasis from the feeder to the food as the basis of classification, is one of the areas of confusion which have arisen during the course of the conceptual and experimental development of FFGs (King et al. 1988).

There have been a number of criticisms of the use and usefulness of the FFG concept (Lake et al. 1985, Winterbourn and Collier 1987, Barmuta 1988, King et al. 1988). In this section, each of three areas of confusion identified by King et al. (1988) and investigated in this study are discussed: 1) spatial, temporal and developmental variability in feeding behaviour and diet; 2) problems with gut analysis as a method for ascertaining FFGs ; and 3) the definition of the terms shredder, scraper and brusher. In section 1.9 the application of the FFG concept in the development of a functional classification is discussed.

1.8.1. Spatial, temporal and developmental dietary variability.

This section discusses the suggestion that macroinvertebrates in streams are such opportunistic generalists in their feeding, and have such flexible feeding behaviour (De Moor 1988), that it is meaningless to assign any species to a FFG. Both King et al. (1988) and Minshall (1988) quoted studies in which the feeding style and/or diet of species changed at different life-cycle stages and/or in different locations.

Feeding variability was the area most carefully considered in this work on the feeding of Buffalo River

macroinvertebrates. Spatial, temporal, and developmental differences in diet and behavioural flexibility were investigated, and in Chapters 4 and 5 the aim was to assess whether dietary variability would not preclude the assigning of 16 selected taxa to FFGs. Dietary variability has proved to be problematic in some studies. Barmuta (1988) and Lake and Doeg (1985) use Hawkins and Sedell's (1981) suggestion of assigning different life history stages to different FFGs. This does not address the fact that animals in the same life history stage may exhibit flexibility in their feeding behaviour (Winterbourn et al. 1985), and may behaviourally fit into more than one FFG (McShaffrey and McCafferty 1990). Hawkins et al. (1982) were among the first to suggest that both the diets and feeding methods of many aquatic insects were likely to be more varied than the FFG classification acknowledged. Data from this study are used to discuss the nature of dietary variability.

1.8.2. Gut Content Analysis

Gut content analysis has been the technique most frequently used in the investigation of macroinvertebrate feeding (Coffman et al. 1971, Chessman 1986, Barmuta 1988, 1989, Boulton et al. 1988, Rader and Ward 1989, Hawkins 1985). However the adequacy of this method for assigning taxa to FFGs has been questioned because:

a) Readily assimilable items might disappear from the gut contents more rapidly than more refractory items.

b) It is not possible to identify ingested prey items unless the chitinous exoskeleton of the prey is included. The gut contents of the prey and the predator are indistinguishable. Predation may be occasional or unexpected, and unless observed, may go undetected (McShaffrey and McCafferty 1990).

c) There is no way of relating the size of the particle in the gut to the size of the item ingested: a small leaf fragment (<250 µm) may have been "shredded" from a leaf, or "collected" along with other detritus.

It was therefore questionable whether or not gut contents would be a useful guide to FFGs (King et al. 1988). Gut content analysis was the primary method used to investigate the feeding of 16 selected macroinvertebrates from the Buffalo River. In an effort to make gut content analysis as useful as possible, only foregut contents were analysed, reducing likelihood of loss of easily assimilated items. The advice of McShaffrey and McCafferty (1986, 1988) to use a variety of methods to investigate the feeding of macroinvertebrates was followed and gut analysis was therefore augmented by other methods such as scanning electron microscopy, behavioural observation and food choice experiments.

1.8.3. Definitions of FFGs

A central problem with the FFG concept concerned the definition of functional groups.

Shredder: Although Cummins (1974, 1974) explained the advantages of a definition of FFGs based on the mechanism of feeding, shredders have most often been defined as having organic particles of varying, but specified sizes in their guts. Tracing the confusion surrounding the "shredder" designation, King et al. (1988) noted this shift in the basis for the shredder designation from the mechanism of feeding (that is shredding), to the food ingested (that is coarse particulate organic matter - CPOM). In one of the early RCC papers reference was made to "CPOM shredders " (Bruns et al. 1982). In addition, different patterns of leaf eating behaviour were described as "shredding" including chewing (Cummins, 1973, 1974, Cummins and Klug 1979) and the rasping or scraping of soft leaf tissue by "microshredders" (Wallace et al. 1970, Short et al. 1980, King et al. 1988). Although the size of particle in the gut was frequently given as the criterion for the recognition of shredders, the sizes cited differed and even the earliest references to particle size were inconsistent. Shredders were

associated with organic particles >1000 µm (Cummins, 1973) and >4000 µm (Cummins, 1974). Marchant et al. (1985) suggested that shredders could be recognised on the basis of the presence of gut particles in the size range 50 - 1000 µm in the gut, but Winterbourn et al. (1984) concluded there were no shredders in their streams despite particles in that size range comprising up to 40% of the gut contents of the invertebrates. Considering that Faith (1990) used the FFG definitions of Marchant et al. (1985) to investigate the relationship between environmental variables and FFGs, and then compared his results to the predictions of the RCC (Vannote et al. (1980) and the criticisms of Winterbourn et al. (1981), all of whom have defined shredders differently, it it not surprising that debate surrounds the predictions of changing patterns of FFG distribution in streams. Finally, few researchers define whether the particle size ranges used refer to the particle size ingested, or the particle size in the gut. Quite obviously "the term shredder needs redefinition" (King et al. 1988).

Scraper: The confusion surrounding the term scraper arose out of the expectation that scrapers, feeding from stone surfaces, would include algae in their diet (Cummins 1973, 1974). This was not always the case as heterotrophic epilithic layers can also be ingested by scrapers (Winterbourn et al. 1985).

King et al. (1988) noted that western Cape caddis larvae Petrothrincus spp. and Agapetus sp. were described by Scott (1985) as grazers on rock surfaces, but found their gut contents comprised fine detritus and no algae. The lack of periphyton in the gut led King et al. (1988) to question the herbivore role of scrapers, and to suggest that caddis, baetids and other stone surface feeders feed on epilithon regardless of whether it includes algae. Rounick and Winterbourn (1983) showed that stream macroinvertebrates could make use of heterotrophic

epilithic layers, and suggested that these were likely to play an important role in carbon transfer from dissolved organic matter to the benthos. This was confirmed by Winterbourn et al. (1985).

Brusher: The FFG designation brusher was first suggested by McShaffrey and McCafferty (1986). The term proved useful in describing the feeding of Leptophlebiid mayflies from both the headwaters and middle/lower reaches of the Buffalo River.

Filterer and Gatherer: The definition of filterers and gatherers given by McShaffrey and McCafferty (1988) is accepted and used in this study.

1.9 A Functional Classification

Once the definitions of FFGs were applied consistently, it became possible to discuss how the distribution of FFGs in a river could contribute to an understanding of river processes. A taxonomic classification of the benthic assemblage structure in the Buffalo River was compared with a functional classification based on FFGs. This aspect of the thesis is somewhat speculative. One of the most promising applications of the FFG concept was perceived as the provision of insights into the mechanisms of processes in streams (Cummins 1974, Barmuta and Lake 1982). Recently this aspect has largely been ignored in the muddled usage of functional groups.

1.10 Summary of Thesis Structure

In this thesis the conceptual implications of the River Continuum Concept are considered, and the Functional Feeding Group concept, which is part of the RCC, is clarified using data on the feeding biology of macroinvertebrates from the Buffalo River. Criticism of the RCC has come primarily from the southern hemisphere,

with attention being drawn to the comparatively stochastic nature of southern hemisphere rivers (Winterbourn et al. 1981, Williams 1988, Allanson et al. 1990). Throughout the thesis attention is drawn to the literature on other southern hemisphere rivers so that the Buffalo River can be viewed from a southern hemisphere perspective. The study begins with a general description of the macroinvertebrate assemblage structure and distribution in the Buffalo River. As a result of this preliminary investigation, distinct macro-invertebrate assemblages were recognised in the headwaters and middle/lower reaches, and characteristic taxa from each of these assemblages were selected for feeding studies. The feeding of sixteen macroinvertebrate taxa is described primarily on the basis of gut content analysis, with the goal of ascertaining the nature of dietary variability. Because of the limitations of gut analysis, feeding studies were augmented with experimental, behavioural and morphological studies. The results of these studies clarified aspects of the FFG concept. The thesis is presented in seven chapters, each of which is outlined below.

Chapter 1: An introduction to the conceptual framework within which the research was conducted.

Chapter 2: This chapter describes the study area and sites referred to in all the subsequent chapters. Some of the previously published research on the river is reviewed.

Chapter 3: The patterns of macroinvertebrate assemblage structure in the river are described. These data provided a basis for the subsequent feeding studies.

Chapter 4: The feeding of four abundant taxa from the headwaters of the river is described. Dietary variability and the flexibility of feeding behaviour is investigated;

the shredder functional group is defined; the morphological basis of the brusher functional group is described; and the necessity for linking FFGs to stream function is introduced.

Chapter 5: The feeding of 12 common macroinvertebrate species from the middle and lower reaches of the river is described. Again, dietary variability and the flexibility of feeding behaviour is investigated, and these, together with morphological data are used to assign the species to FFGs. The scraper functional group is defined, the structural basis for the brusher functional group is reiterated, and the facilitation of stream function by macroinvertebrate feeding is discussed.

Chapter 6: Various aspects of functional classification are explored. Multivariate analysis of data on gut contents is used to attempt an objective identification of FFGs. In addition, all the taxa in the benthic faunal assemblage are assigned to FFGs (including the category "unknown") and a functional classification of riffle fauna in the Buffalo River is presented. Future use of FFG classifications in a predictive capacity is considered, and functional feeding classifications as an alternative and/or an addition to taxonomic classifications are discussed.

Chapter 7: In the final chapter, the main ideas presented in the thesis are summarised; the limitations of the research reported in this study are assessed; and possibilities for future work are discussed.

CHAPTER 2
THE BUFFALO RIVER

2.1 General Description

The total area drained by the Buffalo River is approximately 1 353km^2 and the underlying geology consists primarily of easily erodable Beaufort Series mustones and sandstones, intersected by more resistant dolerite intrusions (Mountain 1962, Haughton 1969). The river is a fourth order stream (sensu Strahler 1974, at a scale of 1:250 000) by the time it drains into the estuary and then into the sea at East London (32° 02'S, 27° 45'E), 140km from its source (Fig. 2.1). From the headwaters to the source the water quality in the river varies considerably. A profile of the river showing changes in land use and water quality is shown in Fig. 2.2.

The Buffalo River rises in the Amatole Mountains, at an altitude of 1 300m, from a sponge in mesotrophic grassy fynbos (Campbell 1985), which soon gives way to near pristine closed canopy Eastern Forest and Thicket (Campbell 1985). The headwater sampling site (Site 0, Figs. 2.1 and 2.3) is surrounded by indigenous forest, but is downstream of a stand of exotic oak trees (Quercus robur L.). The headwater stream has a steep gradient of about 200m/km for 6km, before it flows into Maden dam, the first of two small impoundments in the foothills of the mountains (Fig. 2.2). Site 1 is just above Maden dam (specifications of the four impoundments are given in Palmer and O'Keeffe 1989). The upper reaches, up to Maden dam, generate 42% of the runoff of the river (O'Keeffe 1989). They receive a relatively high rainfall (up to 2000mm per annum), 68% of which falls in summer (Department of Environmental Affairs 1986) and act as the "hydrological pump" of the catchment (Allanson et al. 1990). Water supply, forestry, conservation and

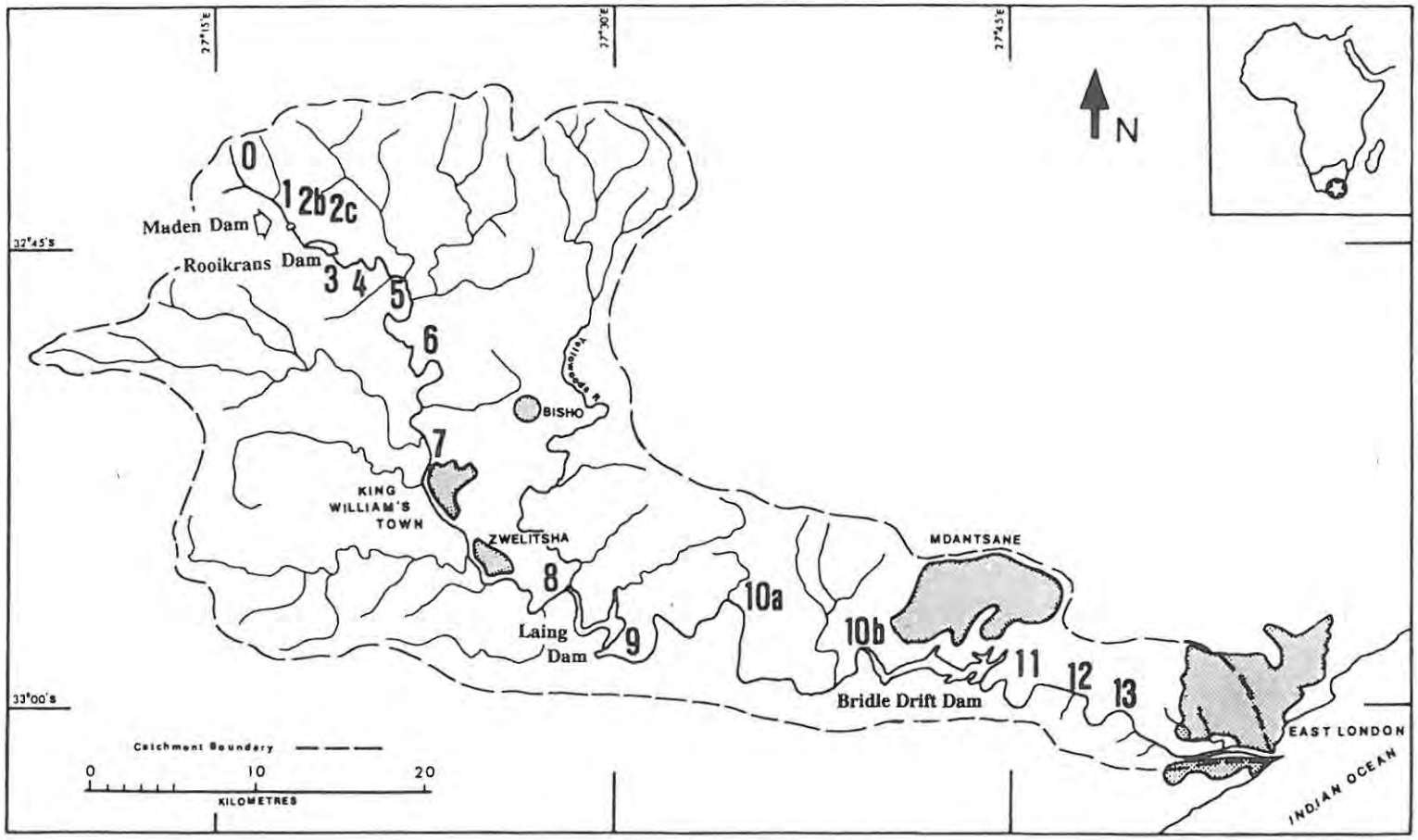


Fig. 2.1. A map of the Buffalo River catchment, eastern Cape, showing the location of the four impoundments and of the sixteen sampling sites (0-13) (from Palmer and O'Keeffe 1989, 1990a). Sample site numbers used in the Buffalo River Programme have been retained to facilitate cross referencing. Various reaches were faunally distinctive. Site 0 - headwaters. Sites 1-13 - middle/lower reaches: Sites 1-4 - upper middle reaches, Sites 5-10a - lower middle reaches, Sites 10b-13 - lower reaches.

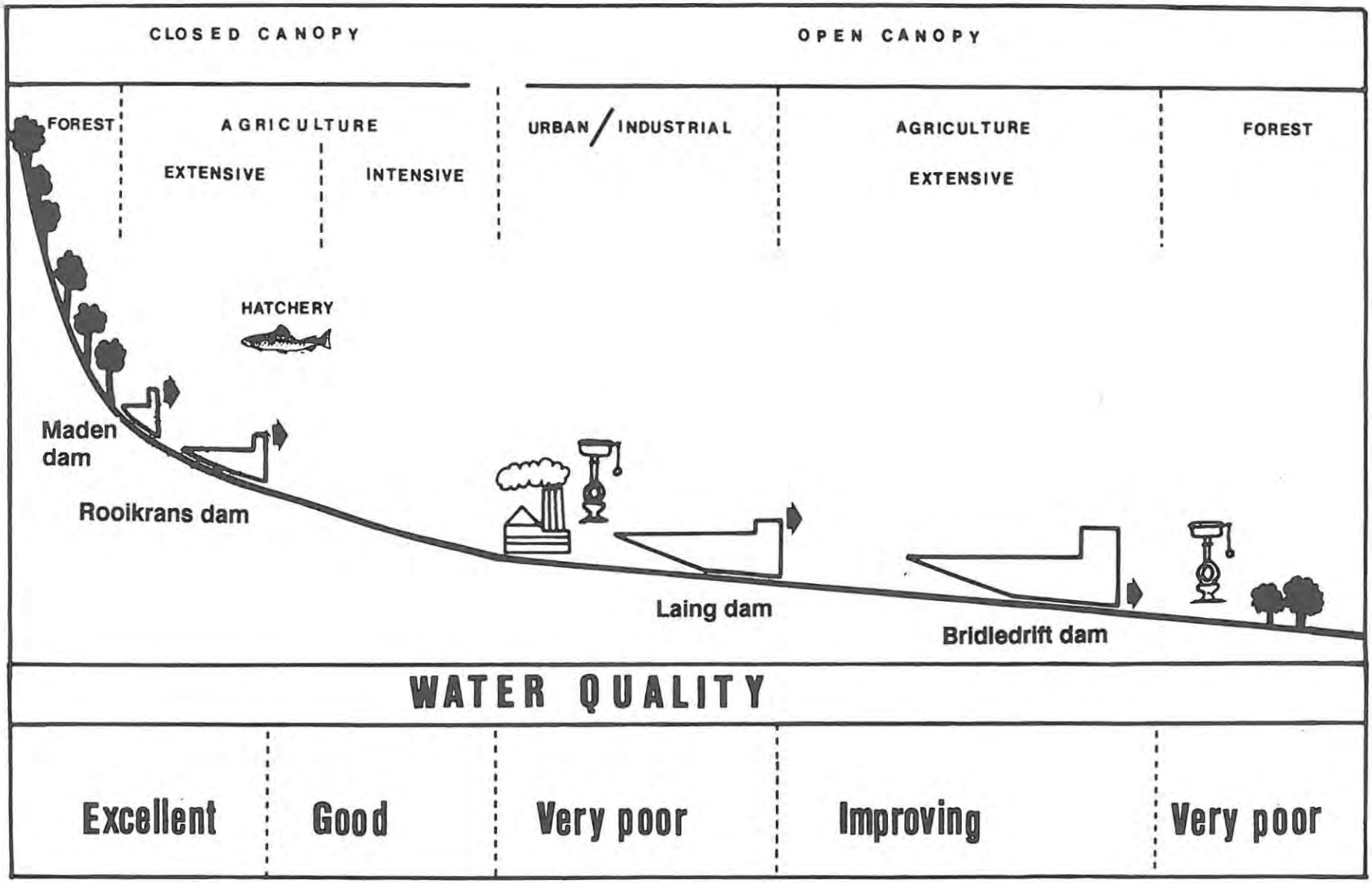
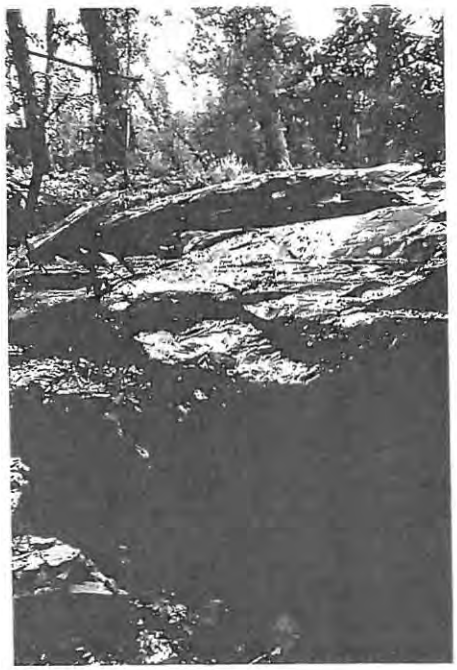


Fig. 2.2 A profile of the Buffalo River showing downstream changes in water quality and catchment land use (from O'Keeffe 1989).

Fig. 2.3 The Headwater Stream: Site 0

Surface flow was absent in winter.



The top of a small waterfall with a winter trickle of water.

The stream in spring.

Alien oak leaves dominated the leaf packs.

recreation (for example hiking, trout fishing, picnic facilities) constitute the primary use of this part of the river and its catchment. King William's Town is supplied with high quality water, though demand for water reduces the impoundment levels in Maden dam in the dry winter months. Rooikrans dam is 5km downstream of Maden dam, and just below it is a small trout hatchery which requires a constant water supply, ensuring continuous water flow below the two impoundments (Fig. 2.2).

In its upper middle reaches (Sites 1-5) the river flows through agricultural lands. Land use in the relic flood plains upstream of King William's Town (Sites 6 and 7) is intensive market gardening, and water quality deteriorates because of fertilizer-rich agricultural run-off carrying suspended solids and nutrients such as nitrates (Palmer and O'Keeffe 1990a). Below Site 7, the river flows through the urban/industrial area of King William's Town/Zwelitsha (Fig. 2.1) 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 for King William's Town, is downstream of Site 8 (Fig. 2.1), and receives eutrophic mineralised water. Laing dam acts as a large settling pond and nutrient levels downstream of the dam are considerably reduced (O'Keeffe 1989, Palmer and O'Keeffe 1990a).

Below Laing reservoir the catchment use is mainly extensive agriculture, and erosion, rather than fertilizer-rich runoff is the major problem (Sites 9, 10a and 10b) (Palmer and O'Keeffe 1990a, b). The last and largest impoundment is Bridle Drift (Fig. 2.1), which is situated in the lower reaches of the river and receives the over spill from Laing dam (Fig. 2.2). The river looks

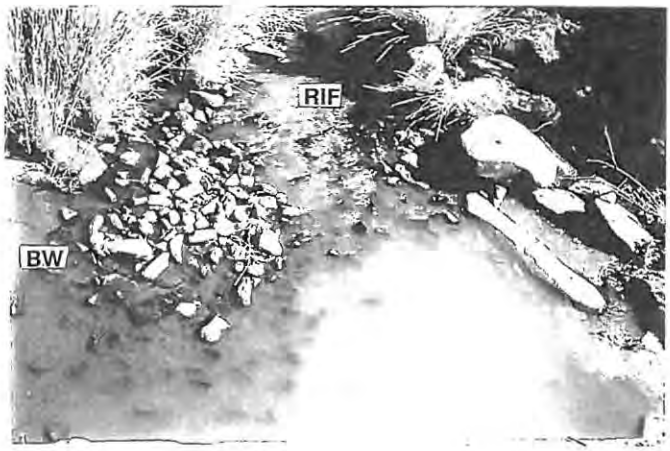
very attractive in these lower reaches and flows between steeply incised valley slopes, covered in Euphorbia spp. dominated succulent thickets (Site 12, Fig. 2.4). However water quality in the river deteriorates because of sewage effluent from Mdantsane (Site 13, Fig. 2.1). Some recreational use is made of Bridle Drift and its immediate environs, for activities such as water sports and hiking.

The river flows through several vegetation types (Comins 1962). The vegetation changes below Rooikrans dam to dense stands of an invasive exotic tree, the black wattle, Acacia mearnsii De Wild. After Site 6 the vegetation is open, and between Sites 6 and 8 the grass Miscanthus capensis (Nees) Anderss. occurs where the river is shallow, and from Sites 6 to 13 the palm Phoenix reclinata Jacq. and the sedge Cyperus textilus Thunb. are common. In the river itself macrophytes are rare. Matricaria nigellifolia DC. grows in shallow, quiet pools, but epilithic algae are scarce. Most of the catchment falls in the vegetation type recognised by Acocks (1988) as Valley Bushveld.

2.2 Zones and Continua

The Buffalo River can be described in terms of the zonation schemes of Illies (1961) and Harrison and Elsworth (1958). The source sponge is located in the mountain source zone and the forested headwaters (Site 0, Fig. 2.3 to Site 1) fall in the epirithron (Illies 1961) or mountain torrent zone (Harrison and Elsworth 1958). The remaining 130km below Maden dam fall within Harrison and Elsworth's (1958) zone II foothill stony run zone, or Illies' (1961) hyporithron, and consist of sedimented pools interspersed with turbulent flow over stony runs. The middle (Sites 1-10a) and lower (Sites 10b-13) reaches of the river all have the characteristics of this zone

Fig. 2.4 The Middle/Lower Reaches: Sites 6 and 12

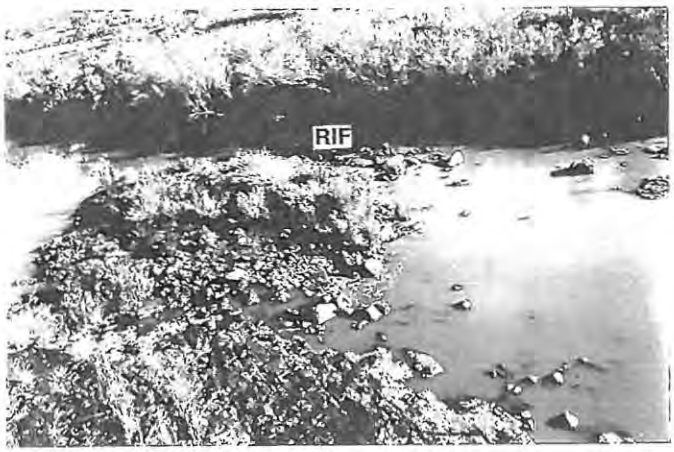


Site 6 At this site the river is braided, these photographs show two of the channels and some of the biotopes which were sampled.

RIF - riffle

BW - stony backwater

MV - marginal vegetation



Site 12 The river is wide and turbid, under the conditions of low flow shown here the marginal vegetation biotope was not inundated.

but the nature of the channel changes from reaches around Site 6 where the river is narrower, to reaches around Site 12 where the channel is wider, and the pools between riffles are longer and deeper (Fig. 2.4).

The description of the river in terms of zones implies abrupt changes at certain points along the river and homogeneity within zones. This has wider implications than simply a choice of descriptive terminology. It encompasses the conceptual framework within which longitudinal patterns in rivers are viewed. Changes in community structure along the length of rivers have frequently been described in terms of zones (Hawkes 1975). Hildrew and Townsend (1987) point out that the question of zones or continua has proved as controversial an area in river communities as it has in plant communities (Austin 1985). The debate relates to the alternative views of community organisation discussed in the previous chapter (Section 1.4): the continuous gradients of the individualistic hypothesis versus the discrete boundaries of the community unit hypothesis. If the River Continuum Concept (RCC, Vannote et al. 1980) contained descriptions of benthic assemblage structure which allied it with the community unit hypothesis, it also quite clearly considered rivers as systems with continuous abiotic gradients. The linkage between successive river reaches was emphasised, with upstream communities influencing those downstream of them by their effects on transported organic material (Fisher 1983). Culp and Davies (1982) were unusual in integrating both a zonational and continuum-based approach in their study of a Canadian river system.

There is evidence that sharp discontinuities do exist. Statzner and Higler (1985) identified abrupt changes in hydraulic characteristics and associated changes in community structure. Efforts were made to identify zones in Australian rivers (Williams 1976, Malipatil and Blyth

1982, Metzeling et al. 1984). In the rivers La Trobe, Coal, Acheron, Bass and Macalister the rithron and potamon could be distinguished (Lake et al. 1985), and in the Thomson river, rithron subdivisions epirithron, metarithron and hyporithron were tentatively distinguished (Malipatil and Blyth 1982). Lake et al. (1985) concluded that zonation in Australian streams may be less consistent than had been found elsewhere. In a later study on the La Trobe river, Marchant et al. (1985) note that despite Metzeling et al.'s (1984) recognition of rithron and potoman zones, none of the major taxanomic groups, or invertebrate families were confined to either zone.

In the Buffalo River, the first impoundment imposes an abrupt discontinuity on the temperature and physico-chemical characteristics of the river (Palmer and O'Keeffe 1989, 1990a). In terms of abiotic factors, either the Illies (1961) or Harrison and Elsworth (1958) zonation schemes are therefore descriptively and conceptually useful, and provided a basis for the selection of study sites for this study. Zonation in macroinvertebrate distribution is less clear and will be discussed in the next chapter.

2.3 Site Selection

The Buffalo River was selected because a research programme was already underway on the downstream effects of the four impoundments on macroinvertebrate distribution and on the physico-chemistry of the river (Palmer and O'Keeffe 1989, 1990a, b, c, O'Keeffe et al. 1990). Participation in this programme provided an opportunity to sample the river in such a way as to answer the specific questions of this study, and to have the advantages of additional, simultaneously gathered data collected along the whole length of the river (Fig. 2.1). In addition, the Buffalo River is an essential

natural resource in an economically depressed region with a burgeoning population. O'Keeffe (1989) noted that the river was already being exploited to its sustainable limit. The multiple-use zones of the river are evident in Fig. 2.2. Information is necessary for effective management of natural resources.

The disadvantage of selecting the Buffalo River was the degree of disturbance in the river. The predictions of the RCC were meant to apply to pristine river conditions, although Ward and Stanford (1983) extended them to include the downstream effects of impoundments. The Buffalo River has multiple impoundments and problems with industrial, agricultural and sewage pollution. But these are problems facing all the major rivers in the arid sub-continent of southern Africa. Only isolated headwater streams are pristine, and the Buffalo River's headwaters are very close to being pristine. The advantages of studying the Buffalo River outweighed the disadvantages, and specific study sites were selected so as to be as little affected by impoundments and pollution as possible.

With the aim of investigating the changing proportions of FFGs down the river in view, three main study sites were selected, one each in the upper, middle and lower reaches of the river. Site 0 (Figs. 2.1 and 2.3) was the upper reaches site. Situated in the natural forest of the Amatole mountains, Site 0 was representative of headwater tributaries of the Buffalo River at a point where they do not dry out completely in the dry winter months, even if flow is subterranean and above-ground water is reduced to a series of pools. The site was unaffected by pollution and impoundment, but could not be said to be in a pristine state because of the presence upstream of plantations of alien trees and a small weir. However conditions were close to the pristine state.

Site 6 (Figs. 2.1 and 2.4) was selected as the middle reaches study site. The site is at the furthest point downstream of Rooikrans dam, while being upstream of the industrial and sewage effluent pollution from the King William's Town area. The land use around Site 6 is agricultural market gardening and the water in somewhat enriched as a result of fertilizer runoff (Palmer and O'Keeffe 1990a).

Site 12 (Figs. 2.1 and 2.4) was selected as the lower reaches site. The site is as far downstream as possible from Bridle Drift dam, while still being upstream of the sewage effluent input from Mdantsane.

Three sites were selected and were sampled in each of four seasons. At each site three replicate invertebrate samples were collected from each of several biotopes. Riffles, stony backwaters and sediments were sampled at all three sites, and leaf packs and a waterfall face were only sampled at Site 0 because these biotopes did not occur at the two lower sites. Samples were collected from a range of biotopes so that proportions of FFGs would be representative of as complete a range of the river's fauna as possible. The separate sampling of biotopes in different seasons enabled a comparison of the diets of selected macroinvertebrate taxa under various spatial and temporal conditions.

During the course of sampling, it appeared that Site 1, just above Maden dam (Fig. 2.1), might be transitional, with characteristics of both the headwaters and the upper middle reaches. It therefore became important to characterise the macroinvertebrate assemblage at that point in the river. Site 1 was included in the sampling regime for Sites 0, 6 and 12 in winter and spring 1987. The faunal affinities of Site 1 are described in Section 3.3.3.

The detailed study of only three sites led to a problem of pseudoreplication which is elaborated in the next chapter. It is enough to point out here that a more complete longitudinal picture of invertebrate composition was gained by the analysis of one set of riffle samples collected in summer from all 16 of the sites (Fig. 2.1) routinely sampled during the course of the more extensive Buffalo River Programme. In addition physico-chemical data were collected from all 16 sites on each sampling occasion (Palmer and O'Keeffe 1989, 1990a) and it was possible to show that none of the three sites selected for this study was atypical, and that they fitted into a sequence of downstream physico-chemical changes (see Sections 3.2.2 and 3.3.3).

This study was conducted as part of the more extensive Buffalo River Programme (BRP). The results of the BRP are of particular interest as they provide a detailed background to conditions in the river at the same time as samples were collected for this study.

2.4 The Buffalo River Programme

The river was sampled approximately monthly (April 1986 - April 1988) at 16 sites (Fig. 2.1). from the headwaters to just upstream of the estuary. At each site the macroinvertebrate assemblages in riffles were sampled by collecting three replicate 0.09m^2 box samples. A variety of physico-chemical variables were measured concurrently. Details of the methods and the physico-chemical characteristics of the river are given in O'Keeffe *et al.* (1990) and Palmer and O'Keeffe (1989, 1990 a, b, c).

Temperature changes in the Buffalo River were more pronounced seasonally than spatially. Palmer and O'Keeffe (1989) ascribed this to the short length of the river and the fact that it rises at a modest altitude, however they noted that the four impoundments had a considerable

effect on temperatures for between 1.5 and 15km downstream. Whether temperatures were increased or decreased below dams depended on the downstream location of the dam, and the nature of the release, i.e. surface or low level. Water temperatures below the two impoundments in the upper catchment increased, but temperatures decreased below the impoundments in the middle and lower reaches. Water flowing into the small, shallow dam from the shaded, groundwater fed upper reaches, was subject to rapid solar heating and the greatest changes in the annual temperature range were recorded in its tailwaters. The impoundments in the lower reaches were larger and deeper, and water temperatures downstream were cooler in summer. In the case of Laing dam, downstream water temperatures were relatively unchanged in winter, but in the case of Bridle Drift dam, with its cold bottom-released outflow, winter temperatures were depressed.

In contrast, water chemistry varied spatially more than seasonally (Palmer and O'Keeffe 1990a). Three chemical categories were identified: a) clean upper middle reaches (Sites 1 - 5), b) moderately polluted lower middle and lower reaches (Sites 6 - 7 and 9 - 11) and two highly polluted sites (8 and 13). This pattern was altered at high flow rates (summer) with water quality improving in the region of Sites 6 and 7. One of the most significant impoundment effects was the improvement of water quality downstream of Laing dam, as nutrients and pollutants were incorporated into the sediments. During periods of low flow, Laing dam is managed as a "closed loop" with water being extracted from the impoundment to supply King William's Town and Zwelitsha, and being returned to the river as sewage effluent, and waste water upstream of the dam. The downstream effects on water chemistry of the impoundments in the Buffalo River were compared with a similar study conducted on the Palmiet River in the Western Cape (O'Keeffe et al. 1990). In both cases small

dams in the upper reaches caused major thermal modifications, and low intensity chemical changes with a shorter recovery distance. Larger dams caused larger chemical disturbances with longer recovery distances, and the consequences of low-level outlets were more severe.

Another characteristic of the Buffalo River is its turbidity. Except for its headwaters, the Buffalo River is turbid. Palmer and O'Keeffe (1990b) noted that ultrafine particles (< 80µm) comprised more than 95% of the dissolved and particulate matter in transport. These fine particle predominate in the river and CPOM is common only in the headwaters. This led Palmer and O'Keeffe (1990b) to suggest that the emphasis placed on CPOM processing in the RCC is inappropriate and that most of the downstream changes in transported organic matter in the Buffalo River are due to inflows of agricultural and urban effluent, and that these disturbances to the river cause greater perturbations than do the impoundments.

CHAPTER 3

MACROINVERTEBRATE ASSEMBLAGES IN THE BUFFALO RIVER: PATTERNS IN TIME AND SPACE

An abbreviated version of this chapter entitled "Are macroinvertebrate species assemblages associated with particular biotopes in the Buffalo River, southern Africa?" has been accepted for publication in the Journal of the North American Benthological Society, and will appear in Volume 10 Number 4, November 1991.

3.1 Introduction

A stream may be viewed as a mosaic of patches characterised by different environmental conditions (Pringle et al. 1988). Patches with similar substrata and hydraulic patterns have been termed habitats or biotopes. The terms habitat, biotope and community have become ambiguous (Whittaker 1973), and require clarification. In this study, the place that an organism occupies in time and space is termed the habitat (sensu Southwood 1977), whereas the location of the community in time and space is the biotope (sensu Udvardy 1959, Whittaker 1973). The term community has been used both to describe groups of populations whose boundaries coincide (Shipley and Keddy 1987) and those which are the sum of the constituent species plus the interactions between them (Begon et al. 1986). So as to make no assumptions about the interactions between taxa, the term species assemblage has been used rather than community and the term biotope is used to describe the location of a species assemblage.

The distinction between species assemblage and community was made because the RCC assumed that species assemblages in streams were highly organized and closely inter-linked, so that downstream communities were adapted to feed on the fine organic debris from inefficient feeding

upstream. In contrast, Winterbourn et al. (1981) suggested that the physical environment played a more important role than biotic interactions in determining the distribution of stream invertebrates and therefore that populations reacted individually rather than communally to environmental influences. In the latter case populations would form a species assemblage rather than a community.

The distribution of macroinvertebrate assemblages in streams is frequently discussed in terms of the nature of the physical environment (Boulton et al. 1988, Whetmore et al. 1990, Jowett and Richardson 1990) and erosional and depositional biotopes have consistently been distinguished (e.g. Minshall and Minshall 1977, Minshall et al. 1983, Cummins and Merritt 1984). In this study the subjective recognition of erosional and depositional biotopes formed the basis of the sampling procedure. There is however conflicting evidence for and against the association of species assemblages with particular biotopes. For example, Chutter (1970), Scullion et al. (1982), and Ormerod (1988) all found discrete species assemblages associated with particular biotopes. In contrast, Rabeni and Minshall (1977), Wright et al. (1983), and Jenkins et al. (1984) each concluded that few invertebrate taxa were confined to particular biotopes. These apparent contradictions may be explained in terms of differences of scale.

Minshall (1988) has emphasized the importance of defining the scale at which investigations are undertaken and reported. In an approach which takes scale into account, Statzner et al. (1988) emphasized the role of water flow in governing macroinvertebrate distribution. They demonstrated significant correlations between macroinvertebrate distribution and complex hydraulics over the entire spatial range, from the scale of individual microhabitat flow environments up to the scale

of river reaches. In contrast, two South African studies show how distribution patterns change at different spatial scales. King et al. (1987a) concluded that macroinvertebrate distribution in their small headwater stream was apparently uniform, with no detectable biotope-associated variation. In the lower reaches of the same river, King (1981) sampled in stony bed and marginal vegetation biotopes, and recorded a different species assemblage in each biotope.

Criteria used to distinguish biotopes have frequently been subjective. Allen (1951) defined several biotopes, such as riffles: "shallow water with a rapid current and usually broken flow." These definitions were reiterated and used by Harrison and Elsworth (1958), and also form the basis of the habitat classification system of Cummins and Merritt (1984). In many investigations (e.g. Chutter 1970, King 1981, Furse et al. 1984, Bunn et al. 1986, Harrison and Hynes 1988, Ormerod 1987, 1988) these definitions have been used as the basis for stratified random sampling programmes (sensu Southwood 1978). There has been an intuitive acknowledgement that biotope characteristics affect the distribution of macroinvertebrate assemblages in streams. As a result, an assumption commonly implicit in these studies is that subjectively identified biotopes will be inhabited by distinct species assemblages.

Several of Allen's (1951) definitions were used in this study to identify biotopes in the Buffalo River: riffles, leaf packs (from riffles), a waterfall face, stony backwaters, marginal vegetation, and the sediments. The aim of this part of the study was to investigate spatial and temporal patterns in the structure of macroinvertebrate assemblages by: 1) assessing whether particular macroinvertebrate species assemblages were associated with subjectively defined biotopes; 2) establishing whether these associations, when they occur,

were consistent seasonally and/or spatially; and 3) establishing whether particular taxa were specific to particular biotopes.

3.2 Methods

3.2.1 Field Collecting Methods

Samples were collected from Sites 0, 6, and 12 (Fig. 2.1). At each site, riffles (erosional biotopes - defined as areas where hydraulic conditions resulted in visibly turbulent flow); stony backwaters (depositional biotopes - defined as areas of still water where an OTT current meter recorded less than 3 cm s^{-1}) and sediments were sampled. At Site 0 two additional erosional biotopes which did not occur at the two lower sites were sampled: leaf-packs from riffles and a waterfall face. At Sites 6 and 12 marginal vegetation in- and out-of-current was sampled. The marginal vegetation biotopes were only inundated, and therefore only sampled, during summer. On the first sampling occasion leaf-packs from riffles were distinguished from leaf packs in pools. Since leaves were included in stony backwater and sediment samples, subsequently all leaf pack samples were collected from riffles. Stony backwater samples were collected from the perimeter of pools in depths up to 0.5m. The stones in both riffles and stony backwaters samples ranged from small to medium cobbles (sensu Cummins 1962, Hynes 1970). Samples were collected seasonally in 1987: February (summer), May (autumn), August (winter) and November (spring). It should be noted the seasonal patterns in the Buffalo River are erratic with regard both to taxonomic composition, and environmental variables such as flow (Palmer 1991 and pers. comm.). The spring, summer, autumn, and winter samples referred to in this and subsequent chapters are not necessarily representative of these seasons.

On each sampling occasion 3 separate replicate samples (Chutter and Noble 1966) were collected in each biotope, at each of the sites. Both riffle and stony backwater samples were collected using a netted (80µm) box sampler ($0.09m^2$) (Merritt et al. 1984b). In stony backwater biotopes stones were scrubbed inside the net with a soft brush and the water and sediments were stirred so as to sweep animals into the net. Leaf packs were collected by holding a net (80µm) downstream and dislodging leaves into it (King et al. 1987b). The marginal vegetation was sampled by back sweeping a metre stretch with an 80um mesh net (Chutter 1970). Sediment samples were collected as three 5cm diameter sediment cores to a maximum depth of 10cm (Merritt et al. 1984b). On the waterfall face (Fig. 2.3) a $1m^2$ area was scrubbed and washed into a D-frame net (80 µm) (Merritt et al. 1984b).

3.2.2. Sample processing and analysis.

Throughout this thesis data are analysed using multivariate techniques, a brief outline of these, together with a list of relevant references is given in Appendix 1.1.

In the laboratory, samples were washed through a 1mm mesh net, into an 80µm mesh net. The retained macroinvertebrates were either counted totally, or if numbers were high (>500), counted using a sub-sampling method based on that of Allanson and Kerrich (1961), and described in detail in Palmer and 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. coleopteran families, oligochaete class, and nematode phylum). Authors for species names are given in Appendix 1.2. Voucher specimens and sorted samples are lodged with the national collection of freshwater invertebrates at the Albany Museum, Grahamstown.

The three study sites were selected to represent the upper, middle, and lower reaches of the Buffalo River. Only one site per reach was chosen and features ascribed to the 'upper', 'middle' or 'lower' reaches may have been nothing more than site effects. The fact that replicate samples were collected from biotopes within each site, and at different seasons is no mitigation. In the terminology of Hurlbert (1984) problems of pseudo-replication could have resulted. This would be most serious if any of the sites were atypical, because it would then have been impossible to discuss invertebrate distribution patterns in terms of downstream changes in the river. Although it was not possible to sample at several sites within each of the reaches, thus replicating sites within each reach, it was possible to test whether any of the study sites were atypical, by checking that each fitted sequentially into the set of 16 Buffalo River Programme (BRP) study sites down the river (Fig. 2.1).

In order to do this, macroinvertebrate relative abundance data from 16 sets of riffle samples from each BRP site down the river were classified using two-way indicator species analysis (TWINSPAN) (Hill 1979a). A month of elevated discharge (February 1987) was selected, and three replicate riffle samples from 16 sites were sorted and the taxa identified. A month of elevated discharge was selected because riffle biotopes at some of the sites disappear at low flows.

In addition, fourteen environmental variables, collected from each BRP site at the same time as the invertebrate riffle samples, were used in canonical correspondence analysis (CCA) (Ter Braak 1988) to model the species-environment relationship. The absolute numbers of animals per sample were transformed to relative abundance scores. Percentage frequencies were assigned to 8 class ranges: 0-1, 2, 3-5, 6-10, 16-25, 26-50, 51-75, 76-100.

If the entire sample comprised fewer than 5 individuals these were recorded at the 0-1% frequency class. Sample scores were weighted mean species scores and rare species were not down-weighted.

In order to detect patterns in the distribution of macroinvertebrates in the Buffalo River samples from all biotopes and seasons at Sites 0, 6 and 12 were ordinated using detrended correspondence analysis (DCA) (Hill 1979b), and classified using TWINSPAN. Each sample in the sequence of samples organised by TWINSPAN carried information about the site, season and biotope from which it was collected. The TWINSPAN programme divides the sample sequence into a dichotomous, hierarchical set of groups each characterised by the presence, absence and relative abundance of particular species. The sample sequence was subjectively checked to assess whether samples from the same season, site, or biotope were grouped together. In the case of the ordination diagram the lines delineating groups of samples were drawn by eye. Thus, the classification and ordination were visually linked to season, distance down the river, and biotope to discern trend.

Fifty of the most frequent taxa were selected to examine species/biotope associations. Data from all the seasons were pooled and the percentage occurrence of each species in each of eight habitats was calculated. The observed distribution of occurrences in these habitats was compared with expected frequencies. Expected or even frequencies were calculated by dividing the total for each species by the eight possible biotope types. Deviation in the observed frequencies from this even distribution was identified using a Chi-squared test. Specific biotope associations were not identified, but where the deviation from even distribution was significant, the biotope associations were inferred from the percentage occurrences (sensu Ormerod 1988).

3.3 Results

3.3.1 Classification of the macroinvertebrate fauna

The most obvious pattern in macroinvertebrate species assemblage structure was the difference in species composition between the headwater site and the middle/lower reaches sites (Figs 3.1a and b and 3.2). At the headwater site a waterfall assemblage could be distinguished from the rest of the stream. Within the riffle-pool sequence of the headwater stream, a seasonal shift in species assemblage structure was more apparent than any biotope association. At the middle/lower reaches sites there was an association of particular species assemblages and the biotopes. These patterns were identified after the classification and ordination of 138 samples, collected from the three study sites, using the reciprocal averaging sub-routines in TWINSPAN and DCA. A total of 103 taxa were identified, and a summary of the TWINSPAN classification (Fig. 3.1b), shows the 49 most commonly found taxa, grouped into nine species assemblages.

Site 0 was distinguished from Sites 6 and 12 on the basis of faunal composition at Level 1 in the hierarchical classification (Fig. 3.1a). This differentiation fitted the descriptions of two Harrison and Elsworth (1958) zones, the mountain torrent zone and the foothill stony run zone. The fauna of the headwater site was distinguished from the fauna of the middle/lower reaches sites primarily by the abundance of larvae of the stoneflies Afronemoura spp., the mayfly Adenophlebia auriculata, the caddisfly Goerodes caffrariae, and the blackfly Simulium dentulosum s.l.; and the absence of Planaria spp. and the freshwater limpet Burnupia sp. The latter taxa were abundant in the middle and lower section of the Buffalo River.

The waterfall assemblage (II.B), could be distinguished

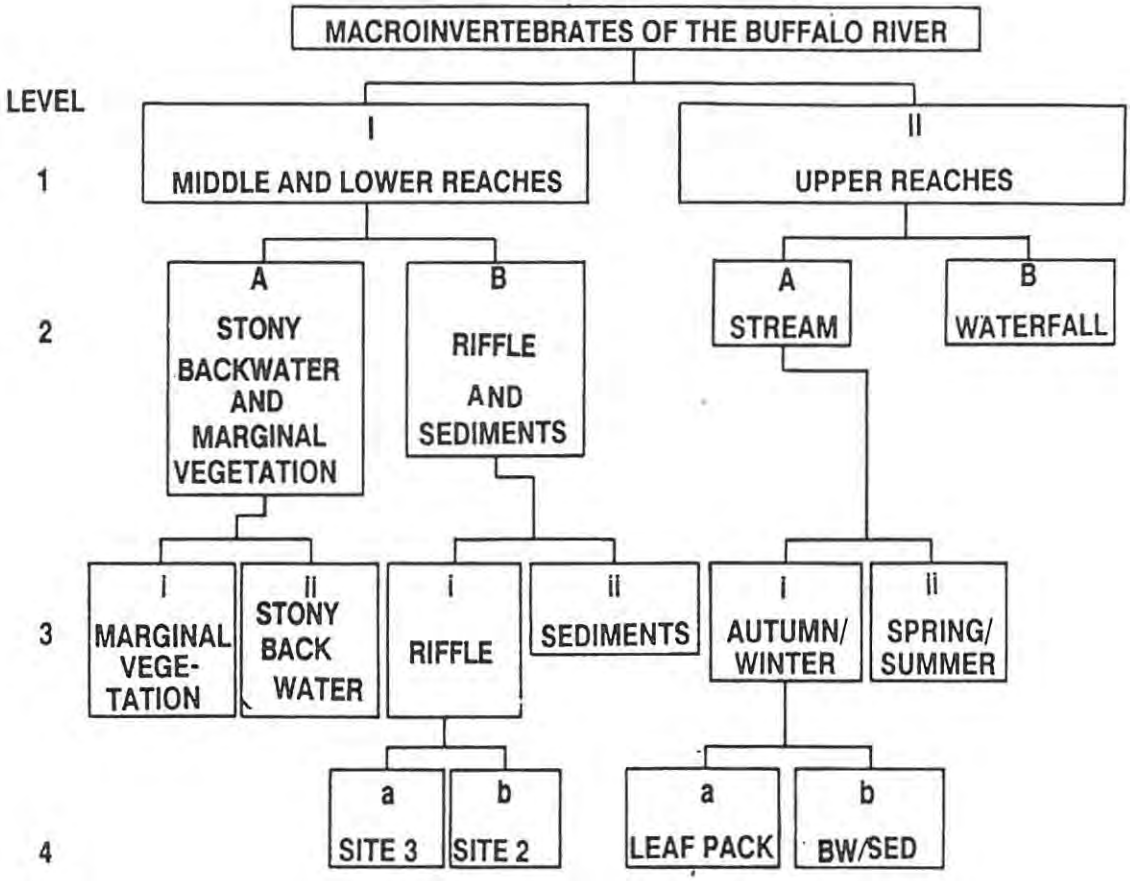


Fig. 3.1a. In an hierarchical classification (TWINSPAN, Hill 1979a) of the macroinvertebrate species assemblages in the Buffalo River, the faunal assemblage from the upper reaches (Site 0) was quite distinct from that of the middle and lower reaches (Sites 6 and 12). At Site 0 the fauna in the stream were distinct from those of the waterfall, and there were distinguishable seasonal changes in the stream assemblage structure. At Sites 6 and 12 benthic assemblages were associated with biotopes that had been subjectively recognised on the basis of their erosional or depositional nature. A summary of the species composition on which this is based follows in Fig. 3.1b.

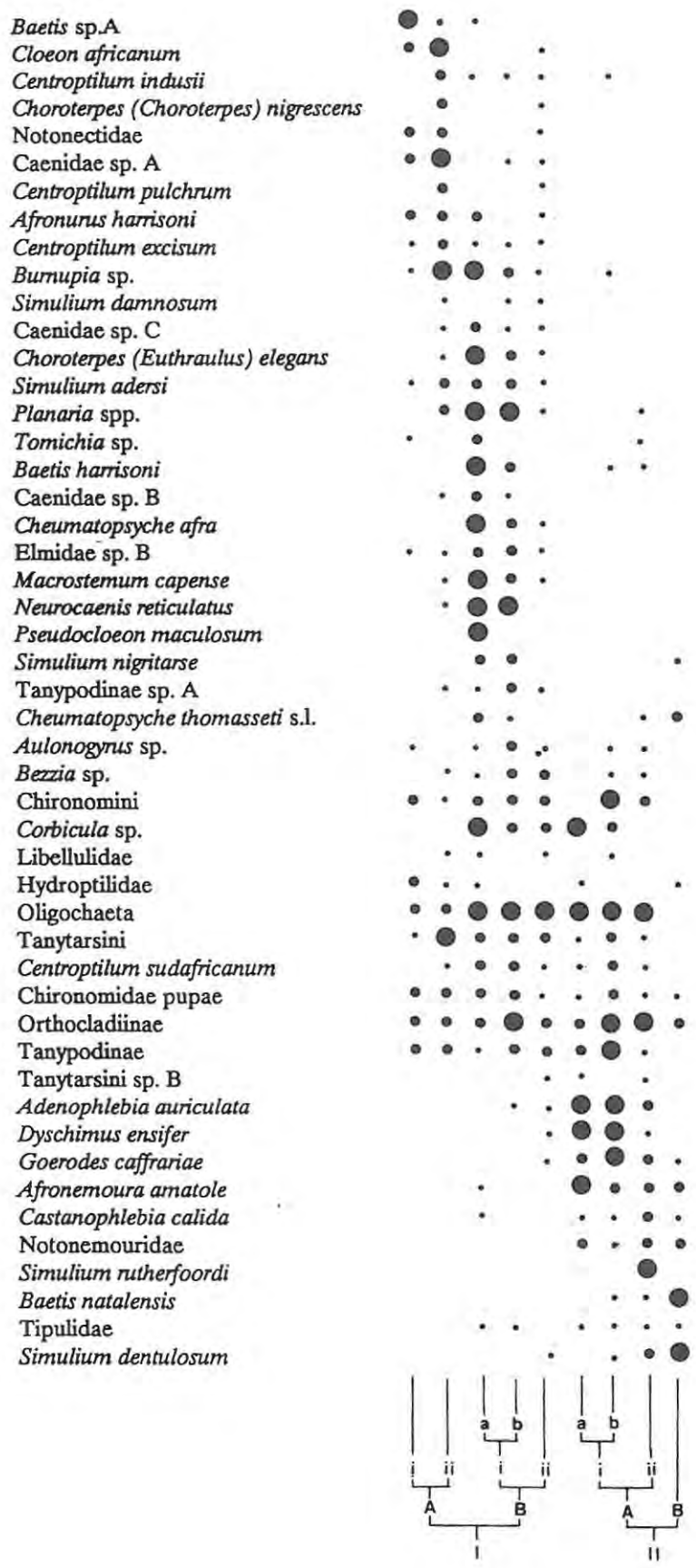


Fig. 3.1b. A summary of the TWINSPAN (Hill 1979a) classification of the macroinvertebrate species assemblages in the Buffalo River. A total of 119 taxa were used to achieve the classification. These 49 taxa were selected by a TWINSPAN sub-routine to summarise the salient features of the classification. The circles show the percentage of occurrences per taxon in each of the nine assemblages (small- 1-30%; medium- 31-70%; large- >70%). The dendrogram below the circles is related to biotopes in Fig. 3.1a.

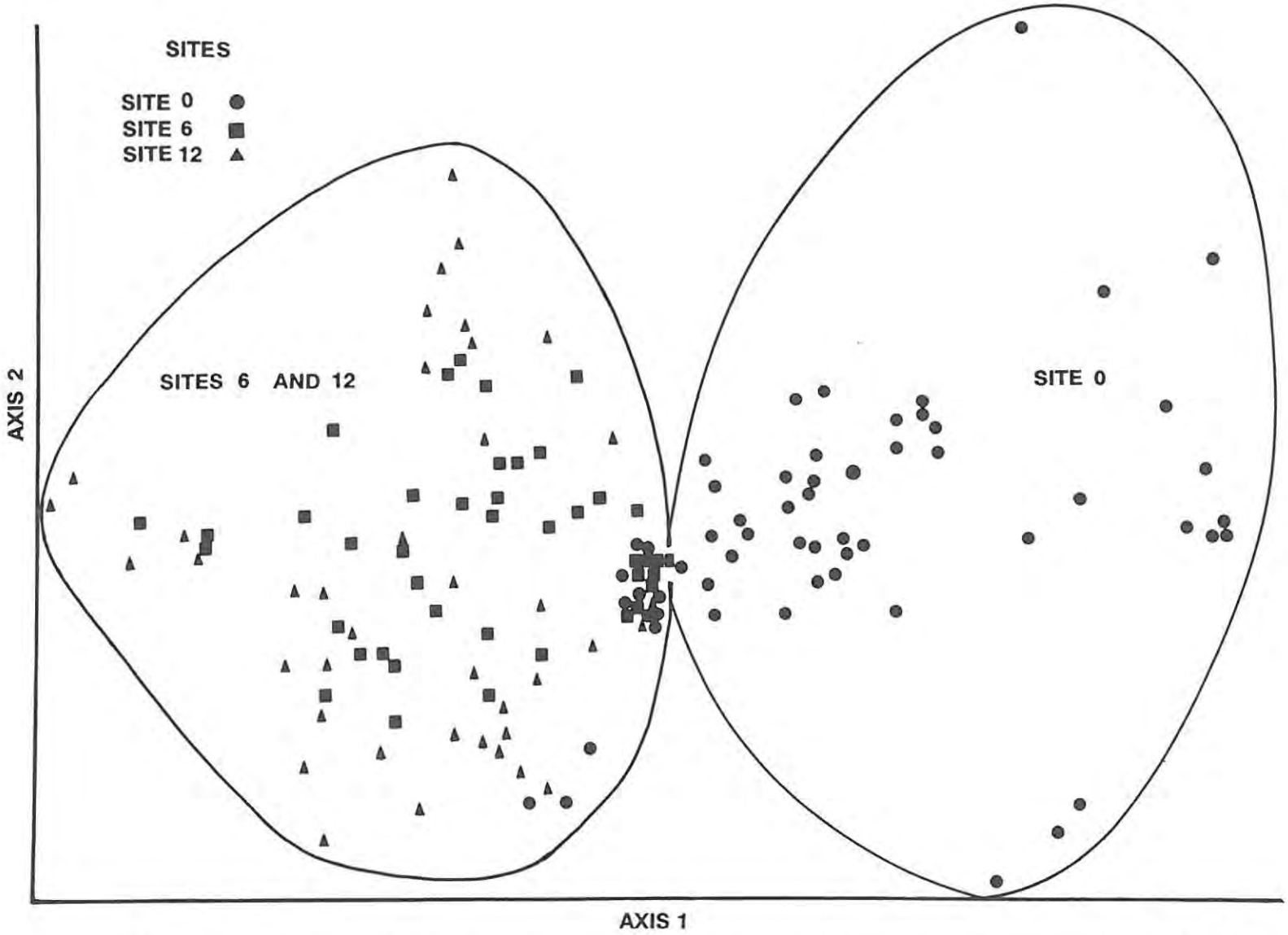


Fig. 3.2. Ordination (DECORANA, Hill 1979b) of taxa collected seasonally from a range of biotopes at Sites 0, 6, and 12 in the Buffalo River, shows a clear grouping of the fauna from Sites 6 and 12 (squares and triangles) together, separately from that of Site 0 (circles).

from the rest of the Site 0 biotopes, which are loosely grouped and described as the stream (II.A) at Level 2 (Fig. 3.1a). The stream included riffles, stony backwaters, leaf packs and sediments. This split is a reflection of seasonal patterns of flow. During summer, water flowed swiftly over the waterfall, feeding the stream below. During winter, while flow over the waterfall was reduced to a trickle (Fig. 2.3), surface flow in the stream ceased and became subterranean, with the result that the stream was reduced to a series of pools. The various biotopes sampled in the headwater stream could not be distinguished by differences in faunal composition.

The stream grouping (II.A), was characterised by Oligochaeta, larvae of the chironomid tribe Tanypodinae, the leptophlebiid mayfly A. auriculata, and the pisulid caddis Dyschimus ensifer. These were absent from the waterfall (II.B), where larvae of the blackfly S. dentulosum s.l., and the mayfly Baetis capensis were characteristic.

Finer groupings within the stream were separated at Level 3 (Fig. 3.1a):

II.A.i: Autumn-Winter Stream: This assemblage was identified by the presence of the caddisfly larvae D. ensifer and the chironomid tribe Tanypodinae. These organisms persisted in the isolated pools when stream flow ceased.

II.A.ii: Spring-Summer Stream: The presence of the blackfly larva Simulium rutherfoordi was characteristic of the spring and summer stream.

In the Autumn/Winter Stream grouping, two biotope-associated assemblages could be distinguished (Level 4, Fig. 3.1a):

II.A.i.a: a leaf-pack assemblage with notonemourid stoneflies as the key group; and

II.A.i.b: a stony backwater-sediment assemblage,

characterised by nematode worms and chironomids from the tribe Chironomini.

These last two were the only instances in the headwater stream where the recognised biotopes were associated with particular fauna.

The middle and lower reaches were characterised by the limpet Burnupia sp. and the platyhelminth Planaria spp. (Level 1, Fig. 3.1a). The stony backwater and marginal vegetation biotopes (I.A), characterised by larvae of the baetid mayflies Cloeon africanum and Baetis sp. A, could be distinguished from riffle and sediment (I.B) biotopes, characterised by the freshwater mussel Corbicula sp.. The apparently anomolous riffle/sediment association is a consequence of the inclusion of hyporheic sediments in the riffle biotope samples. At Level 3 (Fig. 3.1a), four assemblages were evident, each associated with a particular biotope:

I.A.i: Marginal vegetation: This group was characterised by the baetid mayfly Baetis sp. A and numerous Hemiptera, particularly Macroveliidae sp. A. These were the indicator taxa for all the marginal vegetation biotopes, both in- and out-of-current.

I.A.ii: Stony backwaters: The key taxa in this group were the limpet Burnupia sp., the chironomid sub-family Tanytarsini and the heptageniid mayfly Afronurus harrisoni.

I.B.i: Riffles: The mayflies Baetis harrisoni, and Neurocaenis reticulatus were characteristic of this biotope. Riffles were the only biotope in which any difference between Site 6 and Site 12 could be distinguished:
At Level 4 (Fig. 3.1a), group I.B.i.a has two key mayflies, Pseudocloeon maculosum and Caenidae sp. B, which were characteristic of Site 12, but absent from Site 6 (group I.B.i.b).

I.B.ii: Sediments: these samples were dominated by oligochaetes and nematodes.

3.3.2 Species-biotope associations

Twenty seven taxa occurred in sufficient numbers to enable a Chi-squared test to investigate biotope-association. The percentage frequency of occurrence of 25 of these species was significantly different from that which would have been expected if the animals had been evenly distributed over all the biotopes (Table 3.1).

Notonectidae, Caenidae sp. A, and A.harrisoni were strongly associated with stony backwaters and occured in sediment samples because they move over the surface of sediments in still backwaters (Table 3.1). Notonectidae and Caenidae sp. A were found in marginal vegetation out-of-current.

Choroterpes elegans and Simulium adersi were both primarily associated with riffles, and secondarily with stony backwaters (Table 3.1). They both appeared in the riffles area in the ordination plot (Fig. 3.3). C. elegans was also found in sediments samples, whereas S.adersi occurred in marginal vegetation, so that, although they co-existed in 3 biotopes (riffles, stony backwaters, sediments), the extent of their distribution in the various biotopes differed, with each occurring in a biotope from which the other was absent.

Table 3.1 Species-biotope associations in the Buffalo River, showing the percentage occurrence of 25 taxa in each of eight biotopes. The biotope associations of some of the species in the much larger Vaal River (Chutter 1970) are indicated. The number of occurrences (n) is shown, and p indicates the probability of even distribution among the biotopes (for example there is a <0.001% chance of notonectid distribution being even). (X^2 2d.f.) Biotopes: SED (sediments), BW (stony backwaters), RIF (riffles), MVO (marginal vegetation out-of-current, MVI (marginal vegetation in-current), LPO (leaf packs out-of-current), LPI (leaf packs in-current), WF (waterfall). b (taxon with >50% occurrence in one biotope).

Biotope	SED	BW	RIF	MVO	MVI	LPO	LPI	WF	n	p	Vaal R.[a]
Notonectidae	17	61[b]	-	22	-	-	-	-	18	<.001	BW/MVO
Caenidae sp. A	16	68[b]	3	10	-	3	-	-	31	<.001	
Afronurus harrisonii	17	83[b]	-	-	-	-	-	-	22	<.05	RIF/BW
Choroterpes (Euthraulus) elegans	31	23	46	-	-	-	-	-	22	<.001	RIF/BW
Simulium adersi	-	36	45	5	14	-	-	-	22	<.001	RIF/MVI
Planaria sp.	5	34	58[b]	-	-	-	3	-	38	<.001	RIF/BW
Baetis harrisoni	-	-	94[b]	6	-	-	-	-	18	<.05	RIF/MVI
Cheumatopsyche afra	-	11	89[b]	-	-	-	-	-	18	<.001	RIF
Macrostemum capense	-	5	95[b]	-	-	-	-	-	19	<.001	RIF
Neurocaenis reticulatus	-	10	90[b]	-	-	-	-	-	21	<.001	RIF
Burnupia sp.	-	55[b]	41	4	-	-	-	-	44	<.001	All
Centroptilum sudafricanum	-	25	55[b]	-	15	-	5	-	20	<.001	RIF/BW/MVI
Bezzia sp.	32	19	39	-	-	3	7	-	31	<.001	All
Chironomini	23	14	35	7	7	5	8	-	57	<.001	MVI/MVO
Corbicula sp.	36	14	34	-	-	7	9	-	44	<.001	
Tanytarsini	24	41	17	3	5	5	5	-	63	<.001	All
Tanypodinae	14	46	16	5	6	6	7	-	56	<.001	
Centroptilum excisum	14	37	14	3	32	-	-	-	35	<.001	RIF/BW/MVI
Dyschimus ensifer	18	27	-	-	-	18	36	-	22	<.001	
Goerodes caffrariae	9	26	14	-	-	14	29	8	24	<.05	
Orthocladiinae	14	25	28	5	6	5	8	9	78	<.001	All
Adenophlebia auriculata	23	29	13	-	-	3	19	13	31	<.001	
Notonemouridae	-	-	13	-	-	-	50[b]	37	16	<.001	
Simulium dentulosum	11	5	16	-	-	-	5	63[b]	19	<.001	RIF
Cheumatopsyche thomasseti s.l.	-	-	56[b]	5	-	-	-	39	18	<.001	RIF

[a]Chutter (1970)

Not unexpectedly, for both Planaria spp. and the freshwater limpet Burnupia sp. the percentage frequency of occurrence in stony biotopes (riffles and stony backwaters) was more than 90%. This indicated a strong association with stony substrata, regardless of the hydraulic conditions.

Several species and taxa which were not distributed evenly among different biotopes were not specifically associated with a particular biotope. In the case of the chironomid sub-families and tribes (groups which could not be identified to species), individual specific preferences could have been masked by the occurrence of multiple species groups.

Three species from the upper reaches were associated with one biotope in more than half the samples in which they occurred. Notonemourid stonefly larvae were associated with leaf packs. S. dentulosum with the waterfall and Cheumatopsyche thomasseti s.l. with riffles. Other upper reach species show general distribution in the stream (Fig. 3.3). The two case-building caddisfly larvae, G. caffrariae and D. ensifer, were both most common in leaf packs, but G. caffrariae was found in all the other headwater stream biotopes, whereas D. ensifer was absent from the two biotopes directly in-current, riffles and the waterfall; and was more commonly associated with sediment samples than G. caffrariae.

3.3.3 Classification of study sites and their fauna along a downstream gradient.

The relative abundance of benthic invertebrates in samples collected from riffles at all 16 sites, in spring 1987, were classified using TWINSPAN (Fig. 3.4). The results of this analysis revealed that the river sites were ranked in a downstream sequence, with Sites 0, 6, and 12 of this study ranked in sequence with the other sites. This suggests that it was reasonable to accept

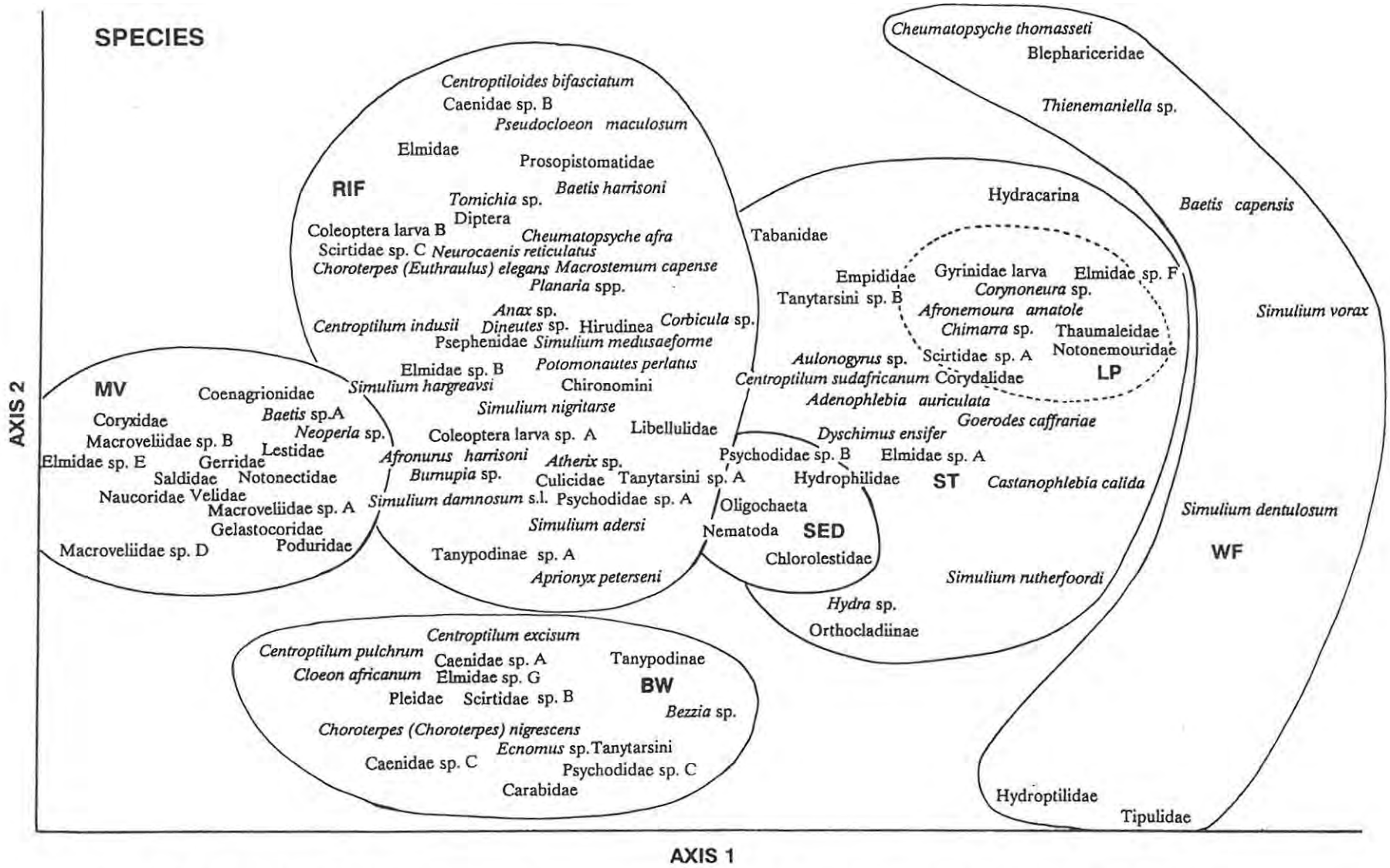


Fig. 3.3. Ordination (DECORANA, Hill 1979b) of the macroinvertebrate taxa collected seasonally from a range of biotopes at Sites 0, 6, and 12 in the Buffalo River. The biotope associations are shown, where RIF = riffles; MV = marginal vegetation; BW = stony backwaters; SED = sediments; ST = stream; LP = leaf packs and WF = waterfall. The broken line indicates a group taxa within the stream group which were associated with leaf packs.

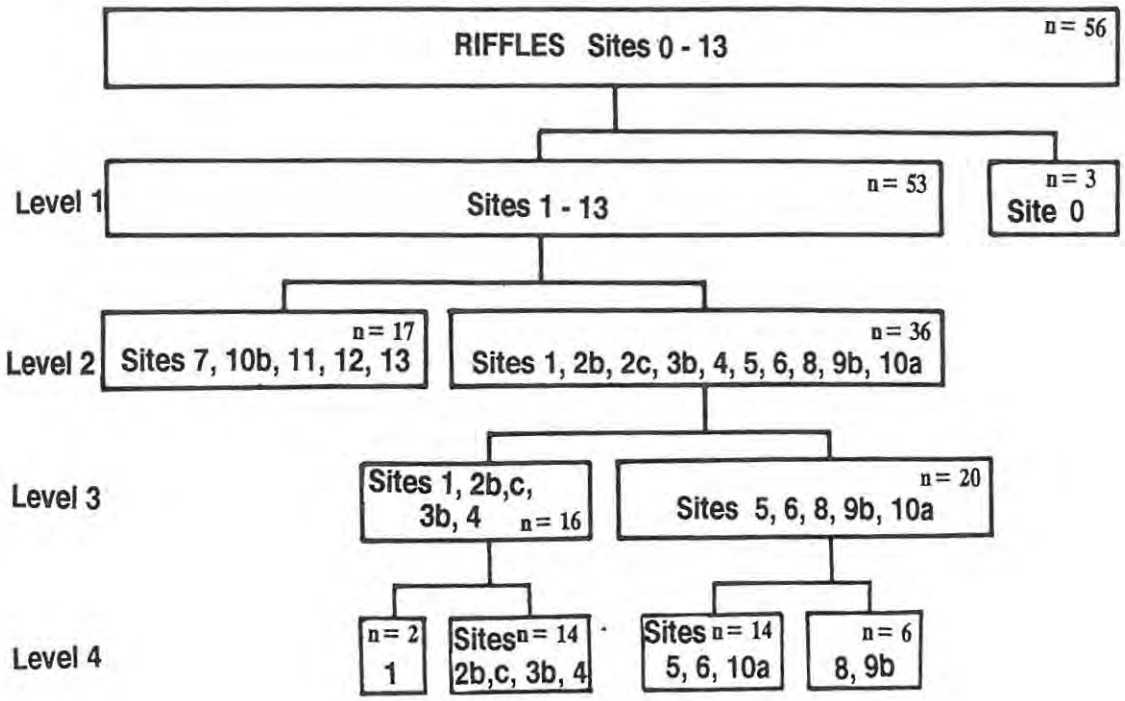


Fig. 3.4. The results of a TWINSPAN (Hill 1979a) classification of the benthic riffle fauna collected in summer (February 1987) from all the sampling sites down the river (Sites 0-13). At level 1, the fauna from Site 0 is separated from that of the rest of the river. At level 2, the fauna of the middle reaches (Sites 1-10a) can be distinguished from that of the lower reaches (Sites 10b-13). In this set of samples Site 7 was included in the lower reaches group. At level 3 the upper middle reaches (Sites 1-4) are distinguished from the lower middle reaches (Sites 5-10a), and at level 4, in the upper middle reaches, Site 1 is faunally distinctive. (n = number of samples)

them as representative of the upper, middle, and lower reaches of the river.

Ordination of summer riffle samples from all the sites using canonical correspondence analysis (CCA) also showed the downstream gradient in the distribution of macroinvertebrate assemblages. Fauna from Site 0 are separated from the rest of the river's fauna along the first axis (x-axis Fig. 3.5). Fauna from Site 1 are distinct at the top of the second axis (y-axis Fig. 3.5), while the fauna from all the other sites are grouped together further down axis 2.

The eigen values of the first four axes of CCA were 0.635, 0.394, 0.346 and 0.268 respectively, indicating that the invertebrate assemblage gradient is pronounced. The ordination revealed no marked outliers. Species axis 1 correlates strongly with environmental axis 1 (0.9728). Axis 1 (22.9) and axis 2 (36.9) account for significant amounts of the variance in the species-environment bi-plot (Fig. 3.5). Environmental arrows point towards the maximum change of a parameter and arrow length indicates its importance in data interpretation. The position of the environmental arrow depends on the eigen values of the axes and the intraset correlations of that arrow (Ter Braak 1988, Dixit et al. 1989).

3.3.4 Correlation of riffle assemblages with environmental gradients.

All the environmental variables correlate negatively with both axis 1 and axis 2, with pH displaying the strongest correlation with axis 1 (-0.698). This parallels the increase in pH from Site 0 to Site 13. Water temperature has a negative correlation (-0.6058) with axis 2, and parallels the increasing water temperature down the river. The biplots of species-environment (Fig. 3.5) and site-environment (Fig. 3.6) reflect the downstream changes in physico-chemical gradients already identified

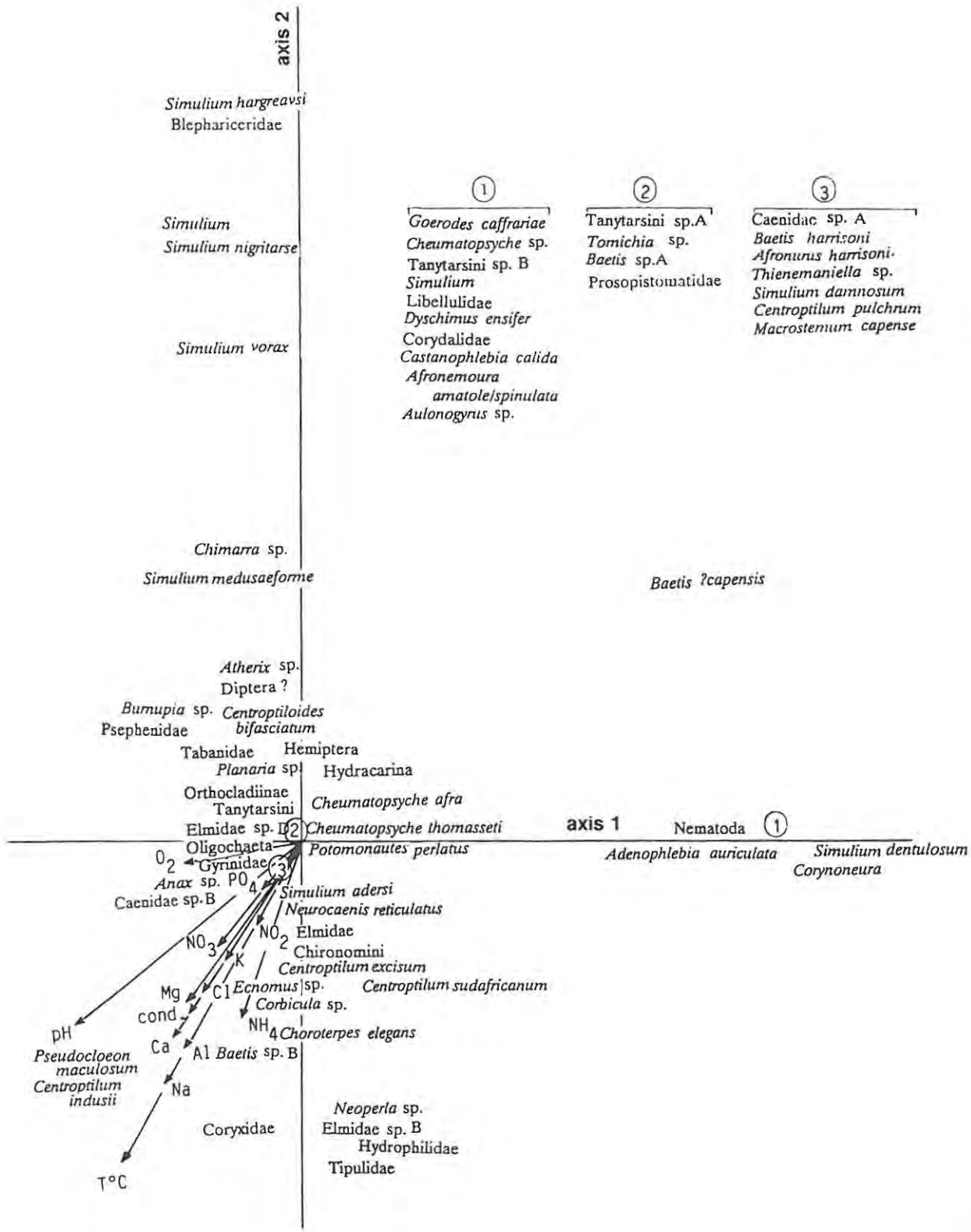


Fig. 3.5. Ordination (CCA, Ter Braak 1988) of the summer riffle fauna from Sites 0-13, in relation to a downstream gradient of environmental variables. Along axis 1, the fauna from the headwater stream (Site 0) are distinguished from the fauna of the rest of the river (Sites 1-13). Along axis 2, the fauna from Site 1 are grouped at the top, and fauna from the other sites (2b-13) cluster around the intersection of the axes. The taxa grouped in brackets are located together at points 1, 2, and 3. The direction of the arrows indicates the direction of increasing magnitude of that variable. The length of the arrow is proportional to the rate of change of the variable in that direction. Environmental variables with long arrows (temperature, pH, and sodium ion levels) are more strongly correlated with with the ordination axes than those with short arrows, and are therefore more closely related to the pattern of taxon distribution shown in the diagram (Ter Braak 1987). In the Buffalo River, taxonomic composition follows a downstream gradient of increasing temperature, pH and ionic concentration (the strongest of which was sodium).

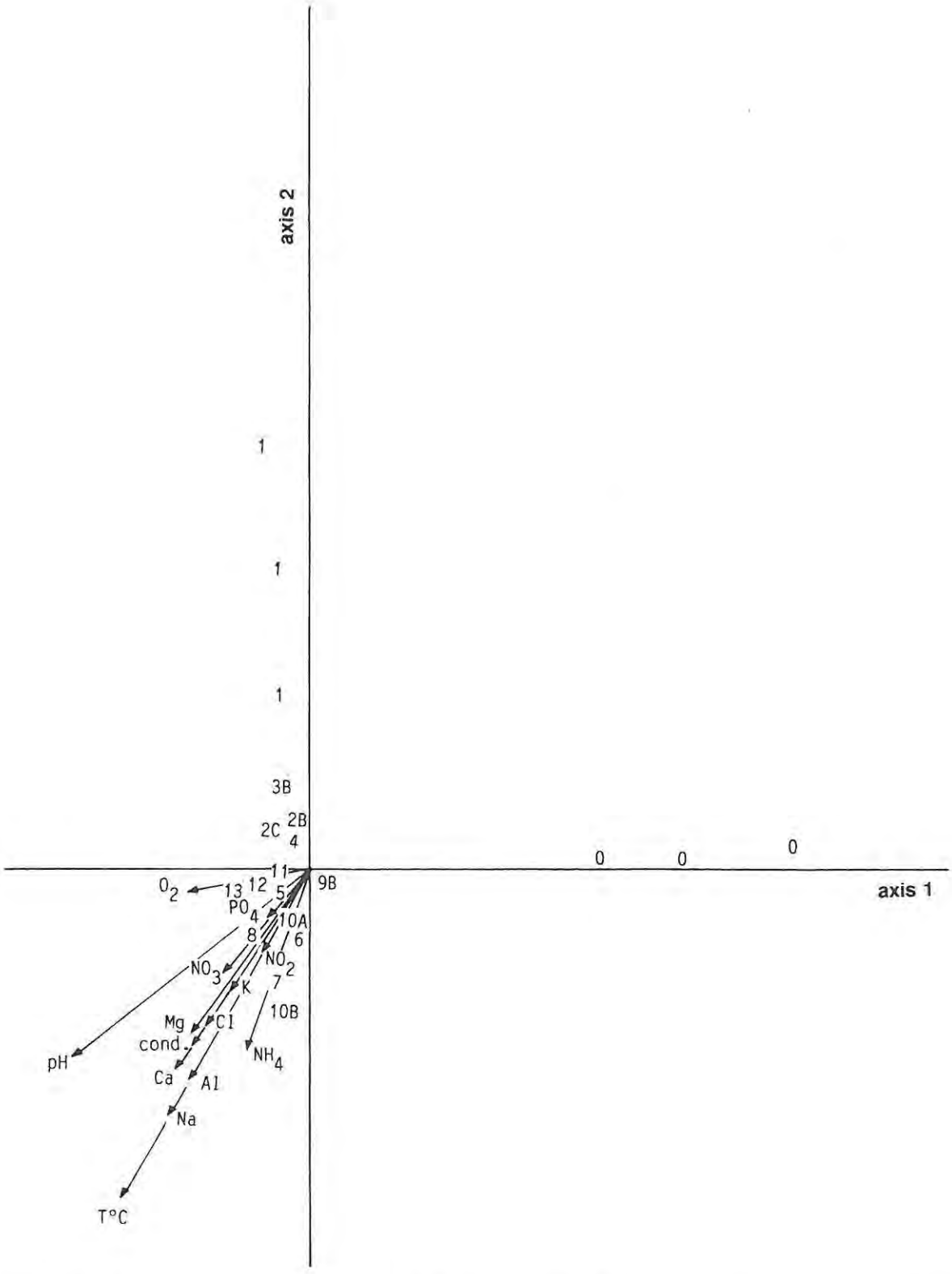


Fig. 3.6. Ordination (CCA, Ter Braak 1988) of the summer riffle fauna from Sites 0-13, in relation to a downstream gradient of environmental variables. The result is the same as that shown in Fig. 3.5, but here the sites are shown. Along axis 1, the fauna from the headwater stream (Site 0) are distinguished from the fauna of the rest of the river (Sites 1-13). Along axis 2, the fauna from Site 1 are grouped at the top, and fauna from the other sites (2b-13) cluster around the intersection of the axes.

for the Buffalo river (O'Keeffe et al. 1990). The position of Sites 0, 6 and 12 along axis 1 of the sample-environment bi-plot helps to justify their selection as typical of the upper, middle and lower reaches of the river.

3.4 Discussion

3.4.1 Patterns of composition and distribution

Both the taxonomic composition and the distribution patterns of macroinvertebrates in the headwaters of the Buffalo River were quite different from those of the middle and lower reaches. In the headwater stream the waterfall face supported a different fauna from the stream bed, but within the stream there was no evidence of biotope-assemblage association, and seasonal changes were more obvious. In the middle and lower reaches invertebrate assemblages were associated with subjectively identified biotopes (riffles, stony backwaters and sediments). As a result of the distinctive benthic assemblage structure and distribution recorded in the two river zones, the feeding biology of taxa from each zone is considered separately in each of the next two chapters.

3.4.2 The importance of scale

Minshall (1988) has recently pointed out that different ecological processes are important when spatial and temporal scales vary. The differences in assemblage composition and distribution between the two zones in the Buffalo River may be a consequence of scale. The dimensions of the headwater stream were considerably smaller than the middle/lower reaches. At Site 0 the stream was only 2.5m broad, and the subjectively recognised biotopes formed a mosaic of small patches. Physical conditions in these patches changed frequently, due to the variable discharge, which fluctuated from occasional spates to a seasonal absence of surface flow.

This contrasted with the middle and lower reaches (22-30m broad), where biotopes formed larger discrete units, and changes in discharge were more gradual and less frequent.

The recognition that stream channels are spatially less diverse in the headwaters than in the middle/lower reaches is not new: King et al. (1987a) investigated a small western Cape mountain stream, at the same scale as Site 0 and could not distinguish different biotopes, but recognised and sampled different biotopes in the middle reaches of the same river (King 1981). Pridmore and Roper (1985) studied macroinvertebrate distribution and assemblage composition in three New Zealand headwater streams where they identified riffles (high current and turbulent flow), and runs (lower current and more laminar flow). They noted that all the species found in runs were also present in riffles, with the exception of one trichopteran species which was exclusive to riffles; and that in two streams, runs and riffles supported similar macroinvertebrate densities.

One consequence of scale in the headwater stream of the Buffalo River was the seasonality of flow. The stream was intermittent (sensu Boulton and Lake 1988) and in the dry winter months groundwater seeped into the remaining pools. Boulton and Lake (1990) noted that physico-chemical variation was more extreme in two intermittent Australian streams than in neighbouring permanent streams and that this affected the macroinvertebrate structure. The intermittent nature of the Buffalo River headwater stream probably accounted for the seasonal patterns of presence and absence of taxa in the headwaters (Fig.3.1a).

The association between the structure of macroinvertebrate assemblages and season is variable. Seasonal changes have been shown to influence macroinvertebrate associations in other headwater streams (Bunn et al. 1986, King 1981). Seasonal changes in the

Acheron River, Australia, were gradual and were attributed by Barmuta (1989) to the persistence of habitats even during drought conditions. He noted that seasonal changes were most marked in riffles, habitats which were readily affected by alteration in discharge. The importance of seasonal fluctuations in discharge was emphasised by Power et al. (1988): "As water levels rise and fall, river and stream habitats expand and contract, resource availabilities shift, certain habitats become more or less isolated from others, and flow regimes change, altering other physical gradients". At high discharge in the Buffalo River, most of the channel in the upper reaches was erosional, and riffles were extensive in the middle and lower reaches. As the water level dropped, some areas of the river which had been erosional became depositional, with a gradual conversion from turbulent to laminar flow, and in some places, from laminar flow to still water. In the upper reaches, when flow became subterranean, riffle biotopes dried out, and only pools remained. Low discharge in the lower reaches resulted in smaller riffles and larger depositional areas.

By subjectively distinguishing between erosional and depositional biotopes, it was implicitly accepted that water velocity was an important factor which differentiated biotopes in the Buffalo River. In the middle and lower reaches, the separate grouping of depositional biotopes (stony backwater and marginal vegetation) and erosional biotopes (riffle and associated sediments) by TWINSPAN (Fig. 3.1a), suggested that water velocity differences affected the composition of macroinvertebrate assemblages. In the middle/lower reaches, marginal vegetation, stony backwater, riffle, and sediment biotopes were individually distinguished in the TWINSPAN classification (Fig 3.1a). Each of these biotopes encompassed a variety of variables, such as substratum type, which also affected patterns of

macroinvertebrate distribution.

At the larger scale of the middle and lower reaches in the Buffalo River, although riffle, stony backwater and sediment biotopes were associated with characteristic groups of taxa (Figs 3.1a and 3.3), some taxa occurred in all these biotopes (Table 3.1). Chutter (1970) and De Moor (1982), working in the large Vaal River system in South Africa, identified the biotopes used in the present study and recorded similar species-biotope associations. Eighteen taxa were common to Chutter's (1970) study, and this study and of these fifteen species-biotope associations were the same (Table 3.1), indicating a consistent biotope choice by particular species in the spatially diverse middle/lower reaches of quite different river systems. In the River Teifi, Jenkins et al. (1984) arbitrarily identified three biotopes (eroding, depositing and vegetation) and found that these were necessary to describe the macroinvertebrate fauna adequately at each site - an argument implying that some species were exclusive to each of the biotopes. However they noted that species were not generally restricted to particular biotopes, but that ecdyonurid mayflies predominated in riffles and one leptocerid caddisfly was found in tree roots. Barmuta (1989) recognised a gradual transition in assemblage structure from erosional to depositional biotopes in the Acheron River. The results reported in this chapter have shown that in the Buffalo River species could be found in a range of biotopes, but still show a greater abundance in one particular biotope, that two species may be concurrent in some biotopes and not in others, and that some species were exclusive to particular biotopes.

The classification procedure (TWINSPAN) produces dichotomies with discrete boundaries between the groups of samples which it distinguishes, implying consonant boundaries in species distribution (Begon et al. 1986).

The subjectively recognised biotopes in the Buffalo River were associated with groups of species in the middle/lower reaches, but not necessarily with specific taxa. A percentage frequency of occurrence greater than 85% in a single biotope was only recorded for the larvae of four riffle-dwelling insect species (Table 3.1). However, a frequency of occurrence of more than 50% was recorded for 15 species (Table 3.1). This indicates a strong association of some species with an individual biotope, but also showed that their distribution extended to a variety of other biotopes. Comparison of species-biotope associations (Table 3.1) with assemblage-biotope associations (Fig. 3.1a) suggested that groups of species were associated with particular biotopes sufficiently often to permit recognition of biotope-assemblage associations. However associations at the level of biotope masked subtleties of distribution that were revealed at the species level. Most species seem to extend their range beyond the defined biotopes. Barmuta (1989) reported similar results and concluded: 1) that it seemed more likely the stream organisms were distributed unimodally along environmental gradients in an individualistic manner, and 2) that the scale of environmental sampling is probably frequently too coarse to be relevant to stream organisms.

3.4.3 Conclusions

It is therefore essential to define a scale which is applicable to each study, and, more importantly to search for scales that are relevant to the organisms themselves (Davis and Barmuta 1989). The traditional subjectively identified biotopes such as riffles, runs, and pools are descriptively useful at higher stream orders, where flow is present all year round. They can certainly serve as the basis for stratified sampling programmes and/or biogeographical studies (e.g. Harrison and Hynes 1988). However this study has shown that it cannot be assumed that distinct faunal groups will necessarily be found in

different biotopes in headwater streams where such biotopes are spatially adjacent and may be subject to seasonal variation in discharge.

CHAPTER 4

FEEDING PATTERNS OF FOUR MACROINVERTEBRATE TAXA IN THE HEADWATERS OF THE BUFFALO RIVER, EASTERN CAPE.

Most of this chapter, together with part of Chapter 6 has been accepted for publication in the journal Hydrobiologia in a paper entitled: "Feeding patterns of four macroinvertebrate taxa in the headwaters of the Buffalo River, eastern Cape."

4.1 Introduction

> "One of the most ubiquitous features of freshwater habitats is their present rate of change in response to man engendered perturbations. Any rehabilitation or management strategy characterised by a high probability of success must rely on fundamental knowledge of the intracacies of freshwater ecosystem structure and function. A basic facet of this structure and function is material cycling and energy flow. In turn, a significant portion of such cycling and flow involves the processing of various forms of organic matter by freshwater invertebrate animals, especially insects. This constitutes a basis for interest in aquatic insect trophic relations." (Cummins 1973)

The above introduction to Cummins' (1973) review of the feeding of aquatic insect larvae remains the most cogent raison d'etre for an investigation of macroinvertebrate feeding, as it relates a fundamental understanding of macroinvertebrate feeding activities to processes in the river and consequently to decision making and management. The Functional Feeding Group (FFG) concept, which aimed to develop a classification of aquatic invertebrates based on feeding, was introduced in Chapter 1, together with the need for clarification of the concept. Two aspects of the concept are clarified in this chapter.

Spatial, temporal and developmental variability: During the development of the FFG concept it became clear that many aquatic invertebrates were generalist feeders (Coffman et al. 1971). This was the reason that FFGs were initially described in terms of morphology and the mechanism of feeding. However gut analysis became a common research approach to investigating FFGs (Section 1.7.2), and evidence was presented which suggested that diet varied spatially, temporally and with development (Cummins 1973, Feminella and Stewart 1986, Chessman 1986). This raised the question whether dietary variability was so great that FFG designations were meaningless.

In this chapter the feeding of four macroinvertebrate taxa from the headwaters of the Buffalo River is reported. The aim was to establish the degree of spatial, seasonal and developmental variation in their gut contents and to assess whether they could be assigned to FFGs as taxonomic entities. The following questions were asked:

a) What food did each taxon ingest ?
b) How did diet vary with season, biotope, and larval size ?
c) Were taxa food specialists or generalists ?
d) Could taxa be assigned to FFGs ?

Definitions: The shift in basis for the assigning of taxa to FFGs from feeding mechanism and morphology to the size and type of food ingested created confusion (King et al. 1988, Section 1.7.3). One of the first predictions of the River Continuum Concept (RCC) (Vannote et al. (1980) to be challenged (Winterbourn et al. 1981) was the prediction that shredders would predominate in headwater streams. Shredders have subsequently been subject to much debate but seldom with the same concept being debated (Section 1.7.3). In this chapter, data on the feeding of three shredders from the headwaters of the Buffalo River are used to clarify the

term shredder and to suggest a basis upon which animals could be termed shredders.

Brusher was a new functional designation coined by McShaffrey and McCafferty (1986) to describe organisms which use setae to remove loosely deposited fine organic material. Brusher was used in the same sense as the term browser which had previously been used to describe the functional feeding of New Zealand leptophlebiid mayfly larvae (Rounick and Winterbourn 1983, Winterbourn et al. 1984, Campbell 1985). However browser had been used interchangably with the term grazer (Collier and Winterbourn 1990, Jowett and Richardson 1990) and this created further opportunities for confusion with the term scraper. The term brusher is descriptively accurate, and in this study a morphological basis for the term is presented.

The results of this part of the thesis are also used to explore the application of the FFG concept in a more speculative manner. In this chapter the use of the FFG concept to elucidate the role of macroinvertebrate feeding in the facilitation of river function is discussed. In Chapter 6 the development of a functional classification based on the size and type of food items found in the foregut, and the use of FFGs in a predictive capacity, are considered.

4.2 Methods

4.2.1. Field sampling and curation

The headwater stream was sampled monthly from January 1987 to March 1988. On each occasion three replicate box samples (0.09m^2, mesh 80um) were collected in each of five biotopes: riffles, waterfall face, leaf packs from riffles, stony backwaters, and sediments. Organisms were sorted and counted using a sub-sampling technique described in Palmer and O'Keeffe (1990c).

The macroinvertebrate assemblage comprised 49 taxa. (A total of 5258 individuals were collected, and voucher specimens are lodged with the Albany Museum, Grahamstown.) Three simuliid species were the most numerous taxa. I assumed these were predominantly filter feeders (Wallace and Merritt, 1980), while noting recent evidence of simuliid behavioural flexibility (Currie and Craig, 1987). Four other 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 A. spinulata (Balinsky), as adults of these species were collected from the site.

4.2.2. Observation of Feeding Behaviour

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 (25x25x100mm). A small stone, a leaf, a twig and 2ml loose detritus from the stream were included, and observations were made in a constant temperature room (15 ^{o}C), under daylight conditions, continuously for 12 hours. Each larva was watched for 5 minutes every hour, and its behaviour was recorded every 30s 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.

In an investigation of whether A.auriculata larvae were able to shred leaves, 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.

4.2.3. Food Choice Experiments

A. auriculata larvae (late instar) were offered different types and different sizes of food, and D. ensifer larvae (late instar) were offered different types of food. G. caffrariae larvae were too scarce in the field at the time when these experiments were conducted to be included and stoneflies were not tested.

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 and 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 ^{o}C (winter maximum, summer minimum stream temperature). This was cool enough to prevent the rapid emergence which occurred above 20 ^{o}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 (Fig. 4.1a).

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 Rhodophyte 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. 4.1a). Five replicate aquaria were set up to ensure that factors other than food were not affecting the

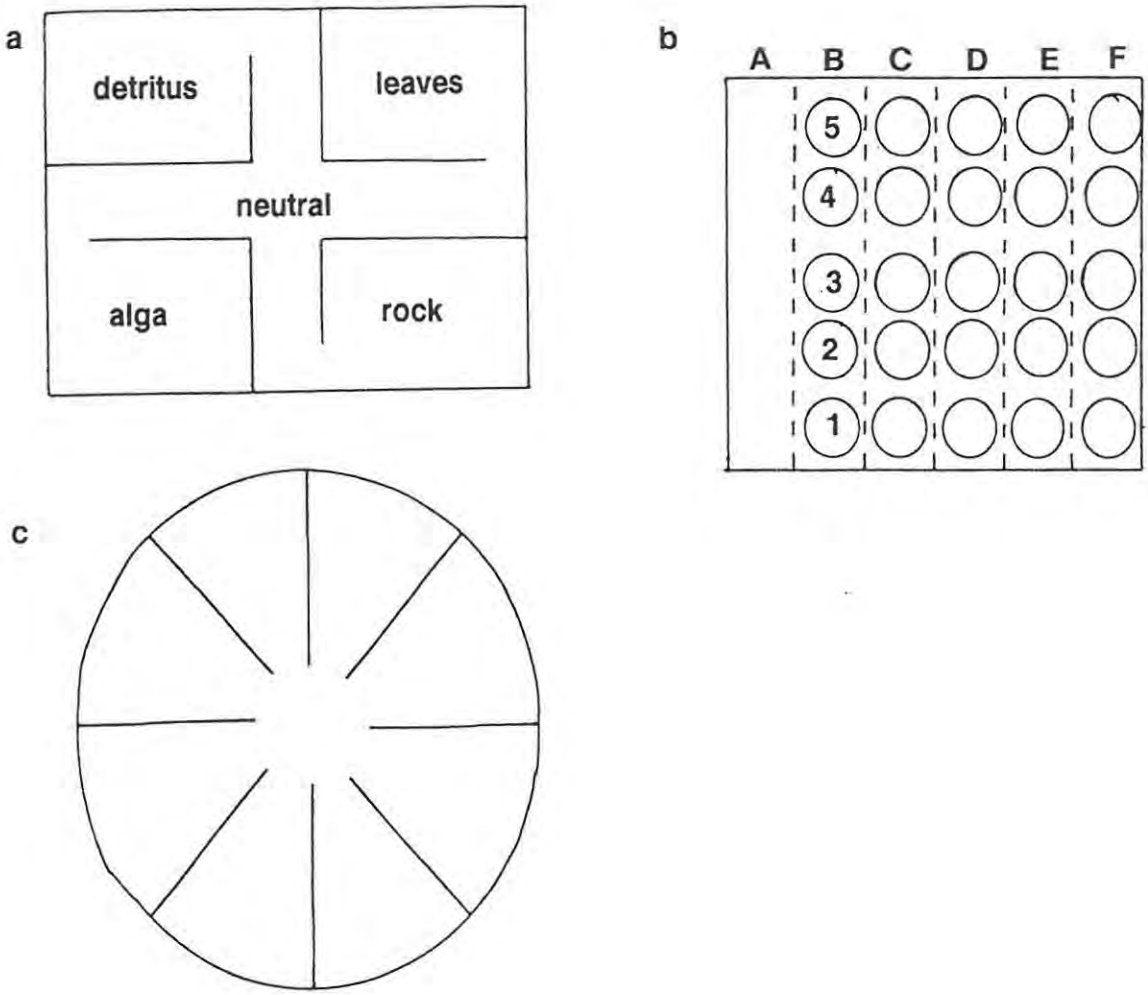


Figure 4.1. Diagrams of food choice experiment aquaria: a) A. auriculata was given a choice of 4 food types; b) A. auriculata was given a choice of 5 food particle sizes: 1 = 80-250µm, 2 = 250-500µm, 3 = 500-850µm, 4 = 850-4000µm, 5 = > 4000µm, (A-F = gauze separated compartments); and c) D. ensifer was given a choice of the same four food types as A. auriculata, with each food type in two of the compartments.

distribution of the larvae in the aquaria. After a 48 hour laboratory acclimation period, twenty five larvae were 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 (Fig. 2.3), though indigenous leaves were relatively more common in summer leaf packs. Irons et al. (1988) reported 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: 80-250µm, 250-500µm; 500-1000µm; 1-4mm, >4mm. 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. 4.1b). A single aquarium was used so that water was of 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 was tested using 5 circular white trays with eight compartments (300mm diameter/30mm depth, Fig. 4.1c). 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 and 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.

4.2.4 Shredding of Leaf Discs

D. ensifer and the Afronemoura spp. larvae were offered weighed leaf discs, to confirm that they were primarily shredders. G. caffrariae larvae were too scarce to be included in these experiments. These three taxa were frequently collected from leaf packs in the stream, so 23 caddis, and 50 stoneflies were placed in two flat white trays (300mm diameter, depth 25mm) with 25 and 20 pre-weighed, damp dried, oak leaf discs (20mm 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.

4.2.5 Morphology

The morphology of the mouthparts of A. auriculata were investigated using scanning electron microscopy (SEM). Specimens were dehydrated in 100% alcohol, subjected to critical point drying, and sputter coated with a thin film of gold before viewing and being photographed (Cross 1987). The aim was to establish the structural basis of brushing, and therefore the morphology of the other headwater taxa was not investigated.

4.2.6. 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 4.1). One large and one small individual were dissected for each slide. The foregut contents were dispersed in distilled water, mixed using a Fisons's "Whirlimixer" and filtered through a 0.45μm

Table 4.1. The size range, and number of individuals used to determine gut contents.

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

Millipore filter. This was cleared with immersion oil, and 10 fields at 400x magnification were viewed and enumerated for each slide (Gray and Ward 1979, Rader and Ward 1987). Thirteen food categories were identified: amorphous detritus in the size ranges: 1) 0.5-50μm (UFPOM); 2) 50-250μm (FPOMa); 3)250μm-1mm (FPOMb); 4) Fungi; 5) sestonic diatoms; 6) other diatoms; 7) multicellular algae; 8) leaf fragments, 0.5-50μm (L.UFPOM); 9)leaf fragments, 50-250μm (L.FPOMa); 10) leaf fragments, 250μm-1mm (L.FPOMb); 11) pollen; 12) invertebrate remains; and 13) inorganic 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). The selection of these food categories was somewhat abitrary. Categories used by Chessman (1986) were used as a basis, and others were added after observation of material in this study. It is important to note that fine detritus, even when differentiated on the basis of size, as was done in this study, is an area of uncertainty. The nature of this organic material may be revealed more precisely using scanning electron microscopy. This was not undertaken in this study.

Dietary composition was compared using a multifactor ANOVA. The ANOVA procedure assumes equality of variance, but Bartletts test (Sokal and Rohlf 1969) 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 the value (which must be a proportion) is needed to stabilise the variance more effectively. 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 and Ward 1987, Becker 1990) 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 were tested (two-way ANOVA without interaction, with food type and sample as the two factors). Once it was established that 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 counting extra fields for the existing slides gave a better reflection of the dietary range of the animals. These repeated count data were included to enable a balanced ANOVA design as a Generalised Linear Modelling package was not available. Two-way ANOVA with interaction was used to assess dietary differences associated with size, biotope and season.

4.3 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 generated a set of tables where larval size, biotope, and seasonal effects on dietary composition were considered separately (Tables 4.2, 4.3, and 4.4; Appendices 2.1, 2.2, and 2.3). While this did not analyse the combined interactions of these factors as a 4-way ANOVA would have done, the raw data for each taxon

Table 4.2 Size comparisons: The gut contents of large larvae are compared with those of small larvae. Separate large versus small comparisons of larvae collected from different seasons and biotopes were made. Gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae were compared using a 3-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: ** $p < 0.01$, * $p < 0.05$.

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

Table 4.3 Biotope comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one biotope were compared with those of larvae collected from one or more different biotopes. In each 3-way ANOVA with interaction, the gut contents of one species, of one size, collected in one season, but from two or more biotopes 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: ** $p < 0.01$, * $p < 0.05$.

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

Table 4.4 Seasonal comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one season were compared with those of larvae collected from one or more different seasons. In each 3-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: ** $p < 0.01$, * $p < 0.05$.

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

(Fig. 4.2a and b, Appendix 3), 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 in the foreguts of the larger individuals.

The range of food types in the foreguts of all individuals from each taxon was basically the same (Fig. 4.2 a and b, Appendix 3). 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 recognised such variations as significant differences, but they were of limited biological significance, and have been given little weight in the conclusions.

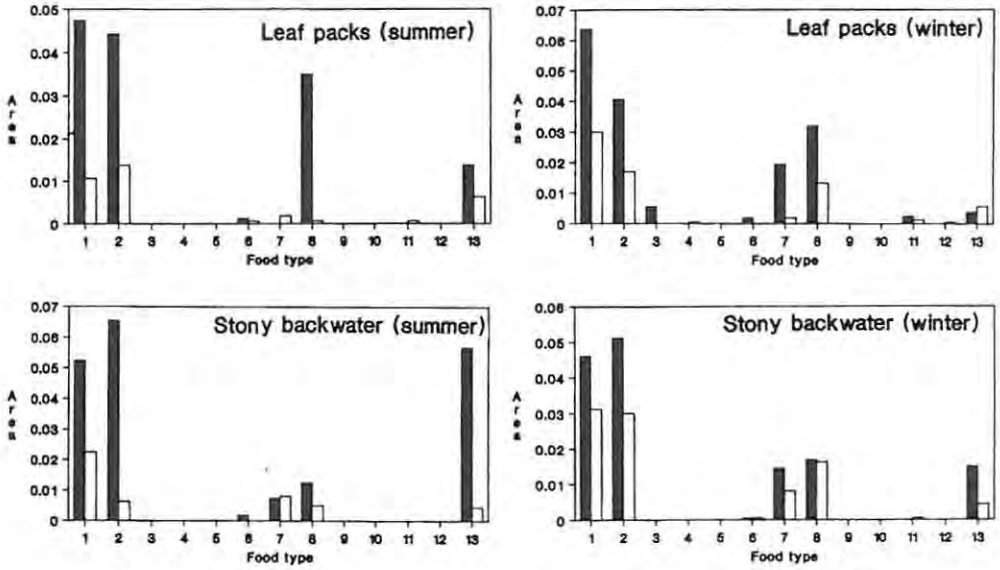
Where there were significant differences in gut contents, the ANOVA indicated whether there was interaction between dietary composition and the factor under consideration, whether size, biotope, or season. Where there was no interaction, the same food types had been ingested, and their relative proportions were not significantly different, but the amount of food ingested was different. Where there was 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 (see also Section 5.2.2).

4.3.1 Adenophlebia auriculata

Observation: 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 (500-1000μm)), and nibbling

GUT CONTENTS

Adenophlebia auriculata



Afronemoura spp.

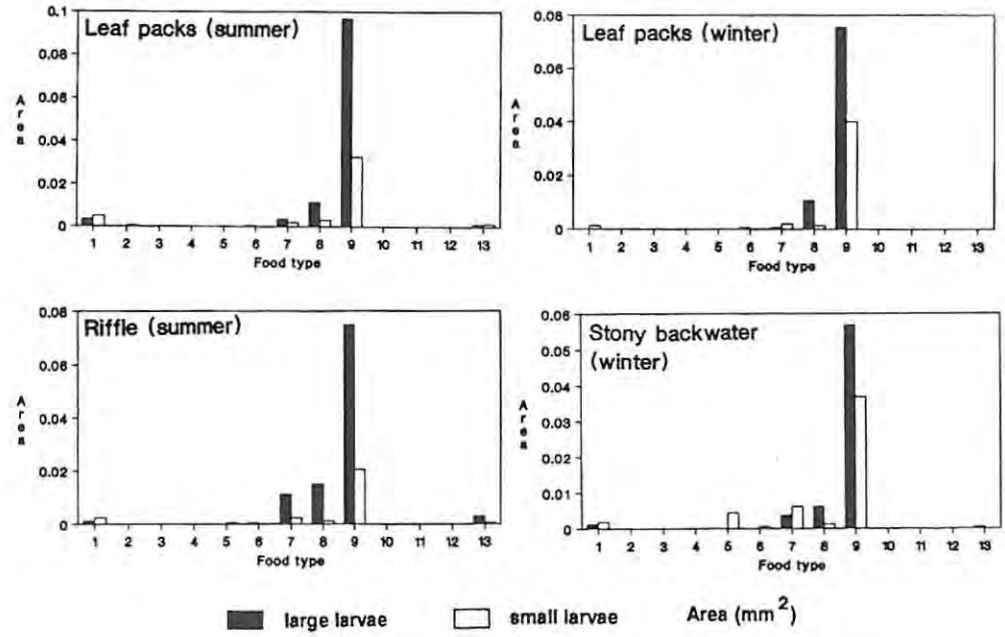


Fig. 4.2a. Typical examples of the gut contents of Adenophlebia auriculata and Afronemoura spp. larvae. The gut contents of large (shaded) and small (unshaded) animals collected from riffles, stony backwater and leaf pack biotopes in summer and winter are shown. These biotopes and seasons illustrate the trends described in the text. The complete set of gut content data is in Appendix 3. The area value given is the mean area covered in 10 microscope fields (400x) by each food type for 3 replicate gut contents slides. 1 = detritus (0.5-50µm), 2 = detritus (50-250µm), 3 = detritus (250µm-1mm), 4 = fungi, 5 = planktonic algae, 6 = diatoms, 7 = filamentous algae, 8 = leaf fragments (0-50µm), 9 = leaf fragments (50-250µm), 10 = leaf fragments (250µm-1mm), 11 = pollen, 12 = invertebrate remains, 13 = inorganic silt. A. auriculata is a collector/brusher which ingests mainly fine detritus, and Afronemoura spp. are shredders, with their gut contents dominated by leaf fragments. (Drawings from Barnard (1932).)

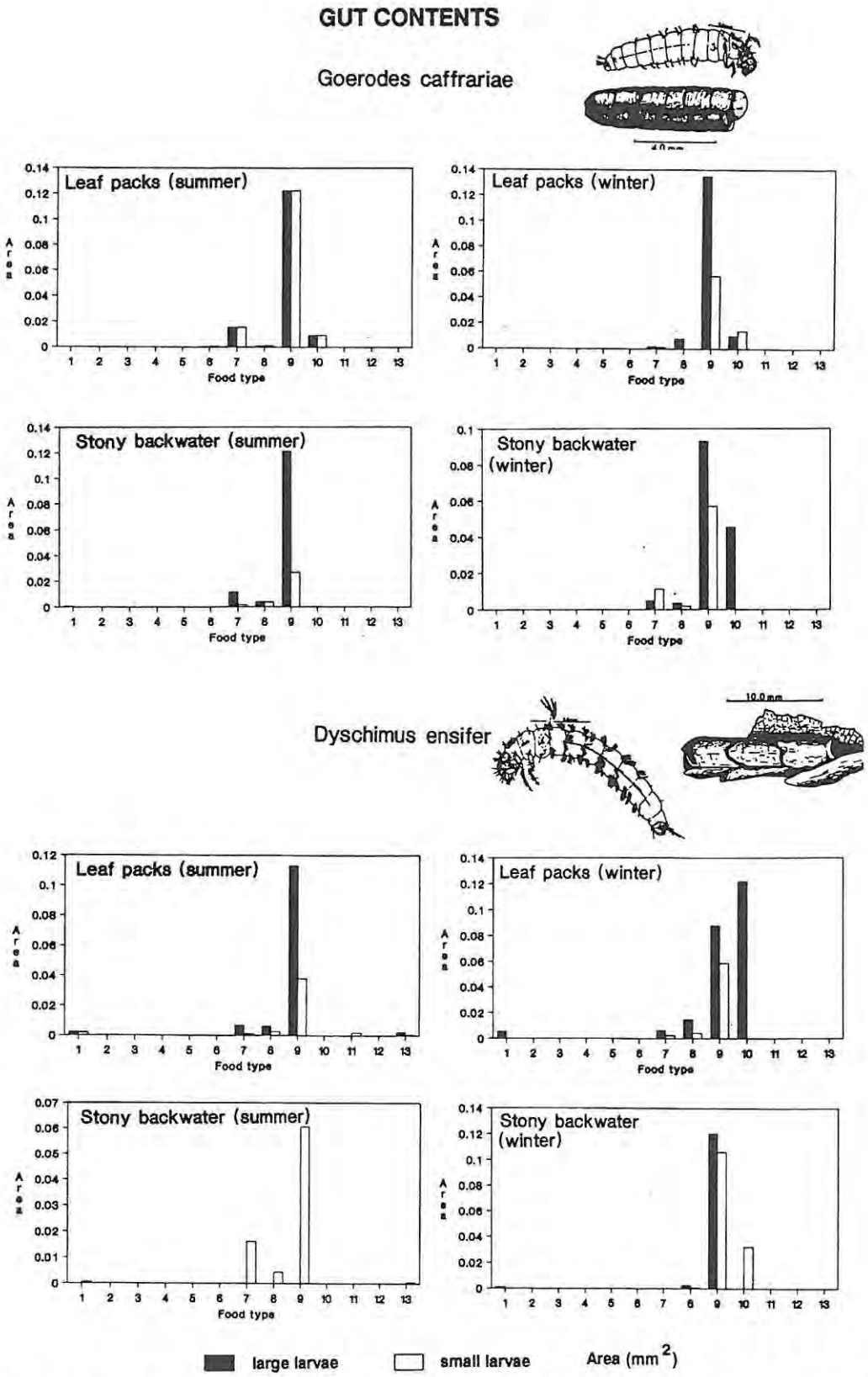


Fig. 4.2b. Typical examples of the gut contents of Dyschimus ensifer and Goerodes caffrariae larvae. The gut contents of large (shaded) and small (unshaded) animals collected from stony backwater and leaf pack biotopes in summer and winter are shown. These biotopes and seasons illustrate the trends described in the text. The complete set of gut content data is in Appendix 3 . The area value given is the mean area covered in 10 microscope fields (400x) by each food type for 3 replicate gut contents slides. 1 = detritus (0.5-50µm), 2 = detritus (50-250µm), 3 = detritus (250µm-1mm), 4 = fungi, 5 = planktonic algae, 6 = diatoms, 7 = filamentous algae, 8 = leaf fragments (0-50µm), 9 = leaf fragments (50-250µm), 10 = leaf fragments (250µm-1mm), 11 = pollen, 12 = invertebrate remains, 13 = inorganic silt. G. caffrariae, and D. ensifer are shredders, with their gut contents dominated by leaf fragments. (Drawings from Dr. K.M.F. Scott (unpublished).)

(observed when larvae ingested Batrachospermum sp. algae by feeding a strand into their mouth and nibbling the end). A. auriculata larvae kept in aquaria with only filtered water and leaves survived for several weeks, 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 a generalist, but they more often brushed the surface of substrata than any other feeding activity (Table 4.5, where feeding events in the neutral area were brushing).

Gut analysis: The 67 A. auriculata larvae which were dissected had ingested mainly fine detritus (UFPOM, FPOMa, L.FPOMa) with some filamentous algae (Fig. 4.2a).

The gut contents of small individuals comprised only fine detritus, whereas the foreguts of larger larvae contained more material and a wider variety of food (Fig. 4.2a, Table 4.2). There were significant variations

Table 4.5. A Chi-squared test was used to 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. (Food size ranges are expressed in μm)

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 ersifer

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. **

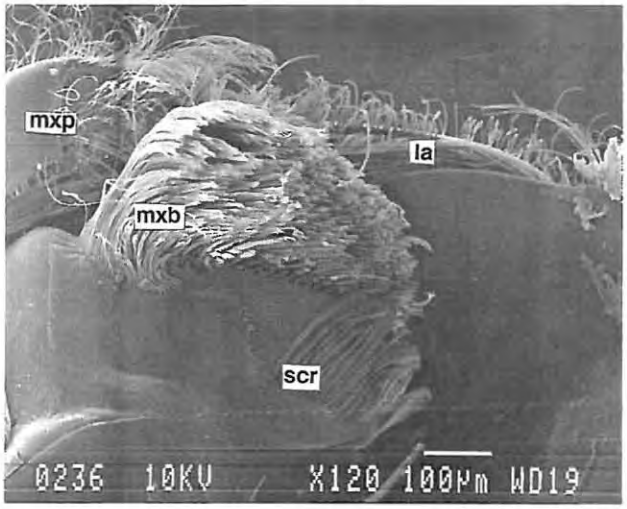
in the gut contents of larvae from different seasons and biotopes (Tables 4.3 and 4.4). These were due to different proportions of the less frequent dietary components such as pollen, fungi, invertebrate remains and larger leaf fragments. Any leaf fragments ingested would have been brushed up rather than shredded and are simply a part of the fine detritus which is the major food source of this species.

Morphology: A. auriculata larvae were equipped with maxillary brushes for brushing (Figs. 4.3 a-e). Each brush comprises a gradient of setae, from curved stout bristles at the base, to long fine setae at the top, each with a double row of fine, curved microtrichia. A. auriculata had a wider range of food items in the gut than two other leptophlebiids from the middle and lower reaches of the Buffalo River (Chapter 5), and also has a more complex range of setae on the mouth parts. In addition to the maxillary brushes, there was a set of setae on the inside face of each maxilla which might have served to remove more tightly accreted material (Fig. 4.3c).

On this basis, A. auriculata was classified as an opportunistic collector: brusher (sensu McShaffrey and McCafferty 1986); with size playing a more important role than biotope or season in dietary variation.

4.3.2 Goerodes caffrariae

Gut analysis: G. caffrariae (49 dissected) was the most specialised feeder, and leaf fragments (0.5µm - 250µm) almost exclusively filled the foregut (Fig. 4.2). Larger animals had chewed off and ingested bigger pieces (250µm-1mm) (Fig. 4.2b, Table 4.2), but there were no variations with biotope or season (Tables 4.3 and 4.4). Shredding by Lepidostomatidae is well documented (Anderson and Grafius, 1975; Anderson et al., 1979; Grafius and Anderson, 1979; 1980), and this study



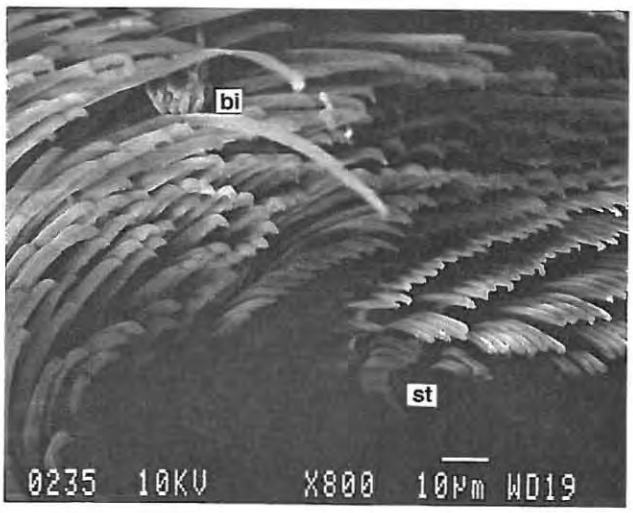
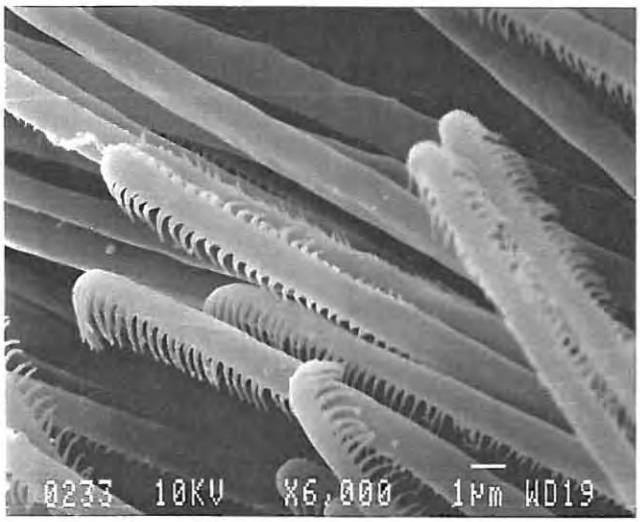


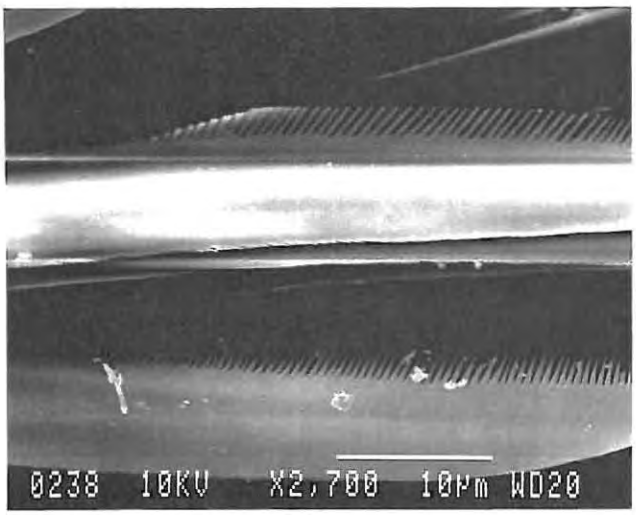
Fig. 4.3 Ultrastructure of the mouthparts of A. auriculata: a. maxillary brush (mxb) and scraping setae (scr), (la = labrum, mxp = maxillary palp)

b. maxillary brush (st = stout curved setae, bi = fine bipectinate setae)

c. scraping setae from a maxilla



d. fine, curved, bipectinate setae with microtrichia, from the top of a maxillary brush



e. fine combs on setae from the labial palps.

confirmed that G. caffrariae was a shredder.

4.3.3. 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 18mg animal^{-1} week^{-1} (Fig. 4.4a). Frass and faecal fragments produced were in the 50-250um size range, a size reduction of two orders of magnitude. D. ensifer tended to wear away the surface of leaf discs evenly (Figs. 4.4b and c).

Food choice: D. ensifer larvae showed a significant preference for chambers containing leaves (Table 4.5). 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. 4.2b).

Large larvae had chewed off and ingested proportionally more of the larger leaf fragments (Fig. 4.2b), which contributed to the detection of differences in the gut contents of large and small larvae (Table 4.2). Seasonal and biotope differences could be ascribed to differing proportions of filamentous algae in the gut (Fig. 4.2b and Tables 4.3 and 4.4).

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

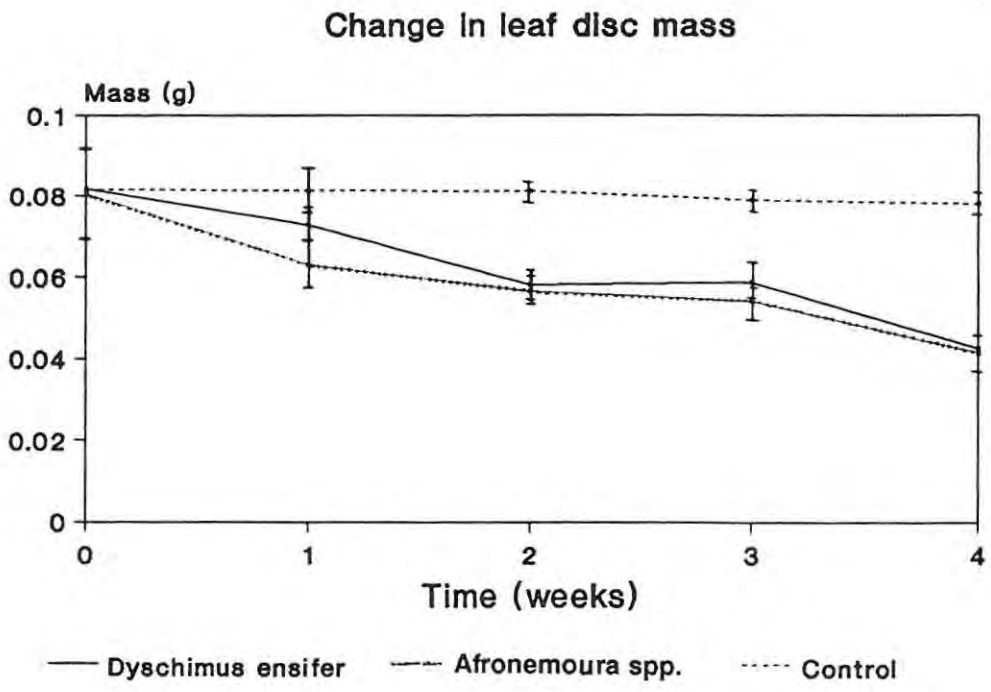
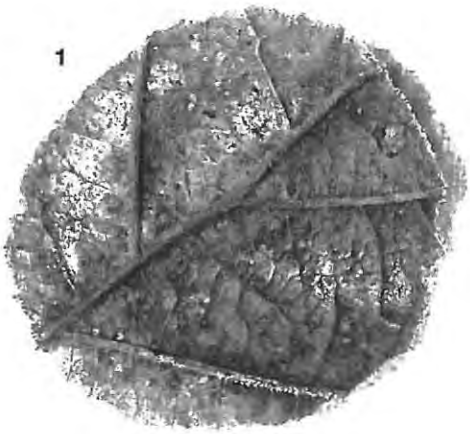
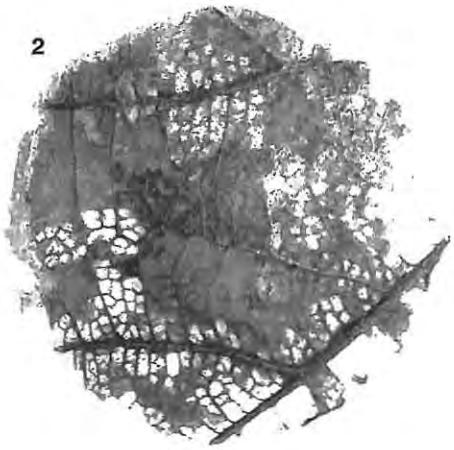


Fig. 4.4a. Shredding activity: change in mean leaf disc mass over time. The mass of pre-weighed oak leaf discs was steadily reduced by the feeding activities of D. ensifer and Afronemoura spp. larvae, over a period of four weeks. The mass of control leaf discs remained unchanged. (vertical bars - 95% confidence limits)

Fig. 4.4b. An oak leaf disc (20mm diameter) before shredding.





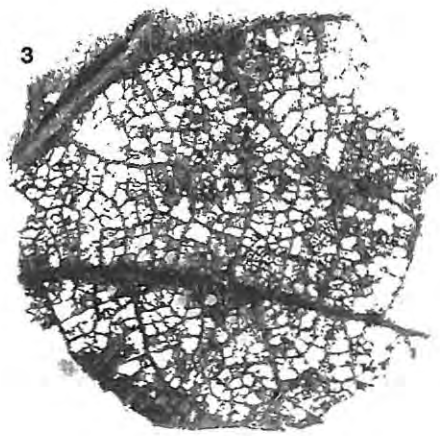
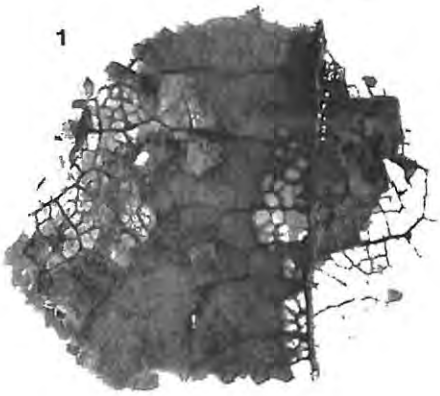
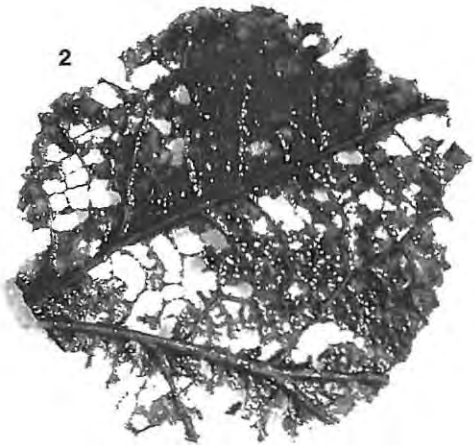


Fig. 4.4c. Three 20mm oak leaf discs (1,2,3) shredded to varying degrees by D. ensifer larvae. These larvae skeletonise leaves by rasping the entire leaf surface evenly.





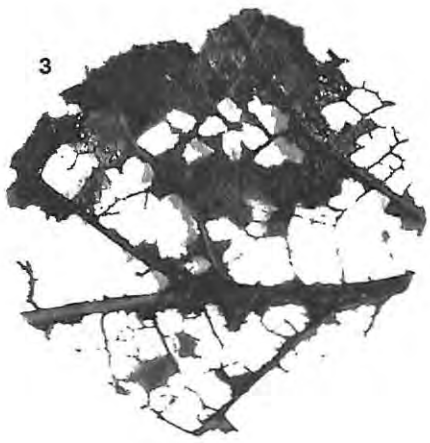


Fig. 4.4d. Three 20mm oak leaf discs (1,2,3) shredded to varying degrees by Afronemoura spp. larvae. These larvae skeletonise one section of the leaf at a time.

4.3.4 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 (Fig. 4.4b and d) 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. 4.4a). The mean rate of consumption was 8 mg animal^{-1} week^{-1}.

Gut analysis: The stoneflies, Afronemoura spp. (64 dissected) were also shredders, differing from the caddisflies in that their gut contents contained a wider variety of material (Fig. 4.2a), 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 4.2) 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 leaf fragments in the gut (Fig. 4.2a), and feeding behaviour in the laboratory (Fig 4.4a and d), indicated that the Afronemoura spp. were members of the shredder guild.

4.4 Discussion

4.4.1 Dietary composition and variability

The questions posed in the introduction concerning the feeding of four macroinvertebrates from the headwaters of the Buffalo River were answered.

a) Type of food ingested: A. auriculata ingested mainly fine detritus, and G. caffrariae, D. ensifer and the Afronemoura spp. shredded leaves and ingested leaf fragments.

b) Dietary variability: In all four taxa diet varied with size, though most of this variation was simply in

the amount of material in the foregut. Some small stoneflies differed from large ones in the predominance of fine detritus, and an 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.

c) 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.

d) Functional Feeding Groups: One of the major concerns about the applicability of the FFG concept identified by King et al. (1988) was that spatial, developmental and temporal dietary variability would preclude the realistic assigning of macroinvertebrate taxa to FFGs. 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 confirmed Hawkins' (1985) findings that although size does influence diet, it does so in a specific way, with larger organisms ingesting larger particles, and a usually a wider range of food. The variation associated with different seasons and biotopes reflected the degree of opportunism within each taxon, as found by Irons (1988) in a group of Arctic caddisflies.

Gut analysis has also been criticised as being unsuitable as a single method on which to base feeding studies (see King et al. 1988). In this study it proved to be a useful tool in assigning taxa to FFGs. Foregut contents reflect the material an organism has ingested though not necessarily that which is assimilated. On the basis that feeding behaviour contributes to the fitness of an organism (Calow 1977, Cummins and Klug 1979), Hawkins (1985) made the reasonable assumption that gut contents do reflect ingestion of assimilable food items. In this study attention was given to the type of material ingested, and the manner of ingestion, in an effort to understand processes in the stream. Together with behavioural and morphological data, gut content analysis can contribute to an understanding of invertebrate feeding (McShaffrey and McCafferty 1988), and ecology (Chessman 1986).

4.4.2 Definition of the term brusher

The FFG designation brusher was first suggested by McShaffrey and McCafferty (1986). Their behavioural description of the brushing activities of Stenacron interpunctatum (Heptageniidae) larvae corresponded to the observed behaviour of A. auriculata larvae, which were found to have maxillary brushes, and were observed brushing surfaces more often than any other feeding behaviour. Chessman (1986) drew attention to the radiation of the leptophlebiids in Australia and New Zealand to occupy niches commonly held by the heptageniids in North America, and leptophlebiids from New Zealand have been described as feeding on loose detritus and organic layers by brushing (Rounick and Winterbourn 1983, Winterbourn et al. 1984) with the latter authors mentioning maxillary brushes, but not describing them. Drawings of a range of other South African leptophlebiids (Barnard 1932, Crass 1947) show maxillary brushes that would probably have the same ultrastructure as three described in this study (two

others in Chapter 5). A. auriculata larvae ingested a wide range of foods, including diatoms. The larvae have a set of scraping setae on the inside face of the maxilla, similar to those found on the ventral surface of the maxillary palps of the North American scraper Rithrogena pellucida (McShaffrey and McCafferty 1988). These might enable A. auriculata larvae to add diatoms and other more tightly accreted material to its diet, but their function is deduced, and was not observed. A. auriculata was assigned to the brusher FFG.

It is suggested that the basis for assigning organisms to the brusher FFG should be both behavioural: the observation of brushing feeding cycles, and structural: the possession of brushes.

4.4.3 Definitions of function

The original FFG concept was envisioned as contributing to an understanding of stream processes (Cummins 1973, 1974, Vannote et al., 1980). 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 and McCafferty (1986, 1988) had a mechanistic view of function. They used morphology and behavioural studies to elucidate how animals fed, and together with gut analysis, to indicate the functional role of the species. They discussed their work in the context of the distribution of stream macroinvertebrates, on the basis that food is distributed in streams in response to flow characteristics (food is either suspended, loosely deposited, or tightly accreted), and animals are found where they feed.

The term function can be approached 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 sizes; retention or mobilisation of organic matter; mineralisation of organic matter; and enhancement of substrata for microbial colonisation. Filterers convert UFPOM and FPOM to animal biomass and faeces, consequently increasing organic particle size, retaining organic matter, and providing substrata for microbial colonisation. Collectors, both feeding on and excreting fine particles probably contribute mainly to retention and the enhancement of substrata 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. The mention of the size of faecal particles is speculative. Such faeces as were collected from Buffalo River mayfly larvae were indistiguishable from amorphous fine detritus, but this aspect was not investigated in any detail, and may be a fruitful avenue to pursue. If two organisms produced similar faeces which became part of the loosely deposited fine detrital pool, but one was a filterer and the other a gatherer they would be involved in different river processes. The filterer would facilitate organic particle retention, converting seston to deposited material, whereas the gather would be recycling loosely deposited material.

One of the FFG debates which is clarified by this approach concerns the definition of the term shredder. King et al. (1988) elaborated 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 functionally 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 were 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, together with the observation of shredding behaviour, the confusion in the literature surrounding the "shredder" definition on the basis of particle size could be avoided.

In the Buffalo River, the shredders G. caffrariae, D. ensifer and the Afronemoura spp. primarily performed 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 and Holland (1989) showed that hydropsychid caddis larvae increased the retention of leaves in a 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 and 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 performed the function of retaining fine particles. This process was aided by the physical retention of fine particles in leaf packs and backwaters.

CHAPTER 5

MACROINVERTEBRATE FUNCTIONAL FEEDING GROUPS IN THE MIDDLE AND LOWER REACHES OF THE BUFFALO RIVER.

5.1 Introduction

In the previous chapter results were described which showed that dietary variability in early and late instar larvae collected seasonally from different biotopes, did not preclude four taxa from the upper reaches of the Buffalo River being assigned to FFGs. The FFG term shredder was clarified and a structural basis for the term brusher was described. The link between FFGs and river function was emphasised. The structure of this chapter is similar. Gut content analysis is again used as an index to compare diet. Twelve numerically abundant macroinvertebrate species from the middle and lower reaches (Sites 1-13, Fig. 2.1) 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 reticulatus Barnard; two caenid mayflies, Caenidae sp. A, and sp. B; and two hydropsychid caddisflies Cheumatopsyche afra (Mosely) and Macrostemum capense (Walker). The foregut contents of large and small larvae of these 12 species, collected seasonally from 15 sites down the river, and in three biotopes at three of the sites, are compared to assess dietary variability. The term scraper is clarified, and the link between FFGs and an understanding of river processes is discussed.

The Buffalo River is a turbid river in its middle and lower reaches, with 95% of the transported particulate material falling in the ultrafine (<80 um) size range (Palmer and O'Keeffe 1990b). The proportion of transported

fine material (<250 µm) that is organic is variable, but it is a potential food resource and is probably deposited in areas of low water velocity. This assumption is uncertain since no data concerning the distribution of deposited benthic organic matter (BOM) have been collected in the Buffalo River (Palmer and O'Keeffe 1990b). If, as suggested by Barmuta and Lake (1982), the functional classification of stream macroinvertebrates facilitates the understanding of processes in streams, it would be expected that the feeding patterns of benthic microvores in the Buffalo River would reflect the river's preponderance of fine material. Suspended FPOM would be available to filter feeders directly and would be available to collectors after deposition.

5.2 Methods

5.2.1 Field sampling and gut analysis

The benthic macroinvertebrate fauna was sampled from Sites 1 to 13 (Fig. 2.1), seasonally in 1987: summer (February), autumn (May), winter (August) and spring (November). At each site, three replicate box samples (0.09m^2, net mesh 80µm) 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 in previous chapters.

In order to assess spatial, temporal and developmental dietary variability, large (late instar) and small (early instar) larvae from all 12 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 which could be identified positively. As with the headwaters taxa, both head capsule width and body length were measured, and there was no overlap in size between larvae termed 'small' and those termed 'large'. One large and one small

individual were dissected for each slide and slides of the gut contents of 3 large and 3 small larvae were prepared. 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 recognised: amorphous detritus in the size ranges 1) 0.5-50 µm (UFPOM); 2) 50-250 µm (FPOM a); 3) 250µm-1mm (FPOM b) 4) fungi; 5) unicellular algae; 6) diatoms; 7) filamentous algae; 8) leaf fragments; 9) pollen; 10) invertebrate remains and 11) inorganic silt. The method of gut analysis first described by Coffman et al (1971), was used in the manner described in Chapter 4. In all instances the term "diet" has been used synonymously with gut contents. Food items from the foregut which were counted may not constitute the entire diet, but they have been used in this study as an index of dietary content.

5.2.2 Data analysis

Dietary composition of large and small larvae from the different sites, biotopes and seasons, was compared using analysis of variance (ANOVA). 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 11 sets in which there was a difference were one set each from 11 different species. Each set of replicates was therefore assumed to represent the range of food items consumed by the 12 species under the conditions prevailing at the time of sample collection. Subsequently, sets of replicates were compared for differences in the diet. Comparisons were made between large and small larvae, and between those collected from

various sites, seasons and biotopes (three-way ANOVA with interaction, of food, the replicates, and size or site or 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 both at Rhodes University and the University of Cape Town were unable to tolerate the extent to which the data were unbalanced. After many manipulations, and the advice and assistance of statisticians (Mrs. S. Radloff and Dr. T. Dunne) a stratified ANOVA procedure was followed. Analysis of the data using multivariate ANOVA may be possible, and is currently being researched by Dr. T. Dunne, but the results were not available. Separate 3-way ANOVAS were calculated to compare gut content composition. Firstly, 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.

The information that was lost by not performing a 4- or 5- way ANOVA, is the degree to which there were composite interactions. In each of the individual ANOVA's there is information as to how the 3 factors under consideration interact. The interaction term gives specific information. The ANOVA result may show a significant difference in diet ($p<0.01$), or not. If there is a significant difference, it may follow one of two patterns. If there is no significant interaction (interaction term $p>0,05$) then although there were different amounts of each food type, they were consumed in the same proportions. If there was significant

interaction (interaction term $p<0.05$) then the food types were ingested in differing proportions. By stratifying the ANOVA procedure it is possible to detect patterns of difference and interaction. In ANOVA, where significant interaction is indicated, general comparisons within a single factor (eg. site alone) are inappropriate, because differences in dietary composition between sites will not be regular across the various biotopes, seasons and sites. Therefore, if sites are to be compared it is appropriate that comparisons be made within a specified biotope or season or size combination. Similarly for each of the other three factors, comparisons were restricted to those arising from the specified three-factor combinations.

In all these comparisons, the 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 sub-optimal 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 the dietary composition, and variability in the data. (The reason for the arcsin transformation is given in Chapter 4.)

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).

5.2.3 Observations

The feeding activities of all species except the baetid mayflies were observed, using a dissecting microscope adapted so as to have its objective lens at right angles to the side of a holding aquarium. The baetids were too small, fast, and difficult to identify when alive and

moving, to observe in sufficient detail to describe their feeding accurately.

5.2.4 Morphology

The ultrastructural morphology of the mouthparts of all the mayfly larvae was investigated using scanning electron microscopy. The morphology of the baetids was of particular interest, as their feeding behaviour was not observed. Morphological studies were initiated when it became clear that the gut contents of several of the mayflies, with observably different feeding mechanisms, were indistinguishable. The gut contents of the hydropsychid caddisfly larvae were distinctive and in this study the ultrastructure of their mouthparts was not investigated. Specimens were dehydrated in 100% alcohol, subjected to critical point drying, and sputter coated with a thin film of gold before viewing and being photographed (Cross 1987).

5.3 Results

5.3.1 Dietary variability: comparison of foregut analyses

Gut analysis revealed that fine, amorphous detritus (UFPOM 0.5-50μm and FPOM 50-250 μm) was the most abundant material in the foregut of all mayfly and small caddisfly larvae (Fig. 5.1). Large caddisfly larvae had also ingested UFPOM and FPOM as major dietary items, but were characterised by a mixed diet, including leaf fragments, diatoms and, particularly, abundant invertebrate remains (Fig. 5.1). Fine inorganic silt particles regularly constituted a small proportion of all the foregut contents. The gut contents shown in Fig. 5.1 are a typical example of the gut contents of each of the species, the complete range of gut contents results can be found in Appendix 3.

For all species, significant differences in the gut

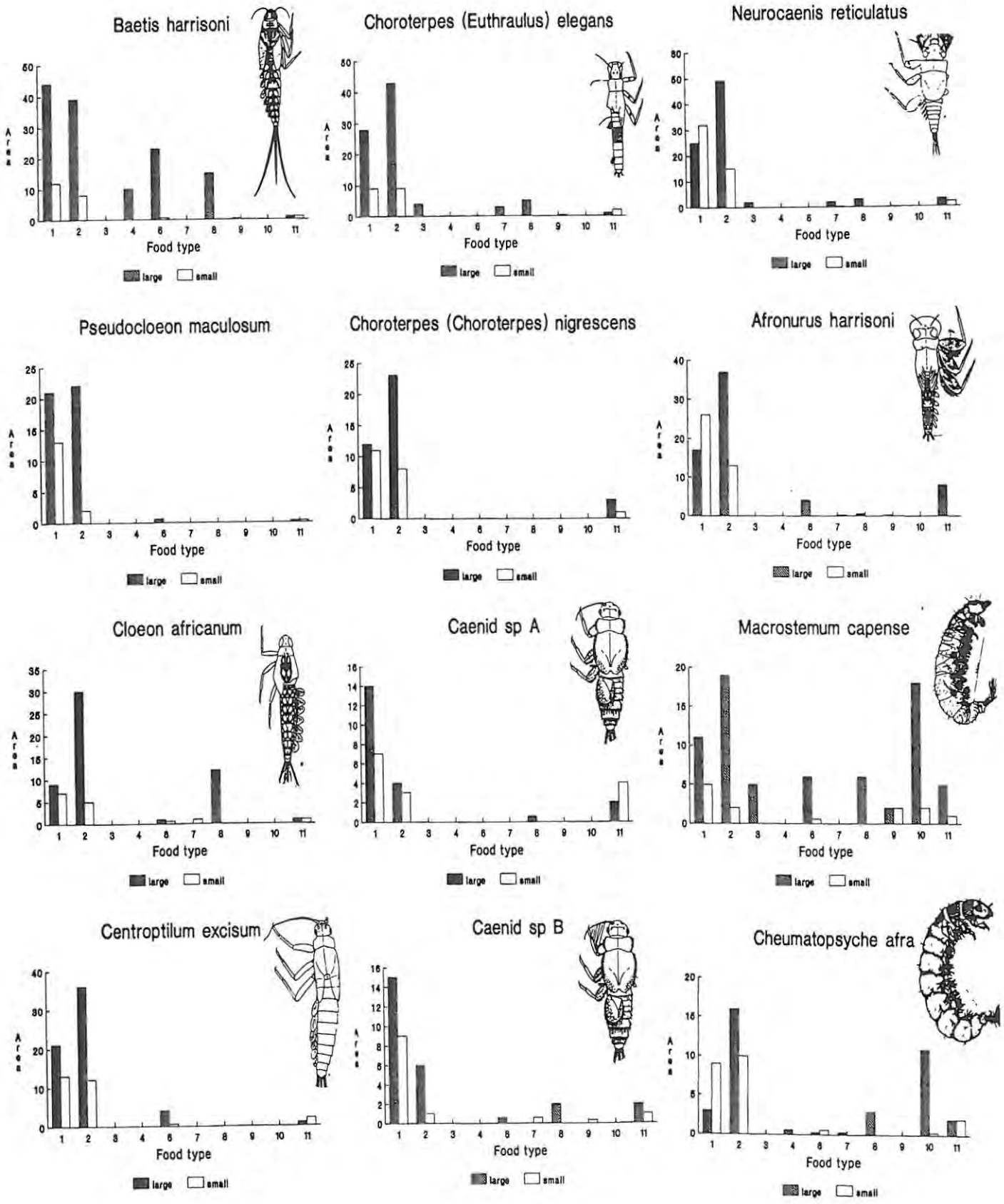


Fig. 5.1 Typical examples of the gut contents of large (shaded) and small (unshaded) larvae of the 12 selected species from the middle/lower reaches of the Buffalo River. The complete set of gut content data is givenin Appendix 5.1. The area value given (mm2) is the mean area covered in 10 microscope fields (400x) by each food type for 3 replicate gut contents slides. 1 = detritus (0.5-50μm), 2 = detritus (50-250 μm), 3 = detritus (250μm-1mm), 4 = fungi, 5 = planktonic algae, 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 (1985).)

contents were most frequent between large and small larvae (Table 5.1). 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 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 (Appendix 3). Only 5 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 (Table 5.4). Tables 5.1-5.4 are summary tables, details of the ANOVA results are presented in Appendix 2 (2.4-2.7).

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 the small animals. Variation in the consumption of these 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. Therefore, dietary variability did not prevent species from being assigned to FFGs, but gut analysis results alone did not enable species to be assigned to FFGs.

5.3.2 Species specific gut contents, feeding behaviour, mouthpart ultrastructure and FFG designations:

Species were assigned to the FFG categories suggested by McShaffrey and McCafferty (1988):

Table 5.1. Size comparisons: The gut contents of large larvae are compared with those of small larvae. Separate large versus 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 3-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, MV - marginal vegetation (out of current)

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

Table 5.2 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 3-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 reticulatus				
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

Table 5.3. Seasonal comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one season were compared with those of larvae collected from one or more different seasons (given in brackets). In each 3-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 6 (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 reticulatus		
RIF	L Site 6 (A, W, Sp)	:
	12 (A, W, Sp)	:
RIF	S Site 6 (A, W, Sp)	:
	12 (A, W, Sp)	:
Hydropsychidae		
Macrostemum 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)	:

Table 5.4 Biotope comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one biotope were compared with those of larvae collected from one or more different biotopes (given in brachets). In each 3-way ANOVA with interaction, the gut contents of one species, of one size, collected in one season, but from two or more biotopes 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, MV-marginal vegetation (out of current).
Sizes: L - large, S - small.

Baetidae				
Cloeon africanum				
Su	Site 6	L	(BW, MV) :	
		S	(BW, MV) :	
Su	Site 12	L	(BW, MV) :	
		S	(BW, MV) :	
Centroptilum excisum				
Sp	Site 12	L	(BW, RIF):	
W	Site 12	L	(BW, RIF):	
Heptageniidae				
Afronurus harrisoni				
A	Site 12	L	(BW, RIF):	x
		S	(BW, RIF):	
W	Site 12	L	(BW, RIF):	
Leptophlebiidae				
Choroterpes elegans				
A	Site 6	L	(BW, RFI):	
		S	(BW, RFI):	
Caenidae				
Caenidae sp. A				
Su	Site 12	L	(BW, RIF):	

a) Filterers

i) passive - feed on seston which is moved by a current, using silk nets or body parts,

ii) active - resuspend deposits which are filtered using silk nets or body parts,

b) Collectors

i) gatherers - use structures other than setae to remove lightly attached, or loosely deposited organic material,

ii) brushers - use setae to remove lightly attached, or loosely deposited organic material,

iii) scrapers - have structural adaptations which allow them to feed on tightly accreted material.

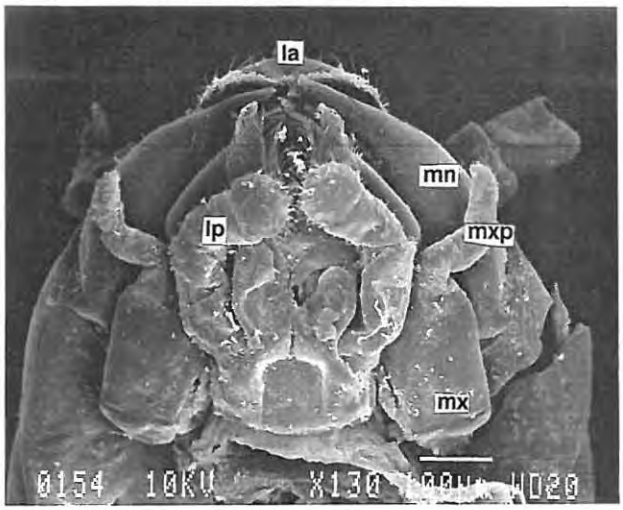
Baetis harrisoni was the most abundant and widely distributed mayfly in the Buffalo River. Larvae were collected from riffles where they were always observed on the surfaces of rocks and stones. In the summer of 1987, large and small individuals were collected from Sites 1, 2c, 3, 6, 7, 8, 10a, 11, 12 and 13, and in autumn and spring from Sites 6 and 12. Larvae were absent in winter. A total of 84 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. 5.1). 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 5.1, which shows a significant difference between large and small individuals in more than half of the comparisons made.

There is an interaction between food and size (Table 5.1), which means that not only is there a difference in the area covered by each of the food types, but there is also a difference in the relative proportions of the different foods.

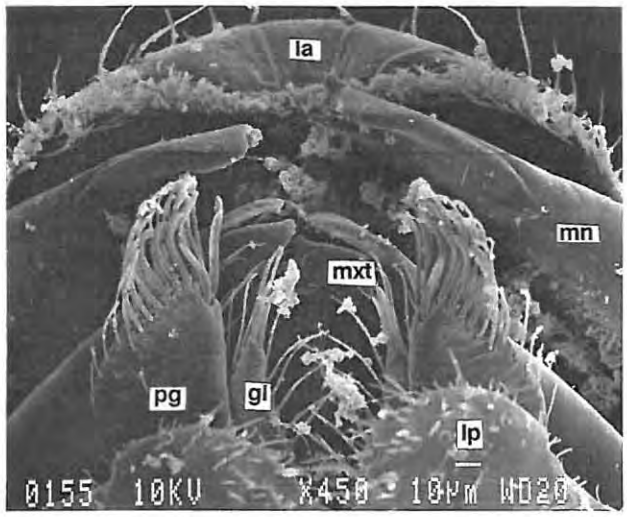
The diets of large and small B. harrisoni collected from different sites were compared (Table 5.2), and they were significantly different. Inspection of gut contents data (Appendix 3) showed that B. harrisoni larvae ingested a much wider range of food types at Site 1 than at any of the other sites. The only seasonal differences in gut contents (Table 5.3), 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.

On the basis of gut contents dietary variability was not sufficient reason not to assign B. harrisoni to a FFG. However, gut content analysis provided insufficient information to assign B. harrisoni larvae to a FFG positively. Ultrastructure of the labium and maxillae provided additional evidence of the way in which the larvae feed (Fig. 5.2 a-e). Morphologically, the labium and maxillae of B. harrisoni larvae were characterised by a relative paucity of bipectinate filtering setae. There were blunt, scoop-like setae at the apices of the labial paraglossae (Fig. 5.2 b, e). The maxillae ended in four blunt teeth (Fig. 5.2 d), and there was a small group of bipectinate, filtering setae laterally on the maxillae (Fig 5.2 d). It seemed likely that the larvae were collector-gatherers, using the paraglossae to remove loose detrital fragments from stone surfaces, and the maxillae to manipulate the mass of fine detritus into the alimentary tract (Fig. 5.2 c). The presence of diatoms in the foregut of large larvae in spring, suggested that

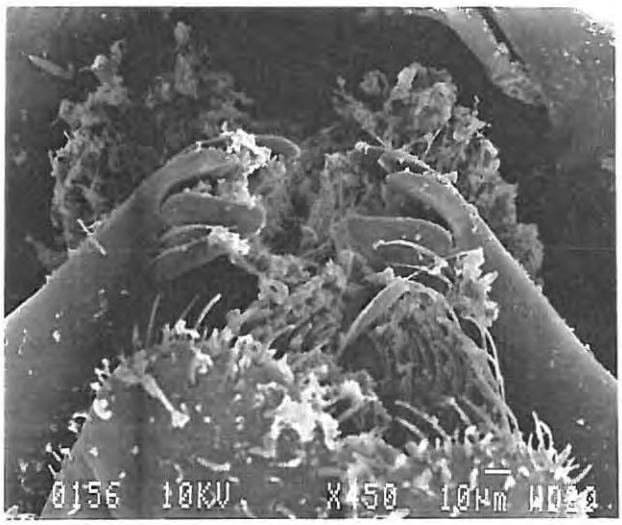
Fig. 5.2 Mouthparts of B. harrisoni:



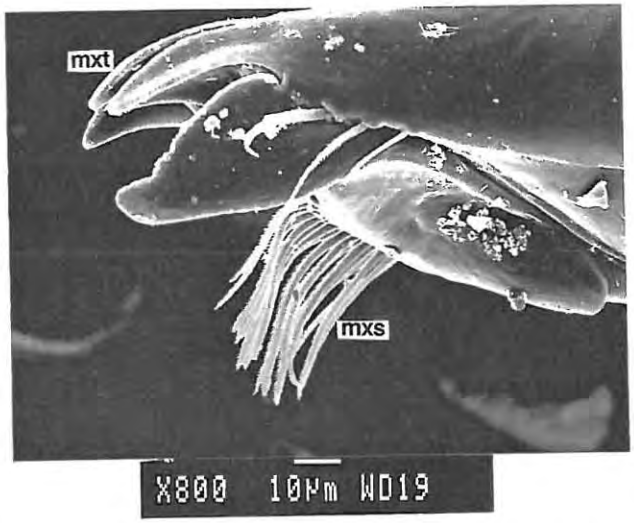
a. Ventral view of the mouthparts. (la = labrum lp = labial palp, mn = mandible, mx = maxilla, mxp = maxillary palp)



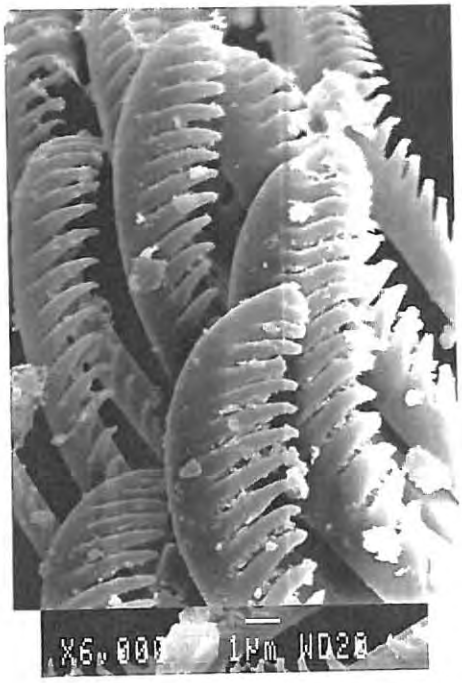
b. Closer ventral view. (mxt = maxillary teeth, gl = glossa, pg = paraglossa)



c. Detritus gathered into oral cavity by maxillary teeth. The paraglossal setae are obscured by the labial palps.



d. Apical maxillary teeth and bipectinate setae (mxs).



e. Apical scoop-like paraglossal setae .

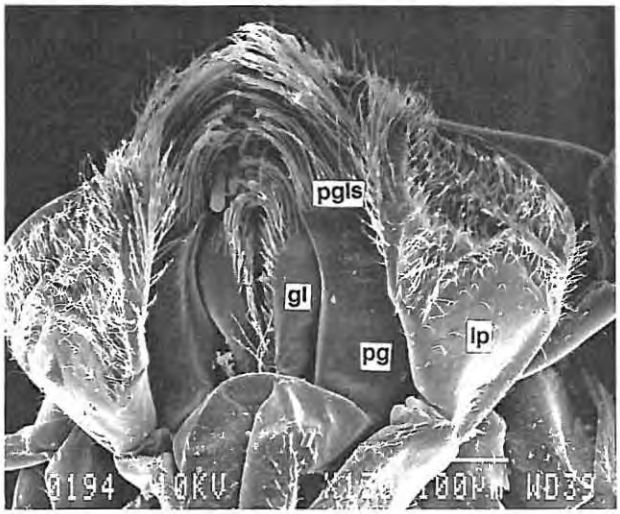
they may remove more tightly accreted material, and that possibly they make use of stone surface organic layers. (However, the diatoms were not positively identified as benthic species.)

Pseudocloeon maculosum was the next most common baetid. Also riffle dwellers, P. maculosum larvae 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 seasons. A total of 30 individuals were dissected, and the gut contents comprised predominantly UFPOM, FPOMa and silt (Fig 5.1). 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.

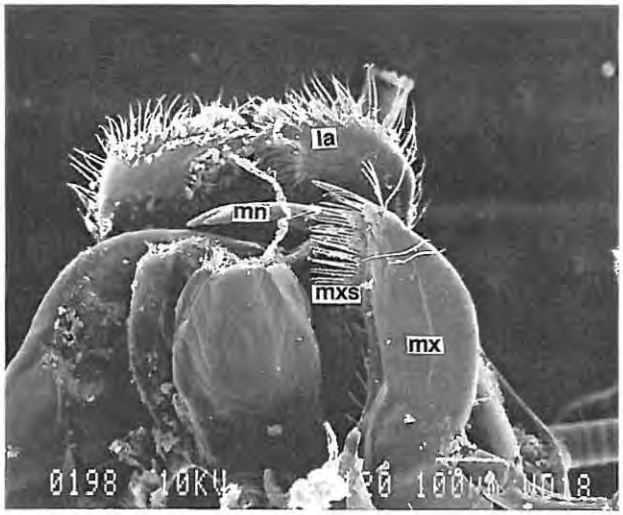
There was no clear pattern of spatial or temporal differences in the proportions and amounts of ingested food, though there was evidence of size related differences (Table 5.1), with smaller animals having less food in the foregut and proportionally less of the larger detrital fragments than large nymphs (Fig. 5.1). There was no difference in the dietary composition of either large or small larvae at Site 12 as compared with Site 13 (Table 5.2), but seasonally, gut content composition was significantly different ($p<0.05$, Table 5.3).

Morphology of the mouthparts of P. maculosum indicated that it may have acquired fine detritus in a different way from B. harrisoni. The larvae had large paddle shaped labial palps, the significance of which was unknown. The labium and maxillae were liberally fringed with bipectinate, filtering, setae (Fig. 5.3 a-e). This suggested the larvae were probably filterers, possibly active filterers, stirring up fine loose fragments on stone surfaces, then collecting them with fine filtering setae.

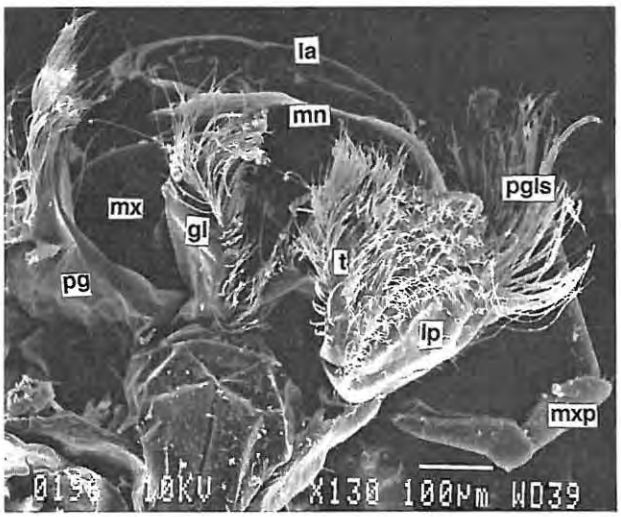
Fig. 5.3 Mouthparts of Pseudocloen maculosum:



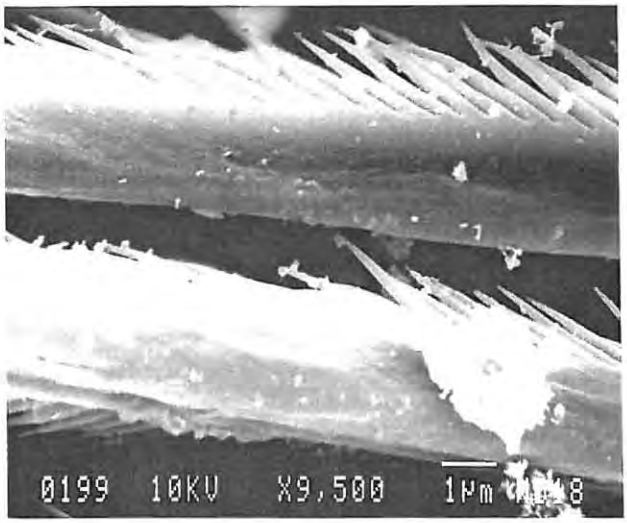
a) Ventral view of the mouthparts. (gl = glossa lp = labial palp, pg = paraglossa, pgls = paraglossal setae)



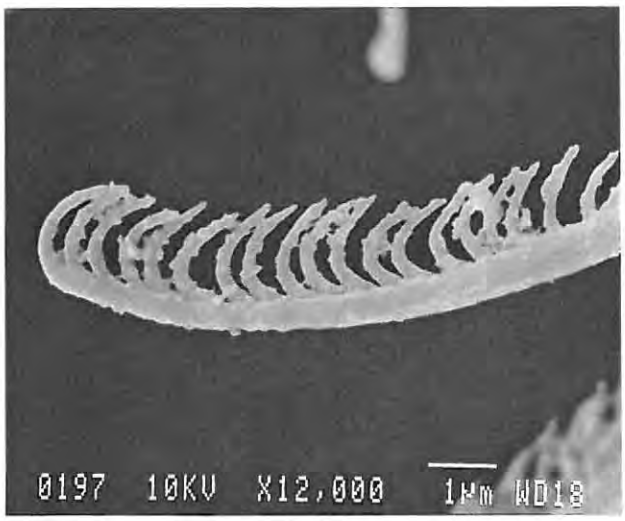
b. Ventral view with labium removed. (la = labrum, mn = mandible, mx = maxilla, mxs = maxillary setae)



c. Labium displaced to show mandible and maxillary palp (mxp). (t = labial palp thumb)



d. Horizontal bristle-like maxillary setae.



e. Bipectinate seta with curved microtrichia, typical of setae found fringing the glossae and paraglossae.

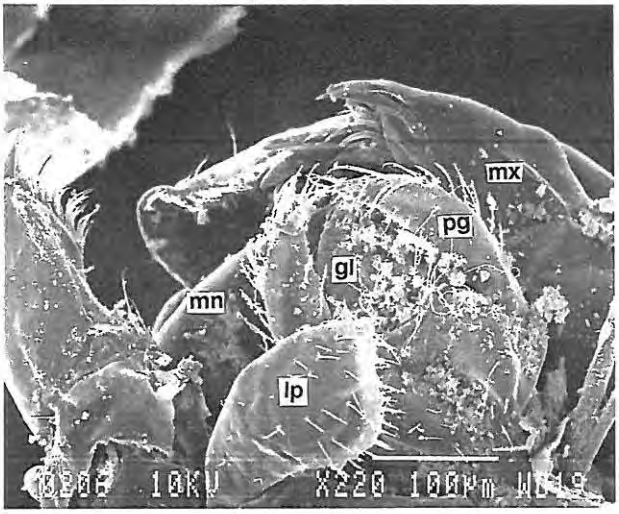
Cloeon africanum, a baetid mayfly, was found exclusively in depositional biotopes - stony backwaters and in the marginal vegetation fringing these backwaters. These biotopes were only sampled at Sites 1, 6 and 12, and C. africanum was found at both Sites 6 and 12. A total of 57 individuals were dissected 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 5.1).

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 5.1). In no case was there any significant difference in the diets of larvae from Site 6 compared with Site 12 (Table 5.2), or between those collected in different seasons (Table 5.3), or from stony backwaters compared with marginal vegetation biotopes (Table 5.4).

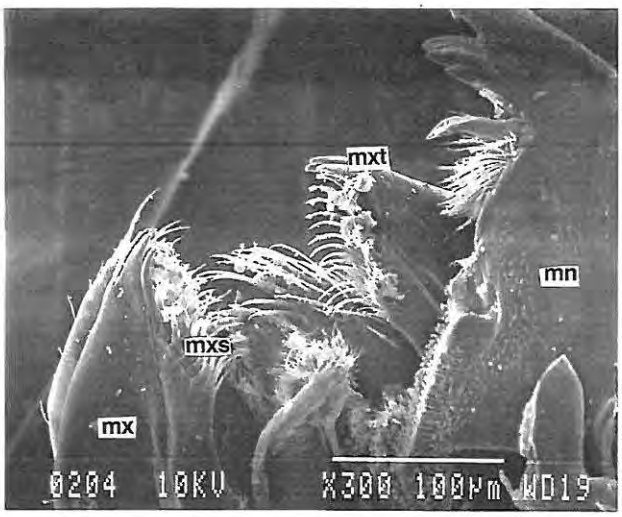
C. africanum larvae had unspecialised mouthparts, with simple bipectinate setae on the paraglossae and at the apices of the maxillae (Fig. 5.4 a-d), which suggested they were collector-gatherers.

Centroptilum excisum larvae were found in both riffle and stony backwater biotopes, at Sites 6 and 12, in all seasons. These baetid larvae had ingested mainly UFPOM and FPOMa (85% of all the food items counted), along with small amounts of silt, and occasional diatoms (Fig. 5.1). There were few dietary differences, although in one instance of size related differences (Table 5.1), 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 5.3, Appendix 3). There were no discernible dietary

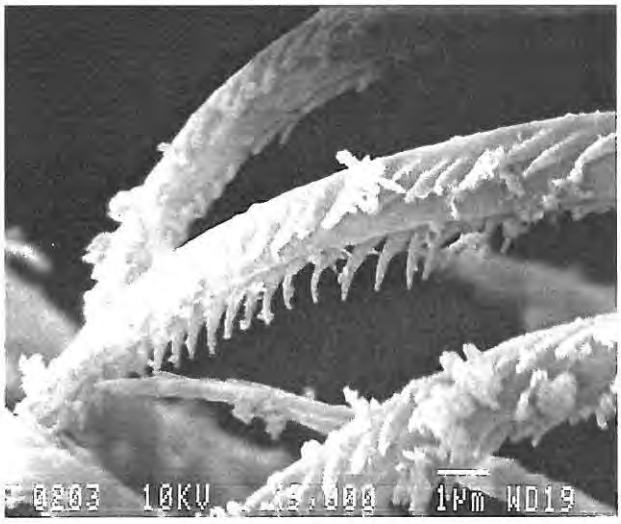
Fig. 5.4 Mouthparts of Cloeon africanum:



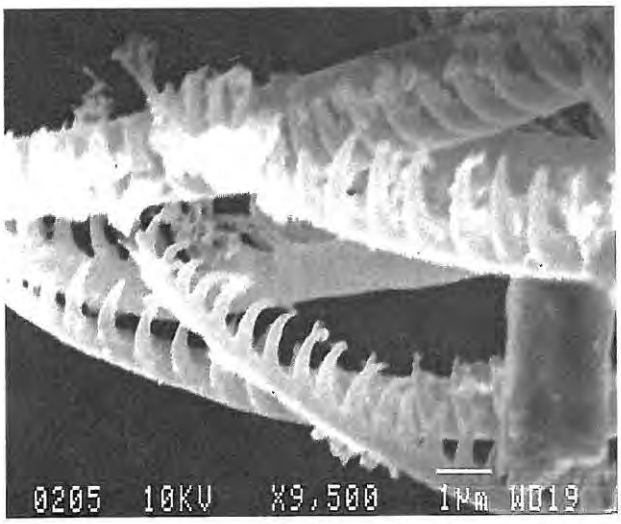
a. Ventral view of the mouth parts. (gl = glossa, lp = labial palp, mn = mandible, mx = maxilla, pg = paraglossa)



b. Dorsal view. (mxs = maxillary setae, mxt = maxillary teeth)



c. Bipectinate paraglossal setae.



d. Bipectinate maxillary setae.

differences between larvae collected from different sites and biotopes (Tables 5.2 and 5.4).

The mouthparts of C. excisum larvae (Fig. 5.5 a-c) closely resembled those of C. africanum (Fig. 5.4 a-d) in their unspecialised nature. They were sparsely setose, with bipectinate setae at the apex of the paraglosssae, and along the inside margin of the maxillae. Both C. excisum and C. africanum inhabited depositional habitats though C. excisum was also collected from riffles, and it seemed likely that C. excisum was also a collector-gatherer.

It is important to note that it was not possible to observe the feeding behaviour of any of the baetids. Without the insight provided by observation, the use of structural features, together with the gut analysis results, to assign species to FFGs, is surmise. This is the reason for simply suggesting FFGs for these species. The only other mayfly whose feeding was not observed was Caenidae sp. B.

Choroterpes elegans 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 78 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 5.1). There was consistently a significant difference in the amount and proportions of food ingested by large and small larvae (Table 5.1). 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 5.2) and seasons (Table 5.3), were also attributable to variable amounts of the rarer dietary items. There were no such differences in the gut contents of small larvae (Tables

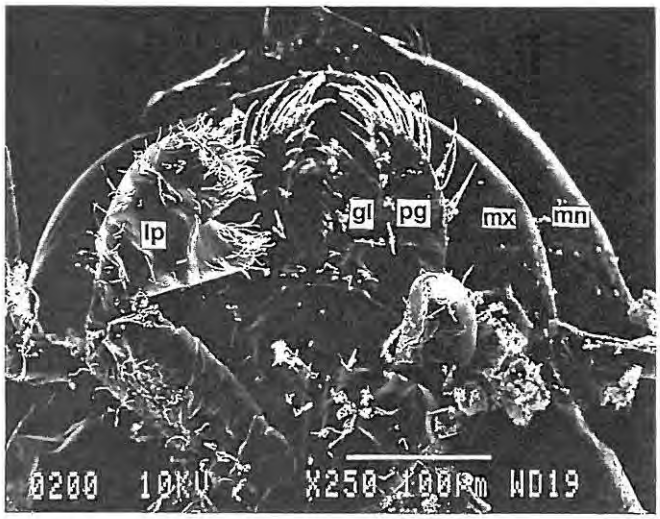
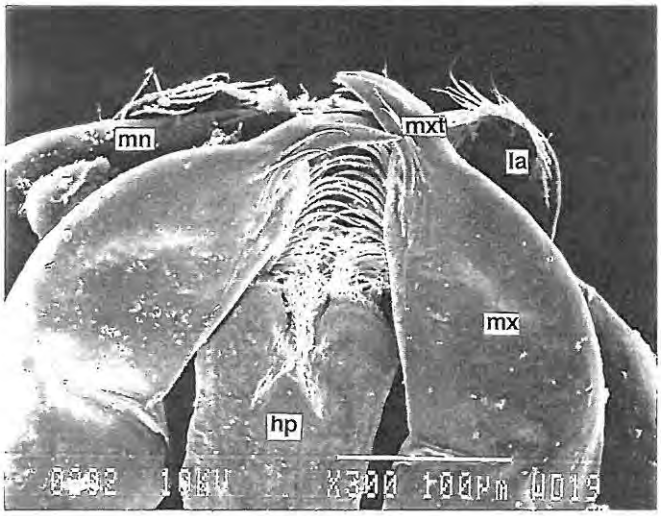
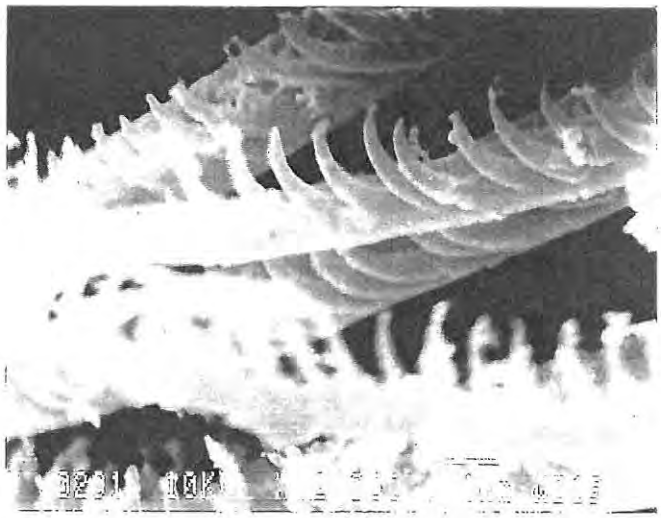


Fig. 5.5 Mouthparts of Centroptilum excisum:
a. Ventral view of the mouthparts. (gl = glossa, lp = labial palp, mn = mandible, mx = maxilla, pg = paraglossa)



b. Ventral view with labium removed. (hp = hypopharynx, la = labrum, mxs = maxillary setae, mxt = maxillary teeth)



c. Bipectinate setae typical of the apices of the paraglossae, and the inner margins of the maxillae.

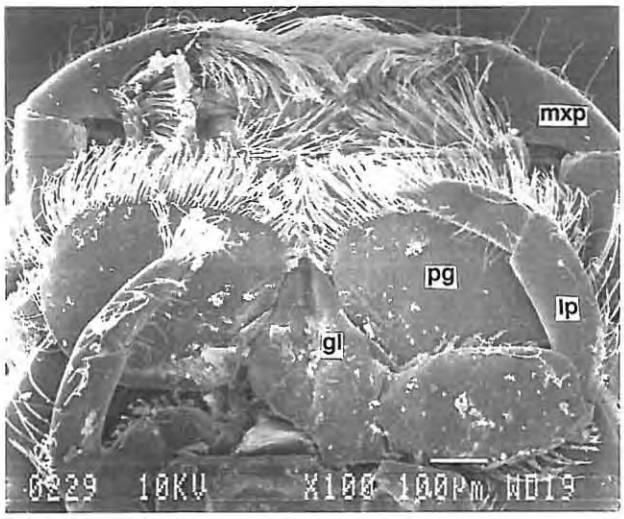
5.2 and 5.3), which contained only the three major categories of food - UFPOM, FPOMa and silt. There were no differences in the gut contents of either large or small larvae collected from different biotopes (Table 5.4).

The ultrastructural features of mouthparts of C. elegans larvae are complex (Fig. 5.6 a-e). The paraglossae, labial palps, and maxillary palps were liberally fringed with bipectinate setae (Fig. 5.6 a,b). The maxillae were equipped with the structural basis for the brusher FFG: brushes. Maxillary brushes comprised a sequence of setae ranging from stout bristles, through setae with curved tips and two rows of wide microtrichia, to bipectinate setae with fine microtrichia (Fig. 5.6 c,d,e). Larvae were observed feeding in the laboratory, and displayed typical brushing cycles (sensu McShaffrey and McCafferty 1986). Behaviour and morphology indicated that C. elegans was a collector: brusher.

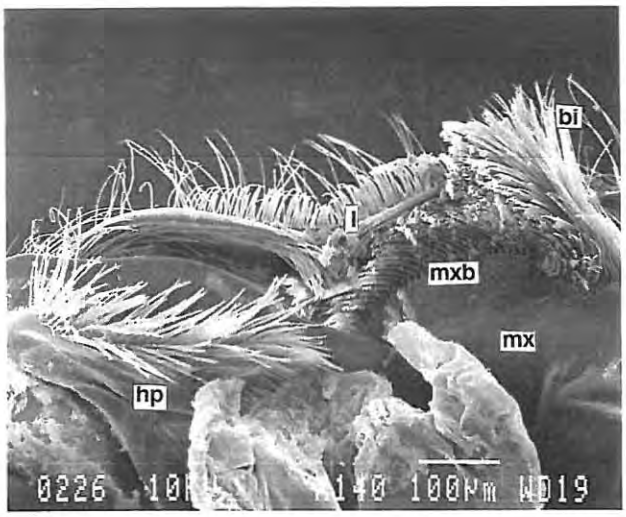
Choroterpes nigrescens was a rare member of the macroinvertebrate assemblage, and was included in this study because it was a leptophlebiid closely related to C. elegans, but found exclusively in depositional backwater biotopes. Only 15 larvae were dissected and UFPOM, FPOMa, silt and isolated diatoms were found in the gut (Fig. 5.1, Appendix 3). Differences in the foregut contents of large and small larvae (Table 5.1) could be ascribed to greater amounts of material in foreguts of larger larvae (Fig. 5.1). There were no seasonal differences in the gut contents (Tables 5.2) and larvae were absent from summer samples.

The mouthparts of these larvae (Fig. 5.7 a-c) were very similar to those of C. elegans (Fig. 5.6) larvae. Abundant setae fringed both the labium and maxillae, which were equipped with maxillary brushes (Fig. 5.7 a,b). The curved setae two thirds of the way up the brush (Fig. 5.7 c) had finer microtrichia than those in a

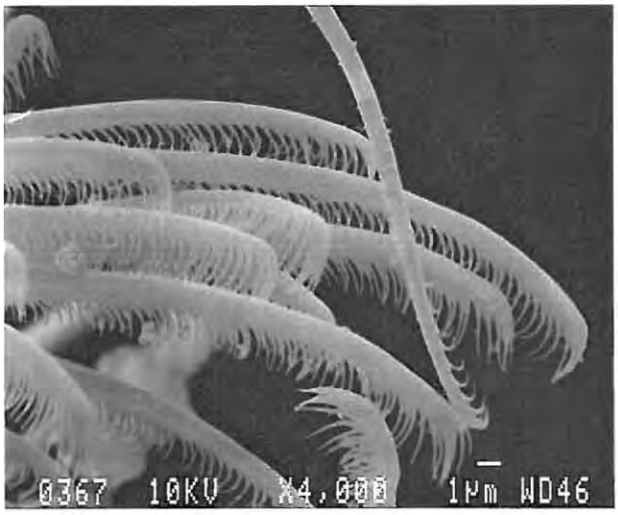
Fig. 5.6 Mouthparts of Choroterpes elegans:



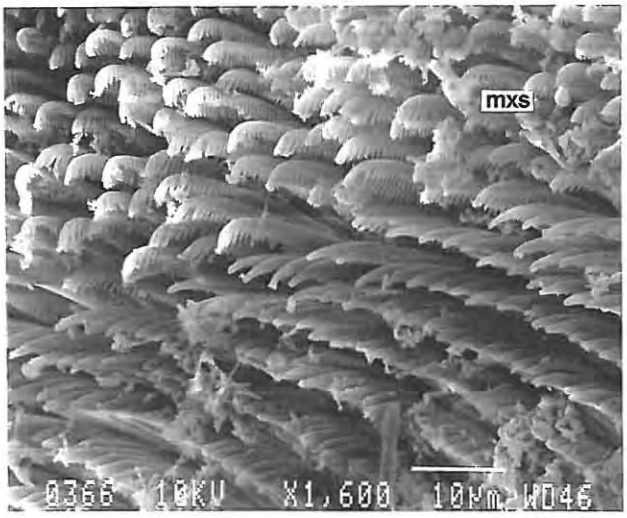
a. Ventral view of the mouthparts. (gl = glossa, lp = labial palp, mxp = maxillary palp pg=paraglossa)



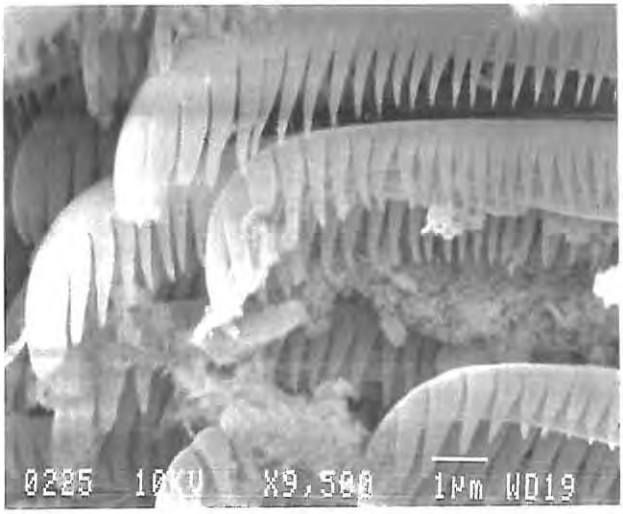
b. Ventral view with labium removed. (bi = bipectinate setae, hp = hypopharynx, l = labrum, mx = maxilla, mxb = maxillary brush)



c. Bipectinate setae from the outer margin of the maxillary brush (bi in b above).

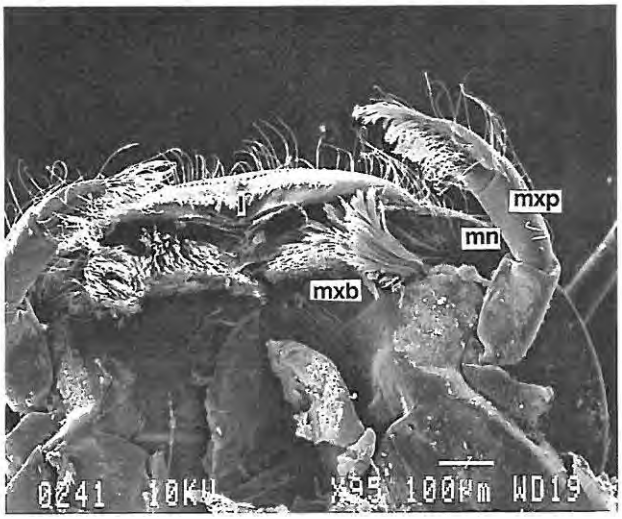


d. Maxillary brush (mxs = curved bipectinate maxillary brush setae)

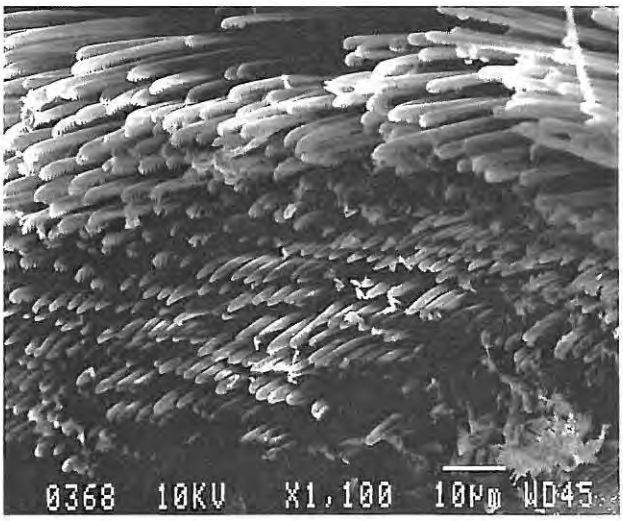


e. Maxillary brush setae (mxs in d above).

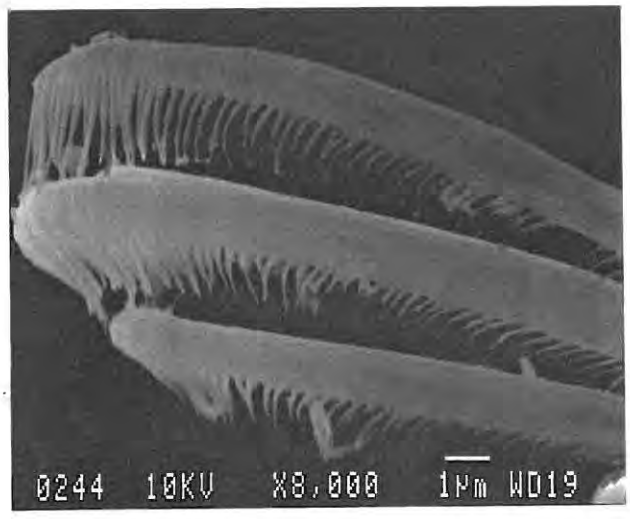
Fig. 5.7 Mouthparts of Choroterpes nigrescens:



a. Ventral view with labium removed. (l = labrum, mn = mandible, mxb = maxillary brush, mxp = maxillary palp)



b. Maxillary brush, structurally similar to those of A. auriculata and C. elegans. (Figs. 4.3b and 5.6e)



c. Maxillary brush setae somewhat finer than those of C. elegans (Fig. 5.6e).

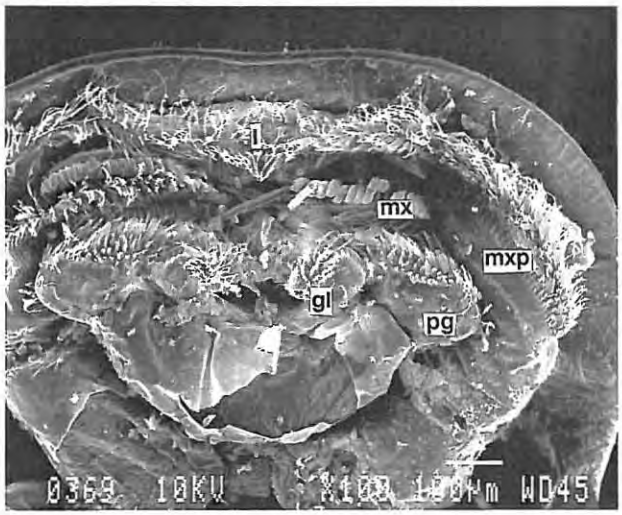
similar position in the maxillary brushes of C. elegans (Fig. 5.6 e). This may be related to the preference of C. nigrescens for depositional biotopes, where fine organic particles might be expected to form the basis of its food. The gut contents of these larvae contained UFPOM and FPOM almost exclusively. The larvae exhibited typical brushing behaviour and were assigned to the brusher FFG.

Afronurus harrisoni is a heptageniid mayfly, found between Sites 1 and 13, in both riffle and stony backwater biotopes. A total of 72 larvae were dissected, with UFPOM, FPOMa and silt comprising 84% of the food items counted (Fig. 5.1). Diatoms were the most common of the infrequent dietary items, which also included occasional fungal hyphae, leaf fragments and pollen grains (Fig. 5.1). 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 5.1). These differences followed a common trend, larger 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 5.2 and 5.3), whereas there were no such differences between small larvae. There was no significant difference in the diet of either large or small larvae collected from riffles or stony backwaters (Table 5.4).

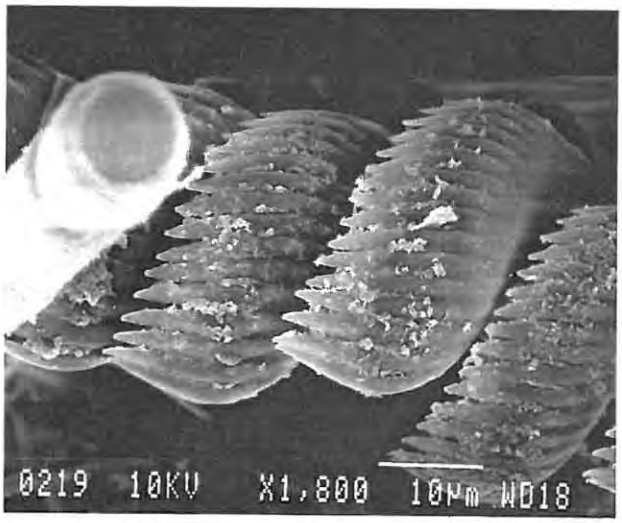
A. harrisoni larvae had complex mouthparts (Fig. 5.8 a-h). Despite the fact that diatoms were recorded in the gut contents of A. harrisoni larvae more frequently than in any of the other larvae, diatoms were still a

Fig. 5.8 Mouthparts of Afronurus harrisoni:

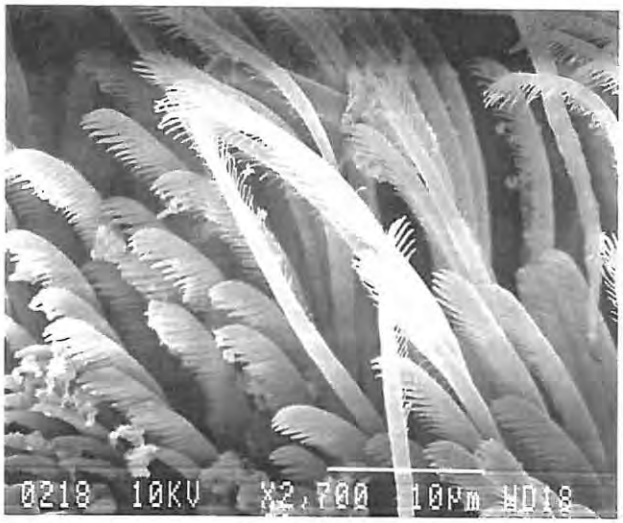


a. Ventral view of the mouthparts. (l = labrum, gl = glossa, pg = paraglossa, mx = maxilla, mxp = maxillary palp)

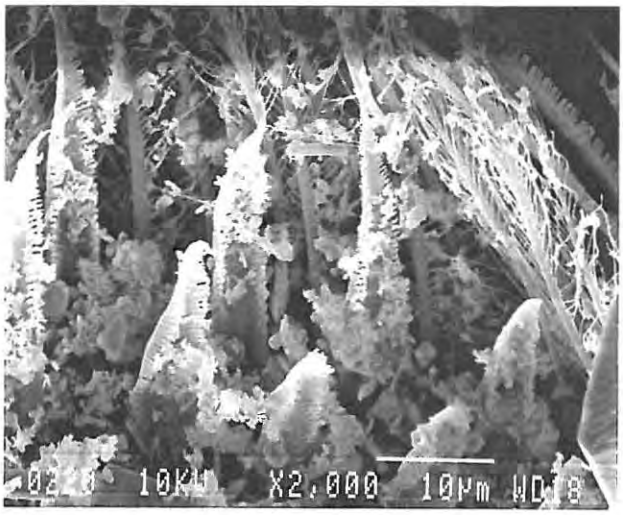
b. Maxillary palp brush, which is structurally similar to the brushes of the Leptophlebiids, with a sequence of setae from stout, curved bristle-like setae to fine, curved bipectinate setae.

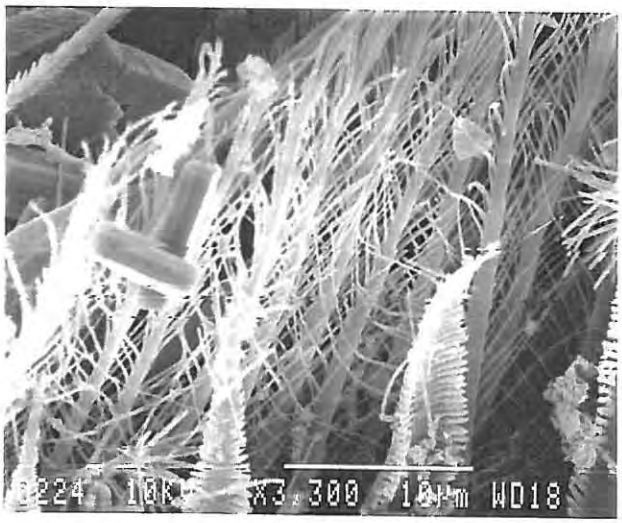


c. Chitinous scraping bars on the maxilla. Here these scraping bars have removed diatoms.



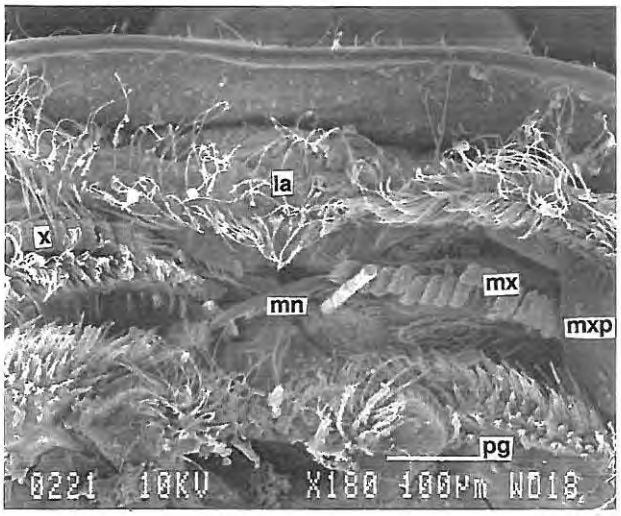
d. Fine curved setae from the top of the maxillary palp brush.



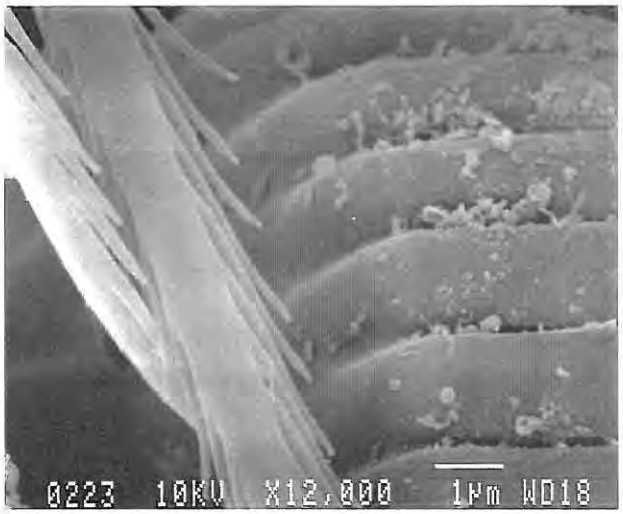


e. and f. Bipectinate setae and upright combs on paraglossa.

Fig. 5.8 Afronurus harrisoni continued:



g. Ventral view of mouthparts. (la = labrum, mn = mandible, mx = maxilla, mxp = maxillary palp, pg = paraglossa, x = area enlarged in h below)



h. Bipectinate setae from the labrum sweeping the surface of a scraping bar.

relatively infrequent dietary component. Therefore it was with some surprise that chitinous maxillary scrapers were discovered (Fig. 5.8 a,b,e,g). In addition, the apices of the maxillary palps had brushes (Fig 5.8 b,d), with setae ranging from stout to fine, which were structurally similar to the leptophlebiid maxillary brushes (Figs. 4.3b, 5.6d, 5.7b). The paraglossae had rows of upright curved combs, with stout bipectinate setae behind them (Fig. 5.8 e,f). These setae had long overlapping microtrichia. This sequence of structures looks ideally adapted for the removal of fine particles (Fig. 5.8 e,f). The long fine setae from the top of the maxillary palp brushes (Fig. 5.8 d) seemed to be able to brush the surface of the scraping teeth (Fig. 5.8g,h), and may possibly be pulled through the combs to remove attached material. A. harrisoni would be an excellent choice for videomacroscopy techniques, which would be necessary to establish the sequence of feeding events, and the function of this complex set of structures. Structurally, the larvae were equipped equally for brushing or scraping, and they probably made use of any material on rock surfaces, whether tightly accreted or loosely attached. A. harrisoni has therefore been assigned to both the brusher and scraper FFG categories.

Neurocaenis reticulatus, a tricorythid mayfly, was found in riffles between Sites 5 and 13. A total of 66 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. 5.1). There was a difference in the proportion and amounts of food ingested by large and small larvae (Table 5.1), but the gut contents of neither large nor small larvae collected from different sites or seasons differed significantly from one another (Tables 5.2 and 5.3).

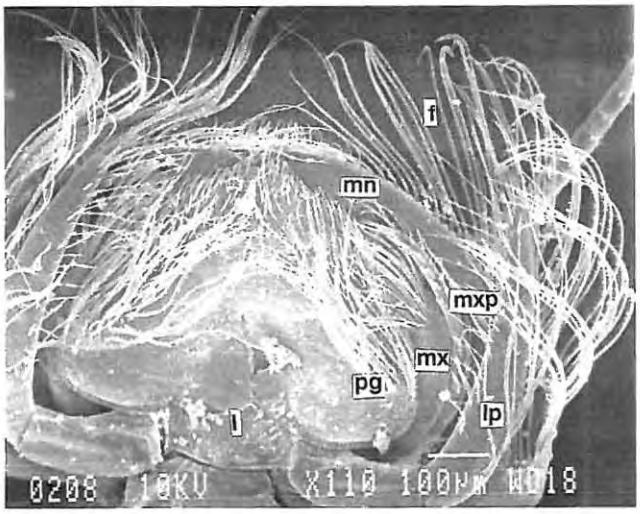
N. reticulatus larvae were associated with the swift currents of the riffle biotope, and in the laboratory

larvae were observed passively filter feeding, using the long fringe of setae on the outer rim of the mandibles, maxillae, paraglossae, and labial palps (Fig 5.9 a,b). These filtering setae, with long microtrichia interspersed with a set of 4-6 short microtrichia (Fig. 5.9e), were structurally similar to those of simuliids and filter feeding oligoneurid mayflies which inhabit high velocity habitats (Braimah 1987). The outer edge of the maxillae had simple bipectinate setae (Fig 5.9 c,d), and the maxillary palps were equipped with combs (Fig. 5.9 d,f), which could be used to clean food particles from the setae. In the laboratory, when larvae were observed passively filtering, they selected positions in an area of maximum velocity. Larvae also swept the surface of stones while under observation. Since they lack the distinctive brushes of the leptophlebiids and A. harrisoni, it is possible that they were actively filtering, by stirring up fine particles which were caught by their abundant setae. Active filtering may account for the presence of leaf fragments and algae in the gut. Neurocaenis reticulatus has therefore been assigned to both the active and passive filterer FFGs.

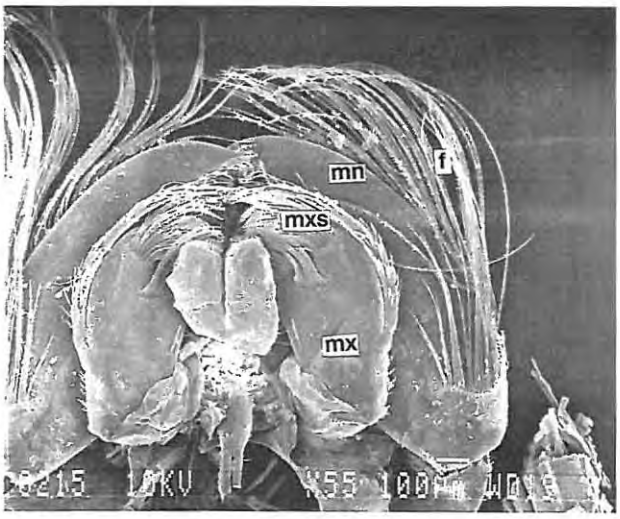
Caenidae sp. A was one of two caenid mayflies which could not be named at a species level. The larvae had mandibles with no marginal setae and the abdominal segments did not protrude posterolaterally. Larvae were collected from riffles and stony backwaters from Site 5 to Site 13. The gut contents consisted predominantly of UFPOM, FPOMa and silt, with occasional diatoms, filamentous algal fragments and leaf fragments (Fig. 5.1). 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 (Table 5.1- 5.4).

Morphologically, the labium and maxillae were quite simple, and are modestly fringed with simple bipectinate

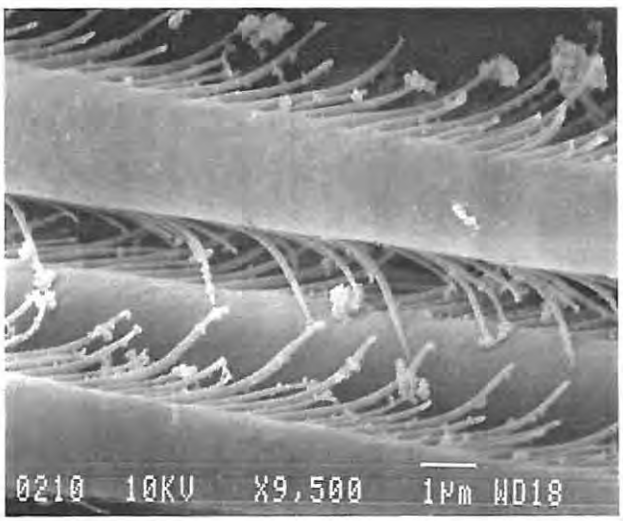
Fig. 5.9 Mouthparts of Neurocaenis reticulatus:



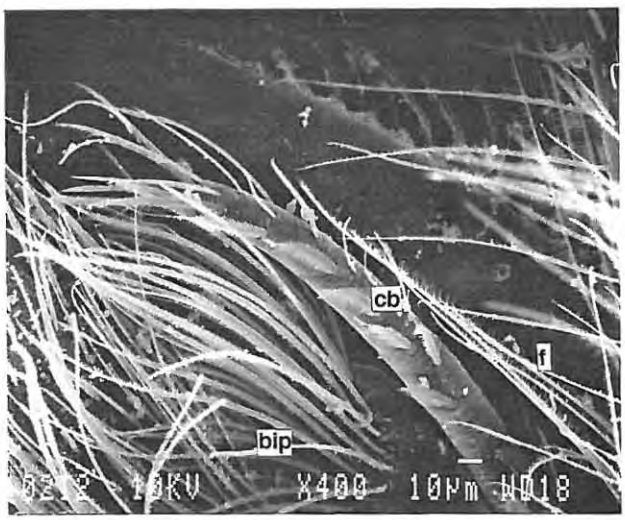
a. Ventral view of the mouthparts. (f = filtering setae, l = labium, lp = labial palp, mn = mandible, mx = maxilla, mxp = maxillary palp, pg = paraglossa)



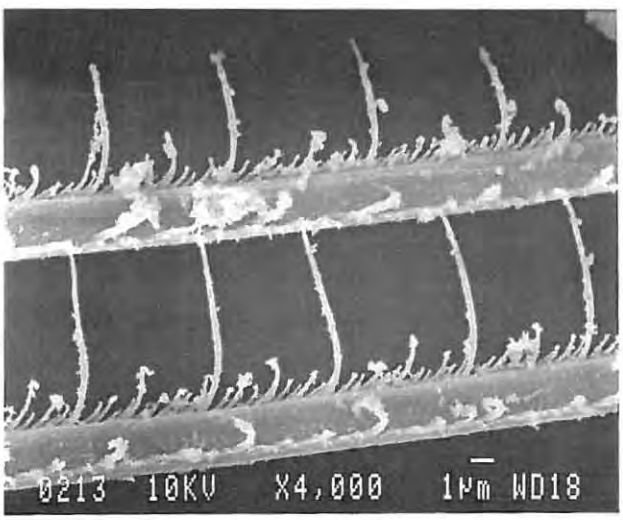
b. Ventral view with labium removed. (mxs = maxillary setae)



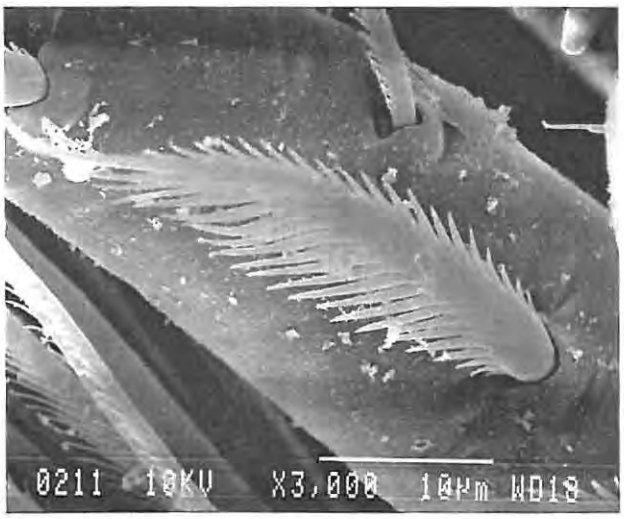
c. Stout bipectinate setae on the maxilla, next to the maxillary palp. Their location next to the palp is shown in 5.9 d.



d. Maxillary palp with combs (cb), and adjacent setae (bip).



e. Filtering setae found fringing the mandibles, and the labial and maxillary palps. (f in a, b, and d above)



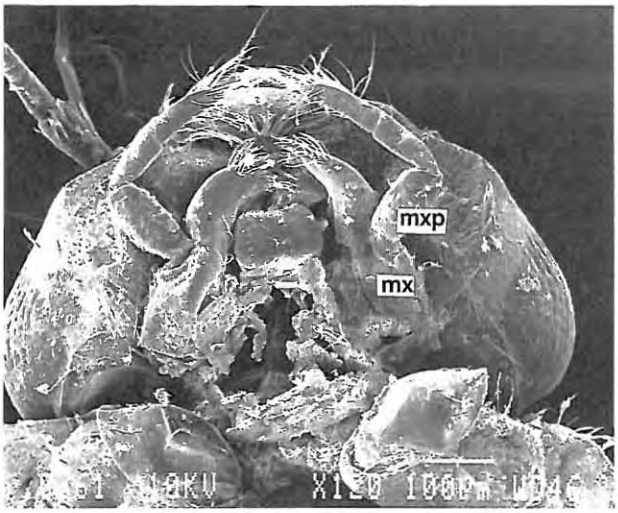
f. Detail of maxillary palp comb.

setae (Fig. 5.10 a-d), resembling the mouthparts of C. excisum and C. africanum (Figs. 5.4 and 5.5). The larvae were observed gathering a mass of detritus between their front legs, holding it there, and feeding from it. The larvae did not have the leg setae which characterise Caenidae sp. B. Caenidae sp. A was assigned to the collector-gatherer FFG.

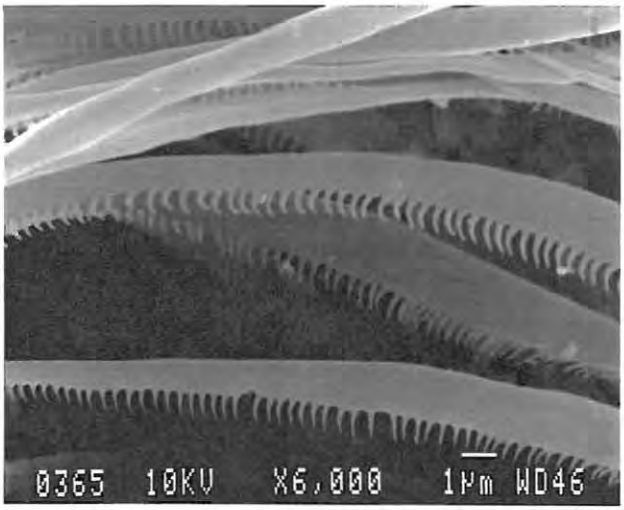
Caenidae sp. B: This caenid belongs to an undescribed genus (W. P. McCafferty pers. comm.) and was less common (24 individuals dissected) than species A. The larvae had mandibles with marginal setae, abdominal segments which protruded posterolaterally and long distinguishing setae on the forelegs (Fig.5.11 a,b). Larvae were only collected from riffles at Sites 12 and 13. The diet was very similar to Caenidae sp. A (Fig. 5.1), there were no significant differences in the foregut contents of larvae collected from different sites, and rare seasonal differences (Tables 5.1-5.3).

The distribution of this caenid in riffles is significant as it has long setae on its first pair of legs (Fig. 5.11 a,b). When these larvae were examined by Prof. W.P. McCafferty, and recognised as belonging to an undescribed genus, he surmised that the leg setae were used for passive filter feeding. However, the leg setae are without microtrichia (Fig. 5.11e) and therefore do not seem to be structurally adapted for passive filtering. There are abundant bipectinate filtering setae fringing the paraglossae, labial palps, maxillae, and maxillary palps (Fig. 5.11 c,d,f). This may indicate that the larvae are active filterers, stirring up fine particles with the long leg setae, and then filtering them. I was not able to collect live specimens and observe them, but their restriction to the rapid currents of riffles suggests at least the possibility of passive filtering. The species was assigned to the active filterer FFG category.

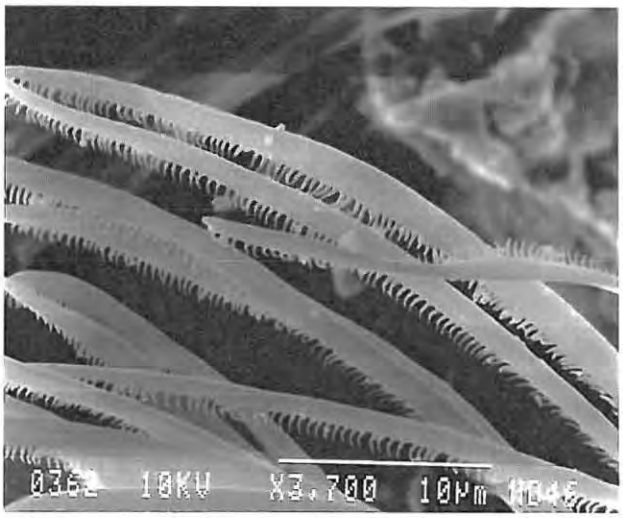
Fig. 5.10 Mouthparts of Caenid sp. A:



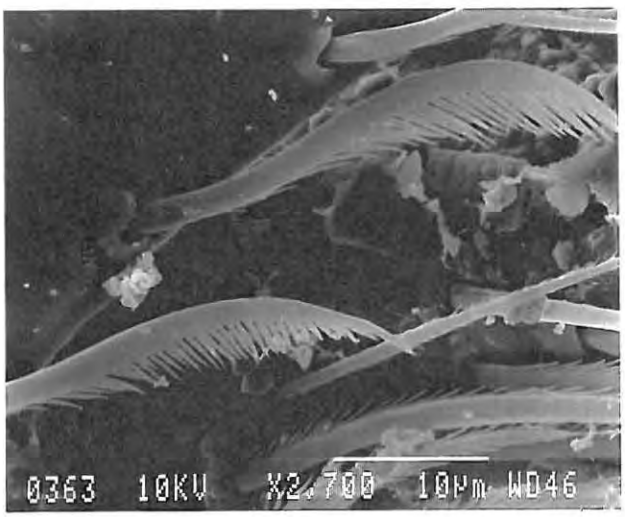
a. Ventral view of mouthparts with the labium removed. (mx = maxilla, mxp = maxillary palp)



b. Fine bipectinate setae from the labial palps.

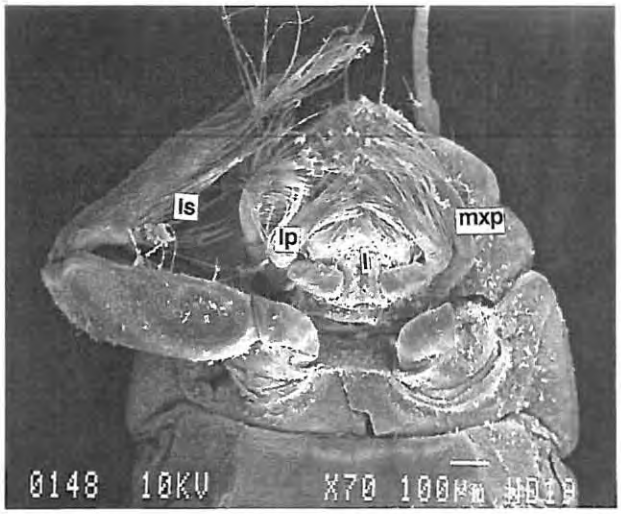


c. Fine bipectinate setae from the maxillary palps.

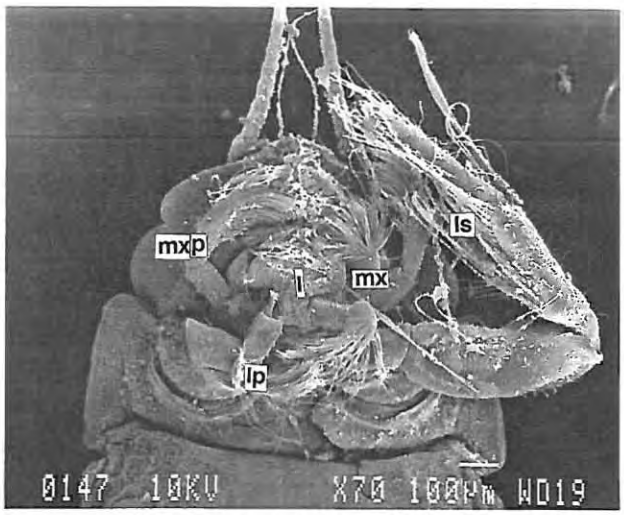


d. Maxillary palp combs.

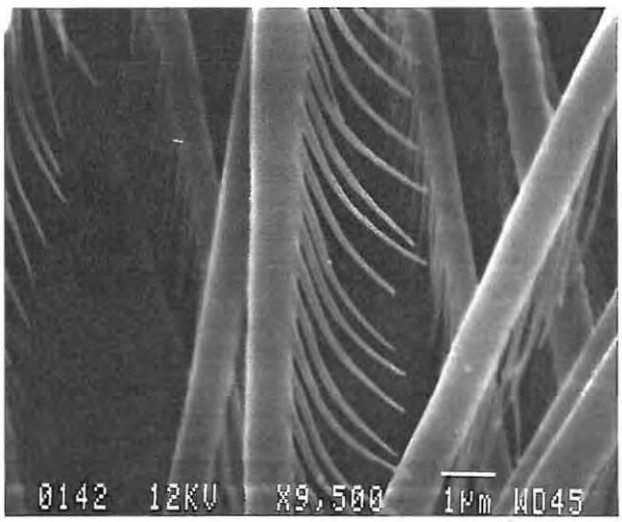
Fig. 5.11 Mouthparts of Caenid sp. B:



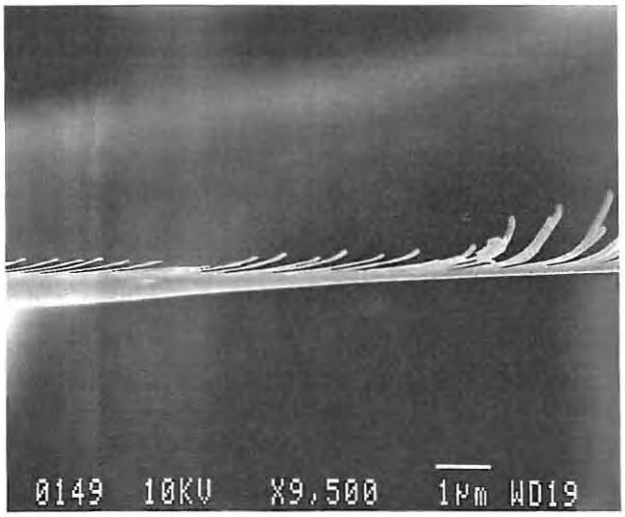
a. Ventral view of the mouthparts. (l = labium, lp = labial palp, ls = leg setae, mxp = maxillary palp)



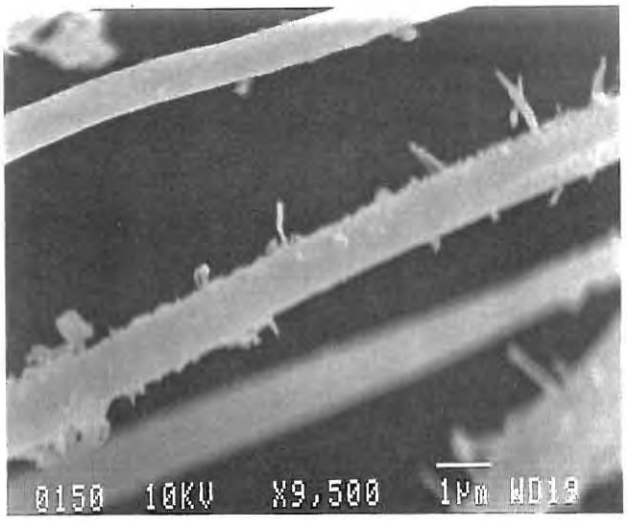
b. Ventral view with labial palps bent down. (mx = maxilla)



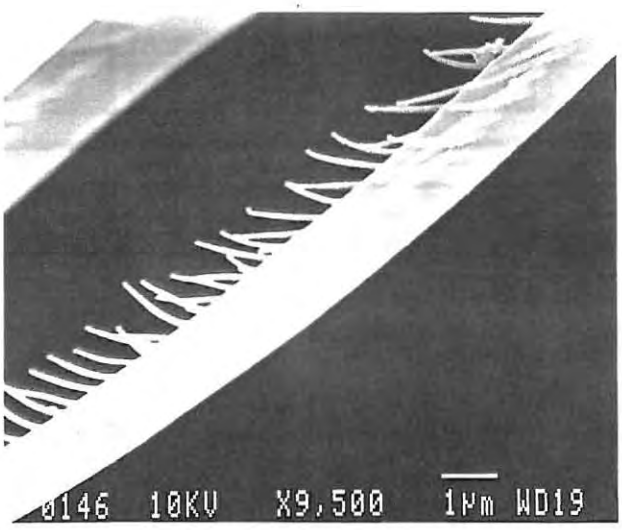
c. Bipectinate labial palp setae.



d. Bipectinate maxillary palp setae.



e) Leg setae with sparse microtrichia.



f) Bipectinate maxillary setae.

Table 5.5 gives comparative data on the ultrastructure of the labia and maxillae of the 11 species of mayfly larvae (including A. auriculata, a leptophlebiid mayfly from the upper reaches, described in Chapter 4).

Cheumatopsyche afra was a net-spinning hydropsychid caddis collected from riffles between Sites 1 and 13, in all seasons, and 78 larvae were dissected. Large larvae had ingested a wide range of foods, while 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 characterised by a high proportion of leaf fragments and invertebrate remains (Fig 5.1). These size differences were consistently significant (Table 5.1). 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 5.2), but not, in general, in those collected from different seasons (Table 5.3). The collection of food items in nets led to C. afra being termed a passive filterer.

Macrostemum capense was the other trichopteran selected for study. Also a net spinner, it resembled C. afra in the breadth of dietary items in the foregut (Fig 5.1), and in the consistency of differences between the gut contents of large and small larvae (Table 5.1). There were significant differences in the diets of both large and small larvae collected from different sites. A multiple range test showed there was no clear downstream pattern in the dietary differences between either large or small larvae collected from different sites. For large larvae, the gut contents from those collected at Sites 1 and 5 differed from all the other sites and from each other. Larva from Site 5 had ingested the widest variety of food, and 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 the other

Table 5.5. A comparative table of ultrastuctural features of the labium and maxilla of 11 Buffalo River mayfly larvae. Many of the structures are illustrated in micrographs (Figs. 4.3 and 5.2-5.11).
The dimensions of setal microtrichia are given as:
e.g. 2/µm x 2µm = 2 microtrichia per µm, each of 2µm length (bipectinate setae); or
2/µm & 4-6 x 1µm 1 x 4µm = 2 microtrichia per µm, 4-6 each of 1µm followed by 1 of 4µm length (filtering setae).
bips = bipectinate setae

	FFG	labial paraglossa	labial palp	maxilla	maxillary palp
A. harrisoni (Fig. 5.8)	scraper	upright combs bips 2/µm x 5um	sparse short setae	chitinous scraping bars	brush curved bips 2/µm x 2µm
C. elegans (Fig. 5.6)	brusher	setose fringe	setose fringe & apical tuft	brush curved bips 2/µm x 2µm	bips
C. nigrescens (Fig. 5.7)	brusher	setose fringe	setose fringe & apical tuft	brush curved bips 4/µm x 3µm	bips
A. auriculata (Fig. 4.3)	brusher	fine combs 2/µm	apical tuft	brush curved bips 2-3/µm x 1µm	apical tuft of setae
B. harrisoni (Fig. 5.2)	gatherer	scoop-like setae	sparse short setae, no microtrichia, no thumb	blunt teeth small group bips	no setae
C. excisum (Fig. 5.5)	gatherer	bips 2/µm x 1µm	sparse short setae, no microtrichia, blunt thumb	long teeth straight bristle-like bips	no setae
C. africanum (Fig. 5.4)	gatherer	short bips 2/µm x 1µm	sparse short setae, no microtrichia, no thumb	short teeth straight bristle-like bips 2/µm x 1.5µm	no setae
Caenidae sp. A (Fig. 5.10)	gatherer	bips 2/µm x 1µm	bips 3/µm x 1µm	short teeth bips 3/µm x 1µm	sparse bips
Caenidae sp. B (Fig. 5.11)	active filterer	bips 2/µm x 2µm	short bips 3/µm x 3-4µm	bips 2/µm x 2µm	bips 2/µm x 2µm
	Other feature: long leg setae without microtrichia.				
P. maculosum (Fig. 5.3)	active filterer	bips 2/µm x 2µm curved	setose long thumb	long teeth straight bristle-like bips 2/µm x 3µm	no setae
N. reticulatus (Fig. 5.9)	passive filterer	long bips	long filtering setae 2/µm 4-6 x 1µm, 1 x 4µm	long filtering setae 2/µm 4-6 x 1µm, 1 x 4µm	small bips 3/µm 1 x 2µm 1 x 4µm
	Other feature: fringe of filtering setae along the edge of the mandibles.				

sites, with an unusually high variety of items. Only large larvae showed seasonal differences in gut contents. M. capense larvae were assigned to the passive filterer FFG.

FFG designations: Using the FFG definitions of McShaffrey and McCafferty (1988), the 12 species from the middle/lower reaches of the Buffalo River were assigned to the following FFGs:

a) Filterers
- i) passive
  - net - C. afra, M. capense,
  - setal - N. reticulatus;
- ii) active - Caenidae sp. B, P. maculosum, N. reticulatus;

b) Collectors
- i) gatherers - Caenidae sp. A, B. harrisoni, C. excisum; C. africanum;
- ii) brushers - C. elegans, C. nigrescens, A. harrisoni;
- iii) scrapers - A. harrisoni.

Where only one FFG designation is given (Table 5.5, Fig. 6.5) N. reticulatus was designated a passive filterer and A. harrisoni a scraper.

5.4 Discussion

The original FFG descriptions (Cummins 1973, 1974) implied that stream macroinvertebrates could quite readily be distinguished on the basis of their diets, despite stating that many aquatic invertebrates were trophic generalists. There was an emphasis on gut content analysis as the primary technique for investigating diet (eg. Coffman et al. 1971, Cummins 1973). However, the most obvious feature of the gut contents of the 12 species studied from the middle/lower reaches of the Buffalo River, was the similarity in the predominance of

amorphous, fine detritus in their foreguts. Species adapted as scrapers, as passive filterers, as brushers, feeding on particles either suspended in the seston, loosely deposited, or tightly accreted on stone surfaces, all had mainly the same material in their foregut: fine, amorphous detritus. These results seemed to render the FFG concept meaningless. However, an investigation of the literature showed that such results were commonplace, and that the gut contents of benthic stream fauna have frequently been shown to contain mainly detritus. It may be that this is more a reflection of insufficient differentiation of components of fine detritus. If so, electron microscopy would be required to achieve a finer level of differentiation.

A study of Australian stonefly larvae reported that 13 out of 19 species had gut contents consisting of between 69 and 100% detritus (Sephton and Hynes 1982). Fine detritus was similarly important in the diets of Australian oligoneurid and siphlonurid mayflies (Campbell 1985), and in the diets of 127 macroinvertebrate taxa from two Victorian rivers (Chessman 1986). Slides of gut contents prepared from 25 New Zealand macroinvertebrate species contained mainly particles in the size range 0.45 - 75um (Winterbourn et al. 1984). Examples of FPOM feeding are abundant from North American studies (Gilpin and Brusven 1970, Koslucher and Minshall 1973, Clifford et al. 1979, Gray and Ward 1979, Hamilton and Clifford 1983, Short 1983, Hawkins 1985, Wallace et al. 1987, Rader and Ward 1987, 1989, McShaffrey and 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. It seems from the literature, that FFGs have routinely been recognised on the basis of less common dietary items and that fine detritus, which is ubiquitous in streams, forms the staple diet of many stream macroinvertebrates.

This was certainly the case for 12 macroinvertebrates from the middle/lower reaches of the Buffalo River. Consequently, on the basis of the gut analysis results alone, it was only possible to identify two broad FFGs: 1) UFPOM/FPOM microvores, which included all the mayfly species, and 2) mixed diet microvores, characterised by the inclusion of invertebrate remains in the diet, which included both the net spinning caddisfly species.

Behaviour and morphology provided complementary evidence used in the development of a functional classification and determined the degree of certainty with which species could be assigned to FFGs. The four baetid species and Caenidae sp. B were not observed feeding and FFG designations could only be inferred using morphological evidence. B. harrisoni, C. excisum, and C. africanum were assigned to the gatherer FFG because they lacked specialised filtering structures, but were equipped with bipectinate setae which McShaffrey and McCafferty (1990) associated with feeding on fine material. In addition they were structurally similar to the larvae of Caenidae sp. A which were observed gathering fine detritus between their front legs and feeding from it. The scoop-like setae on the apices of the labial paraglossae (Fig. 5.2 e) of B. harrisoni larvae may have enabled it to remove more tightly accreted material. B. harrisoni was an abundant riffle dweller and it seemed likely it would have been able to feed on material which would be washed away if not attached. However, without behavioural verification that is supposition. The mouthparts of P. maculosum and Caenidae sp. B were considerably more setose (Figs. 5.3 and 5.11). This, and their location mainly in riffles suggested that they may be filterers. They did not have the specialised filtering setae of passive filterers like simuliids and N. reticulatus (Fig. 5.9e) and were assigned to the active filterer FFG. In terms of river function, provided their faeces are of the same size and consistency, there is no difference in the

river functions facilitated by gatherers and active filterers since both FFGs collect and excrete fine deposited detritus.

Behavioural observation of feeding, together with morphology and the gut contents data provided the most certain FFG designations. The filtering activities of N. reticulatus were observed in the laboratory, and closely resembled those described for the caddisfly Brachycentrus occidentalis (Brachycentridae) which used leg setae to filter feed, and jostled for position in hydraulically favourable positions (Whetmore et al. 1990). The ultrastructure of the filtering setae on the mandibles, maxillae and labium of N. reticulatus larvae closely resembled cephalic fan setae of simuliids (Braimah 1987, Palmer 1991), and leg setae of siphlonurid (Wallace and O'Hop 1979) and oligoneurid (Braimah) mayflies. The leg setae of Caenidae sp. B superficially resembled the filtering leg setae of the siphlonurid Ionychia spp. (Wallace and O'Hop 1979), however, electron microscopy revealed the absence of filtering microtrichia on the leg setae of Caenidae sp. B. It was the absence of filtering microtrichia on the leg setae of Caenidae Sp. B that prevented its designation as a passive filterer.

The brushing cycles of C. elegans and C. nigrescens were observed, and these larvae had setose maxillary brushes, structurally similar to those described in the previous chapter for the headwaters leptophlebiid A. auriculata. Brushes are morphological adaptations for the removal of loose and lightly attached detritus, which, like filtering setae, have evolved in different macroinvertebrate lineages. Southern African (Barnard 1932, Crass 1947, this study) and New Zealand (Winterbourn et al. 1984) leptophlebiids have maxillary brushes, as does the heptageniid mayfly from the Buffalo River, A. harrisoni (not on the maxillae as with the leptophlebiids, but on the maxillary palps).

Morphological adaptations such as filtering setae and brushes provide firm bases for a functional classification that cuts across taxonomic boundaries and groups animals on the basis of their feeding.

The hydropsychid caddis larvae had characteristic gut contents. Although fine detritus was the predominant food type present, particularly in small larvae, the presence of the chitinous exoskeletons of invertebrate prey were distinctive. McShaffrey and McCafferty (1988) group all passive filterers together, whether they use setae or nets for filtration, yet they distinguish between brushers and gatherers, which feed on the same food source, the former using setae and the latter using other body parts. In this study setal and net filterers have been distinguished because of differences in their gut contents. This distinction also accommodates the predatory nature of net filtration.

Comparison of the foregut contents enabled an assessment of dietary variability. As was the case with the headwater taxa, variation in the foregut contents of the 12 macroinvertebrates from the middle and lower reaches of the Buffalo River did not preclude the assigning of these species to functional groups. Dietary variation was greatest between large and small larvae, following a previously described pattern of larger animals having more material in the foregut, together with larger fragments, and a wider range of items (Chapter 4). 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).

One of the features of the gut contents analysed in this study was a paucity of diatoms. In many of the North American studies mentioned earlier in the context of a mainly FPOM diet, and in the European work of Becker

(1990) diatoms were frequently second in abundance to fine detritus. For a few species, they were the most common dietary items. Of the species studied from the Buffalo River, only A. harrisoni was equipped with externally chitinised 'scraping bars' (sensu Morgan 1911), though these occurred on the maxillae, and not on the distal labial palp segment as in the scraping heptageniid Epoerus fragilis (Morgan 1911). A. harrisoni was also the only species in this study which had diatoms as a regular, if minor dietary component. This contrasts with North American studies which frequently mention scrapers using diatoms as a primary food source, as they were for certain Australian chironomids (Chessman 1986). Specialised algal scrapers were absent from the New Zealand macrobenthic fauna (Winterbourn 1986). This conclusion prompted research on the utilisation of non-photosynthetic organic layers by brushing (=browsing) or scraping, particularly by the leptophlebiid Deleatidium spp., (Winterbourn et al. 1984, Winterbourn 1990, Jowett and Richardson 1990). Deleatidium spp. larvae are the functional equivalent of both the North American brusher Stenacron interpunctatum (McShaffrey and McCafferty 1986), and the leptophlebiid brushers in the Buffalo River (Adenophlebia auriculata in the headwaters, and C. elegans and C. nigrescens in the middle and lower reaches). It seems likely that in the Buffalo River these brushers, and the scraper A. harrisoni, utilise stone surface organic layers.

Having placed these 12 species in FFGs with varying levels of certainty, the question arises whether this process achieves one of the stated aims of FFGs: that they should facilitate an understanding of river function. The most obvious feature of the middle and lower reaches of the Buffalo River is the overwhelming abundance and availability of suspended fine material (Palmer and O'Keeffe 1990b). This is reflected in the feeding of the macroinvertebrate fauna by the

preponderance of fine detritus in the foreguts of these animals. The way in which feeding activities can facilitate river function was introduced in the previous chapter (Section 4.4.3). The way in which the filterers, gatherers, brushers and scrapers of the middle and lower reaches contribute to the retention, mobilisation, microbial colonisation and size transformation of fine organic material would be a worthwhile avenue of research.

CHAPTER 6
THE APPLICATION OF FFGs AS A BASIS FOR CLASSIFICATION

6.1 Introduction

Patterns in natural systems are complex and are neither easily described nor easily understood. The patterns which are most frequently described are those of taxonomic composition, with the term "community structure" frequently being synonymous with taxonomic composition. Recently, Shipley et al. (1989) have suggested that because of the vast number of species and even greater range of environments "it will be necessary to abandon taxonomic units as the standard variables " used in the development of predictive models of assemblage composition in relation to environmental variables. This echo's Cummins' (1974) assertion that problems with taxonomic identification would seriously limit the development of a functional understanding of stream ecosystems. The idea of replacing taxonomic units with functional units is not new. One of the earliest attempts at functional classification was a classification of plants on the basis of growth form (Raunkiaer 1934), and the concept of ecologically meaningful units was implicit in the coining of the term "guild" (Root 1967). Guilds may be reproductive, as has been shown extensively in fishes (Balon 1975a, b, Bruton and Merron 1990), morpho-behavioural (Dahl et al. 1988, Corkum and Ciborowski 1988), size-based (Sprules 1984), or trophic, as are Functional Feeding Groups (FFGs).

However, it is probably a mistake to view taxonomic and functional classifications as being opposing alternatives. Organisms will continue to be recognised and described on the basis of distinguishing morphological features and will be incorporated into the existing body of taxonomic knowledge. Indeed the evolutionary affinities of organisms frequently yield

valuable ecological insights (McCafferty 1981). Much of this thesis has investigated whether taxa can be assigned to FFGs, which presupposes a level of taxonomic description, even if not always to species level. Furthermore, the recognition of functional categories is not always easier than the recognition of specific characteristics. This study has demonstrated the difficulties of achieving an unambiguous FFG classification. Therefore the question addressed in this chapter is not whether functional classifications should replace the taxonomic approach but rather whether they can usefully augment the taxonomic approach.

Two aspects of the FFG classification of macroinvertebrates from the Buffalo River were explored:

Classification of food items: Gut analysis remains the simplest method for the investigation of macroinvertebrate feeding. Selected headwaters and middle/lower reaches taxa were classified on the basis of the size and type of food in their foreguts, with the aim of establishing whether the resultant groups could be associated with either taxa or FFGs. It was hoped that the results would provide objective evidence of the usefulness of gut contents data in the recognition of FFGs.

Classification of macroinvertebrates into FFGs: Each taxon in the macroinvertebrate assemblage from the Buffalo River was assigned to a FFG (including the category "unknown"). Samples collected seasonally from several biotopes from Sites 0, 1, 6 and 12 (Fig. 2.1) were classified on the basis of the relative abundances of first, component taxa, and then component FFGs. The classifications were compared to see if there was any pattern to the the distribution of FFGs in the river, and to establish whether any such pattern coincided with the pattern of taxonomic groupings described in Chapter 3.

If patterns of FFG distribution did exist, and if they could be related to environmental gradients in the river, FFGs could be used in the monitoring of water quality. This argument was well developed by Faith (1990). He went on to test whether the apparent association between FFGs and environmental gradients was linear or unimodal, and whether it differed from random. In this study most effort went into establishing a consistent definition of FFGs and the exploration of the distribution patterns of FFGs is more superficial than that of Faith (1990). However the relationship between the spatial distribution of FFGs and environmental gradients in the Buffalo River was investigated. The role of functional classifications is discussed.

6.2 Methods

All the methods used in this chapter have already been described. They are listed and referenced according to their appearance in earlier chapters.

Description of study sites	: Chapter 2
Sampling	: Chapter 3 (3.2.)
Classification using TWINSPAN	: Chapter 3 (3.2.2) and Appendix 1
Ordination using CCA	: Chapter 3 (3.2.2) and Appendix 1

6.2.1 Classification of samples on the basis of the size and type of particle in the foregut

Gut content analysis is a well established method for gathering information on the feeding of aquatic macroinvertebrates. A TWINSPAN analysis was used to develop hierarchical groupings of all the gut content samples in order to achieve an objective functional classification based on the size and type of food items in the gut. The classification is based on food type presence, absence and relative abundance. The food types were the same as those reported in Chapters 4 and 5 for headwaters and middle/lower reaches taxa respectively. Samples collected in all biotopes from a) the headwaters

(Site 0, Fig.2.1), and b) the middle/lower reaches (Sites 1, 6 and 12, Fig. 2.1) were classified separately on the basis of the foregut contents of larvae selected from the samples, using TWINSPAN.

6.2.2 Classification of the macroinvertebrate fauna of the Buffalo River on the basis of FFGs.

All the taxa were assigned to one of 10 FFGs:

1) shredders
2) scrapers
3) brushers
4) active filterers
5) passive filterers (setal)
6) passive filterers (net)
7) gatherers
8) predators
9) deposit feeders
10) unknown.

The FFGs are those of McShaffrey and McCafferty (1988) which have been described in detail in previous chapters, but passive filterers which use nets and those which use setae to collect seston have been distinguished.

The basis for the assigning of taxa to FFGs was established and data on the feeding biology of 16 of the most abundant taxa have been reported in Chapters 4 and 5. During this process it became clear that several methods were necessary to provide data that would enable the assigning of an organism to a FFG. The feeding behaviour of some of the taxa was flexible, and they were assigned to more than one FFG. For the functional classification reported here a decision was made as to which style of feeding was predominant, and each taxon was assigned to one of the 10 FFGs. The results of the feeding studies on the headwaters leptophlebiid A. auriculata (Chapter 4) exemplify the difficulty of assigning an organism to a single FFG. The feeding of A.

auriculata larvae was studied using gut analysis, field and laboratory observation, food choice experiments, and morphology. The species was assigned to the brusher FFG. This designation describes most of the feeding behaviour observed, but larvae also grazed on a red alga, and collected oak leaf particles. They have scraping setae on the maxillae which may allow them to remove tightly accreted material. At best a single functional description provided information on the most frequent form of feeding activity. In the case of taxa whose feeding activities were not observed, FFG designations were even less certain.

In this study 119 macroinvertebrate taxa were identified and it was impossible to study the feeding of all of them in detail. King et al. (1988) have demonstrated that it is inappropriate to apply Merritt and Cummins' (1984) FFG designations for North American taxa, to geographically distant taxa. Apart from the 16 taxa that were studied in detail, there were other taxa which could be assigned to FFGs with reasonable confidence. All the Simuliidae were assigned to the passive filterer group (Scott 1990, Palmer 1991), though the work of Currie and Craig (1987) has shown that even blackfly larvae are flexible in their feeding behaviour. Two other hydropsychid caddis were assigned to the net filterer group, and the Planaria spp., perlid stoneflies, Megaloptera and Tanypodinae were assumed to be predators. The freshwater limpet Burnupia sp. was assigned to the scraper functional group. Once all of these designations were complete, 65% of the macroinvertebrates by numbers were assigned positively to FFGs and the others were designated unknown.

Samples from all biotopes at Sites 0, 1, 6, and 12 were classified on the basis of these FFGs using TWINSPAN (Hill 1979a).

6.2.3 Ordination of summer riffle samples from all sites down the river.

All the taxa from samples collected during summer in riffles at all the sampling sites down the river (Fig. 2.1) were assigned to FFGs as described above, and ordinated using CCA (Ter Braak 1988). The FFG composition was related to the same set of physico-chemical variables used in the ordination of the taxonomic composition in Chapter 3.

6.3 Results

6.3.1 Classification of samples on the basis of the size and type of particle in the foregut.

Headwaters: The hierarchical classification of the headwaters samples on the basis of foregut contents is shown in Fig. 6.1. At level 1, gut content samples with UFPOM (ultrafine particulate organic matter - 0.5-50μm), FPOMa (fine particulate organic matter - 50-250μm), silt and some diatoms (Group I) were distinguished from samples with no FPOMa, less UFPOM and silt, and very few diatoms but with leaf fragments (Group II). Group I included 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. 6.1).

Group I

At level 2, the A. auriculata samples (Group I.A) were distinguished from the small Afronemoura spp. samples (Group I.B). Group I.A was characterised by the predominance of FPOMa and silt, with fungi, pollen and invertebrate remains present, and very little L.UFPOM (leaf fragments 0.5-50μm). Group I.B samples contained little FPOMa (fine particulate organic matter 50-250 μm) and silt, no fungi, pollen or invertebrate remains and

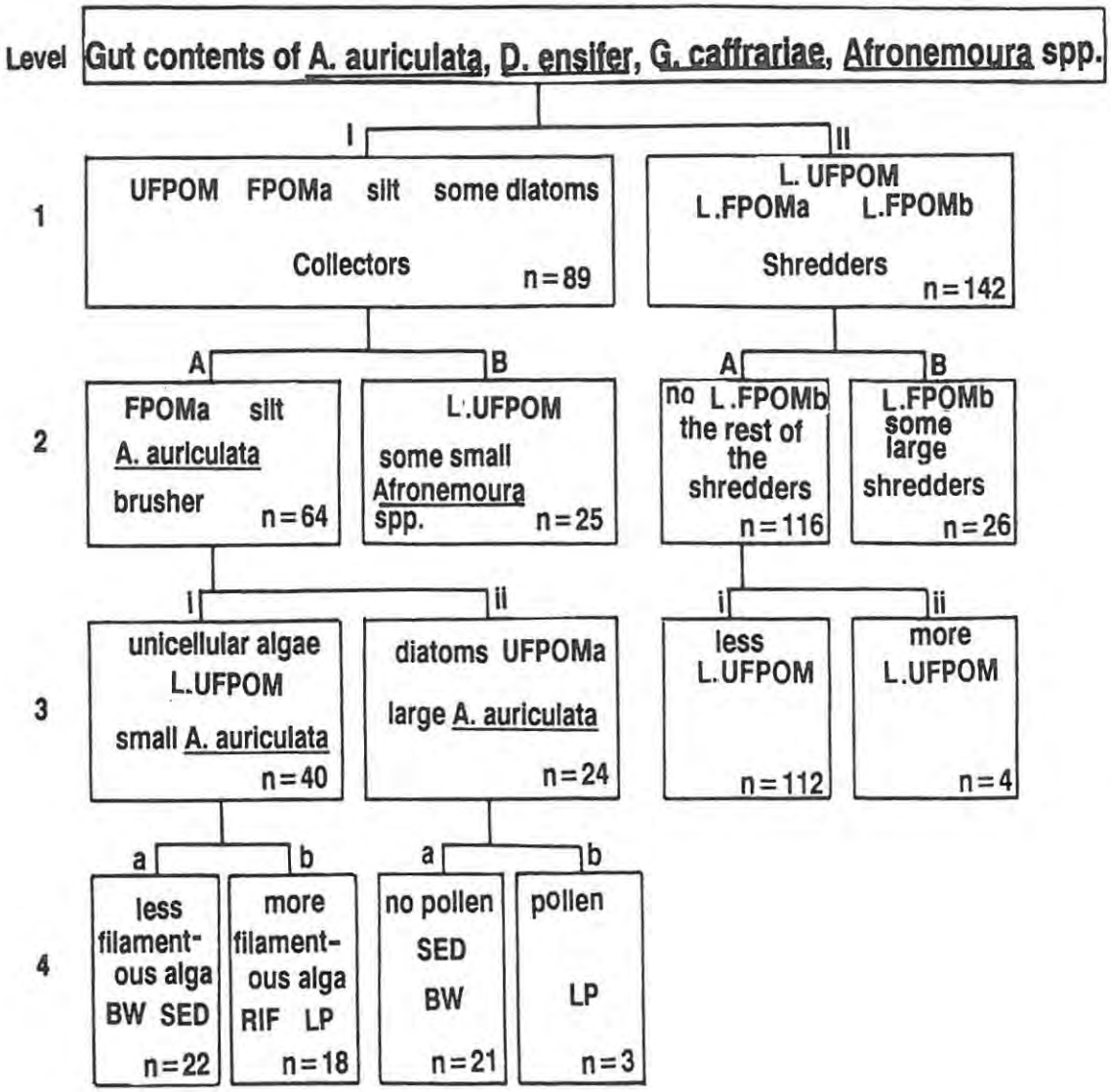


Fig. 6.1 Three large and three small larvae of each of the four headwaters species, collected seasonally from Site 0 in various biotopes, were dissected, and their gut contents enumerated. These gut contents samples were classified using TWINSPAN (Hill 1979a). The gut contents of collectors, which comprised mainly fine detritus and some inorganic silt, were distinguishable from those of the shredders, which comprised leaf fragments almost exclusively. The collectors were the brusher A. auriculata and some small stonefly larvae. The two caddisfly species, and all the large and most small stonefly larvae were shredders. Details of each level are given in the text. (L.UFPOM = leaf fragments (0-50µm), L.FPOMa = leaf fragments (50-250µm), L.FPOMb = leaf fragments (250µm-1mm), RIF = riffle, BW = stony backwater, SED = sediments, LP = leaf pack)

were dominated by L.UFPOM (Fig. 6.1).

At level 3, Group I.A.i samples were distinguished by the presence of unicellular algae and L.UFPOM , fewer FPOMa and diatoms, and the absence of FPOMb (fine particulate organic matter 250µm-1mm). In Group I.A.ii samples, FPOMb was present, while unicellular algae and L.UFPOM were absent. Diatoms and UFPOM were more common than in Group I.A.i. The majority of Group I.A.i samples comprised small A. auriculata individuals, while Group I.A.ii were mainly large individuals (Fig. 6.1).

At level 4, small A. auriculata (Group I.A.i.a) samples from depositional biotopes (stony backwaters and sediments), were distinguished from leaf pack samples (Group I.A.i.b) because they contained less filamentous algae. Large A. auriculata (Group I.A.ii.a) samples from depositional biotopes (stony backwaters and sediments), were separated from erosional (riffle and leaf pack) samples (Group I.A.ii.b) because of the absence of pollen, FPOMb and invertebrate remains (Fig. 6.1).

Group II
At level 2, the presence/absence of L.FPOMb was the distinguishing feature. The gut contents of only the largest G. caffrariae and D. ensifer contained L.FPOMb (leaf fragments 250µm-1mm)(Group I.B), all the rest of the G. caffrariae, D. ensifer and Afronemoura spp. samples did not (Group IA) (Fig. 6.1).

At level 3, a large set of samples, Group II.A.i, was distinguished from a smaller set, Group II.A.ii, because the latter contained more L.UFPOM (Fig. 6.1). These dietary distinctions could not be linked to taxon, organism size, biotope or season.

Middle/Lower Reaches: The hierarchical classification of the middle/lower reaches samples on the basis of foregut

contents is shown in Fig. 6.2. The various dietary combinations were described as diets (1-8, Fig. 6.2). The samples which were grouped in each diet were checked for taxonomic, seasonal, size or site patterns of composition.

At level 1, the distinction was between diets comprising mainly UFPOM and FPOM (Diets 1-7), and a dietary type with a mixture of items, including particularly invertebrate remains (Diet 8). At level 2, a small number of samples contained mainly fine organic particles, but no silt (Diet 1). At level 3 those with silt were distinguished by either having diatoms or not. At level 4 those without diatoms were distinguished either by the addition of vascular plant fragments (Diet 3), filamentous algal fragments (Diet 4), invertebrate remains (Diet 5) or the absence of vascular plant fragments (Diet 2). Diets with diatoms were distinguished by having greater (Diet 7) or lesser (Diet 6) amounts of the basic fine organic material.

Diet 1 (UFPOM, FPOM, no silt: n=9):
Large Ephemeroptera from riffles were classified in this group. Baetis harrisoni was the most frequent species in the group.

Diet 2 (UFPOM, FPOM, silt: n=63):
Small Ephemeroptera, and large individuals of small species (Caenidae sp. A and sp. B, C. africanum) were classified in this group. Both both large and small caenids were classified in this group and they were species which showed no significant differences between the diets of large and small larvae (Table 5.1).

Diet 3 (UFPOM, FPOM, silt, vascular plant fragments: n=27):
More large than small Ephemeroptera fell into this group. C. elegans was the most common mayfly in the group which

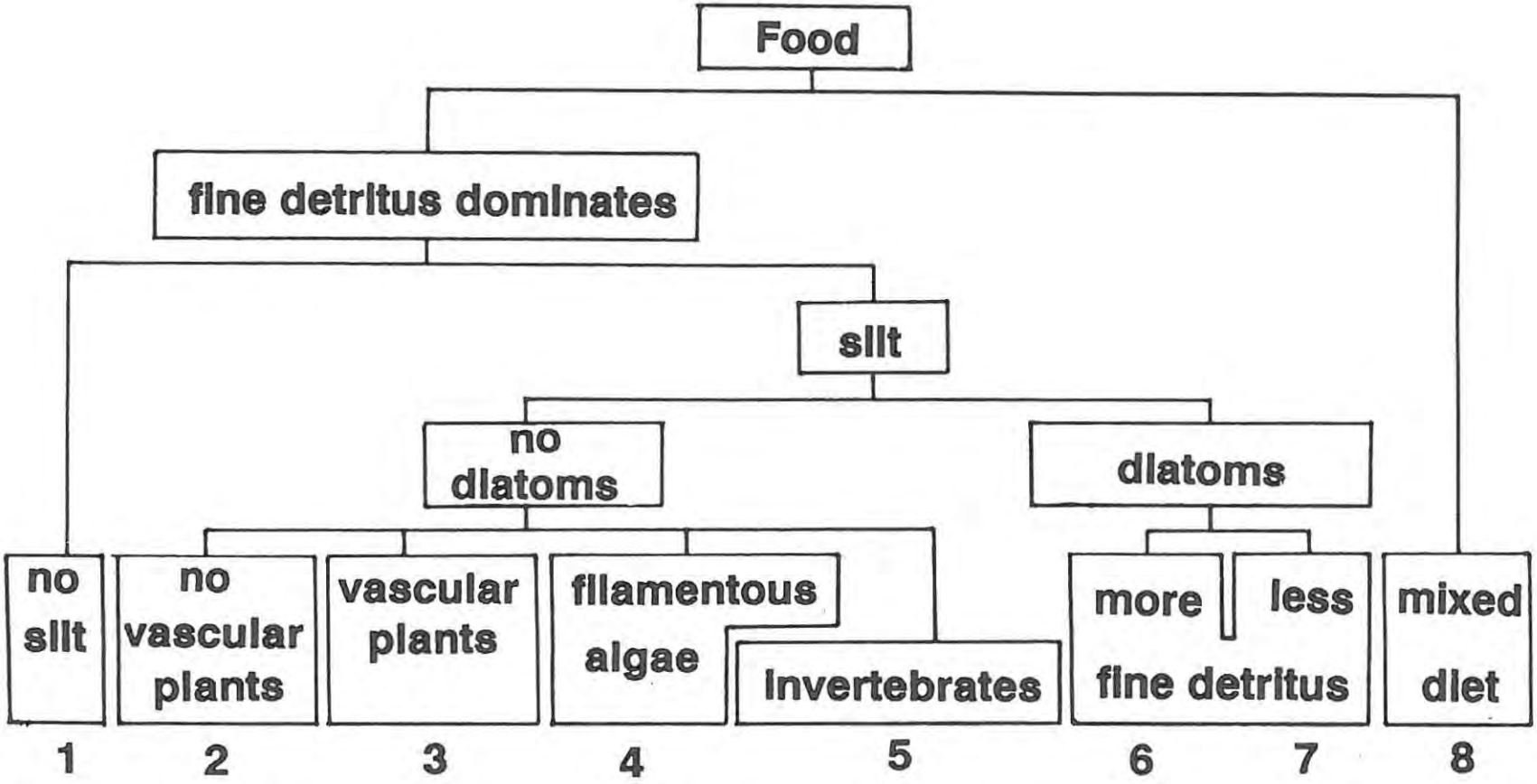


Fig. 6.2 Three large and three small larvae of each of the 12 middle/lower reaches species, collected seasonally from all sites down the river, from riffle, stony backwater and sediment biotopes, were dissected, and their gut contents enumerated. These gut contents samples were classified using TWINSPAN (Hill 1979a). At level 1 gut contents comprising mainly fine detritus (from the ephemeropteran larvae) were distinguished from those with a variety of items, notably invertebrate remains (from the hydropsychid caddisfly larvae). Seven fine detrital diets were distinguished, and are described in the text, but these did not relate in any way to species, or to site, biotope or season from which the larvae were collected.

also included C. afra samples from which invertebrate remains were absent.

Diet 4 (UFPOM, FPOM, silt, filamentous algae: n=7):
All the samples in this group were large Ephemeroptera, of which C. elegans was the most common.

Diet 5 (UFPOM, FPOM, silt, invertebrate remains: n=6):
This group comprised only small hydropsychid caddis, which had included invertebrate remains in a diet of predominantly fine organic matter.

Diet 6 (UFPOM and FPOM (high values), diatoms and silt: n=22):
This diet was exclusively characteristic of small Ephemeroptera, particularly A. harrisoni, B. harrisoni, C. excisum, and C. africanum.

Diet 7 (UFPOM and FPOM (low values), diatoms and silt: n=19):
Ingested by large C. elegans, A. harrisoni, C. excisum and N. reticulatus.

Diet 8 (mixed diet: UFPOM, FPOM, silt, diatoms, filamentous algae, pollen and invertebrate remains: n=44):
Most of the trichopteran and some large ephemeropteran samples were classified in this group. For the caddisflies, invertebrate remains were diagnostic. Foregut samples from which invertebrate remains were absent, but items other than detritus were present, included those from large individuals of B. harrisoni, C. elegans, C. africanum and N. reticulatus, emphasising that large mayflies tended to ingest a wider range of foods.

6.3.2 Classification of the macroinvertebrate fauna of the Buffalo River on the basis of FFGs.

A set of 156 samples collected from Site 0 (riffles, stony backwaters, leaf packs, a waterfall, and sediments), and from Sites 1, 6, and 12 (riffles, stony backwaters, marginal vegetation, and sediments), in four seasons (Figs. 6.3 and 6.4) were classified both on the basis of taxonomic composition and FFGs. A reciprocal averaging procedure (TWINSPAN, Hill 1979a) was used. Although the classifications differed in detail, the patterns of association and distribution were very similar. Equivalent groups (indicated in Figs. 6.3 and 6.4) were identified in both classifications, but at different levels. In both instances the middle/lower reaches are distinguished from the headwaters at level 1, though in the taxonomic classification the sediment samples were grouped with the middle/lower reaches, and in the functional classification they were grouped with the headwaters. In both classifications the sediment samples were distinguished at level 2, comprising mainly deposit feeding (FFG) oligochaetes (taxon).

The taxonomic classification (Fig. 6.3) was very similar to the one generated in the early stages of the study, (Chapter 3, Fig. 3.1a), before Site 1 samples had been included. The same indicator species characterise the major groups, and the taxonomic classification was therefore not described in detail. In the following sections, a comparison of equivalent groups will be described together with details of the functional classification.

Middle/lower reaches stream (Figs. 6.3 and 6.4 ■): In both classifications, samples collected from riffles, stony backwaters, and marginal vegetation from Sites 1, 6, and 12 were grouped together (Group I.A, Fig. 6.3 = Group I, Fig. 6.4). This group was characterised taxonomically by the hemipterans and Baetis sp. A of the marginal vegetation, and Planaria spp. and the limpet Burnupia sp. of the stony benthos; and functionally by

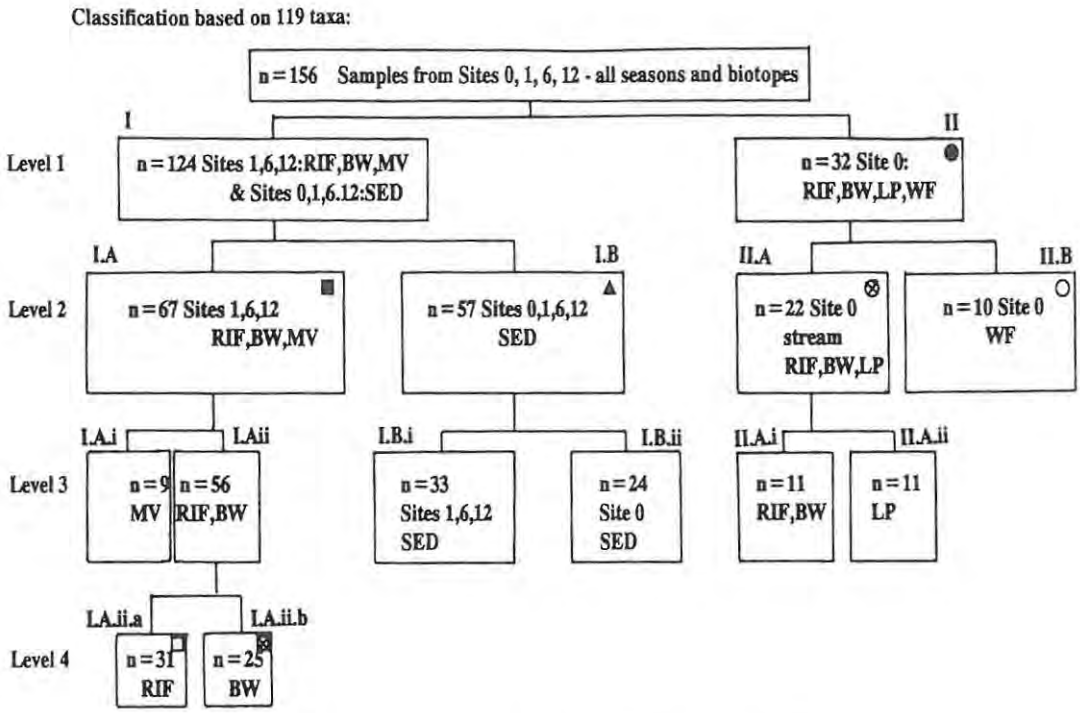


Fig. 6.3 Samples were collected seasonally from Sites 0, 1, 6 and 12, from marginal vegetation, riffles, stony backwaters, the sediments, and from a waterfall face; 119 taxa were recognised. These samples were classified on the basis of their taxonomic composition using TWINSPAN (Hill 1979a). The most notable features are the distinctive headwaters fauna, with different taxa in the stream and on the waterfall face; and a biotope-associated fauna in the middle and lower reaches. Where the same samples were grouped together by this classification and the functional classification (Fig. 6.4), equivalent groups are identified by the same symbols.

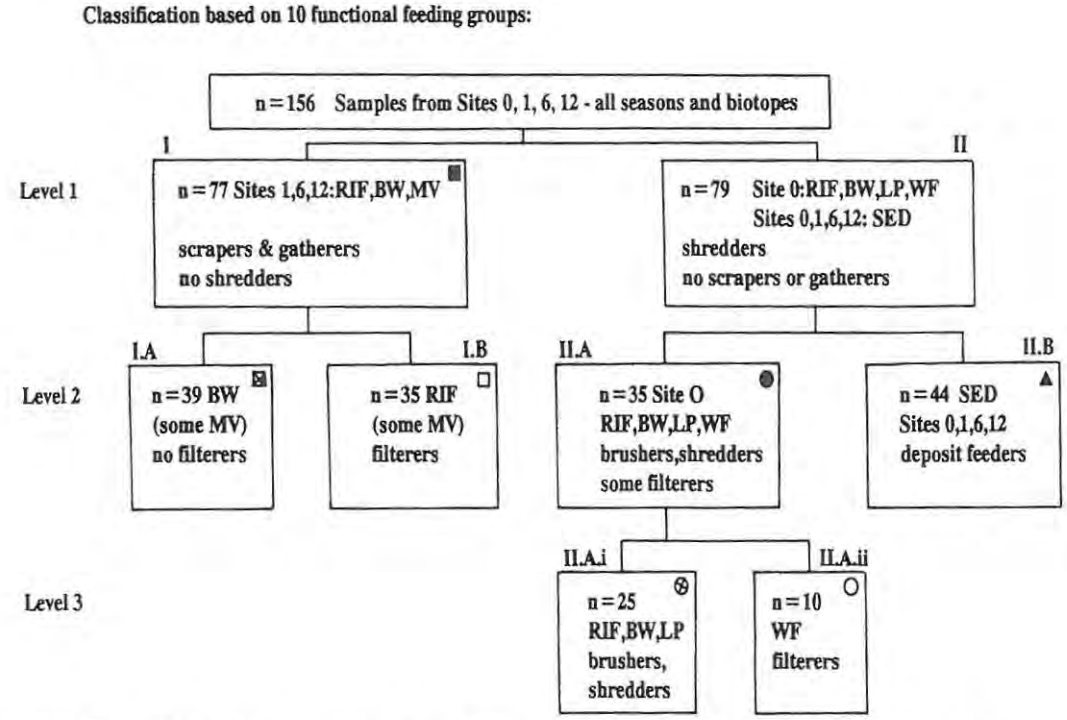


Fig. 6.4 The 119 taxa described above were assigned to 10 FFGs as described in the text, and the samples were classified again, this time on the basis of functional groups. Basically the same samples were grouped together, though in a slightly different order. Where the same samples were grouped together by this classification and the taxonomic classification (Fig. 6.3), equivalent groups are identified by the same symbols, and their functional identity is given. This is the clearest indication the macroinvertebrate assemblages can be meaningfully described in terms of FFGs.

the presence of scrapers and gatherers, and an absence of shredders.

None of the marginal vegetation fauna could be assigned to FFGs, and marginal vegetation samples, while being taxonomically distinct (Group I.A.i, Fig. 6.3), were not distinguished on a functional basis. The assemblages in riffles and stony backwaters were taxonomically and functionally distinct. Riffles (Group I.A.ii.a, Fig. 6.3 = Group I.B, Fig. 6.4) were characterised by Baetis harrisoni, and the net spinning hydropsychid caddis larvae, and functionally by the presence of filterers (active and passive). Indicator species of the stony backwaters included Caenidae sp.A and the baetid C. africanum, and the distinguishing FFG was collector-gatherer (Group I.A.ii.b, Fig. 6.3 = Group I.A, Fig. 6.4).

Sediments (Figs. 6.3 and 6.4 ▲): In both classifications the sediment samples were grouped together (Group I.B, Fig. 6.3 = Group II.B, Fig. 6.4). These samples were distinguished by the predominance of deposit feeding oligochaetes.

Headwater stream and waterfall (Figs. 6.3 and 6.4 ●): In both classifications the headwater stream (riffles, stony backwaters, leaf packs) and waterfall samples were grouped together (Group II, Fig. 6.3 = Group II.A, Fig. 6.4). The indicator taxa were the simuliids S. dentulosum and S. rutherfoordi, the leptophlebiid A. auriculata, and the case-building caddis D. ensifer and G. caffrariae. Indicator FFGs were brushers, shredders, and some passive filterers, and an absence of scrapers and gatherers was characteristic.

At a subsequent level in each case the waterfall was separated from the stream. The waterfall assemblage was characterised by passive setal filterers, and the

dominant simuliid was S. dentulosum (Group II.B, Fig. 6.3 = Group II.A.ii, Fig. 6.4). The stream was distinguished by the presence of shredders and brushers, with the indicator species being the case-building caddis, the stoneflies Afronemoura spp. and A. auriculata (Group II.a, Fig. 6.3 = Group II.A.i, Fig. 6.4).

6.3.3 Ordination of summer riffle samples from all sites down the river.

The results of the ordination of summer riffle samples collected from all sites down the river, based on taxonomic units, are reported in Chapter 3 (3.3.4, Figs. 3.5 and 3.6). The taxa were assigned to FFGs and the same procedure was followed (ordination using CCA (Ter Braak 1988)). The results are presented as a site-environment bi-plot (Fig. 6.5), and a FFG-environment bi-plot (Fig. 6.6), which are interpretable in the same way as in correspondence analysis. In the bi-plots the environmental variables are shown with an arrow. The direction of the arrow indicates the direction of increasing value of the records of that variable. The length of the arrow is proportional to the rate of change in that direction. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows (Ter Braak 1987), and are therefore more closely related to the pattern of site/FFG variation shown in the diagrams.

In the Buffalo River pH increased downstream, and was related to the pattern of distribution of FFGs and the sites at which they occurred. Based on FFGs, the sites were separated along axis 1 (x axis). Site 0 was separated at the left side of the plot, and Sites 12 and 13 at the right (Fig. 6.5). In between, the other sites were grouped without a discernible trend. This is in accordance with the taxonomic interpretation of the headwaters being distinct from the rest of the river.

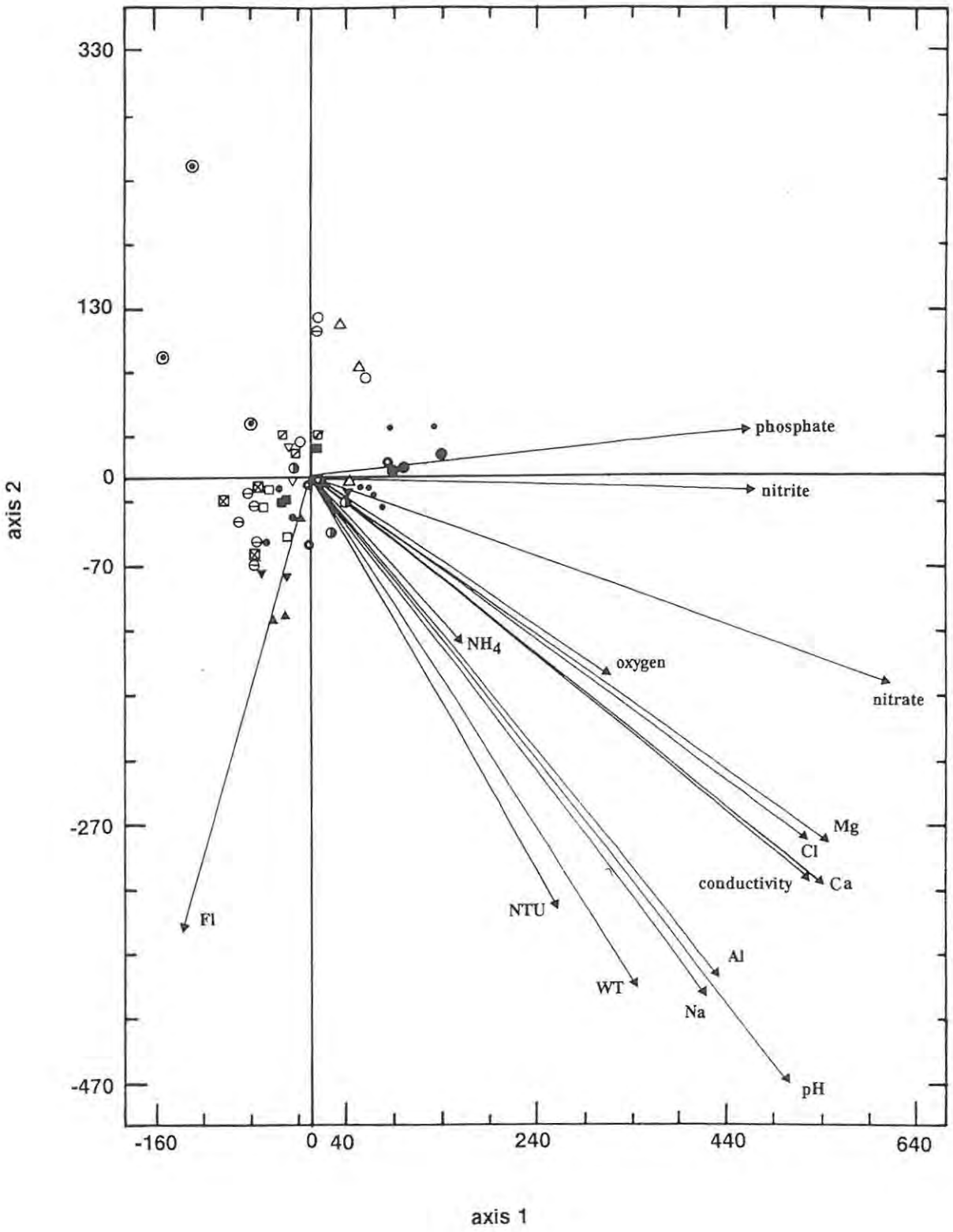


Fig. 6.5. In Chapter 3 there is a description of the ordination (CCA, Ter Braak 1988) of summer riffle samples collected from all sites down the river, based on taxonomic units (Figs. 3.5 and 3.6). The taxa were assigned to FFGs and the ordination procedure repeated. Fig. 6.5 shows a site-environment biplot of these data. Site 0 is distinguished at the top of axis 1, with the other sites grouped together, along increasing gradients of pH, temperature, and sodium and aluminium ions. As with the classification procedure, the result from a FFG based analysis is very similar to that achieved using a taxonomic basis. NTU-turbidity, WT-water temperature, Mg-magnesium ions, Na-sodium ions, Al-aluminium ions, Ca-calcium ions, Cl-chloride ions, Fl-flouride ions, NH_4-ammonium ions.

Site 0 ◉ Site 1 △ Site 2B ▽ Site 2C • Site 3 ○ Site 4 □ Site 5 ■ Site 6 ⊖
Site 7 ⊠ Site 8 ○ Site 9 ▼ Site 10A ▲ Site 10B ⊠ Site 11 ◑ Site 12 • Site 13 ●

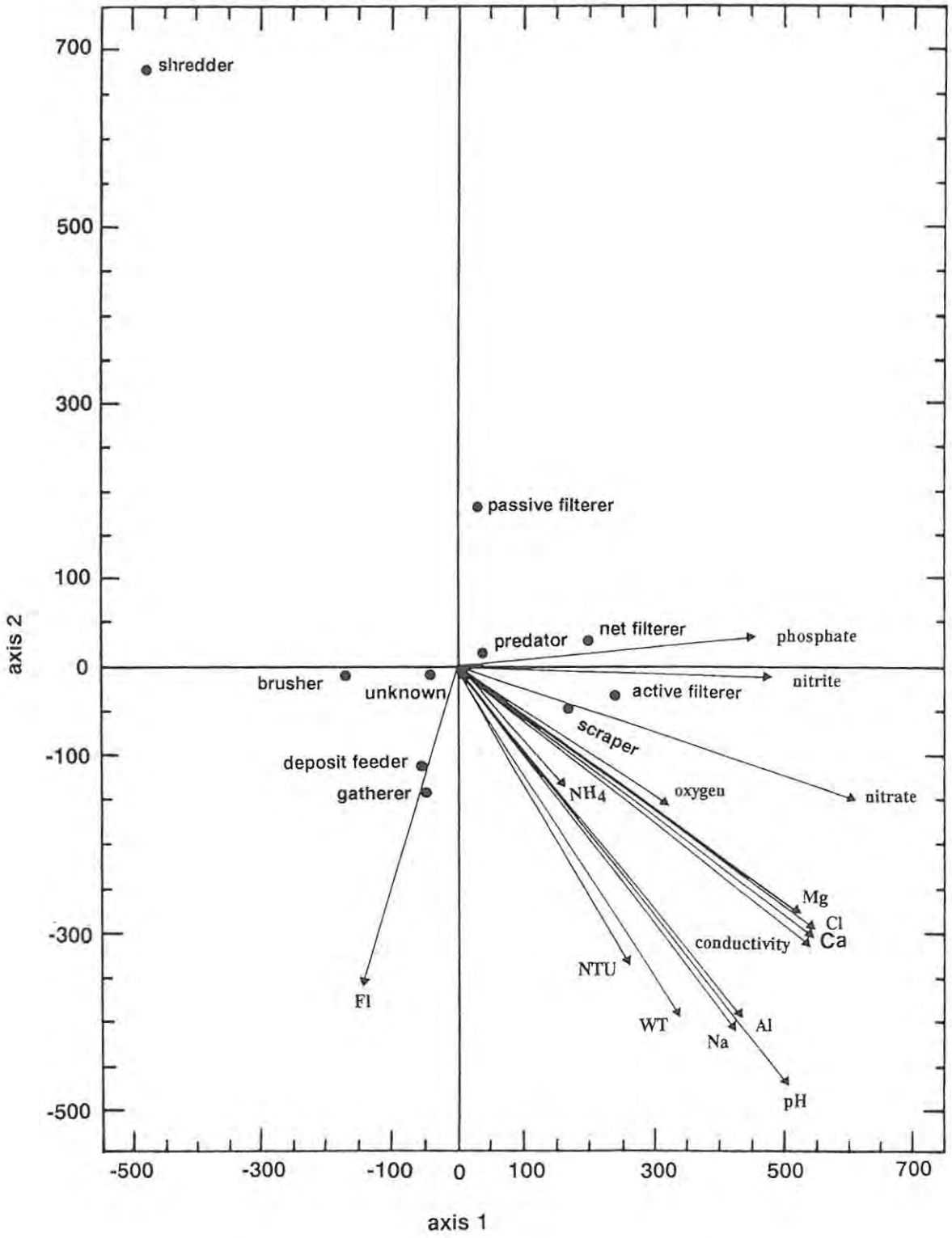


Fig. 6.6. A FFG-environment biplot for riffle samples collected from all sites in February 1987, following canonical correspondence analysis (CCA, Ter Braak 1988). Here FFGs are shown in relation to the environmental gradients. Shredders are clearly distinguished, and are associated with the low pH, temperature and dissolved ions of the headwater stream. NTU-turbidity, WT-water temperature, Mg-magnesium ions, Na-sodium ions, Al-aluminium ions, Ca-calcium ions, Cl-chloride ions, Fl-flouride ions, NH_4-ammonium ions.

In the FFG-environment bi-plot, the pattern of FFG distribution revealed by ordination correlated best to the increasing pH values from Site 0 downstream. The shredders were separated out at the top left corner of the diagram. Their position is the equivalent of the position of Site 0 in the site-environment bi-plot. The "unknown" FFG was located near the origin, which means it had a minimal effect on the structuring of the diagram. The next FFG along axis 1, was the brusher group. This FFG extended from Site 0, with the brusher A. auriculata, down to the middle/lower reaches with the other leptophlebiids. Predators were also near the origin, indicating an even distribution downstream. The second FFG down axis 2 was passive filterer. This is a reflection of the abundance of simuliids (the most abundant passive filterers) from the headwaters all the way down the river. The other FFGs, active filterers, gatherers, deposit feeders and scrapers, were spread out in positions equivalent to the general distribution of the middle/lower reaches sites. Again, the main pattern demonstrated in this analysis was the change from the shredder dominated headwaters down to the rest of the river with a variety of FFGs. The functional groups net filterer, active filterer, and scraper were grouped towards the right side of axis, indicating their relationship with the lower reaches, Sites 12 and 13.

6.4 Discussion

6.4.1. Classification of food items

The FFG categories described by Cummins (1973, 1974), and modified by McShaffrey and McCafferty (1988), were defined in morpho-behavioural terms. Yet studies on the feeding of stream macroinvertebrates more often included information on gut contents (see list of authors in Section 5.4) than behaviour and morphology (Brown 1960, 1961, 1965, McShaffrey and McCafferty 1986, 1988). Gut content analysis formed the foundation of this study, and

the aim of the first part of this chapter was to see if FFGs could be distinguished on the basis of gut contents.

In the headwaters the three shredder taxa were distinguished from the brusher on the basis of gut contents. The shredders had ingested mainly leaf particles, whereas the brusher had ingested a range of items, but mainly fine detritus (Level 1 Fig. 6.1). At subsequent levels in the classification (Fig. 6.1) there was no connection between diet and existing descriptions of FFGs. However, the classification did indicate that size was an important secondary determinant of diet, with biotope type 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. Periphyton has been shown to influence other species ecologically: its abundance affected the distribution of the caddisfly larva Helicopsyche borealis (Lamberti and 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). The inclusion of some small Afronemoura spp. in the collector group is an indication that although primarily shredders, fine detritus forms an important part of the diet of early instar stoneflies. On a scale from generalised collector to specialised shredder the taxa would be: A. auriculata, Afronemoura spp., D. ensifer and G. caffrariae.

In the middle/lower reaches fine microvores were distinguished from passive filterers (net) (Level 1, Fig. 6.2). The fine microvores were all Ephemeroptera which had ingested mainly fine detritus. The fine detritus feeding FFGs such as passive and active filterers, brushers and gatherers could not be distinguished on the basis of food items in the foregut. The net spinning Hydropsychidae were readily apparent from their gut

contents because of the inclusion of invertebrate prey in their diet. The second level discrimination of mayfly larvae which had not ingested inorganic silt particles was probably the result of the chance selection of microscope fields from which silt particles were absent, and seems to be of little biological interest or significance. At level 3 larvae which had ingested diatoms were distinguished from those which did not. The heptageniid A. harrisoni was the species with the highest frequency of diatoms in the foregut, and was equipped with specialised maxillary scraping bars. However not all A. harrisoni larvae had ingested diatoms, which may indicate temporal patchiness of this food type. In the absence of diatoms, the larvae fed on alternative food types such as fine detritus. The presence of diatoms in the foregut may be indicative of a scraping habit, but their absence does not mean the animal is not a scraper. The nature and utilization of tightly attached heterotrophic stone surface layers have been described in New Zealand (Rounick and Winterbourn 1983, Collier 1988) and the United Kingdom (Winterbourn et al. 1985).

Gut analysis did therefore provide some of the data necessary for the assigning of taxa to FFGs, and was particularly useful in the identification of shredders and net spinning filterers, though even these designations required behavioural confirmation.

6.4.2 FFG Classification

There was a pattern in the distribution of FFGs in the Buffalo River, and samples which were grouped together on the basis of their taxonomic identity (Fig. 6.3) were also grouped together on the basis of a functional identity (Fig. 6.4). Both functionally and taxonomically there was a clear difference between the headwaters and the middle/lower reaches (Level 1 Figs. 6.3 and 6.4). There was a distinct headwater fauna composed of waterfall assemblages characterised by passive filter

feeders, and stream assemblages distinguished by shredders and brushers. In the middle/lower reaches a distinct riffle fauna was characterised by filterers, and a stony backwater fauna by gatherers. Scrapers were common to both these biotopes. Throughout the river deposit feeding oligochaetes were characteristic of the sediments. These results closely resemble the FFG distribution predicted by the RCC (Vannote et al. 1980). In the case of the Buffalo River, Minshall's (1988) warning that the ecological meaning would be lost by collapsing the fauna into a few functional feeding groups was unfounded.

6.4.3 Ordination of riffle samples based on FFGs

Riffles constituted 70% by area of the upper reaches of the Buffalo River, and only 30% of the lower reaches, where pools and runs were the more common biotopes (Scott 1990). However riffles were the only biotope which had been sampled at all the sampling sites, and the relationship between environmental gradients and changes in FFG abundance in riffles along a downstream gradient was investigated. The result of the ordination (Figs. 6.5 and 6.6) showed that most of the variables measured in the Buffalo River increased along a downstream gradient, while the relative abundance of different FFGs followed the pH gradient most strongly. Other authors have noted shifts in the relative proportions of FFGs with changes in pH. Townsend et al. (1983) found that acid sites in the Ashdown forest, United Kingdom, had a fauna including shredders, collectors and predators, and that scrapers and filterers only became abundant at less acidic sites. In most acid streams in southern Ontario shredders were associated with lower pH values, and collectors with higher pH values (Mackay and Kersey 1985). Similarly, in the Buffalo River shredders were characteristic of Site 0 riffles (pH 5.3-7.3) while riffles further down the river (pH 7-8.9) contained all the other FFGs, with a preponderance of scrapers and gatherers in the lower

reaches. Winterbourn and Collier (1987) suggested that such shifts may have been a consequence of changes in food resources with pH.

One of the aims of the FFG concept was to provide an alternative classification of benthic macroinvertebrates in streams (Cummins 1974, Anderson and Sedell 1979). The need for an alternative basis for classification arose out of difficulties encountered in the identification of organisms to species, because of a paucity of taxonomic information. This is common in southern African streams where many taxa await description and common groups such as the baetid mayflies are in need of revision. There is evidence from this study that FFGs could be related to environmental gradients in a predictive manner. Functional classifications using FFGs could play a role in the management of ecosystems which are undergoing radical changes in habitat status. The achievement of a functional classification is no easier than a taxonomic one, and functional classifications are also likely to suffer from the problems of incompleteness mentioned by Cummins (1974). 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.

CHAPTER 7
CONCLUDING DISCUSSION

The River Continuum Concept (RCC) (Vannote et al. 1980) and the Functional Feeding Group (FFG) concept (Cummins 1973, 1974) have provided the conceptual framework for this thesis. A fourth order southern African river, the Buffalo River, in the eastern Cape was selected as the study site. The benthic assemblage structure was described and 16 abundant taxa were selected for feeding studies. While investigating the diets, and in most cases the feeding behaviour of these organisms, aspects of the FFG concept which had previously been confused (King et al. 1988, Barmuta 1988) were clarified: 1) dietary variability did not prevent taxa being assigned to FFGs; 2) gut content analysis provided basic data on feeding but additional methods were necessary in order to asssign taxa to FFGs; and 3) the FFG categories shredder, scraper and brusher were clearly defined. The spatial distribution of FFGs followed a discernible pattern and this was related to environmental variables. The FFG concept was therefore found to be both useful and usable. It was suggested that the idea of function in the FFG concept should incorporate the aspects of stream function which are facilitated by the feeding activities of stream invertebrates. Aspects of some of these contributions are amplified:

A description of the benthic fauna of the Buffalo River

The composition of macroinvertebrate assemblages in the headwaters was distinctly different from that of the middle/lower reaches. Additionally, biotope-assemblage associations were not apparent in the narrow headwater stream, but were detected in the wider middle/lower reaches. This was thought to reflect different spatial scales in the headwaters compared with the middle/lower reaches. Seasonal differences in assemblage composition were greater in the headwater stream than in the

middle/lower reaches. A characteristic headwater biotope, and one with a distinct fauna, was the waterfall, yet no references to waterfall fauna were found in the literature.

Dietary variability

The question dealt with most thoroughly in the thesis was that of dietary variablility. One of the areas of concern in the application of the FFG concept was the problem that benthic animals in streams have been thought to be such trophic opportunists and generalists, that the assigning of taxa to FFGs is meaningless. In the Buffalo River 16 numerically abundant taxa were collected seasonally from a range of biotopes and sites down the river. Foregut contents were used as an index of diet, and the dietary composition of both large and small individuals was compared spatially and temporally. In the course of this investigation nearly 1000 larvae were dissected, and differences in dietary composition were detected using ANOVA.

The results indicate that for these taxa, in this river, dietary variability was not so great as to prevent their being assigned to FFGs. There were clear patterns of variation in dietary composition. Leaf fragments were the most common food items found in the foreguts of three shredder taxa, but for the other 13 species fine detritus was the "staple diet". The most obvious and significant dietary differences were between large and small individuals. All small larvae except those of the headwater case-building caddisfly larvae, ingested undifferentiated fine detritus. Large larvae ingested a wider range of food items, and understandably, had more material in the foregut. Seasonal and spatial differences in dietary composition were most common between large larvae, and could be ascribed to differences in the proportions of rarer dietary items.

Definition of FFG terms

A basis for assigning taxa to the functional groups shredders, scrapers and brushers was defined. King et al. (1988) identified the confusion surrounding the terms scraper and shredder. It is suggested that the basis for the identification of shredders should be a predominance of leaf particles in the foregut and that the size of particle in the gut is irrelevant. The observation of shredding behaviour is also essential, so as to exclude the possibility that the leaf particles were gathered. It is suggested that McShaffrey and McCafferty's (1988) definition of scrapers as animals which feed on tightly accreted material should be followed. Scrapers should be identified on a morpho-behavioural basis (for example the possession of scraping bars and the observation of scraping behaviour) and not exclusively on the basis of the presence of algae in the gut, since tightly accreted heterotrophic stone surface layers might be used as a food resource. McShaffrey and McCafferty (1988) introduced the FFG category brusher, which seemed clearer than the equivalent term browser (Winterbourn et al. 1984). Taxa belonging to the brusher functional group should be recognised on a morpho-behavioural basis: the observation of brushing, and the possession of brushes, which were described for the first time.

Distribution of FFGs in the Buffalo River

It was not until FFGs had been clearly defined that their application could be investigated. It was possible to demonstrate a pattern in the distribution of FFGs in the Buffalo River. Functional groups were found to characterise both river reaches, (for example shredders in the headwaters), and biotopes (stony backwaters were inhabited by collectors). If the reliability of these patterns was established, in the Buffalo and other rivers, the use of FFGs as a monitoring tool could be investigated. Faith (1990) has shown that care must be taken to test that any relationship between FFGs and

environmental variables, which seems to be evident after ordination, is not simply random. This was not achieved in this study, so the link to a downstream increase in pH is tentative. This seems to be a promising area for future research.

The hypothesis that shredders are associated with acid headwaters, and scrapers and gatherers with the higher pH values of the middle/lower reaches could be tested. However, it is disconcerting that the level at which river reaches are characterised by particular FFGs is so coarse, and it might be questioned whether such an hypothesis is worth testing. Correlations of FFGs with particular water qualities were elusive. The sampling sites in the Buffalo River which were most polluted (Sites 8 and 13, Palmer and O'Keeffe 1990a) were not distinguished by either changes in taxonomic or FFG composition. This is a warning that either the organisms that have survived to inhabit the Buffalo River are resilient, or the scale and resolution at which the data have been collected or analysed is inappropriate. In either case future research should take these possibilities in account.

Use of the term "function"

The term "function" in the FFG concept has usually had a morpho-behavioural meaning, indicating the way in which organisms feed. In Cummins' (1973, 1974) early descriptions of FFGs, the idea was expressed that FFGs should enable an understanding of river function and this was reiterated by Barmuta and Lake (1982). River functions which could be facilitated by the feeding activities of macroinvertebrates have been listed in Chapter 4. Two examples are that shredders facilitate organic particle size reduction and mobilisation, and enhance organic surfaces for microbial colonisation; and that in riffles, passive filterers are responsible for the retention of organic particles, converting seston to

biomass and deposited faeces. Again these are hypotheses which require testing, but there is evidence that this could also be a worthwhile area for future research.

The role of macroinvertebrates in detritus processing is well documented (Anderson and Sedell 1979, Merritt et al. 1984). There is no doubt that interactions with detritus are important for aquatic insect larvae, but the importance of their feeding activities to the functioning of the stream needed to be established. Much of the evidence for this comes from experimental procedures in which insect larvae are removed from streams by the use of insecticides. In an Appalacian headwater stream, an immediate massive drift reaction resulted in the loss of macroinvertebrates; a reduction in both the rate at which leaf detritus was broken down, and the amount of leaf material that was converted to fine detritus; and downstream of the treated area there was a difference in the amount of transported organic matter, and in the quality and amount of fine benthic organic matter (Wallace et al. 1982, Cuffney et al. 1984, 1990). Two years after the treatment Wallace et al. (1986) found that the macroinvertebrate community had recovered. The taxonomic composition was different but the functional composition was restored: recovery of the shredder populations, comprising new taxa, led to the restoration of leaf litter processing rates (Wallace et al. 1986). Meyer and O'Hop (1983) showed that shredding also makes dissolved organic matter available in streams. These results indicate that macroinvertebrate feeding does mediate the stream processes of organic particle size reduction, retention and mobilisation, and consequently the downstream transport of fine particles. In a Japanese stream Yasuno and Okhita (1982) found that insecticide treatment altered stream processes and resulted in an algal bloom. Changes in the primary production of streams has also been reported as being biotically mediated. Both McAuliffe (1984) and Hart (1985) have reported activities

of grazers which altered the distribution of other primary consumers.

The insecticide studies were conducted in small headwater streams, equivalent to the headwaters of the Buffalo River. In view of the results reported in Chapter 3 concerning differences in spatial scales between headwater streams and larger lower reaches, it seems possible that the significant effect on stream process achieved by the removal of macroinvertebrates from a headwater stream may not be replicated at larger spatial scales. It would be useful to test the hypothesis that: while the feeding activities of macroinvertebrates in small headwater streams facilitate river processes, at higher stream orders physical processes are more important.

This thesis has tested the FFG concept, and aspects of the RCC in a southern African stream for the first time. Perhaps surprisingly, the results have supported both concepts in as far as they were tested. It does appear that in the Buffalo River, stream invertebrates can be assigned to FFGs, that abundant shredders are found in the headwaters, and that collectors characterise the middle/lower reaches. Hopefully, the clarification of FFG definitions, the comparison of a taxonomic and a functional classification, and a re-emphasis on stream function may facilitate future research in this field.

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APPENDIX 1.1

SUMMARY OF MULTIVARIATE METHODS USED IN THE THESIS

The data used in this study were collected, as ecological data frequently are, from several sites (multispatial) and on successive sampling occasions (multitemporal). Many taxa were collected, and several environmental variables were measured simultaneously for each sample. Consequently it was not possible to detect the effects of each single environmental variable on individual taxa or on assemblage composition (direct gradient analysis). In an effort to detect patterns which may be related to complex environmental gradients, multivariate techniques were used to analyse the data. This is indirect gradient analysis (Whittaker 1972). There are many indirect gradient analysis methods available (Gaugh 1982, Ter Braak and Prentice 1988), all of which arrange species and samples along ordination axes. Recent literature supports the choice of reciprocal averaging (Hill 1973) as the algorithm most successful in achieving an ordination pattern which can be related to a set of environmental variables (Parker 1991, Allen et al. 1991)

RECIPROCAL AVERAGING (Gaugh 1982)

Reciprocal averaging is an ordination technique which is computationally similar to principal component analysis and is conceptually similar to weighted averages (Gaugh 1982).

The species ordination scores are averages of the sample ordination scores and reciprocally, the sample ordination scores are averages of the species ordination scores (Hill 1973, Orloci 1975). At the first iteration, arbitrary species ordination scores are assigned. Samples scores are obtained from these species scores using weighted averages. The second iteration produces new species scores by weighted averages of the sample scores and similarly, new sample scores are produced by

weighted averages of the species scores. Iterations are repeated until the scores stablize, which is indicated by an insignificant change in species score between interations. The scores converge to a unique solution. Detailed equations may be found in Orloci (1975: pages 92-96).

TWINSPAN

Two-way indicator species analysis (TWINSPAN) (Cornell Ecological Programs 41; Hill 1979a) arranges sites into two distinct groups along the first axis of a reciprocal averaging ordination. Further dichotomous divisions are achieved using the presence, absence and relative abundances of indicator species. TWINSPAN simultaneously produces groups of species with similar distribution among sites. TWINSPAN is an improvement upon the original indicator species analysis (Hill et al. 1975) in that species are classified as well as samples.

DETRENDED CORRESPONDENCE ANALYSIS (DCA)

Detrended correspondence analysis (DCA)(Cornell Ecology Programs 40; Hill 1979 b; Hill and Gauch 1980) is an ordination procedure which removes the undesirable "arch effect" (Gauch 1982) found in a conventional reciprocal averaging (correspondence analysis) ordination. Sample scores are weighted mean species scores.

CANONICAL CORRESPONDENCE ANALYSIS (CCA)

Canonical correspondence analysis (CCA) (Ter Braak 1986) is an extension of correspondence analysis (CA), where an ordination diagram is interpreted with the help of external data by multiple regression of the ordination axes. The result is that the ordination axes appear in order of variance explained by linear combinations of environmental variables. (A sequence of samples is achieved using CA, and this sequence is improved using multiple regression of environmental variables, so the relationship between species, or changing assemblage structure, with these variables can be described.)

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APPENDIX 1.2

Several of the species mentioned in the thesis appear only in Figs. 3.1b and 3.3 and Table 3.1, where authors are not given. In the text Choroterpes (Choroterpes) nigrescens and Choroterpes (Euthraulus) elegans are called Choroterpes nigrescens and Choroterpes elegans. Baetis sp. A is so designated only for this study, and does not refer to any published species with the same designation. The genus Centroptilum has been revised, and many of the species of this genus have been designated Afroptilum (Gillies 1990). I have used Centroptilum.

Adenophlebia auriculata (Eaton)
Afronemoura amatole (Balinsky)
Afronemoura spinulata (Balinsky)
Afronurus harrisoni Barnard
Aprionyx peterseni (Lestage)
Baetis capensis Barnard
Baetis harrisoni Barnard
Castanophlebia calida Barnard
Centroptiloides bifasciatum (Esben-Petersen)
Centroptilum excisum Barnard
Centroptilum indusii Crass
Centroptilum pulchrum Crass
Centroptilum sudafricanum Lestage
Cheumatopsyche afra (Mosely)
Cheumatopsyche thomasetti (Ulmer)
Choroterpes (Choroterpes) nigrescens Barnard
Choroterpes (Euthraulus) elegans (Barnard)
Cloeon africanum Esben-Petersen
Dyschimus ensifer Barnard
Goerodes caffrariae (Barnard)
Macrostemum capense (Walker)
Neurocaenis reticulatus Barnard
Potomonautes perlatus (Milne-Edwards)
Pseudocloeon maculosum Crass
Simulium adersi Pomeroy

Simulium damnosum s.l. Theobald
Simulium dentulosum Roubard
Simulium hargreavsi Gibbins
Simulium medusaeforme Pomeroy
Simulium nigritarse Coquillett
Simulium rutherfoordi de Miellon
Simulium vorax Pomeroy

REFERENCE

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Appendix 2.1 Size comparisons: The gut contents of large larvae are compared with those of small larvae. Separate large versus small comparisons of larvae collected from different seasons and biotopes were made. Gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae were compared using a 3-way ANOVA with interaction. Interaction is explained in the text.

A. auriculata

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring, riffles					
sample	.0020215	2	.0010107	2.98	.0732
food	.3570724	10	.0357072	105.571	.0000
size	.0261366	1	.0261366	77.275	.0000
Interactions					
sample.food	.0065316	20	.0003266	.966	.5308
sample.size	.0022193	2	.0011096	3.281	.0586
food.size	.0468532	10	.0046853	13.853	.0000
Residual	.0067646	20	3.38229E-004		
Spring, stony backwaters					
sample	.0010986	2	.0005493	1.332	.2863
food	.0872831	10	.0087283	21.170	.0000
size	.0084246	1	.0084246	20.433	.0002
Interactions					
sample.food	.0078278	20	.0003914	.949	.5457
sample.size	.0036969	2	.0018484	4.483	.0246
food.size	.0157270	10	.0015727	3.814	.0052
Residual	.0082459	20	4.12296E-004		
Spring, leaf packs					
sample	.0011480	2	.0005740	5.758	.0106
food	.2089100	10	.0208910	209.558	.0000
size	.0035277	1	.0035277	35.387	.0000
Interactions					
sample.food	.0097081	20	.0004854	4.869	.0004
sample.size	.0006596	2	.0003298	3.308	.0574
food.size	.0106541	10	.0010654	10.687	.0000
Residual	.0019938	20	9.96906E-005		
Summer, riffles					
sample	.0008985	2	.0004492	1.170	.3308
food	.1434544	10	.0143454	37.351	.0000
size	.0027022	1	.0027022	7.036	.0153
Interactions					
sample.food	.0055580	20	.0002779	.724	.7621
sample.size	.0021245	2	.0010623	2.766	.0870
size.food	.0081559	10	.0008156	2.124	.0728
Residual	.0076813	20	3.84067E-004		
Summer, stony backwaters					
sample	.0013705	2	.0006852	.854	.4405
food	.2180554	10	.0218055	27.189	.0000
size	.0275502	1	.0275502	34.352	.0000
Interactions					
sample.food	.0097980	20	.0004899	.611	.8606
sample.size	.0030695	2	.0015348	1.914	.1736
food.size	.0466209	10	.0046621	5.813	.0004
Residual	.0160401	20	8.02007E-004		
Summer, leaf packs					
sample	.0005260	2	.0002630	.564	.5774
food	.1328079	10	.0132808	28.507	.0000
size	.0131639	1	.0131639	28.257	.0000
Interactions					
sample.food	.0079899	20	.0003995	.858	.6328
sample.size	.0023892	2	.0011946	2.564	.1020
food.size	.0196550	10	.0019655	4.219	.0030
Residual	.0093174	20	4.65870E-004		

Appendix 2.1 (continued)

Summer, riffles					
sample	.0005150	2	.0002575	7.130	.0037
food	.2004565	12	.0167047	462.592	.0000
size	.0017812	1	.0017812	49.326	.0000
Interactions					
sample.food	.0044293	24	1.84556E-004	5.111	.0001
sample.size	.0002779	2	1.38937E-004	3.847	.0355
food.size	.0092351	12	7.69595E-004	21.312	.0000
Residual	8.66666E-004	24	3.61111E-005		
Summer, stony backwaters					
sample	.0012083	2	.0006041	.354	.7057
food	.2311684	12	.0192640	11.279	.0000
size	.0110044	1	.0110044	6.443	.0180
Interactions					
sample.food	.0301837	24	.0012577	.736	.7705
sample.size	.0023521	2	.0011760	.689	.5119
food.size	.0418203	12	.0034850	2.040	.0662
Residual	.0409904	24	.0017079		
Summer, leaf packs					
sample	.0003432	2	.0001716	.284	.7555
food	.2913328	12	.0242777	40.122	.0000
size	.0026973	1	.0026973	4.458	.0453
Interactions					
sample.food	.0195257	24	.0008136	1.345	.2369
sample.size	.0043153	2	.0021577	3.566	.0441
food.size	.0210813	12	.0017568	2.903	.0127
Residual	.0145224	24			
Summer, sediments					
sample	.0001599	2	.0000799	.644	.5338
food	.2268350	12	.0189029	152.411	.0000
size	.0018478	1	.0018478	14.899	.0008
Interactions					
sample.food	.0043944	24	.0001831	1.476	.1733
sample.size	.0000242	2	.0000121	.098	.9073
food.size	.0128715	12	.0010726	8.648	.0000
Residual	.0029766	24	1.24026E-004		
Autumn, stony backwaters					
sample	.0027877	2	.0013938	1.555	.2318
food	.2321356	12	.0193446	21.578	.0000
size	.0107965	1	.0107965	12.043	.0020
Interactions					
sample.food	.0236575	24	.0009857	1.100	.4090
sample.size	.0024428	2	.0012214	1.362	.2751
food.size	.0407178	12	.0033932	3.785	.0027
Residual	.0215155	24	8.96478E-004		
Autumn, leaf packs					
sample	.0004212	2	.0002106	1.310	.2885
food	.2595189	12	.0216266	134.521	.0000
size	.0002315	1	.0002315	1.440	.2419
Interactions					
sample.food	.0048796	24	.0002033	1.265	.2848
sample.size	.0001563	2	.0000781	.486	.6210
food.size	.0132665	12	.0011055	6.877	.0000
Residual	.0038584	24	1.60768E-004		

Appendix 2.1 (continued)

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Autumn, stony backwaters					
sample	.0005337	2	.0002668	.487	.6216
food	.1747138	10	.0174714	31.885	.0000
size	.0159622	1	.0159622	29.131	.0000
Interactions					
sample.food	.0060732	20	.0003037	.554	.9022
sample.size	.0034535	2	.0017268	3.151	.0646
food.size	.0244371	10	.0024437	4.460	.0022
Residual	.0109590	20	5.47950E-004		
Autumn, leaf packs					
sample	.0018789	2	.0009395	3.068	.0688
food	.1423608	10	.0142361	46.495	.0000
size	.0010563	1	.0010563	3.450	.0780
Interactions					
sample.food	.0156910	20	.0007845	2.562	.0206
sample.size	.0000634	2	.0000317	.104	.9021
food.size	.0127795	10	.0012780	4.174	.0032
Residual	.0061237	20	3.06187E-004		
Autumn, sediments					
sample	.0024894	2	.0012447	2.789	.0854
food	.1193029	10	.0119303	26.730	.0000
size	.0279640	1	.0279640	62.655	.0000
Interactions					
sample.food	.0097064	20	.0004853	1.087	.4266
sample.size	.0021170	2	.0010585	2.372	.1191
food.size	.0311568	10	.0031157	6.981	.0001
Residual	.0089264	20	4.46319E-004		
Winter, stony backwaters					
sample	.0009136	2	.0004568	1.010	.3821
food	.2233315	10	.0223331	49.378	.0000
size	.0049336	1	.0049336	10.908	.0036
Interactions					
sample.food	.0313848	20	.0015692	3.470	.0038
sample.size	.0001291	2	.0000646	.143	.8678
food.size	.0055561	10	.0005556	1.228	.3320
Residual	.0090458	20	4.52292E-004		
Winter, leaf packs					
sample	.0027964	2	.0013982	2.538	.1042
food	.2343166	10	.0234317	42.529	.0000
size	.0256001	1	.0256001	46.465	.0000
Interactions					
sample.food	.0252545	20	.0012627	2.292	.0354
sample.size	.0002940	2	.0001470	.267	.7685
food.size	.0283750	10	.0028375	5.150	.0009
Residual	.0110192	20	5.50960E-004		

G. caffrariae

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring, leaf packs					
sample	.0002995	2	.0001498	.446	.6455
food	.1986393	12	.0165533	49.284	.0000
size	.0017550	1	.0017550	5.225	.0314
Interactions					
sample.food	.0110807	24	4.61694E-004	1.375	.2207
sample.size	.0001854	2	9.27243E-005	.276	.7611
food.size	.0060439	12	5.03655E-004	1.500	.1921
Residual	.0080610	24	3.35875E-004		

Appendix 2.1 (continued)

Winter, stony backwaters					
sample	.0014569	2	.0007284	1.257	.3026
food	.2487567	12	.0207297	35.770	.0000
size	.0011013	1	.0011013	1.900	.1808
Interactions					
sample.food	.0094945	24	.0003956	.683	.8219
sample.size	.0011650	2	.0005825	1.005	.3809
food.size	.0217412	12	.0018118	3.126	.0084
Residual	.0139085	24	5.79520E-004		
Winter, leaf packs					
sample	.0002871	2	.0001435	.374	.6922
food	.3245982	12	.0270499	70.407	.0000
size	.0054574	1	.0054574	14.205	.0009
Interactions					
sample.food	.0081217	24	.0003384	.881	.6208
sample.size	.0013475	2	.0006738	1.754	.1946
food.size	.0207472	12	.0017289	4.500	.0008
Residual	.0092207	24	3.84194E-004		

D.ensifer

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Summer, riffles.					
sample	.0003786	2	.0001893	.441	.6487
food	.2865217	12	.0238768	55.581	.0000
size	.0005369	1	.0005369	1.250	.2746
Interactions					
sample.food	.0036134	24	.0001506	.350	.9936
sample.size	.0004382	2	.0002191	.510	.6069
food.size	.0259508	12	.0021626	5.034	.0004
Residual	.0103101	24	9.78796E-004		
Summer, leaf packs					
sample	.0004970	2	.0002485	.924	.4105
food	.2318904	12	.0193242	71.870	.0000
size	.0056190	1	.0056190	20.898	.0001
Interactions					
sample.food	.0038743	24	.0001614	.600	.8907
sample.size	.0006303	2	.0003152	1.172	.3268
food.size	.0188455	12	.0015705	5.841	.0001
Residual	.0064531	24	2.68879E-004		
Autumn, stony backwaters					
sample	.0004607	2	.0002303	1.218	.3133
food	.2917300	12	.0243108	128.601	.0000
size	.0124779	1	.0124779	66.006	.0000
Interactions					
sample.food	.0080341	24	.0003348	1.771	.0844
sample.size	.0000060	2	.0000030	.016	.9842
food.size	.0910160	12	.0075847	40.122	.0000
Residual	.0045370	24	1.89041E-004		
Autumn, leaf packs					
sample	.0018500	2	.0009250	2.661	.0904
food	.3158267	12	.0263189	75.716	.0000
size	.0045277	1	.0045277	13.026	.0014
Interactions					
sample.food	.0075143	24	.0003131	.901	.6000
sample.size	.0014358	2	.0007179	2.065	.1487
food.size	.0688034	12	.0057336	16.495	.0000
Residual	.0083424	24	3.47599E-004		

Appendix 2.1 (continued)

Autumn, sediments					
sample	.0008298	2	.0004149	.422	.6607
food	.2744862	12	.0228738	23.249	.0000
size	.0103018	1	.0103018	10.471	.0035
Interactions					
sample.food	.0269343	24	.0011223	1.141	.3749
sample.size	.0014214	2	.0007107	.722	.4959
food.size	.0859463	12	.0071622	7.280	.0000
Residual	.0236127	24	9.83864E-004		
Winter, stony backwaters					
sample	.0008368	2	.0004184	5.086	.0144
food	.4020415	12	.0335035	407.267	.0000
size	.0011725	1	.0011725	14.253	.0009
Interactions					
sample.food	.0056224	24	.0002343	2.848	.0065
sample.size	.0001279	2	.0000640	.777	.4708
food.size	.0364449	12	.0030371	36.919	.0000
Residual	.0019743	24	8.22641E-005		
Winter, leaf packs					
sample	.0026306	2	.0013153	1.344	.2798
food	.3598874	12	.0299906	30.640	.0000
size	.0283906	1	.0283906	29.006	.0000
Interactions					
sample.food	.0166082	24	.0006920	.707	.7991
sample.size	.0000925	2	.0000463	.047	.9539
food.size	.1614962	12	.0134580	13.750	.0000
Residual	.0234911	24	9.78796E-004		

Afronemoura spp.

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring, riffles					
sample	.0000799	2	.0000399	.285	.7544
food	.0830535	12	.0069211	49.433	.0000
size	.0001956	1	.0001956	1.397	.2488
Interactions					
sample.food	.0027496	24	.0001146	.818	.6864
sample.size	.0003447	2	.0001724	1.231	.3098
food.size	.0192049	12	.0016004	11.431	.0000
Residual	.0033602	24	1.40009E-004		
Spring, leaf packs					
sample	.0044023	2	.0022011	2.367	.1153
food	.2213352	12	.0184446	19.832	.0000
size	.0005147	1	.0005147	.553	.4720
Interactions					
sample.food	.0437914	24	.0018246	1.962	.0528
sample.size	.0004012	2	.0002006	.216	.8075
food.size	.0046661	12	.0003888	.418	.9412
Residual	.0223208	24	9.30034E-004		
Summer riffles					
sample	.0008435	2	.0004217	1.227	.3108
food	.1566789	12	.0130566	38.001	.0000
size	.0065715	1	.0065715	19.127	.0002
Interactions					
sample.food	.0094208	24	.0003925	1.142	.3734
sample.size	.0005721	2	.0002860	.833	.4471
food.size	.0214032	12	.0017836	5.191	.0003
Residual	.0082459	24	3.43581E-004		

Appendix 2.1 (continued)

Summer, leaf packs					
sample	.0002316	2	.0001158	.283	.7563
food	.2148561	12	.0179047	43.680	.0000
size	.0024824	1	.0024824	6.056	.0214
Interactions					
sample.food	.0046831	24	.0001951	.476	.9624
sample.size	.0006737	2	.0003368	.822	.4517
food.size	.0168437	12	.0014036	3.424	.0050
Residual	.0098378	24	4.09907E-004		
Autumn, leaf packs					
sample	.0000284	2	.0000142	.065	.9372
food	.2132332	12	.0177694	81.401	.0000
size	.0019084	1	.0019084	8.742	.0069
Interactions					
sample.food	.0037947	24	1.58114E-004	.724	.7824
sample.size	.0001234	2	6.17204E-005	.283	.7562
food.size	.0054099	12	4.50825E-004	2.065	.0631
Residual	.0052391	24	2.18295E-004		
Winter,stony backwaters					
sample	.0000074	2	.0000037	.006	.9944
food	.1256087	12	.0104674	15.890	.0000
size	.0000124	1	.0000124	.019	.8937
Interactions					
sample.food	.0233232	24	.0009718	1.475	.1737
sample.size	.0001991	2	.0000996	.151	.8605
food.size	.0163103	12	.0013592	2.063	.0633
Residual	.0158095	24	6.58730E-004		
Winter, leaf packs					
sample	.0038926	2	.0019463	3.026	.0673
food	.2262740	12	.0188562	29.320	.0000
size	.0002054	1	.0002054	.319	.5832
Interactions					
sample.food	.0125812	24	5.24218E-004	.815	.6897
sample.size	.0013815	2	6.90738E-004	1.074	.3575
food.size	.0051329	12	4.27744E-004	.665	.7666
Residual	.0154347	24	6.43113E-004		
Winter, waterfall					
sample	.0003279	2	.0001639	.196	.8236
food	.1723178	12	.0143598	17.135	.0000
size	.0000881	1	.0000881	.105	.7521
Interactions					
sample.food	.0075346	24	.0003139	.375	.9902
sample.size	.0002849	2	.0001424	.170	.8447
food.size	.0300864	12	.0025072	2.992	.0108
Residual	.0201134	24	8.38059E-004		

Appendix 2.2 Biotope comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one biotope were compared with those of larvae collected from one or more different biotopes. In each 3-way ANOVA with interaction, the gut contents of one species, of one size, collected in one season, but from two or more biotopes were compared. Interaction is explained in the text.

A.auriculata

Spring large larvae (riffles, stony backwaters, leafpacks, sediments)					
sample	.0004216	2	.0002108	1.582	.2181
food	.1666817	10	.0166682	125.111	.0000
biotope	.0050319	2	.0025159	18.885	.0000
Interactions					
sample.food	.0070077	20	.0003504	2.630	.0045
sample.biotope	.0004608	4	.0001152	.865	.4935
food.biotope	.0217317	20	.0010866	8.156	.0000
Residual	.0053291	40	1.33227E-004		
Spring small larvae (riffles, stony backwaters, leafpacks)					
sample	.0004216	2	.0002108	1.582	.2181
food	.1666817	10	.0166682	125.111	.0000
biotope	.0050319	2	.0025159	18.885	.0000
Interactions					
sample.food	.0070077	20	.0003504	2.630	.0045
sample.biotope	.0004608	4	.0001152	.865	.4935
food.biotope	.0217317	20	.0010866	8.156	.0000
Residual	.0053291	40	1.33227E-004		
Summer large larvae (riffles, stony backwaters)					
sample	.0010380	2	.0005190	1.271	.3024
food	.3048809	10	.0304881	74.638	.0000
biotope	.0160855	1	.0160855	39.379	.0000
Interactions					
sample.food	.0122317	20	.0006116	1.497	.1872
sample.biotope	.0010957	2	.0005478	1.341	.2841
food.biotope	.0160459	10	.0016046	3.928	.0045
Residual	.0081696	20	4.08479E-004		
Summer small larvae (riffles, stony backwaters, leafpacks)					
sample	.0064292	2	.0032146	12.086	.0001
food	.1142237	10	.0114224	42.946	.0000
biotope	.0003872	2	.0001936	.728	.4892
Interactions					
sample.food	.0146429	20	7.32146E-004	2.753	.0032
sample.biotope	.0008144	4	2.03611E-004	.766	.5540
food.biotope	.0126208	20	6.31039E-004	2.373	.0099
Residual	.0106388	40	2.65970E-004		
Autumn large larvae (stony backwaters, leaf packs, sediments, pool)					
sample	.00303	2	.00152	3.11	.0528
food	.47627	9	.05292	108.53	.0000
biotope	.01108	3	.00369	7.57	.0003
Interactions					
sample.food	.02322	18	.00129	2.65	.0030
sample.biotope	.00629	6	.00105	2.15	.0623
food.biotope	.05323	27	.00197	4.04	.0000
Residual	.02633	54	.00049		
Autumn small larvae (stony backwaters, leaf packs, sediments)					
sample	.0002796	2	.0001398	.578	.5654
food	.1414097	10	.0141410	58.503	.0000
biotope	.0099357	2	.0049679	20.553	.0000
Interactions					
sample.food	.0036156	20	1.80780E-004	.748	.7541
sample.biotope	.0012022	4	3.00553E-004	1.243	.3082
food.biotope	.0165814	20	8.29070E-004	3.430	.0004
Residual	.0096686	40	2.41715E-004		

Appendix 2.2 (continued)

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Winter large larvae (stony backwaters, leaf packs, pool)					
sample	.0012362	2	.0006181	.835	.4413
food	.4606085	10	.0460609	62.225	.0000
biotope	.0100388	2	.0050194	6.781	.0029
Interactions					
sample.food	.0192485	20	.0009624	1.300	.2345
sample.biotope	.0037526	4	.0009381	1.267	.2988
food.biotope	.0325921	20	.0016296	2.201	.0166
Residual	.0296093	40	7.40232E-004		
Winter small larvae (stony backwaters, leaf packs)					
sample	.0011823	2	.0005911	.735	.4918
food	.1471094	10	.0147109	18.301	.0000
biotope	.0000854	1	.0000854	.106	.7512
Interactions					
sample.food	.0229315	20	.0011466	1.426	.2170
sample.biotope	.0003312	2	.0001656	.206	.8155
food.biotope	.0033896	10	.0003390	.422	.9193
Residual	.0160769	20	8.03845E-004		

G. caffrariae

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring large larvae (stony backwaters, leaf packs)					
sample	.0005142	2	.0002571	.211	.8111
food	.1618804	12	.0134900	11.080	.0000
biotope	.0001669	1	.0001669	.137	.7184
Interactions					
sample.food	.0249920	24	.0010413	.855	.6475
sample.biotope	.0002080	2	.0001040	.085	.9184
food.biotope	.0434002	12	.0036167	2.971	.0112
Residual	.0292198	24	.0012175		
Summer large larvae (riffles, stony backwaters, leaf packs, sediments)					
sample	.00006	2	.00003	.03	.9723
food	.70176	11	.06380	59.14	.0000
biotope	.00455	3	.00152	1.41	.2485
Interactions					
sample.food	.01758	22	.00080	.74	.7811
sample.biotope	.00539	6	.00090	.83	.5494
food.biotope	.03526	33	.00107	.99	.4990
Residual	.07119	66	.00108		
Summer small larvae (riffles, stony backwaters, leaf packs, sediments)					
sample	.00101	2	.00050	1.51	.2280
food	.26762	11	.02433	73.10	.0000
biotope	.00241	3	.00080	2.41	.0744
Interactions					
sample.food	.00574	22	.00026	.78	.7323
sample.biotope	.00362	6	.00060	1.81	.1104
food.biotope	.01093	33	.00033	.99	.4933
Residual	.02197	66	.00033		
Autumn large larvae (stony backwaters, leaf packs)					
sample	.00152	2	.00076	.72	.4979
food	.39878	11	.03625	34.39	.0000
biotope	.00471	1	.00471	4.46	.0462
Interactions					
sample.food	.02037	22	.00093	.88	.6183
sample.biotope	.00448	2	.00224	2.12	.1434
food.biotope	.00799	11	.00073	.69	.7347
Residual	.02319	22	.00105		

Appendix 2.2 (continued)

Autumn small larvae (stony backwaters, leaf packs)					
sample	.00023	2	.00011	.57	.5739
food	.15862	11	.01442	71.63	.0000
biotope	.00003	1	.00003	.14	.7104
Interactions					
sample.food	.00465	22	.00021	1.05	.4555
sample.biotope	.00008	2	.00004	.19	.8246
food.biotope	.00110	11	.00010	.50	.8850
Residual	.00443	22	.00020		
Winter large larvae (stony backwaters, leaf packs)					
sample	.00284	2	.00142	2.89	.0766
food	.38991	11	.03545	72.13	.0000
biotope	.00012	1	.00012	.24	.6300
Interactions					
sample.food	.02021	22	.00092	1.87	.0750
sample.biotope	.00099	2	.00050	1.01	.3807
food.biotope	.01150	11	.00105	2.13	.0635
Residual	.01081	22	.00049		
Winter small larvae (stony backwaters, leaf packs)					
sample	.00015	2	.00007	.24	.7875
food	.20032	11	.01821	59.27	.0000
biotope	.00099	1	.00099	3.23	.0859
Interactions					
sample.food	.00261	22	.00012	.39	.9850
sample.biotope	.00063	2	.00031	1.02	.3768
food.biotope	.00481	11	.00044	1.42	.2314
Residual	.00676	22	.00031		

D. ensifer

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring large larvae (leaf packs, sediments)					
asample	.00632	2	.00316	8.89	.0015
food	.45809	11	.04164	117.24	.0000
biotope	.00069	1	.00069	1.96	.1759
Interactions					
sample.food	.02588	22	.00118	3.31	.0035
sample.biotope	.00045	2	.00023	.64	.5372
food.biotope	.00407	11	.00037	1.04	.4459
Residual	.00781	22	.00036		
Summer large larvae (riffles, leaf packs)					
sample	.0003947	2	.0001974	.822	.4514
food	.3765570	12	.0313797	130.743	.0000
biotope	.0029794	1	.0029794	12.414	.0017
Interactions					
sample.food	.0057144	24	2.38100E-004	.992	.5077
sample.biotope	.0004289	2	2.14468E-004	.894	.4224
food.biotope	.0067788	12	5.64901E-004	2.354	.0359
Residual	.0057603	24	2.40011E-004		
Summer small larvae (riffles, stony backwaters, leaf packs, sediments)					
sample	.00105	2	.00052	.60	.5555
food	.50758	11	.04614	52.66	.0000
biotope	.00521	3	.00174	1.98	.1340
Interactions					
sample.food	.00832	22	.00038	.43	.9797
sample.biotope	.00047	6	.00008	.09	.9970
food.biotope	.03032	33	.00092	1.05	.4432
Residual	.03155	36	.00088		

Appendix 2.2 (continued)

Autumn large larvae (stony backwaters, leaf packs, sediments)					
sample	.00036	2	.00018	.12	.8844
food	.84946	11	.07722	52.26	.0000
biotope	.00108	2	.00054	.37	.6950
Interactions					
sample.food	.00587	22	.00027	.18	1.0000
sample.biotope	.00573	4	.00143	.97	.4340
food.biotope	.03464	22	.00157	1.07	.4159
Residual	.06502	44	.00148		
Autumn small larvae (stony backwaters, leaf packs, sediments)					
sample	.00014	2	.00007	.57	.5700
food	.20663	11	.01878	157.90	.0000
biotope	.00163	2	.00081	6.85	.0026
Interactions					
sample.food	.00235	22	.00011	.90	.5974
sample.biotope	.00028	4	.00007	.58	.6788
food.biotope	.01575	22	.00072	6.02	.0000
Residual	.00523	44	.00012		
Winter large larvae (Stony backwaters, leaf packs)					
sample	.0013455	2	.0006727	1.414	.2628
food	.4652404	12	.0387700	81.476	.0000
biotope	.0206386	1	.0206386	43.373	.0000
Interactions					
sample.food	.0185046	24	.0007710	1.620	.1221
sample.biotope	.0006894	2	.0003447	.724	.4949
food.biotope	.1738571	12	.0144881	30.447	.0000
Residual	.0114203	24	4.75846E-004		
Winter small larvae (stony backwaters, leaf packs)					
sample	.0015834	2	.0007917	4.896	.0165
food	.2787004	12	.0232250	143.620	.0000
biotope	.0034899	1	.0034899	21.581	.0001
Interactions					
sample.food	.0138901	24	.0005788	3.579	.0014
sample.biotope	.0000696	2	.0000348	.215	.8080
food.biotope	.0420721	12	.0035060	21.681	.0000
Residual	.0038811	24	1.61712E-004		

Afronemoura spp.

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Spring large larvae (riffles, leaf packs)					
sample	.0010448	2	.0005224	.685	.5137
food	.1458452	12	.0121538	15.935	.0000
biotope	.0028402	1	.0028402	3.724	.0655
Interactions					
sample.food	.0244134	24	.0010172	1.334	.2429
sample.biotope	.0017540	2	.0008770	1.150	.3335
food.biotope	.0227596	12	.0018966	2.487	.0277
Residual	.0183045	24	7.62689E-004		
Spring small larvae (riffles, leaf packs)					
sample	.0006370	2	.0003185	.598	.5580
food	.1170143	12	.0097512	18.301	.0000
biotope	.0038432	1	.0038432	7.213	.0129
Interactions					
sample.food	.0167163	24	.0006965	1.307	.2583
sample.biotope	.0017922	2	.0008961	1.682	.2072
food.biotope	.0426406	12	.0035534	6.669	.0000
Residual	.0127877	24	5.32823E-004		

Appendix 2.2 (continued)

Summer large larvae (riffles, leaf packs)					
sample	.0004246	2	.0002123	.582	.5667
food	.3109468	12	.0259122	70.985	.0000
biotope	.0000255	1	.0000255	.070	.7967
Interactions					
sample.food	.0098859	24	4.11913E-004	1.128	.3849
sample.biotope	.0014767	2	7.38334E-004	2.023	.1543
food.biotope	.0059548	12	4.96234E-004	1.359	.2513
Residual	.0087610	24	3.65041E-004		
Summer small larvae (riffles, leaf packs)					
sample	.0003133	2	.0001567	.890	.4237
food	.0909886	12	.0075824	43.092	.0000
biotope	.0006861	1	.0006861	3.899	.0599
Interactions					
sample.food	.0093178	24	3.88240E-004	2.206	.0291
sample.biotope	.0001063	2	5.31460E-005	.302	.7421
food.biotope	.0018918	12	1.57649E-004	.896	.5632
Residual	.0042230	24	1.75957E-004		
Autumn large larvae (stony backwaters, leaf packs, waterfall)					
sample	.00009	2	.00004	.16	.8538
food	.22451	11	.02041	74.63	.0000
biotope	.00489	2	.00245	8.94	.0006
Interaction					
sample.food	.00485	22	.00022	.81	.7027
sample.biotope	.00027	4	.00007	.25	.9087
food.biotope	.06360	22	.00289	10.57	.0000
Residual	.01203	44	.00027		
Autumn small larvae (sediments, leaf packs, waterfall)					
	.04146	1	.04146	235.79	.0000
sample	.00002	2	.00001	.04	.9567
food	.14668	11	.01333	75.83	.0000
biotope	.00014	2	.00007	.39	.6800
Interaction					
sample.food	.00438	22	.00020	1.13	.3538
sample.biotope	.00035	4	.00009	.49	.7399
food.biotope	.01065	22	.00048	2.75	.0021
Residual	.00774	44	.00018		
Winter large larvae (stony backwaters, leaf packs, waterfall)					
sample	.00091	2	.00045	.89	.4178
food	.37402	11	.03400	66.84	.0000
biotope	.00016	2	.00008	.16	.8525
Interactions					
sample.food	.00652	22	.00030	.58	.9130
sample.biotope	.00025	4	.00006	.12	.9732
food.biotope	.01782	22	.00081	1.59	.0936
Residual	.02238	44	.00051		
Winter small larvae (stony backwaters, leaf packs, waterfall)					
sample	.00153	2	.00076	.67	.5163
food	.14168	11	.01288	11.31	.0000
biotope	.00021	2	.00011	.09	.9116
sample.food	.01436	22	.00065	.57	.9196
sample.biotope	.00404	4	.00101	.89	.4803
food.biotope	.03075	22	.00140	1.23	.2752
Residual	.05011	44	.00114		

Appendix 2.3 Seasonal comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one season were compared with those of larvae collected from one or more different seasons. In each 3-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. Interaction is explained in the text.

A. auriculata

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Large larvae, riffles (spring, summer)					
sample	.0054201	2	.0027101	11.918	.0004
food	.3847517	10	.0384752	169.196	.0000
season	.0154841	1	.0154841	68.092	.0000
Interactions					
sample.food	.0096597	20	.0004830	2.124	.0500
sample.season	.0004496	2	.0002248	.988	.3896
food.season	.0449014	10	.0044901	19.746	.0000
Residual	.0045480	20	2.27399E-004		
Small larvae, riffles (spring, summer)					
sample	.0001030	2	.0000515	.119	.8885
food	.1232913	10	.0123291	28.473	.0000
season	.0002175	1	.0002175	.502	.4941
Interactions					
sample.food	.0036675	20	1.83376E-004	.423	.9692
sample.season	.0012911	2	6.45529E-004	1.491	.2492
food.season	.0025915	10	2.59151E-004	.598	.7968
Residual	.0086603	20	4.33015E-004		
Large larvae, stony backwaters (spring, summer, autumn, winter)					
sample	.00174	2	.00087	.93	.4014
food	.48947	9	.05439	57.90	.0000
season	.01715	3	.00572	6.09	.0012
Interactions					
sample.food	.00598	18	.00033	.35	.9911
sample.season	.00727	6	.00121	1.29	.2779
food.season	.04845	27	.00179	1.91	.0216
Residual	.05073	54	.00094		
Small larvae, stony backwaters (spring, summer, autumn, winter)					
sample	.00089	2	.00045	.77	.4675
food	.17287	9	.01921	33.24	.0000
season	.01229	3	.00410	7.09	.0004
Interactions					
sample.food	.00865	18	.00048	.83	.6569
sample.season	.00611	6	.00102	1.76	.1243
food.season	.03008	27	.00111	1.93	.0202
Residual	.03121	54	.00058		
Large larvae, leaf packs (spring, autumn, winter)					
sample	.0014430	2	.0007215	1.338	.2739
food	.3698527	10	.0369853	68.576	.0000
season	.0240038	2	.0120019	22.253	.0000
Interactions					
sample.food	.0179954	20	.0008998	1.668	.0831
sample.season	.0039599	4	.0009900	1.836	.1410
food.season	.0378514	20	.0018926	3.509	.0004
Residual	.0215734	40	5.39334E-004		

Appendix 2.3 (continued)

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Small larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00040	2	.00020	.45	.6394
food	.22342	9	.02482	55.84	.0000
season	.00512	3	.00171	3.84	.0146
Interactions					
sample.food	.01212	18	.00067	1.51	.1213
sample.season	.00312	6	.00052	1.17	.3362
food.season	.02405	27	.00089	2.00	.0150
Residual	.02401	54	.00044		
Large larvae, sediments (spring, autumn)					
sample	.0032391	2	.0016195	1.666	.2141
food	.3937862	10	.0393786	40.519	.0000
season	.0007538	1	.0007538	.776	.3982
Interactions					
sample.food	.0402601	20	.0020130	2.071	.0558
sample.season	.0054200	2	.0027100	2.788	.0855
food.season	.0179464	10	.0017946	1.847	.1166
Residual	.0194372	20	9.71861E-004		
Large larvae, pool (autumn, winter)					
sample	.0025828	2	.0012914	2.521	.1056
food	.3647231	10	.0364723	71.198	.0000
season	.0023965	1	.0023965	4.678	.0428
Interactions					
sample.food	.0082829	20	4.14145E-004	.808	.6805
sample.season	.0004411	2	2.20533E-004	.431	.6561
food.season	.0098383	10	9.83833E-004	1.921	.1028
Residual	.0102453	20	5.12263E-004		

G. caffrariae

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Large larvae, stony backwaters (spring, summer, autumn, winter)					
sample	.00453	2	.00227	1.31	.2765
food	.68133	11	.06194	35.77	.0000
season	.00299	2	.00150	.86	.4258
Interactions					
sample.food	.05746	22	.00261	1.51	.0989
sample.season	.00800	4	.00200	1.15	.3380
food.season	.05208	22	.00237	1.37	.1617
sample.food.season	.12556	44	.00285	1.65	.0295
Residual	.12467	72	.00173		
Small larvae, stony backwaters (summer, autumn, winter)					
sample	.00010	2	.00005	.18	.8337
food	.21942	11	.01995	73.09	.0000
season	.00124	2	.00062	2.27	.1153
Interactions					
sample.food	.00762	22	.00035	1.27	.2456
sample.season	.00060	4	.00015	.55	.6988
food.season	.01048	22	.00048	1.75	.0575
Residual	.01201	44	.00027		
Large larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00021	2	.00011	.17	.8473
food	.73828	11	.06712	104.14	.0000
season	.00457	3	.00152	2.36	.0792
Interactions					
sample.food	.01247	22	.00057	.88	.6192
sample.season	.00336	6	.00056	.87	.5233
food.season	.03091	33	.00094	1.45	.0985
Residual	.04254	66	.00064		

Appendix 2.3 (continued)

Small larvae, leaf packs (spring, summer, autumn, winter)

sample	.00076	2	.00038	1.36	.2633
food	.34053	11	.03096	111.12	.0000
season	.00193	3	.00064	2.31	.0847
Interactions					
sample.food	.00462	22	.00021	.75	.7673
sample.season	.00375	6	.00062	2.24	.0498
food.season	.00830	33	.00025	.90	.6186
Residual	.01839	66	.00028		

D. ensifer

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Large larvae, stony backwaters (summer, autumn, winter)					
sample	.0002223	2	.0001111	.376	.6908
food	.4186075	12	.0348840	117.946	.0000
season	.0038566	1	.0038566	13.040	.0014
Interactions					
sample.food	.0033429	24	.0001393	.471	.9644
sample.season	.0002700	2	.0001350	.456	.6389
food.season	.0977968	12	.0081497	27.555	.0000
Residual	.0070983	24	2.95763E-004		
Small larvae, stony backwaters (summer, autumn, winter)					
sample	.00061	2	.00031	1.24	.3006
food	.32480	11	.02953	118.81	.0000
season	.00762	2	.00381	15.33	.0000
Interactions					
sample.food	.00362	22	.00016	.66	.8497
sample.season	.00122	4	.00031	1.23	.3114
food.season	.06665	22	.00303	12.19	.0000
Residual	.01094	44	.00025		
Large larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00521	2	.00260	2.59	.0868
food	.61881	11	.05626	55.85	.0000
season	.01212	2	.00606	6.02	.0049
Interactions					
sample.food	.00813	22	.00037	.37	.9933
sample.season	.00204	4	.00051	.51	.7316
food.season	.18315	22	.00832	8.26	.0000
Residual	.04432	44	.00101		
Small larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00061	2	.00031	1.37	.2644
food	.24201	11	.02200	98.50	.0000
season	.00012	2	.00006	.27	.7633
Interactions					
sample.food	.00884	22	.00040	1.80	.0485
sample.season	.00082	4	.00021	.92	.4601
food.season	.00741	22	.00034	1.51	.1219
Residual	.00983	44	.00022		
Large larvae, sediments (spring, summer, autumn)					
sample	.0030717	2	.0015359	2.628	.0929
food	.5617103	12	.0468092	80.084	.0000
season	.0000589	1	.0000589	.101	.7570
Interactions					
sample.food	.0485617	24	.0020234	3.462	.0017
sample.season	.0012982	2	.0006491	1.111	.3457
food.season	.0058028	12	.0004836	.827	.6231
Residual	.0140280	24	5.84498E-004		

Appendix 2.3 (continued)

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Small larvae, sediments (spring, summer, winter)					
sample	.0002230	2	.0001115	.516	.6034
food	.1189198	12	.0099100	45.858	.0000
season	.0006779	1	.0006779	3.137	.0892
Interactions					
sample.food	.0016692	24	6.95516E-005	.322	.9963
sample.season	.0001112	2	5.56238E-005	.257	.7752
food.season	.0085775	12	7.14788E-004	3.308	.0061
Residual	.0051865	24	2.16103E-004		

Afronemoura spp.

Source of variation	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Large larvae, stony backwaters (autumn, winter)					
sample	.0000397	2	.0000198	.110	.8959
food	.1971913	12	.0164326	91.502	.0000
season	.0007876	1	.0007876	4.386	.0470
Interactions					
sample.food	.0014610	24	6.08757E-005	.339	.9948
sample.season	.0000894	2	4.47187E-005	.249	.7816
food.season	.0023361	12	1.94676E-004	1.084	.4146
Residual	.0043101	24	1.79588E-004		
Large larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00165	2	.00083	1.14	.3265
food	.53339	11	.04849	66.76	.0000
season	.00154	3	.00051	.71	.5507
Interactons					
sample.food	.01127	22	.00051	.71	.8184
sample.season	.00267	6	.00044	.61	.7196
food.season	.01833	33	.00056	.76	.7988
Residual	.04794	66	.00073		
Small larvae, leaf packs (spring, summer, autumn, winter)					
sample	.00264	2	.00132	1.93	.1535
food	.29937	11	.02722	39.73	.0000
season	.00821	3	.00274	4.00	.0112
Interactions					
sample.food	.01170	22	.00053	.78	.7416
sample.season	.00520	6	.00087	1.27	.2850
food.season	.03543	33	.00107	1.57	.0608
Residual	.04521	66	.00068		
Small larvae, sediments (summer, autumn)					
sample	.00021	2	.00010	.44	.6466
food	.06229	11	.00566	24.06	.0000
season	.00013	1	.00013	.56	.4614
Interactions					
sample.food	.01225	22	.00056	2.37	.0246
sample.season	.00010	2	.00005	.22	.8081
food.season	.01493	11	.00136	5.76	.0002
Residual	.00518	22	.00024		
Large larvae, waterfall (autumn, winter)					
sample	.00019	2	.00010	.75	.4863
food	.06139	11	.00558	42.74	.0000
season	.00009	1	.00009	.64	.4234
Interactions					
sample.food	.00204	22	.00009	.71	.7869
sample.season	.00030	2	.00015	1.15	.3360
food.season	.00447	11	.00041	3.11	.0112
Residual	.00287	22	.00013		

Appendix 2.3 (continued)

Small larvae, waterfall (autumn, winter)					
sample	.00060	2	.00030	.40	.6731
food	.15879	11	.01444	19.24	.0000
season	.00231	1	.00231	3.07	.0935
Interactions					
sample.food	.01126	22	.00051	.68	.8116
sample.season	.00016	2	.00008	.11	.8989
food.season	.04883	11	.00444	5.92	.0002
Residual	.01650	22	.00075		

Appendix 2.4 Size comparisons: The gut contents of large larvae are compared with those of small larvae. Separate large versus 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 3-way ANOVA with interaction. Interaction is explained in the text.

		F-value	Food/size interaction	Sig.
Baetidae				
Baetis harrisoni				
Site 1	Su RIF:	5.46	0.00	0.03
Site 2c	Su RIF:	9.02	0.06	0.01
Site 3	Su RIF:	0.33	0.00	0.59
Site 6	Su RIF:	3.54	0.04	0.10
	A RIF :	39.66	0.00	0.00
	Sp RIF :	56.80	0.01	0.00
Site 7	Su RIF:	23.35	0.00	0.00
Site 8	Su RIF:	36.93	0.00	0.00
Site 10a	Su RIF:	4.54	0.17	0.05
Site 11	Su RIF:	10.86	0.00	0.00
Site 12	Su RIF:	3.04	0.00	0.11
	A RIF:	12.10	0.20	0.01
	Sp RIF:	3.50	0.03	0.09
Site 13	Su RIF:	2.96	0.00	0.12
Pseudocloeon maculosum				
Site 12	Su RIF:	22.893	0.010	0.008
	A RIF:	3.340	0.107	0.117
	W RIF:	18.401	0.010	0.005
	Sp RIF:	4.733	0.149	0.161
Site 13	Su RIF:	17.149	0.001	0.006
Cloeon africanum				
Site 6	Su BW :	4.919	0.397	0.057
	MVO:	8.860	0.040	0.024
	A BW :	5.242	0.115	0.041
	Sp BW :	217.681	0.000	0.000
Site 12	Su BW :	1.554	0.103	0.259
	MVO:	0.397	0.015	0.552
	A BW :	6.825	0.000	0.031
	W BW :	4.393	0.207	0.625
	Sp BW :	1.552	0.068	0.280
Centroptilum excisum				
Site 6	A BW :	34.581	0.004	0.000
Site 12	W BW :	3.853	0.318	0.097
	Sp BW :	3.158	0.032	0.105

Appendix 2.4 (continued)

			F-value	Food/size interaction	Sig.
Heptageniidae					
Afronurus harrisoni					
Site 1	Su	RIF:	31.507	0.020	0.000
Site 2c	Su	RIF:	61.020	0.008	0.000
Site 6	A	BW :	2.682	0.229	0.132
Site 10a	Su	RIF:	69.166	0.005	0.000
Site 12	Su	RIF:	35.697	0.015	0.000
		BW :	52.228	0.000	0.000
	A	RIF:	18.345	0.030	0.002
		BW :	2.860	0.254	0.166
	W	RIF:	13.471	0.457	0.010
		BW :	26.091	0.032	0.002
Site 13	Su	RIF:	14.407	0.169	0.005
Leptophlebiidae					
Choroterpes elgans					
Site 5	Su	RIF:	28.273	0.064	0.000
Site 6	Su	RIF:	30.819	0.266	0.000
	A	RIF:	52.023	0.000	0.000
		BW :	34.803	0.003	0.001
	W	BW :	20.640	0.017	0.003
Site 7	Su	RIF:	55.528	0.000	0.000
Site 10a	Su	RIF:	19.895	0.000	0.001
Site 10b	Su	RIF:	12.381	0.005	0.012
Site 12	Su	RIF:	11.358	0.000	0.007
	A	RIF:	4.592	0.038	0.098
	W	RIF:	14.081	0.035	0.009
Site 13	Su	RIF:	254.62	0.000	0.000
Choroterpes nigrescens					
Site 6	A	BW :	9.069	0.120	0.039
	W	BW :	26.543	0.087	0.002
Caenidae					
Caenidae sp. A					
Site 5	Su	RIF:	4.381	0.648	0.062
Site 6	Su	RIF:	0.350	0.438	0.581
	W	BW :	0.940	0.350	0.370
Site 7	Su	RIF:	2.715	0.810	0.138
Site 8	Su	RIF:	0.174	0.443	0.689
Site 10a	Su	RIF:	2.124	0.094	0.183
Site 12	Su	BW :	2.972	0.029	0.159
	A	BW :	0.002	0.957	0.961
Site 13	Su	RIF:	0.013	0.705	0.914
Caenidae sp. B					
Site 12	Su	RIF:	0.959	0.124	0.366
	A	RIF:	1.121	0.136	0.050
	W	RIF:	8.584	0.027	0.042

Appendix 2.4 (continued)

			F-value	Food/size interaction	Sig.
Trichorythidae					
Neurocaenis reticulatus					
Site 5	Su	RIF:	22.703	0.003	0.000
Site 6	A	RIF:	6.576	0.549	0.028
	W	RIF:	43.171	0.145	0.000
Site 7	Su	RIF:	18.366	0.081	0.005
Site 11	Su	RIF:	19.531	0.008	0.004
Site 12	Su	RIF:	41.406	0.001	0.000
	A	RIF:	30.837	0.001	0.000
	W	RIF:	56.891	0.000	0.000
	Sp	RIF:	14.680	0.041	0.008
Site 13	Su	RIF:	32.289	0.000	0.000
Hydropsychidae					
Macrostemum capense					
Site 1	Su	RIF:	18.270	0.000	0.001
Site 5	Su	RIF:	32.345	0.089	0.000
Site 6	A	RIF:	29.666	0.000	0.000
	W	RIF:	31.789	0.027	0.000
	Sp	RIF:	6.237	0.354	0.028
Site 7	Su	RIF:	3.138	0.702	0.095
Site 11	Su	RIF:	8.131	0.199	0.014
Site 12	Su	RIF:	16.122	0.001	0.001
	A	RIF:	7.116	0.139	0.018
	W	RIF:	50.253	0.102	0.000
Site 13	Su	RIF:	16.916	0.020	0.001
Cheumatopsyche afra					
Site 1	Su	RIF:	9.444	0.180	0.008
Site 5	Su	RIF:	14.185	0.006	0.002
Site 6	A	RIF:	36.850	0.000	0.000
	W	RIF:	3.508	0.841	0.082
	Sp	RIF:	30.936	0.004	0.000
Site 7	Su	RIF:	37.527	0.000	0.000
Site 11	Su	RIF:	13.215	0.208	0.006
Site 12	Su	RIF:	0.337	0.009	0.578
	A	RIF:	46.981	0.004	0.000
	W	RIF:	10.237	0.011	0.009
	Sp	RIF:	12.743	0.056	0.003
Site 13	Su	RIF:	16.305	0.131	0.006

Appendix 2.5 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. In each 3-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. Interaction is explained in the text.
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.

				F-value	Food/size interaction	Sig.
Baetidae						
Baetis harrisoni						
Su	RIF	L	(Sites 1,2c,3,6,7,8,10a, 11,12,13)	:4.11	0.00	0.000
		S	(Sites 1,2c,3,6,7,8,10a, 11,12,13)	:4.64	0.607	0.000
Pseudocloeon maculosum						
Su	RIF	L	(Sites 12,13)	:0.491	0.140	0.529
		S	(Sites 12,13)	:0.004	0.007	0.954
Cloeon africanum						
Su	BW	L	(Sites 6,12)	:0.501	0.159	0.506
		S	(Sites 6,12)	:0.906	0.995	0.404
	MVO	L	(Sites 6,12)	:2.480	0.011	0.165
		S	(Sites 6,12)	:0.081	0.754	0.805
A	BW	L	(Sites 6,12)	:1.086	0.132	0.327
		S	(Sites 6,12)	:0.713	0.614	0.431
W	BW	L	(Sites 6,12)	:1.473	0.482	0.259
Sp	BW	L	(Sites 6,12)	:2.444	0.160	0.193
Centroptilum excisum						
Sp	BW	S	(Sites 6,12)	:0.095	0.196	0.768
Heptageniidae						
Afronurus harrisoni						
Su	RIF	L	(Sites 1,2c,5,10a,12,13)	:4.860	0.00	0.002
		S	(Sites 1,2c,5,10a,12,13)	:2.600	0.002	0.075
Leptophlebiidae						
Choroterpes elegans						
Su	RIF	L	(Sites 5,6,7,10a,12 13)	:7.970	0.005	0.000
		S	(Sites 5,6,7,10a,12,13)	:1.480	0.000	0.205

Appendix 2.5 (continued)

	F-value	Food/size interaction	Sig.
Caenidae			
Caenidae sp. A			
Su RIF L (Sites 5,6,7,8, 10a,12,13)	:1.060	0.977	0.389
S (Sites 5,6,7,8, 10a,12,13)	:0.540	0.745	0.706
Caenidae sp. B			
Su RIF L (Site 12,13)	:0.473	0.122	0.518
Tricorythidae			
Neurocaenis reticulatus			
Su RIF L (Sites 2b,5,7,11,12,12)	:2.350	0.727	0.065
S (Sites 2b,5,7,11,12,12)	:1.302	0.223	0.290
Hydropsychidae			
Macrostemum capense			
Su RIF L (Site 1,5,7,11,12,13)	:4.830	0.053	0.000
S (Site 1,5,7,11,12,13)	:3.720	0.054	0.008
Cheumatopsyche afra			
Su RIF L (Site 1,5,7,11,12,13)	:103.900	0.000	0.000
S (Site 1,5,7,11,12,13)	:4.030	0.000	0.003

Appendix 2.6 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. In each 3-way ANOVA with interaction, the gut contents of one species, of one size, collected from one biotope and one site, but in two or more seasons were compared. Interaction is explained in the text.
Seasons: Sp-spring, Su-summer, A-autumn, W-winter.
Biotopes: RIF-riffle, BW-stony backwaters.
Sizes: L-large, S-small.

				F-value	Food/size interaction	Sig.
Baetidae						
Baetis harrisoni						
RIF	L	Site 6	(Su, A, Sp) :	33.198	0.000	0.000
	S	6	(Su, A, Sp) :	0.795	0.265	0.468
	L	Site 12	(Su, A, Sp) :	2.111	0.006	0.143
	S	12	(Su, A, Sp) :	0.023	0.020	0.977
Pseudocloeon maculosum						
RIF	L	Site 12	(Su, A, W, Sp):	3.898	0.010	0.026
	S	Site 12	(Su, A, W, Sp):	4.156	0.000	0.014
Cloeon africanum						
BW	L	Site 6	(Su, A, W, Sp):	0.286	0.144	0.835
		12	(Su, A, W, Sp):	1.834	0.892	0.167
BW	S	Site 6	(Su, A,) :	0.001	0.696	0.975
		12	(Su, A, W, Sp):	0.366	0.400	0.778
Centroptilum excisum						
BW	L	Site 12	(W, Sp) :	0.999	0.645	0.357
BW	S	Site 6	(A, W) :	0.108	0.050	0.754
		12	(W, Sp) :	0.464	0.272	0.521
RIF	L	Site 12	(W, Sp) :	10.126	0.047	0.013
Heptageniidae						
Afonurus harrisoni						
BW	L	Site 12	(Su, A, W) :	17.516	0.000	0.000
	S		(Su, A, W) :	1.594	0.041	0.243
RIF	L	Site 12	(A, W) :	5.568	0.155	0.012
RIF	S	Site 12	(A, W) :	0.831	0.435	0.450
Leptophlebiidae						
Choroterpes elegans						
RIF	L	Site 6	(Su, A) :	19.432	0.546	0.001
		12	(Su, A, W, Sp):	15.372	0.029	0.000
RIF	S	Site 6	(Su, A) :	1.684	0.424	0.242
		12	(Su, A, W) :	0.538	0.400	0.594
BW	L	Site 6	(A, W) :	1.276	0.304	0.291
	S	Site 6	(A, W) :	0.031	0.743	0.867

Appendix 2.6 (continued)

		F-value	Food/size interaction	Sig.
Caenidae				
Caenidae sp. A				
BW L Site 12 (Su, A)	:	2.794	0.448	0.125
S Site 12 (Su, A)	:	2.815	0.244	0.144
Caenidae sp. B				
RIF L Site 12 (Su, A, W, Sp)	:	0.269	0.023	0.847
S Site 12 (Su, A, W)	:	3.960	0.033	0.040
Tricorythidae				
Neurocaenis reticulatus				
RIF L Site 6 (A, W, Sp)	:	0.037	0.109	0.852
12 (A, W, Sp)	:	0.075	0.924	0.928
RIF S Site 6 (A, W, Sp)	:	0.525	0.355	0.602
12 (A, W, Sp)	:	3.364	0.184	0.603
Hydropsychidae				
Macrostemum capense				
RIF L Site 6 (A, W, Sp)	:	5.045	0.000	0.013
12 (Su,A, W)	:	6.054	0.269	0.006
RIF S Site 6 (A, W, Sp)	:	0.502	0.190	0.602
12 (Su,A, W, Sp)	:	0.674	0.715	0.573
Cheumatopsyche afra				
RIF L Site 6 (A, W, Sp)	:	2.235	0.138	0.791
12 (A, W, Sp)	:	0.780	0.001	0.467
RIF S Site 6 (A, W, Sp)	:	7.345	0.143	0.002
12 (A, W, Sp)	:	2.237	0.099	0.128

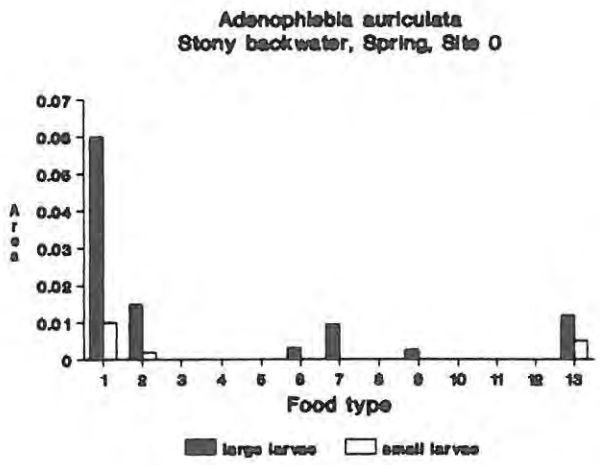
Appendix 2.7 Biotope comparisons: The gut contents of A. auriculata, G. caffrariae, D. ensifer and Afronemoura spp. larvae collected in one biotope were compared with those of larvae collected from one or more different biotopes (given in brachets). In each 3-way ANOVA with interaction, the gut contents of one species, of one size, collected in one season, but from two or more biotopes 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, MV-marginal vegetation (out of current).
Sizes: L - large, S - small.

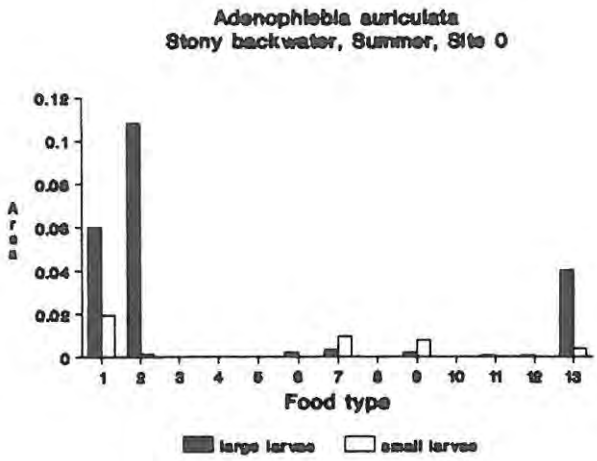
		F-value	Food/biotope Interaction	Sig.
Baetidae				
Cloeon africanum				
Su Site 6	L (BW, MV) :	1.203	0.805	0.304
	S (BW, MV) :	0.007	0.374	0.935
Su Site 12	L (BW, MV) :	0.429	0.146	0.543
	S (BW, MV) :	0.081	0.647	0.788
Centroptilum excisum				
Sp Site 12	L (BW, RIF):	2.139	0.575	0.181
W Site 12	L (BW, RIF):	0.824	0.890	0.400
Heptageniidae				
Afronurus harrisoni				
A Site 12	L (BW, RIF):	1.231	0.001	0.293
	S (BW, RIF):	2.085	0.178	0.222
W Site 12	L (BW, RIF):	0.006	0.514	0.939
	S (BW, RIF):	0.001	0.393	0.982
Leptophlebiidae				
Choroterpes elegans				
A Site 6	L (BW, RIF):	1.415	0.256	0.268
	S (BW, RIF):	0.006	0.073	0.940
Caenidae				
Caenidae sp. A				
Su Site 12	L (BW, RIF):	0.496	0.553	0.515

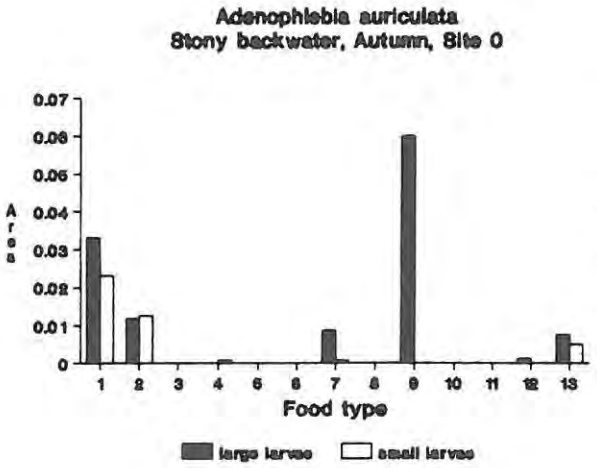
APPENDIX 3

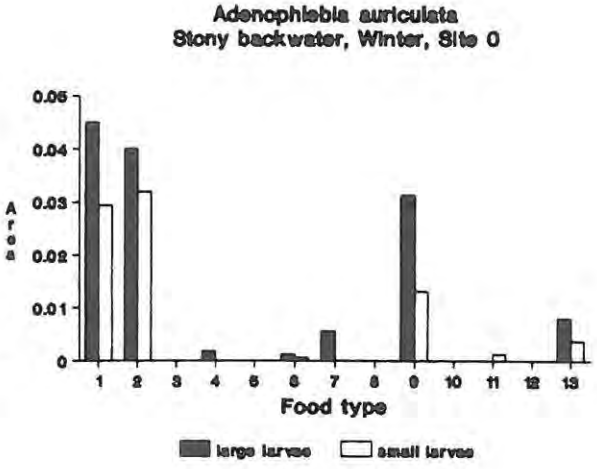
GUT ANALYSIS DATA

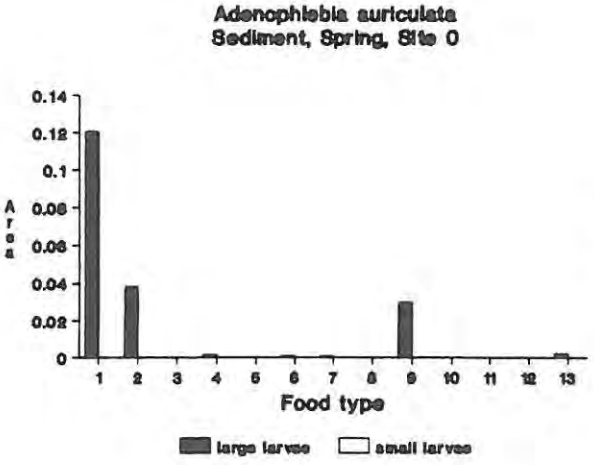
For each of the 16 taxa selected for feeding studies, three large and three small individuals collected from each site, season, and biotope were dissected. Slides of gut contents were prepared and enumerated as described in the text. The gut contents of the three replicate individuals were shown to be not significantly ($p< 0.05$) different. Bar charts of the gut contents of one individual from each taxon under each of the sampling conditions are given. On each bar chart the units of y axis (area) are mm^2. Food types 1-13 (headwater taxa) and 1-11 (middle/lower reaches taxa) are listed in Chapter 4 (Section 4.2.6) and Chapter 5 (Section 5.2.1) respectively.

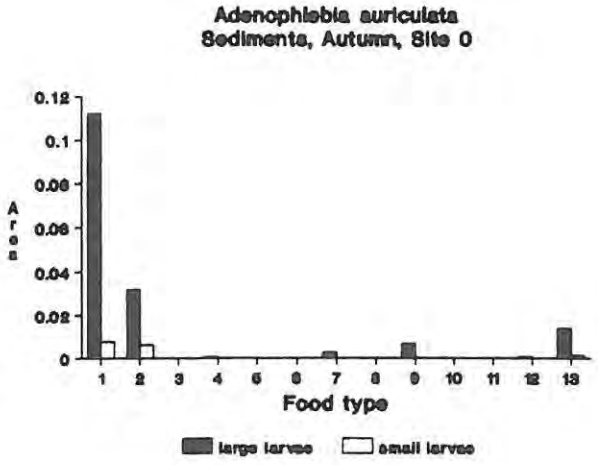

Adenophlebia auriculata
Stony backwater, Spring, Site 0
Area
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

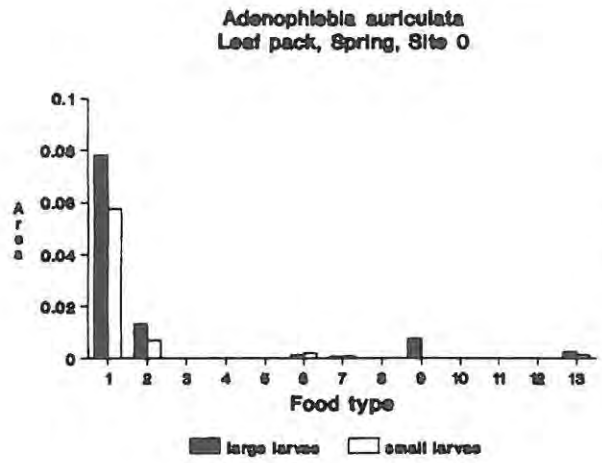

Adenophlebia auriculata
Stony backwater, Summer, Site 0
Area
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

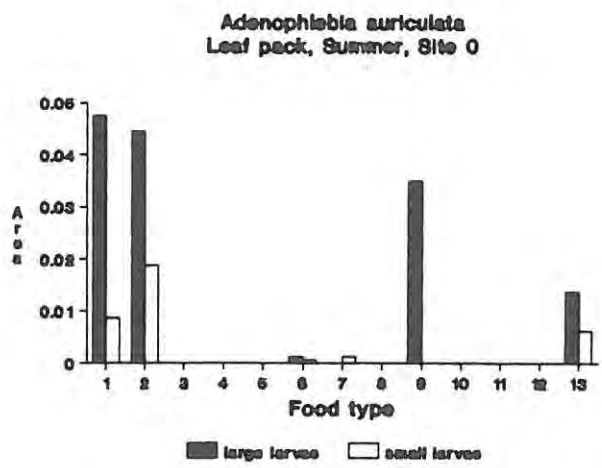

Adenophlebia auriculata
Stony backwater, Autumn, Site 0
Area
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

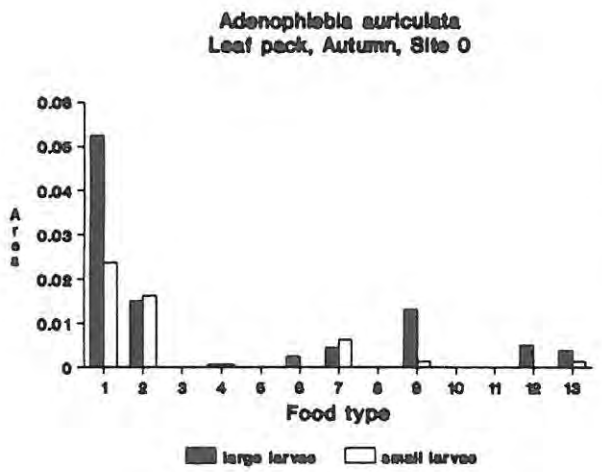

Adenophlebia auriculata
Stony backwater, Winter, Site 0
Area
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

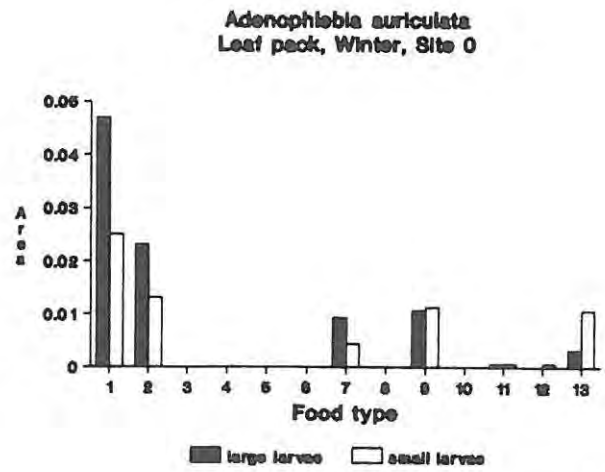

Adenophlebia auriculata
Sediment, Spring, Site 0
Area
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

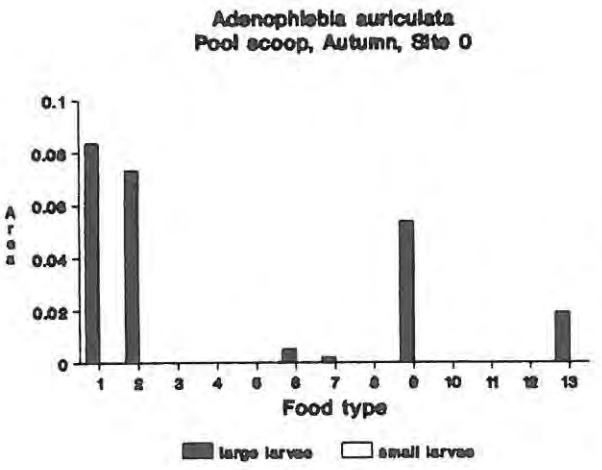

Adenophlebia auriculata
Sediments, Autumn, Site 0
Area
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

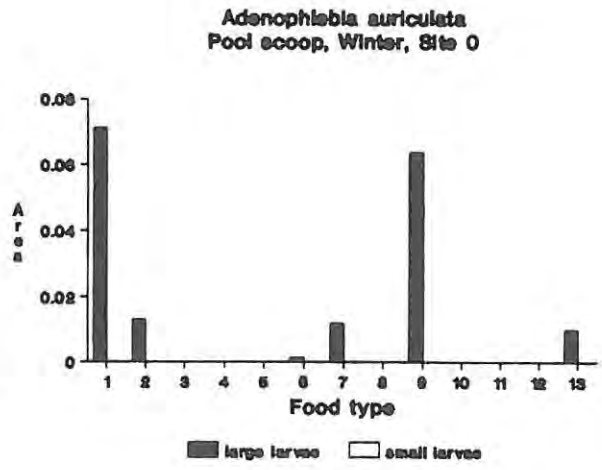

Adenophlebia auriculata
Leaf pack, Spring, Site 0
Area
Food type
large larvae
small larvae

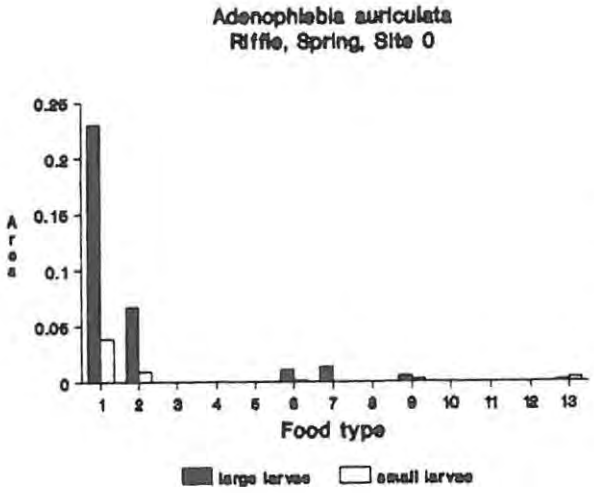

Adenophlebia auriculata
Leaf pack, Summer, Site 0
Area
Food type
large larvae
small larvae

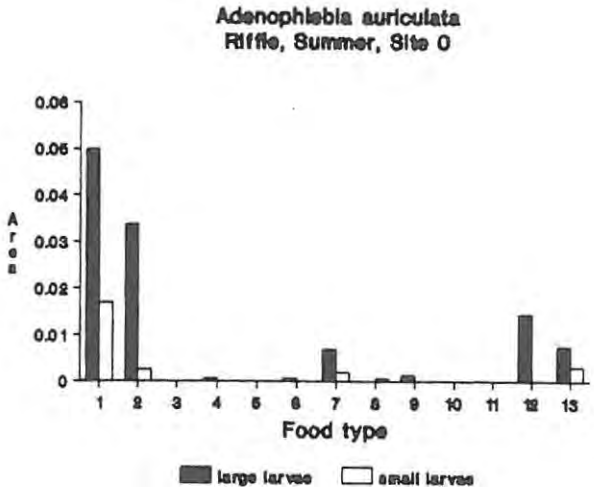

Adenophlebia auriculata
Leaf pack, Autumn, Site 0
Area
Food type
large larvae
small larvae

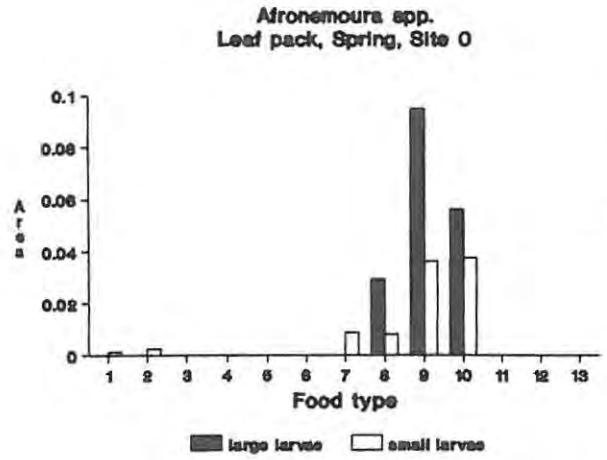

Adenophlebia auriculata
Leaf pack, Winter, Site 0
Area
Food type
large larvae
small larvae

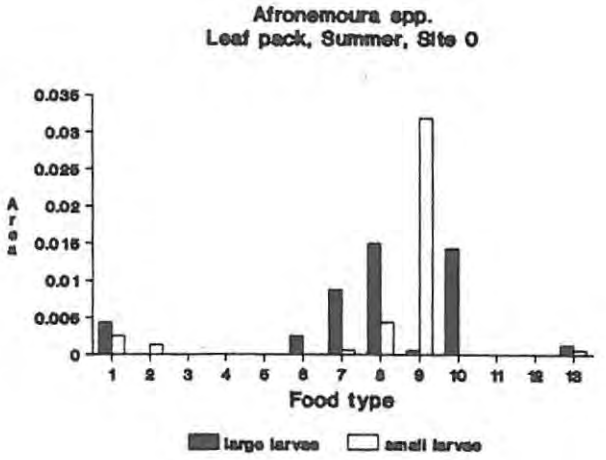

Adenophlebia auriculata
Pool scoop, Autumn, Site 0
Area
Food type
large larvae
small larvae

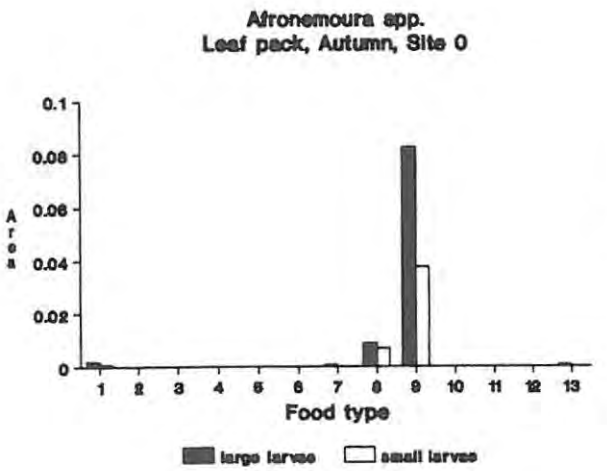

Adenophlebia auriculata
Pool scoop, Winter, Site 0
Area
Food type
large larvae
small larvae

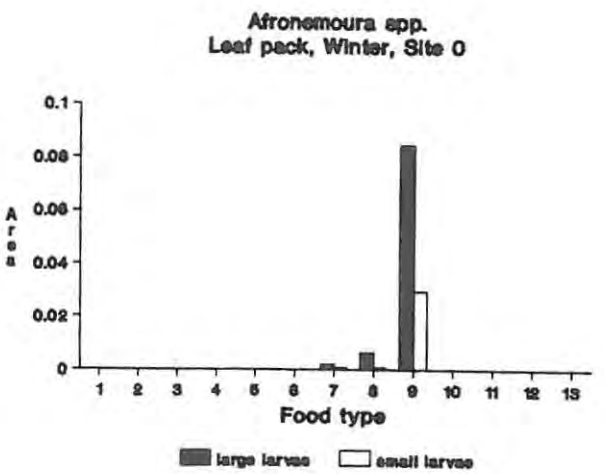

Adenophlebia auriculata
Riffle, Spring, Site 0
Area
0.25
0.2
0.15
0.1
0.05
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

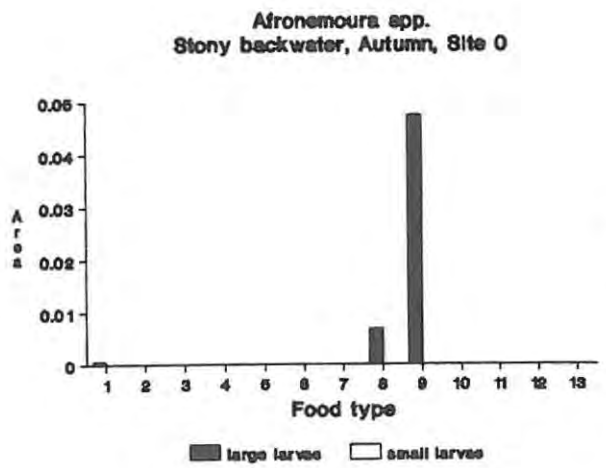

Adenophlebia auriculata
Riffle, Summer, Site 0
Area
0.06
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

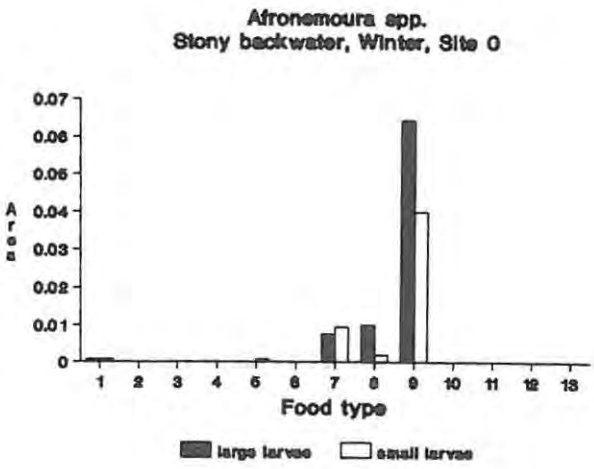

Afronemoura spp.
Leaf pack, Spring, Site 0
Area
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae


Afronemoura spp.
Leaf pack, Summer, Site 0
Area
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae


Afronemoura spp.
Leaf pack, Autumn, Site 0
Area
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

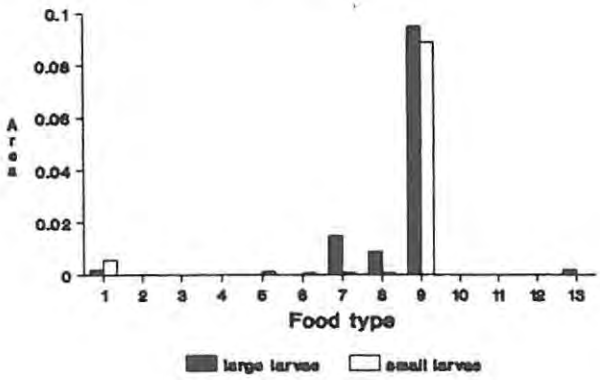

Afronemoura spp.
Leaf pack, Winter, Site 0
Area
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae


Afronemoura spp.
Stony backwater, Autumn, Site 0
Area
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

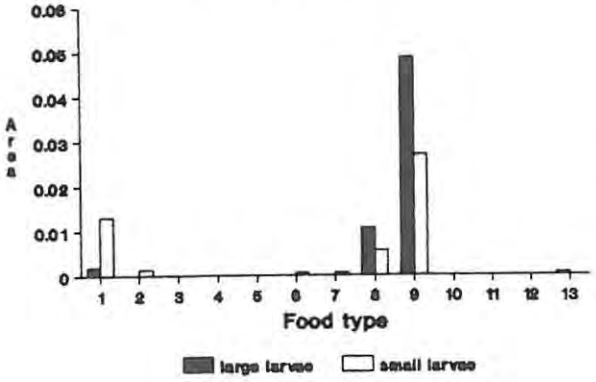

Afronemoura spp.
Stony backwater, Winter, Site 0
Area
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

Afronemoura spp.
Riffle, Spring, Site 0

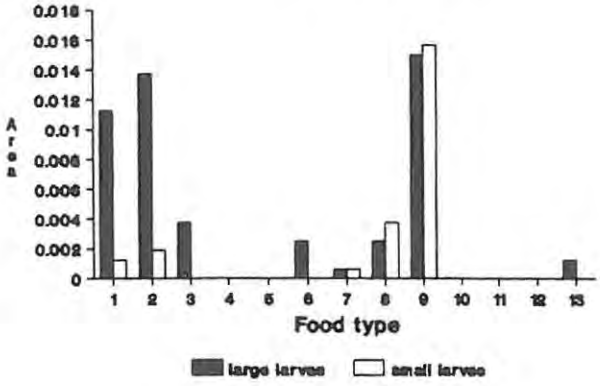
Afronemoura spp.
Riffle, Summer, Site 0



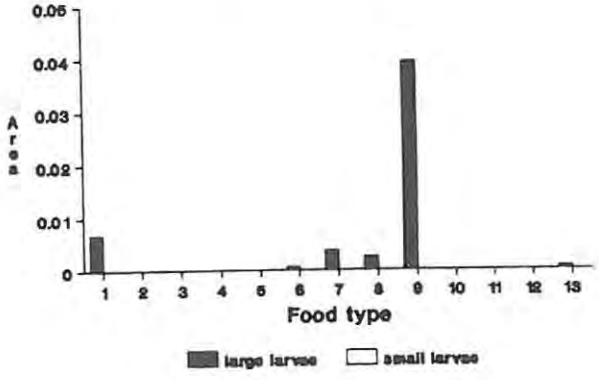
Afronemoura spp.
Waterfall, Winter, Site 0



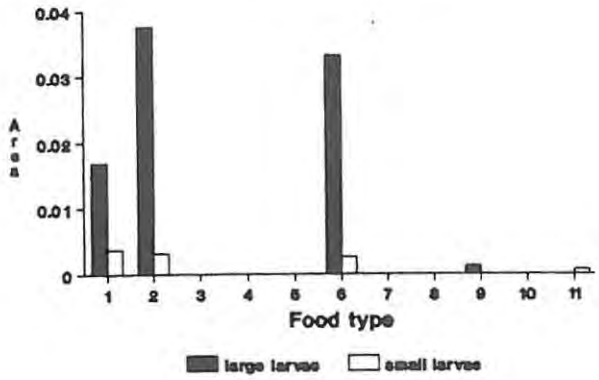
Afronemoura spp.
Waterfall, Autumn, Site 0



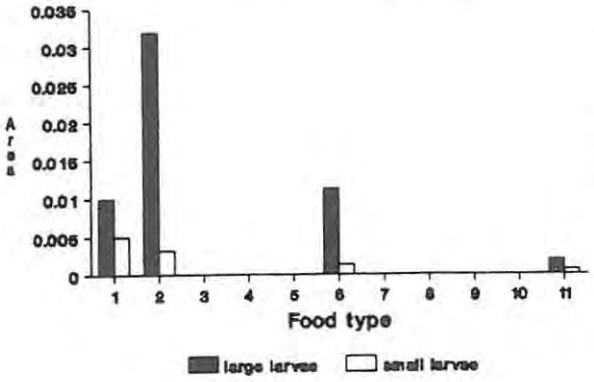
Afronemoura spp.
Leaf disc experiment



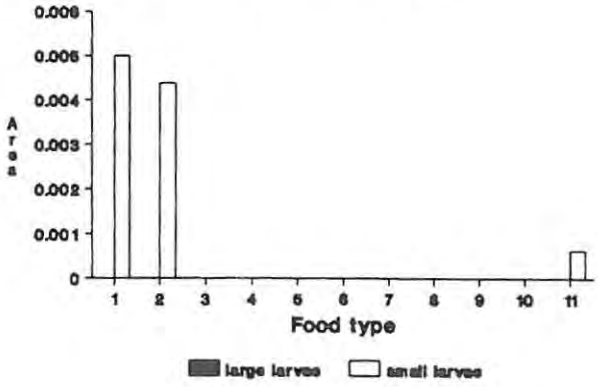
Afronurus harrisoni
Riffle, Summer, Site 1



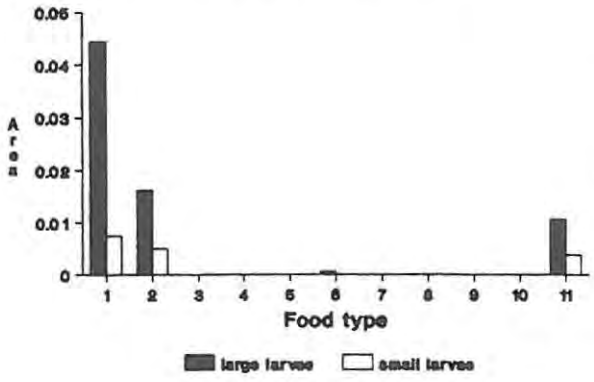
Afronurus harrisoni
Riffle, Summer, Site 2c



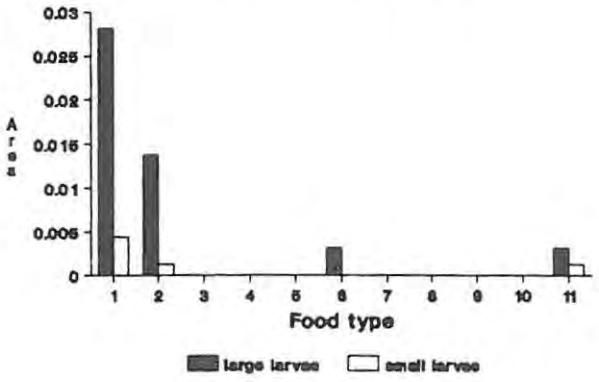
Afronurus harrisoni
Riffle, Summer, Site 5



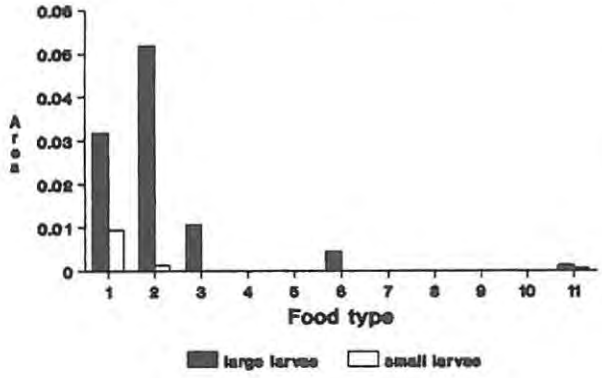
Afronurus harrisoni
Riffle, Summer, Site 10a



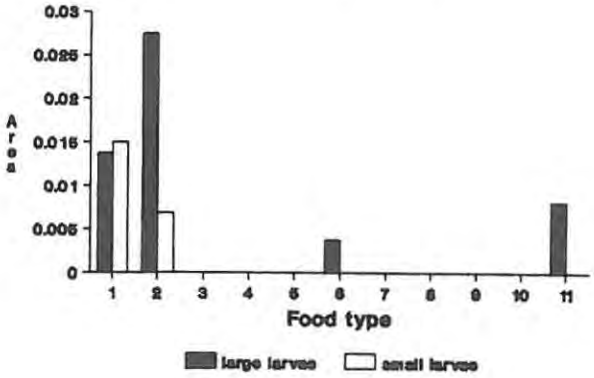
Afronurus harrisoni
Riffle, Summer, Site 12



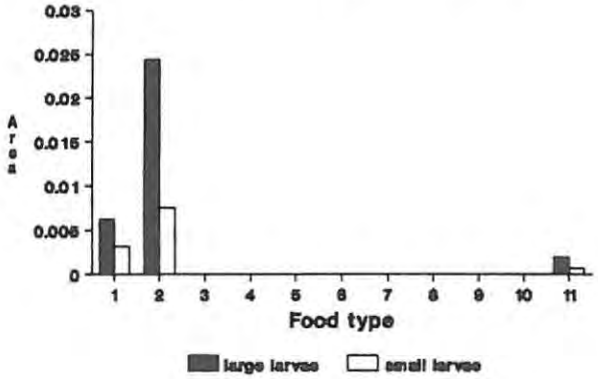
Afronurus harrisoni
Stony backwater, Summer, Site 12



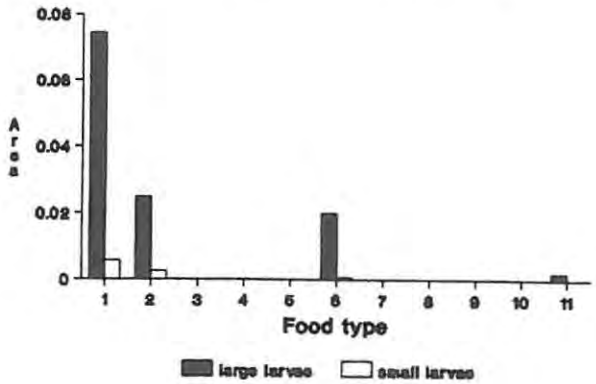
Afronurus harrisoni
Stony backwater, Autumn, Site 6



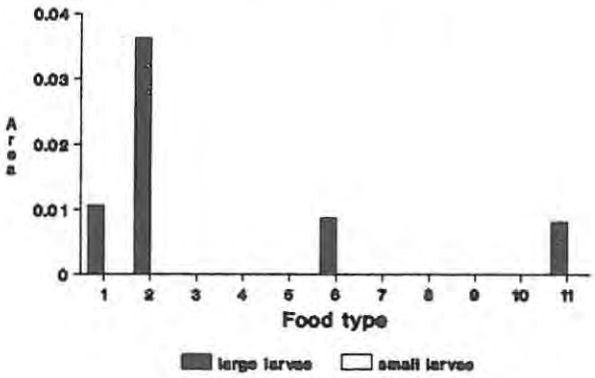
Afronurus harrisoni
Stony backwater, Autumn, Site 12



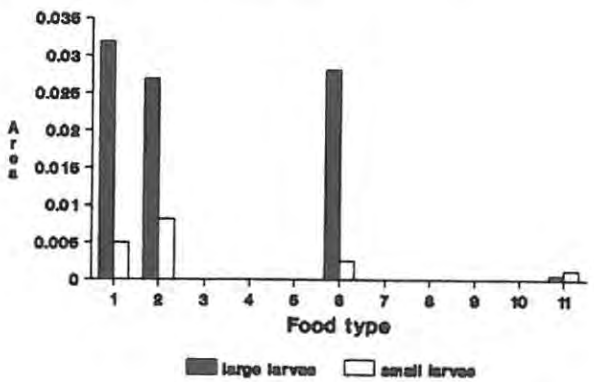
Afronurus harrisoni
Stony backwater, Winter, Site 12

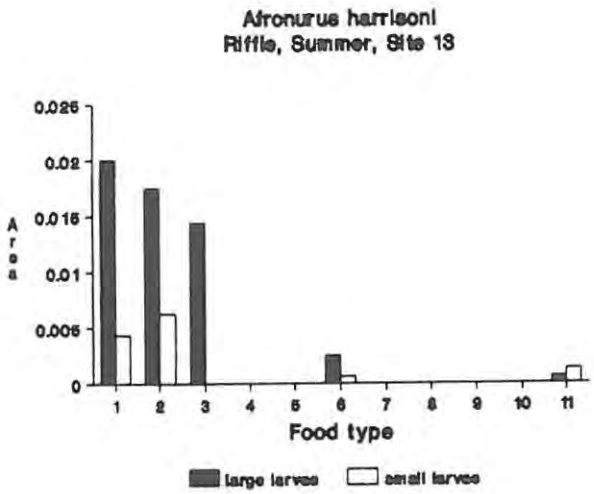


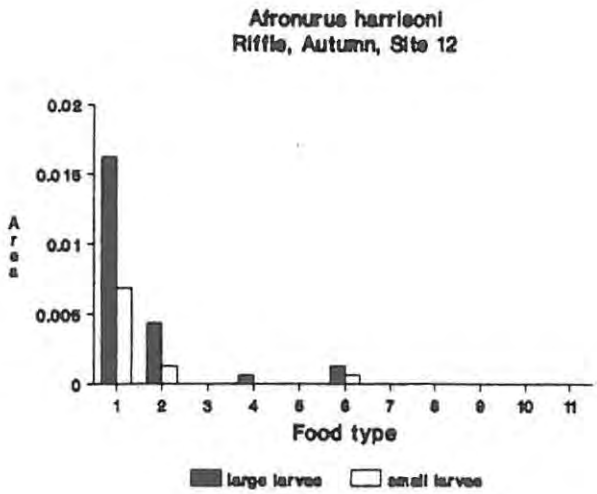
Afronurus harrisoni
Riffle, Winter, Site 6



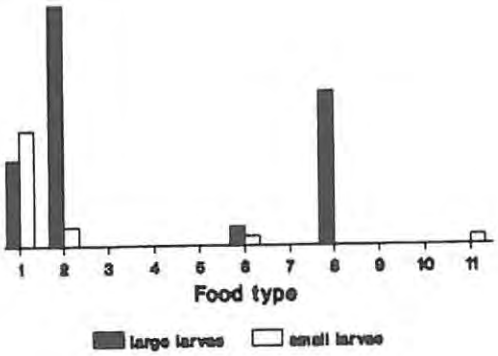
Afronurus harrisoni
Riffle, Winter, Site 12



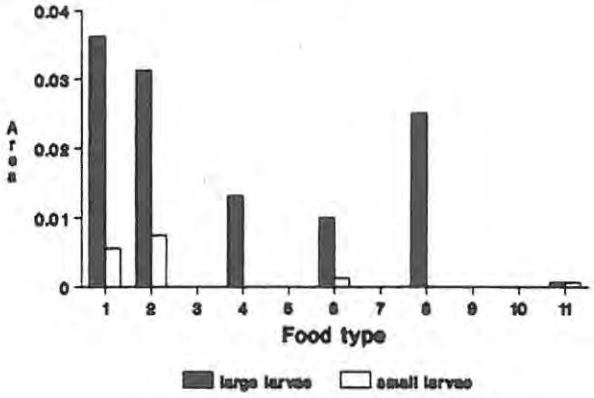

Afronurus harrisoni
Riffle, Summer, Site 13
0.025
0.02
0.015
0.01
0.005
0
Area
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Afronurus harrisoni
Riffle, Autumn, Site 12
0.02
0.015
0.01
0.005
0
Area
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

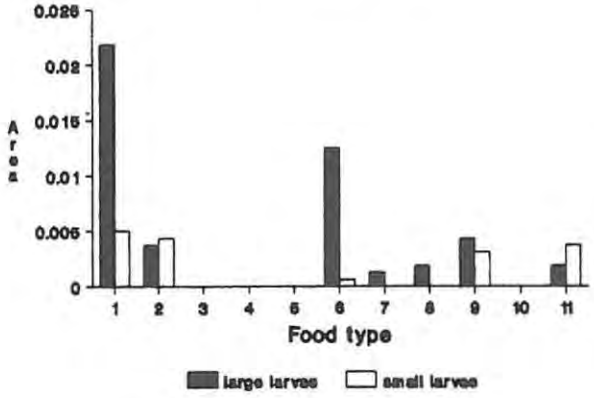
Baetis harrisoni
Riffle, Spring, Site 12



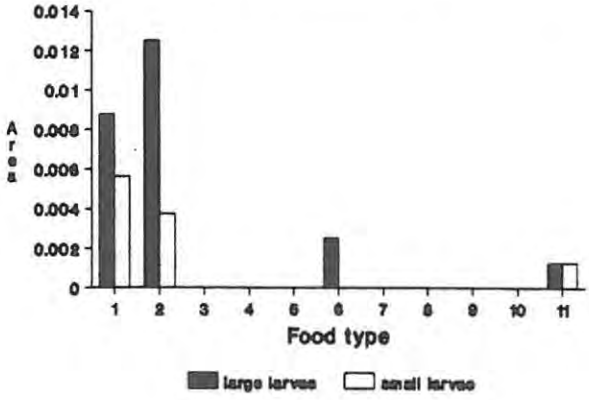
Baetis harrisoni
Riffle, Spring, Site 6



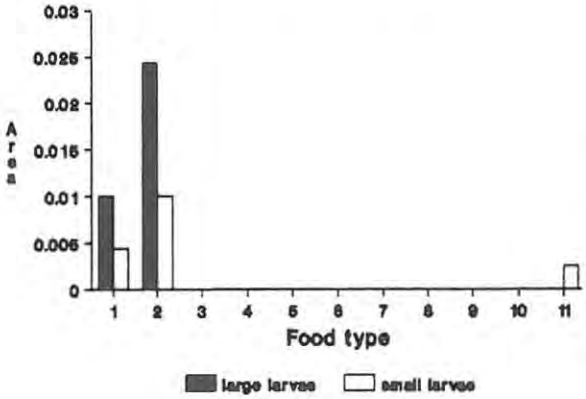
Baetis harrisoni
Riffle, Summer, Site 1



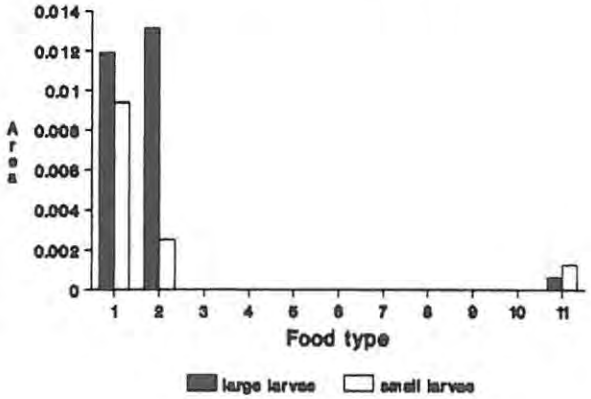
Baetis harrisoni
Riffle, Summer, Site 2c

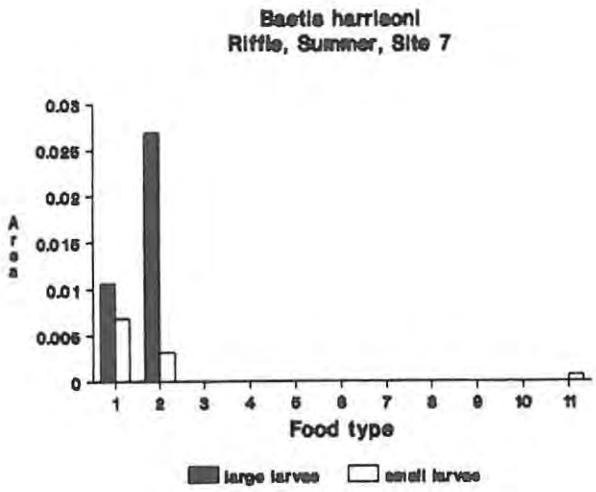


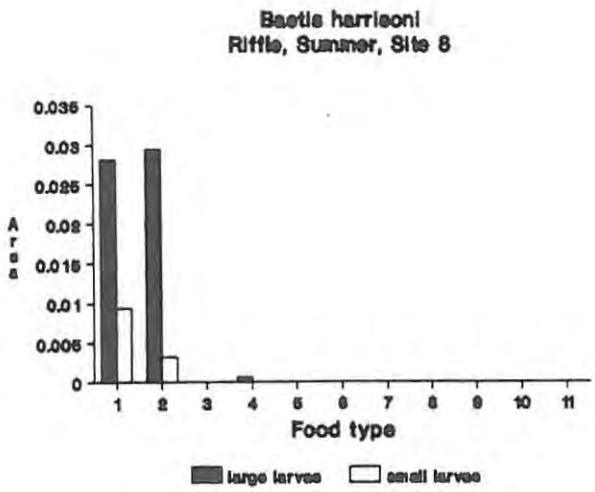
Baetis harrisoni
Riffle, Summer, Site 3

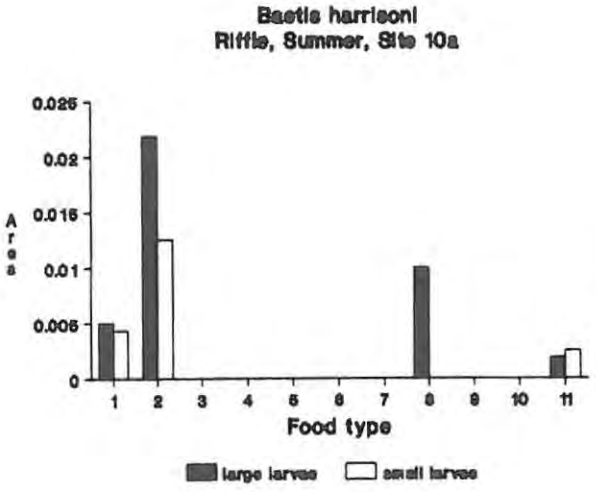


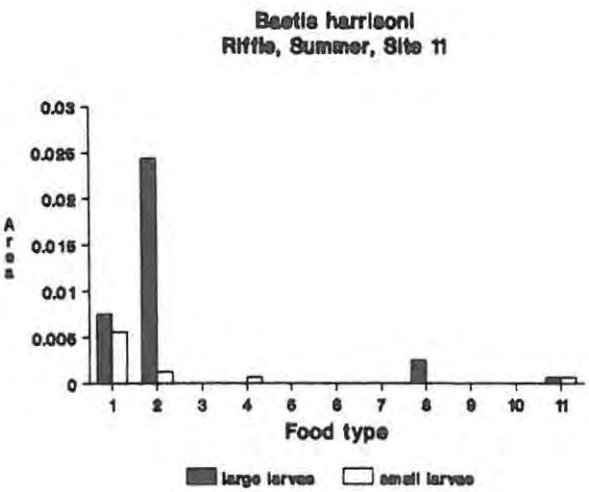
Baetis harrisoni
Riffle, Summer, Site 6

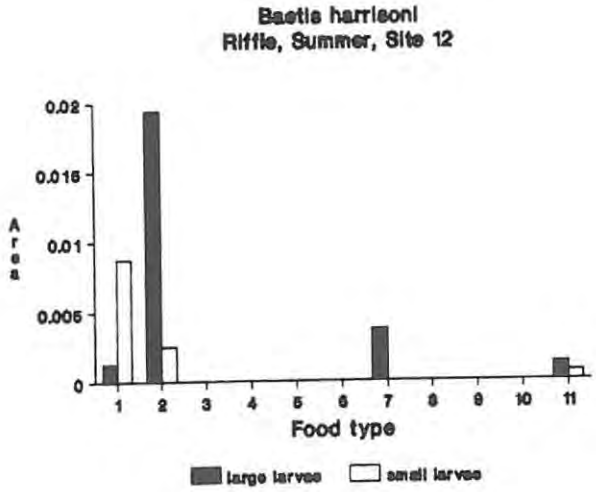


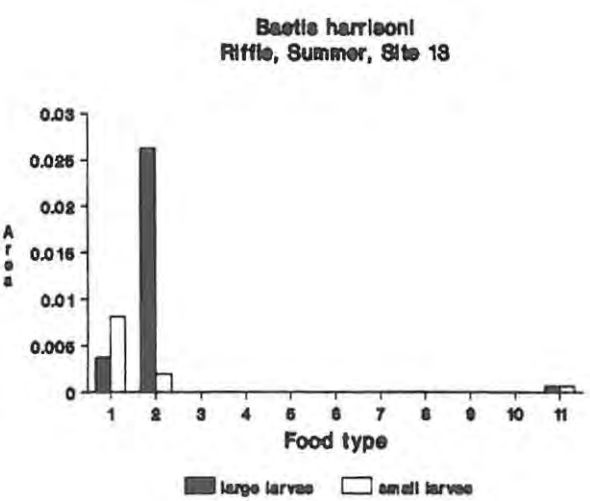

Baetis harrisoni
Riffle, Summer, Site 7
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

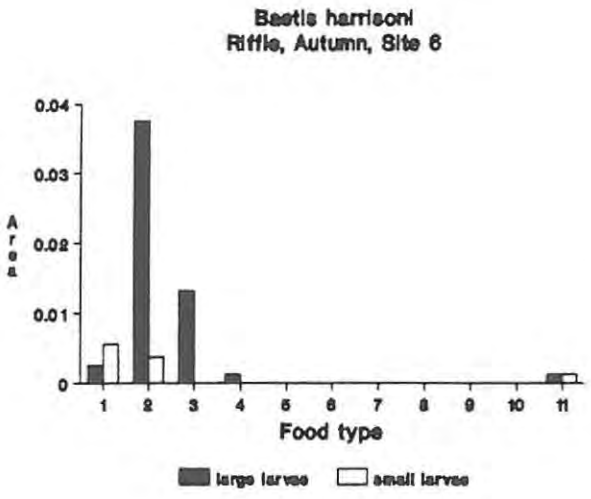

Baetis harrisoni
Riffle, Summer, Site 8
Area
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

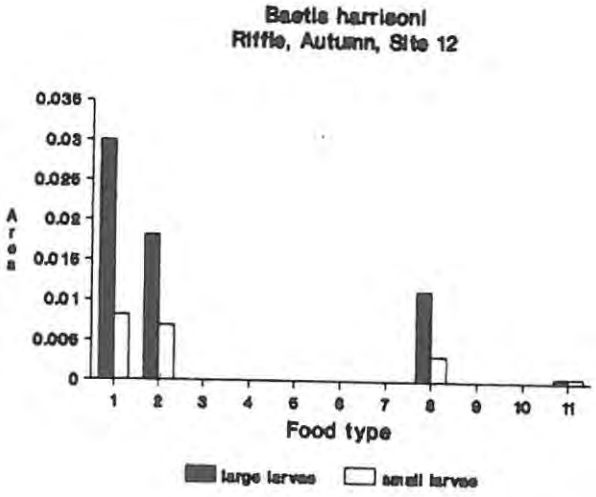

Baetis harrisoni
Riffle, Summer, Site 10a
Area
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Baetis harrisoni
Riffle, Summer, Site 11
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

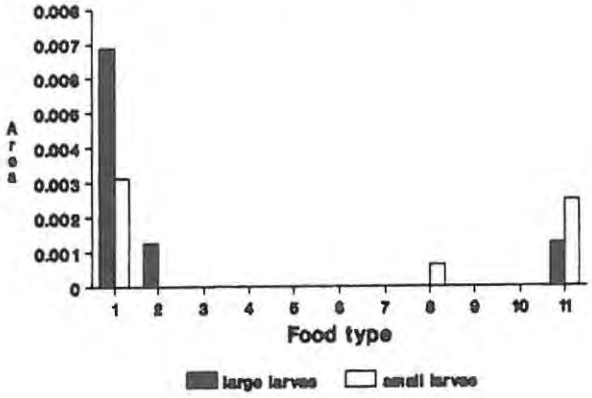

Baetis harrisoni
Riffle, Summer, Site 12
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Baetis harrisoni
Riffle, Summer, Site 13
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

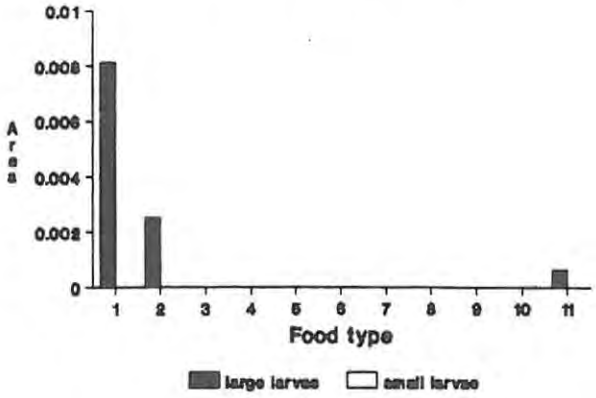

Baetis harrisoni
Riffle, Autumn, Site 6
0.04
0.03
0.02
0.01
0
Area
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Baetis harrisoni
Riffle, Autumn, Site 12
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
Area
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

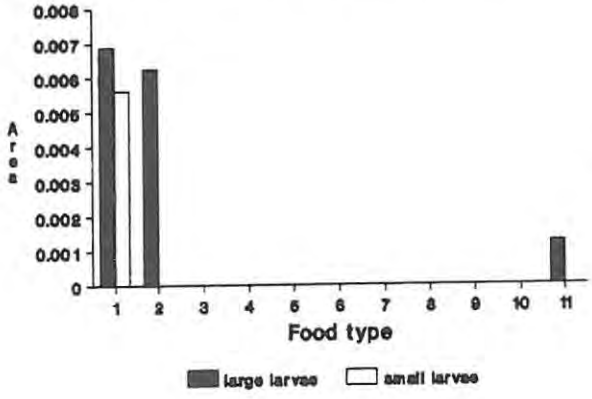
Caenidae sp A
Riffle, Summer, Site 10a



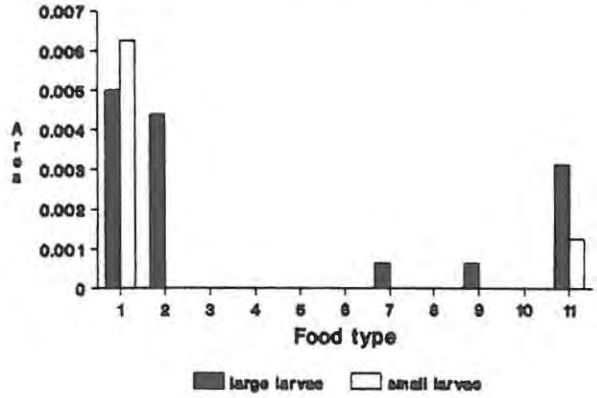
Caenidae sp A
Riffle, Summer, Site 12



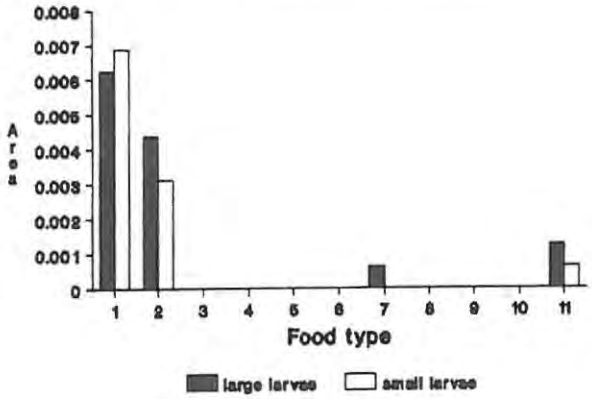
Caenidae sp A
Stony backwater, Summer, Site 12

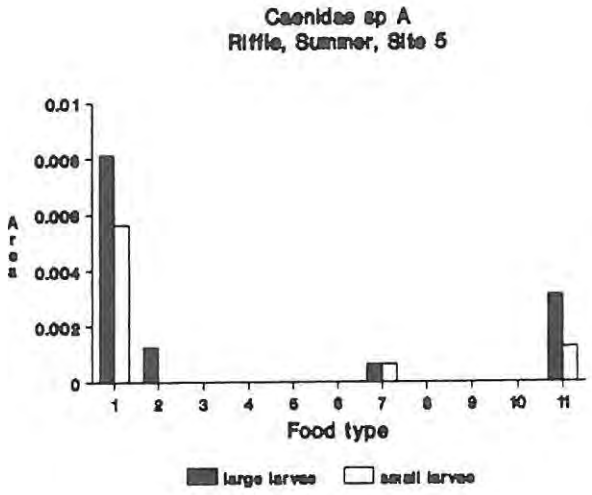


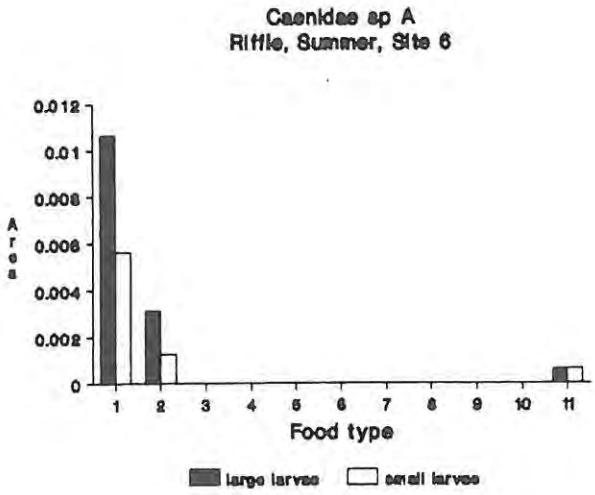
Caenidae sp A
Stony backwater, Autumn, Site 12

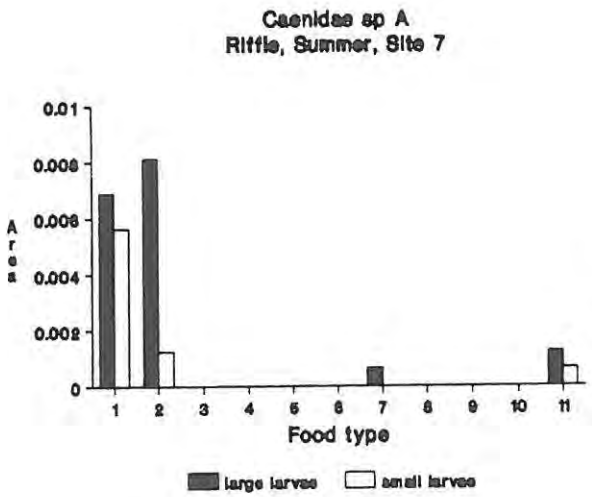


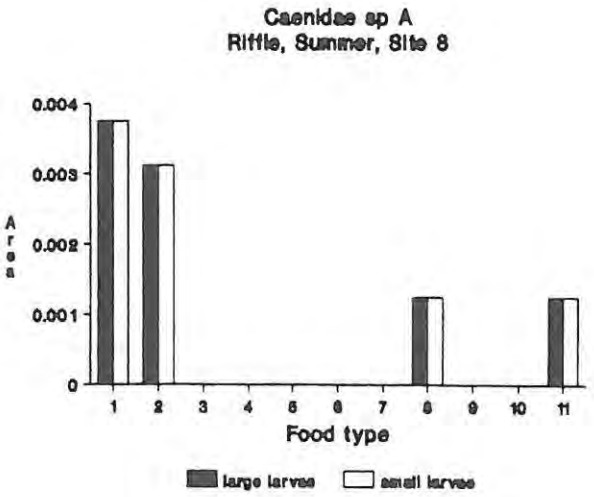
Caenidae sp A
Stony backwater, Winter, Site 6



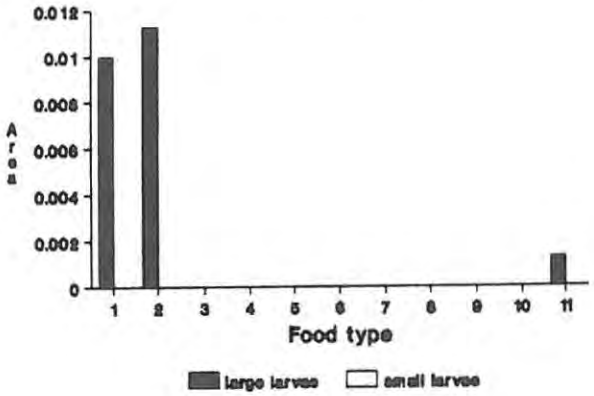

Caenidae sp A
Riffle, Summer, Site 5
Area
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Caenidae sp A
Riffle, Summer, Site 6
Area
0.012
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

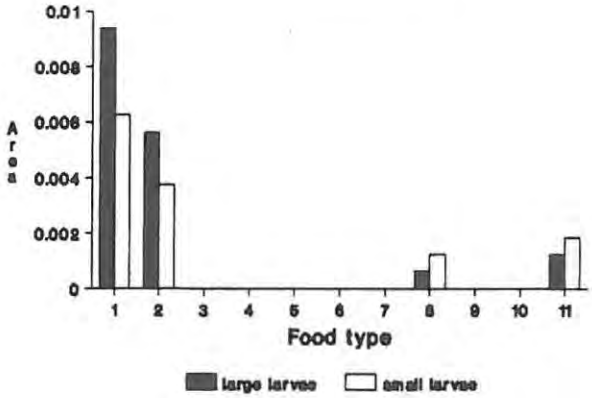

Caenidae sp A
Riffle, Summer, Site 7
Area
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Caenidae sp A
Riffle, Summer, Site 8
Area
0.004
0.003
0.002
0.001
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

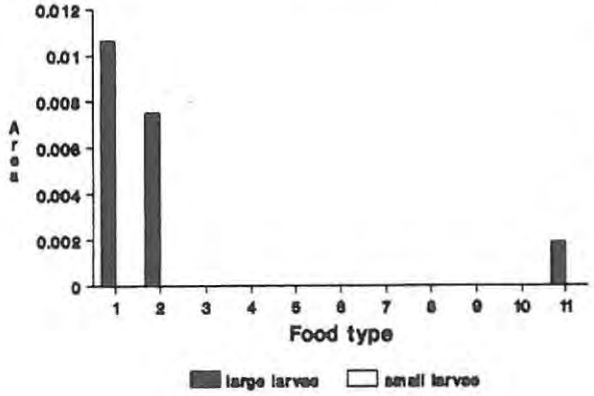
Caenidae sp B
Riffle, Spring, Site 12



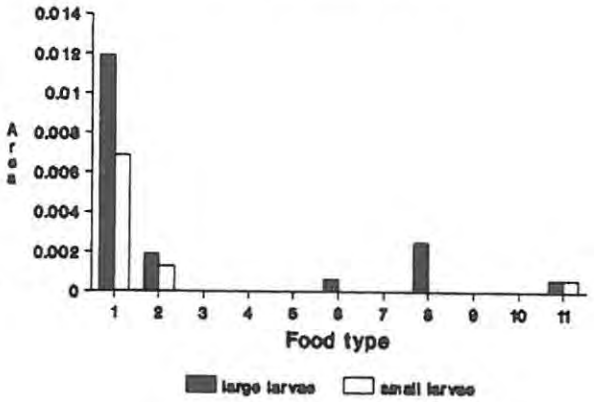
Caenidae sp B
Riffle, Summer, Site 12



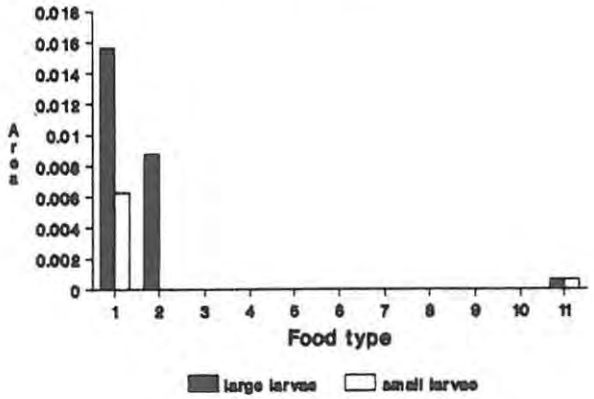
Caenidae sp B
Riffle, Summer, Site 13



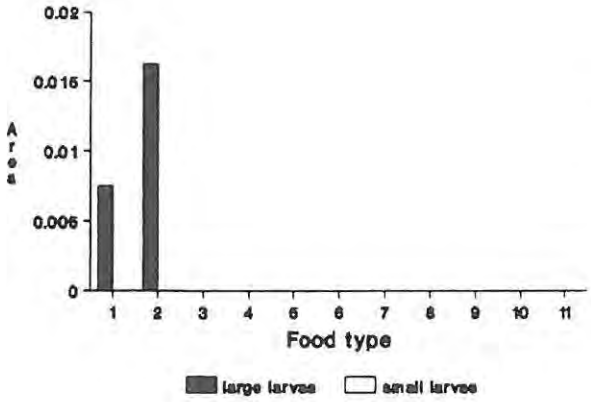
Caenidae sp B
Riffle, Autumn, Site 12



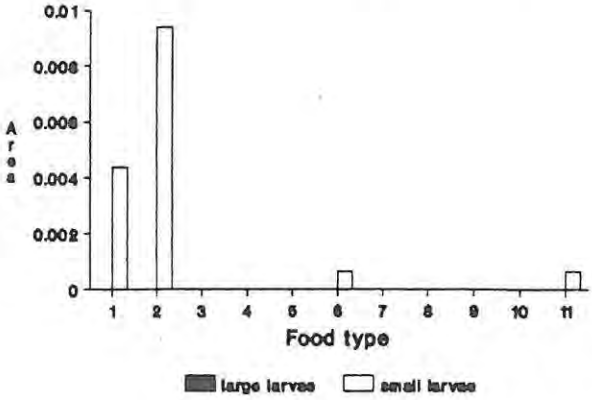
Caenidae sp B
Riffle, Winter, Site 12



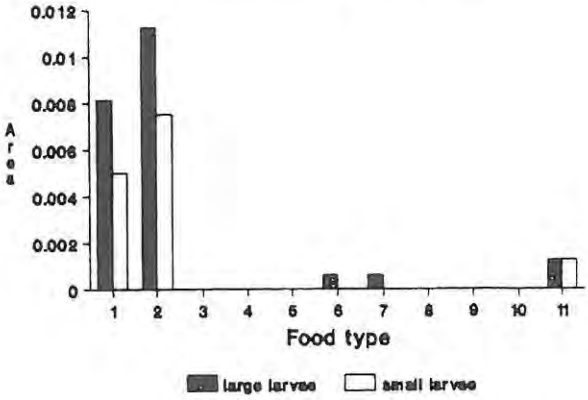
Centroptilum excisum
Riffle, Spring, Site 12



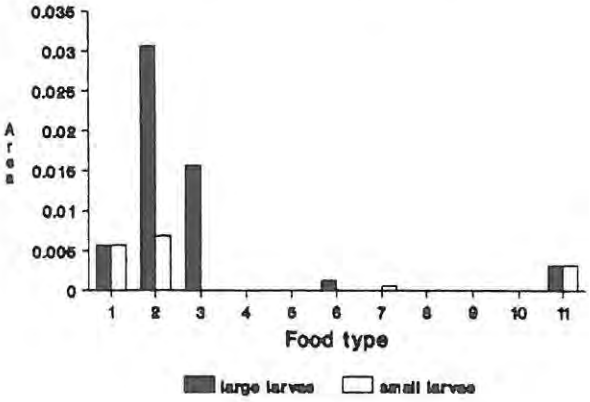
Centroptilum excisum
Stony backwater, Spring, Site 6



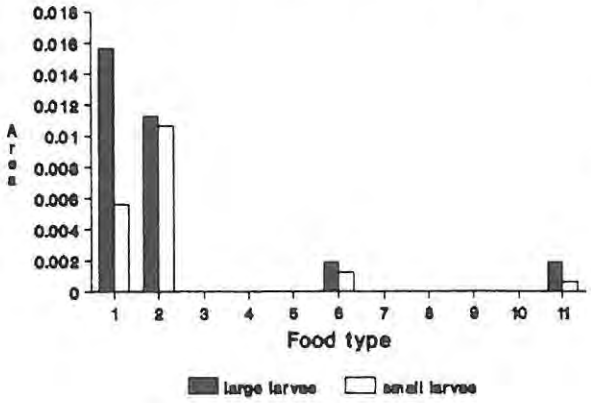
Centroptilum excisum
Stony backwater, Spring, Site 12



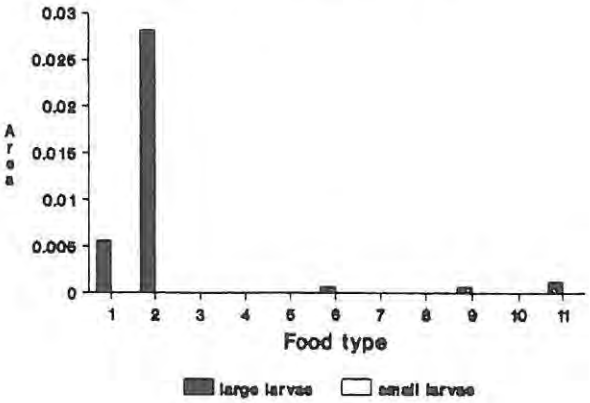
Centroptilum excisum
Stony backwater, Autumn, Site 6

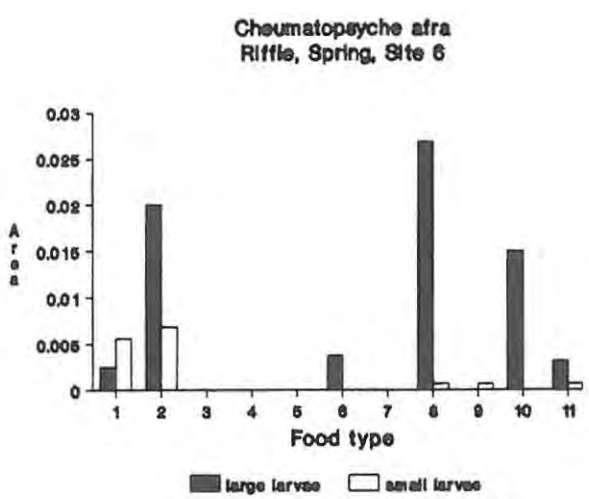


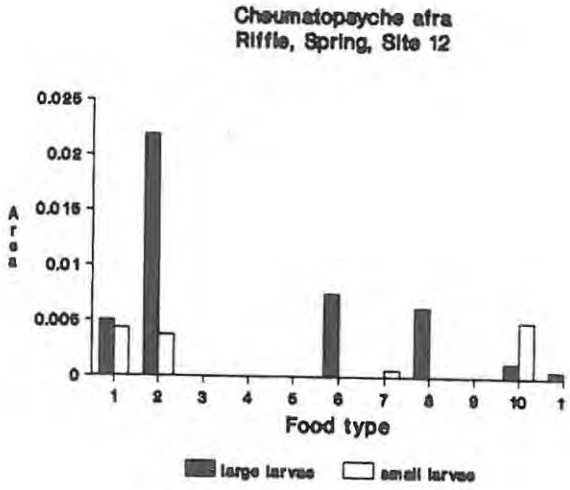
Centroptilum excisum
Stony backwater, Winter, Site 12

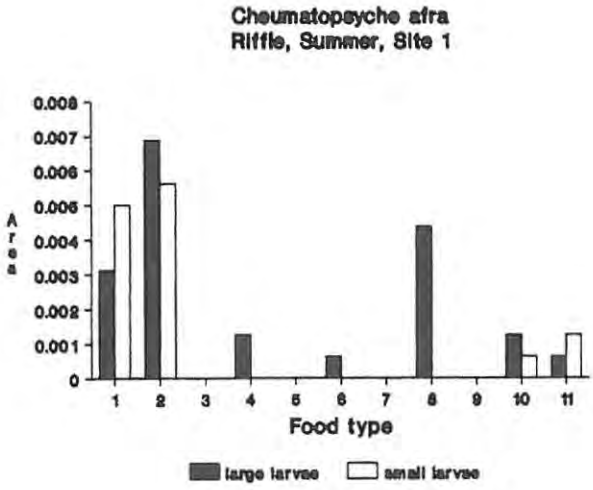


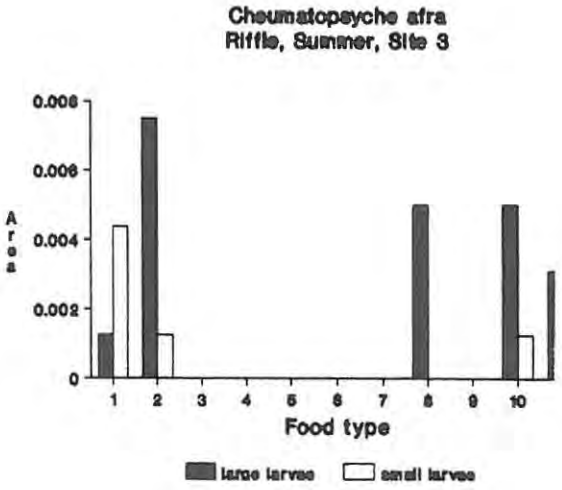
Centroptilum excisum
Riffle, Winter, Site 12

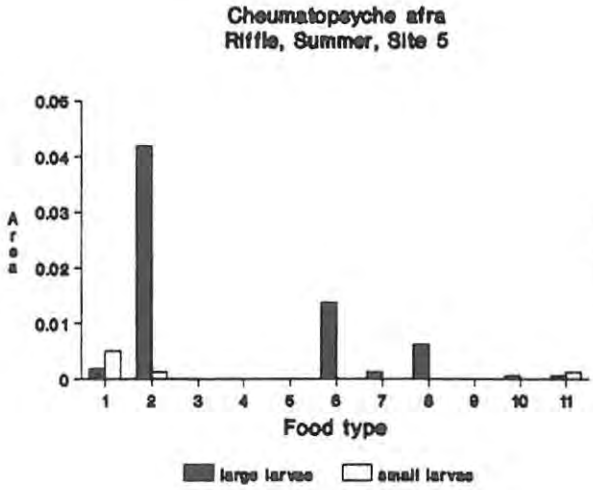


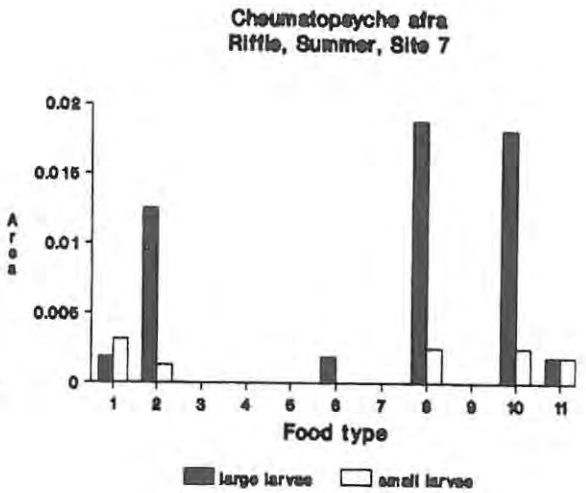

Cheumatopsyche afra
Riffle, Spring, Site 6
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

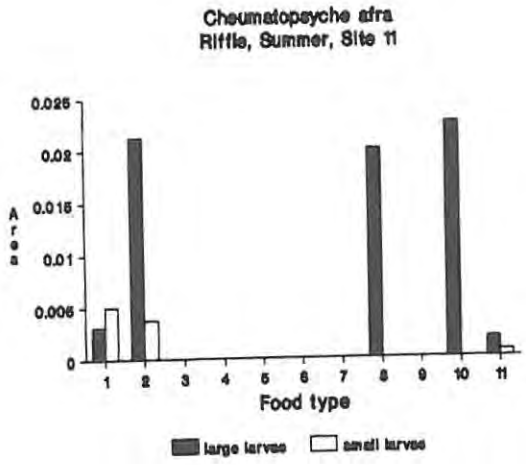

Cheumatopsyche afra
Riffle, Spring, Site 12
Area
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10
Food type
large larvae
small larvae

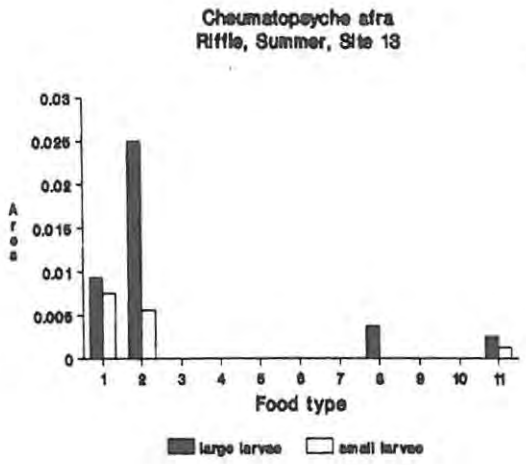

Cheumatopsyche afra
Riffle, Summer, Site 1
Area
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

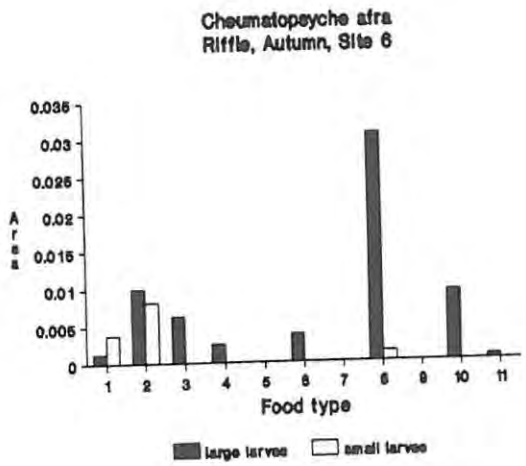

Cheumatopsyche afra
Riffle, Summer, Site 3
Area
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10
Food type
large larvae
small larvae

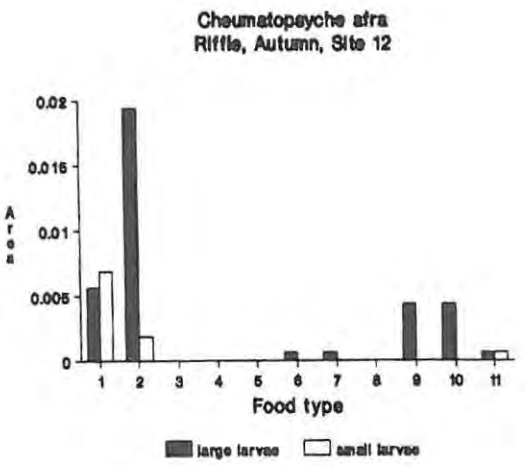

Cheumatopsyche afra
Riffle, Summer, Site 5
Area
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

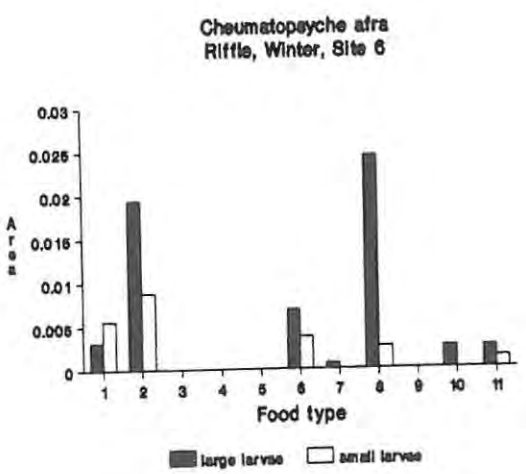

Cheumatopsyche afra
Riffle, Summer, Site 7
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

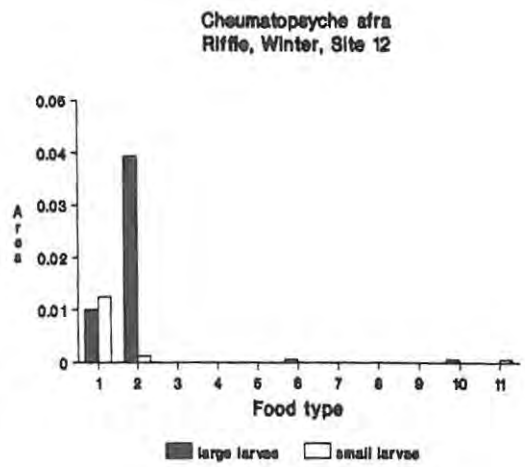

Cheumatopsyche afra
Riffle, Summer, Site 11
Area
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Cheumatopsyche afra
Riffle, Summer, Site 13
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

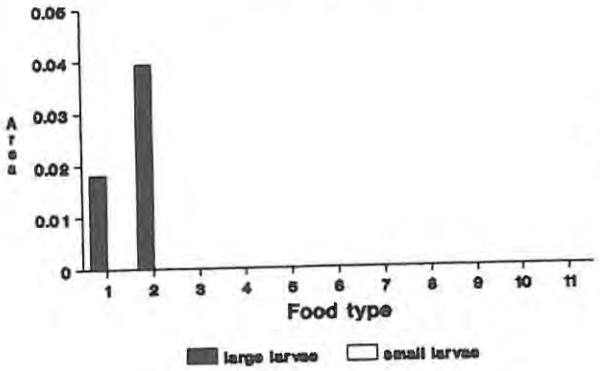

Cheumatopsyche afra
Riffle, Autumn, Site 6
Area
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Cheumatopsyche afra
Riffle, Autumn, Site 12
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

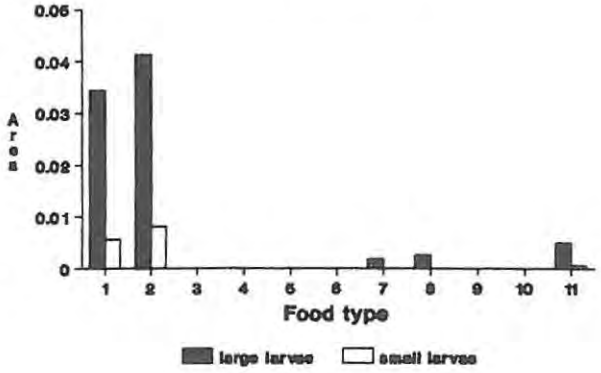

Cheumatopsyche afra
Riffle, Winter, Site 6
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Cheumatopsyche afra
Riffle, Winter, Site 12
Area
0.05
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

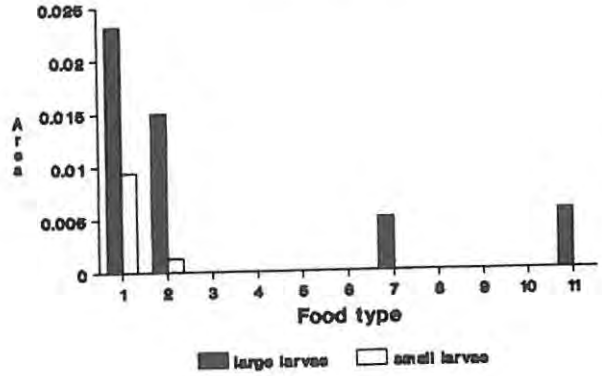
Choroterpes elegans
Riffle, Spring, Site 12



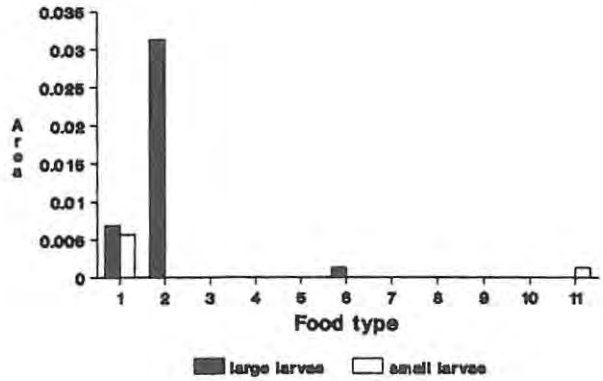
Choroterpes elegans
Riffle, Summer, Site 6



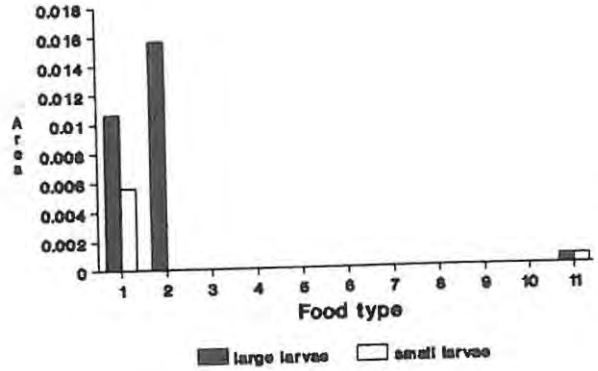
Choroterpes elegans
Riffle, Summer, Site 7



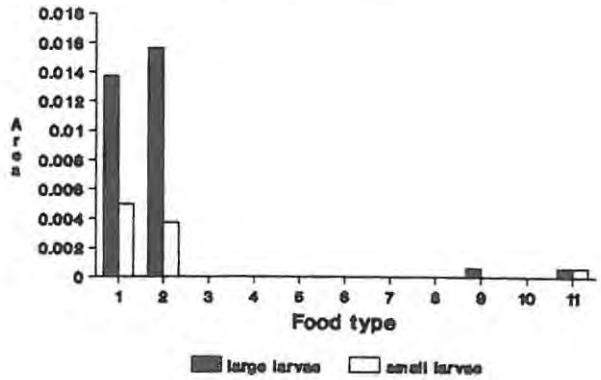
Choroterpes elegans
Riffle, Summer, Site 10a



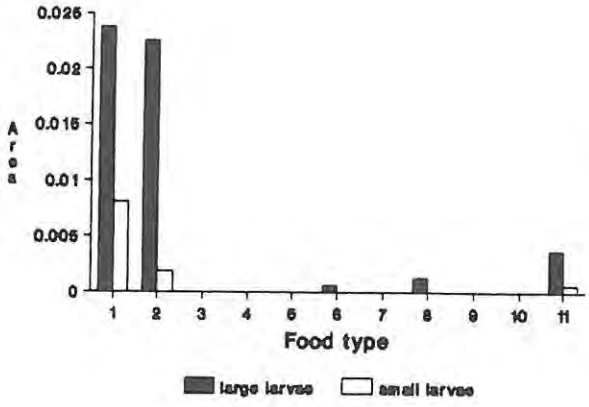
Choroterpes elegans
Riffle, Summer, Site 10b



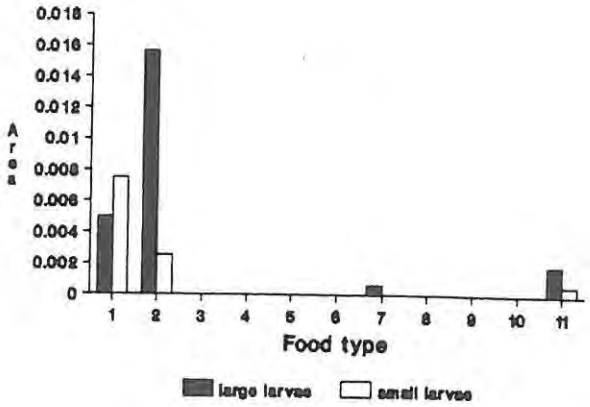
Choroterpes elegans
Riffle, Summer, Site 12



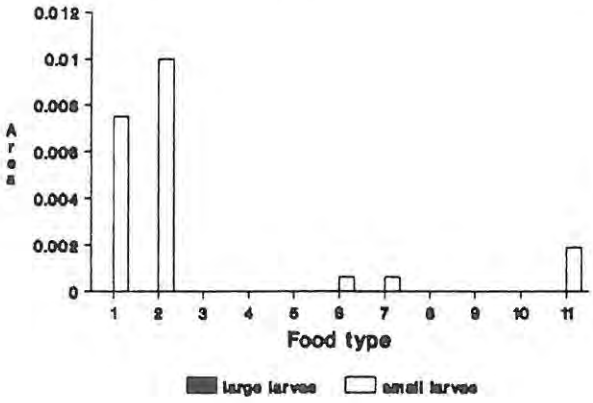
Choroterpes elegans
Riffle, Summer, Site 13



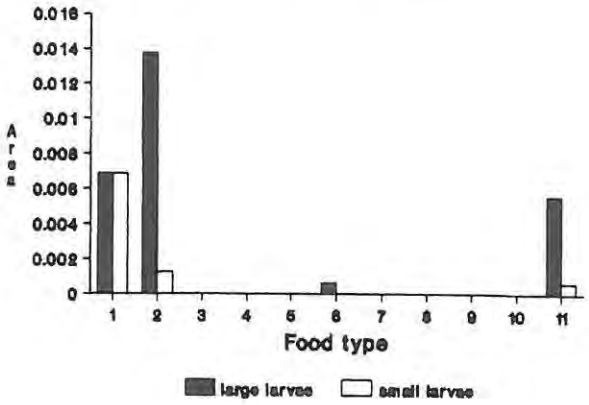
Choroterpes elegans
Riffle, Autumn, Site 6



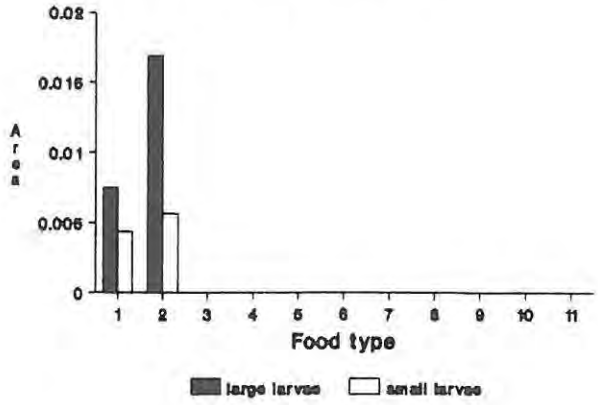
Choroterpes elegans
Riffle, Summer, Site 4



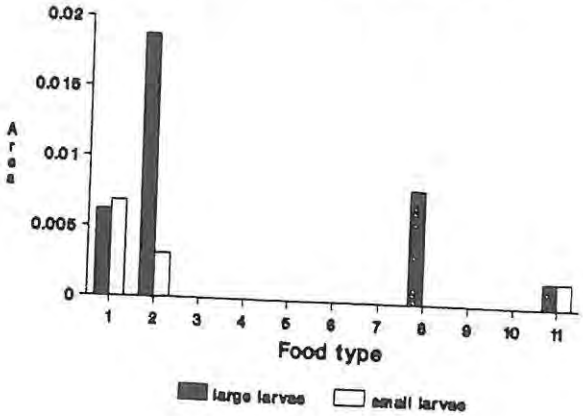
Choroterpes elegans
Stony backwater, Autumn, Site 6

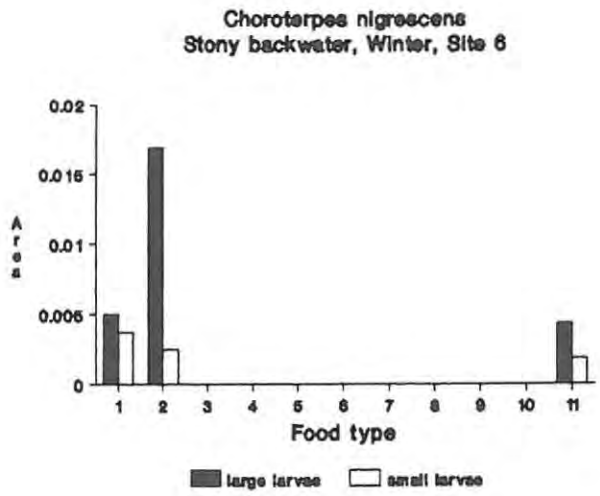


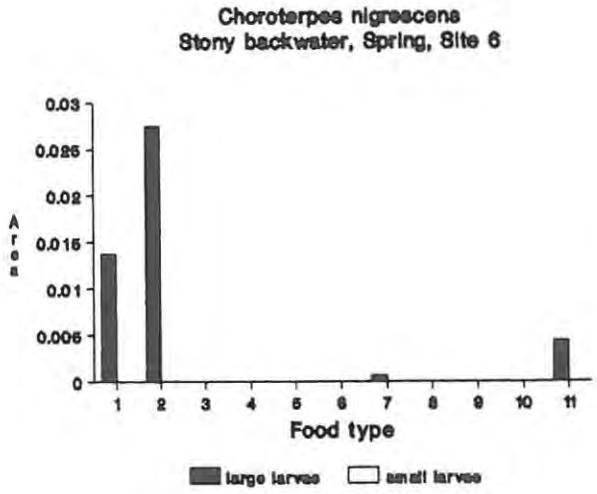
Choroterpes elegans
Riffle, Autumn, Site 12

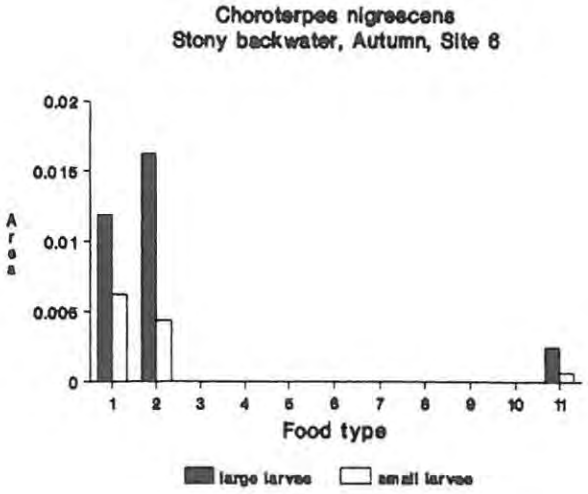


Choroterpes elegans
Stony backwater, Winter, Site 6

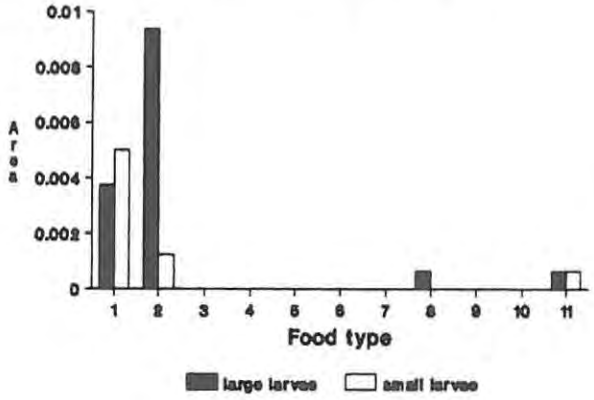



Choroterpes nigrescens
Stony backwater, Winter, Site 6
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

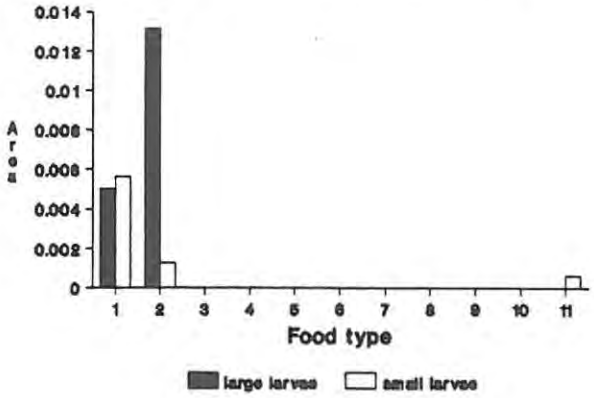

Choroterpes nigrescens
Stony backwater, Spring, Site 6
Area
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Choroterpes nigrescens
Stony backwater, Autumn, Site 6
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

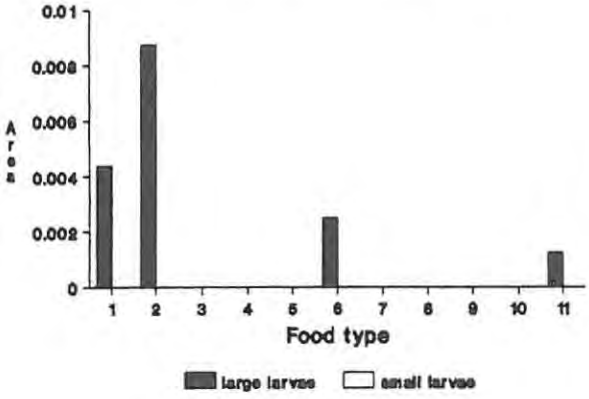
Cloeon africanum
Stony backwater, Autumn, Site 6



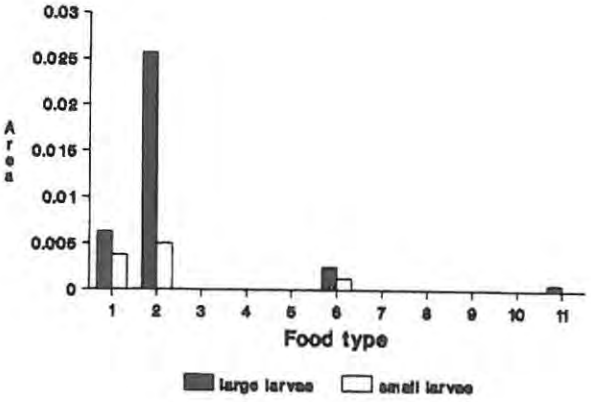
Cloeon africanum
Stony backwater, Autumn, Site 12



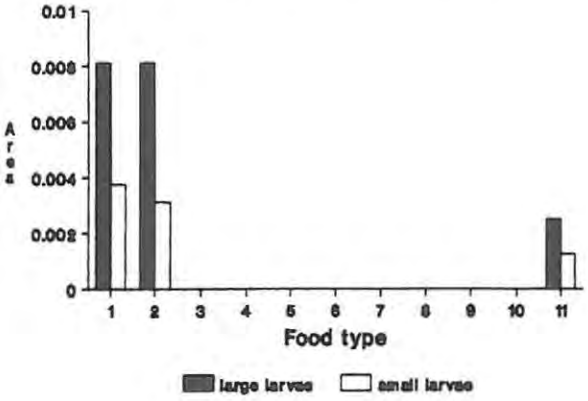
Cloeon africanum
Stony backwater, Winter, Site 6



Cloeon africanum
Stony backwater, Winter, Site 12

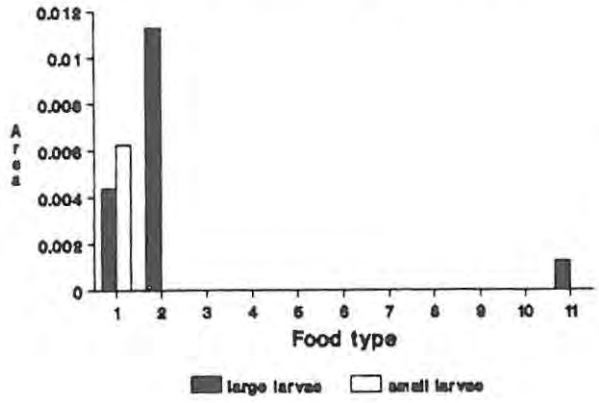


Cloeon africanum
Marginal vegetation, Summer, Site 6

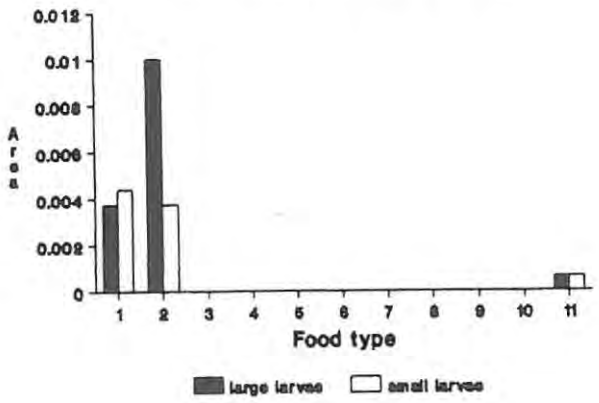


Cloeon africanum
Marginal vegetation, Summer, Site 12

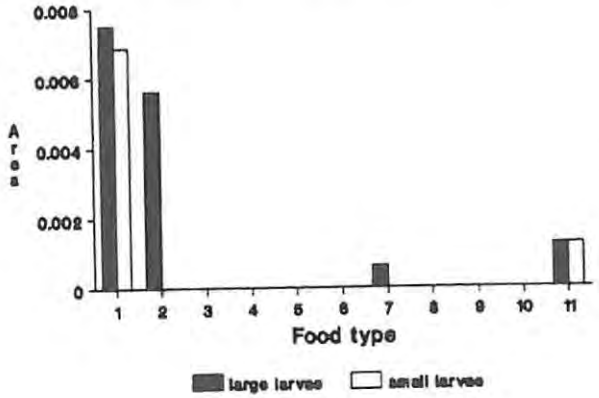
Cloeon africanum
Stony backwater, Spring, Site 6



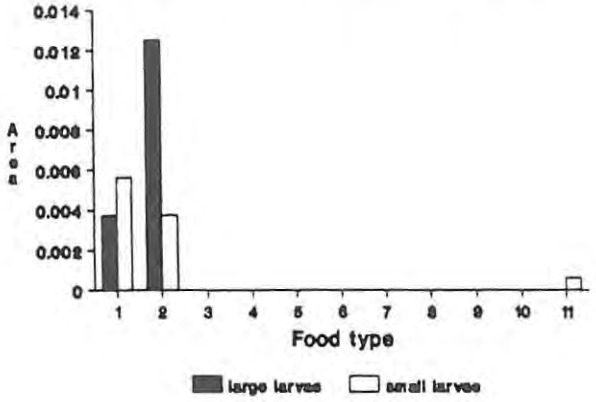
Cloeon africanum
Stony backwater, Spring, Site 12



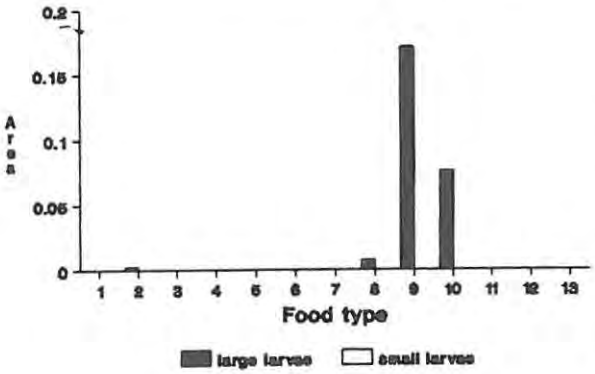
Cloeon africanum
Stony backwater, Summer, Site 6



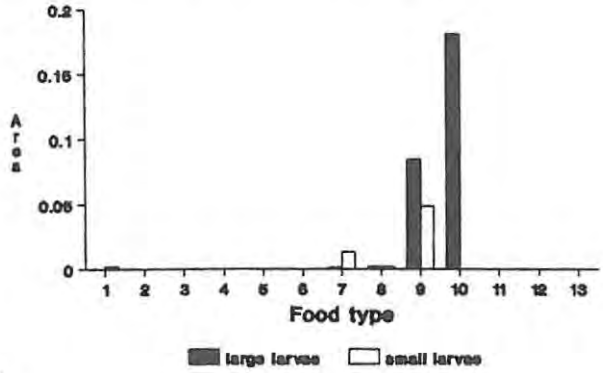
Cloeon africanum
Stony backwater, Summer, Site 12



Dyschimus enaifer
Leaf pack, Spring, Site 0

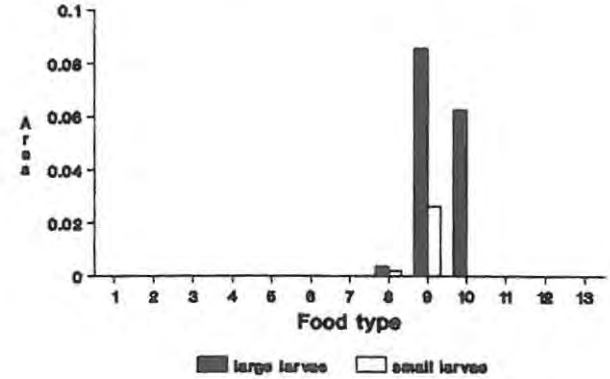


Dyschimus enaifer
Leaf pack, Autumn, Site 0

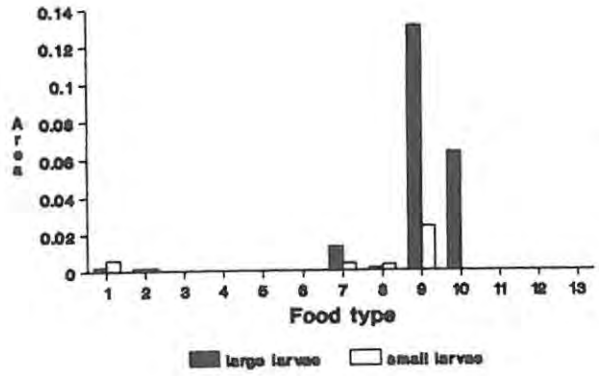


Dyschimus enaifer
Leaf pack, Winter, Site 0

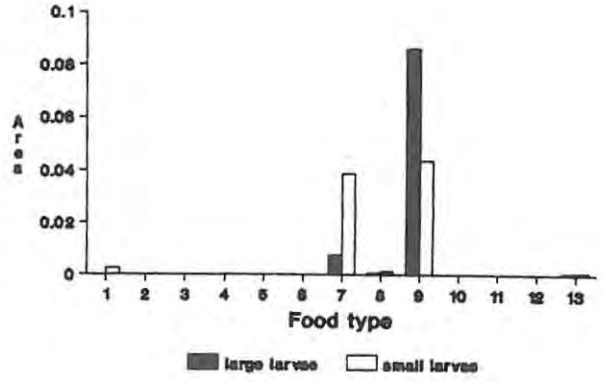
Dyschimus enaifer
Stony backwater, Autumn, Site 0

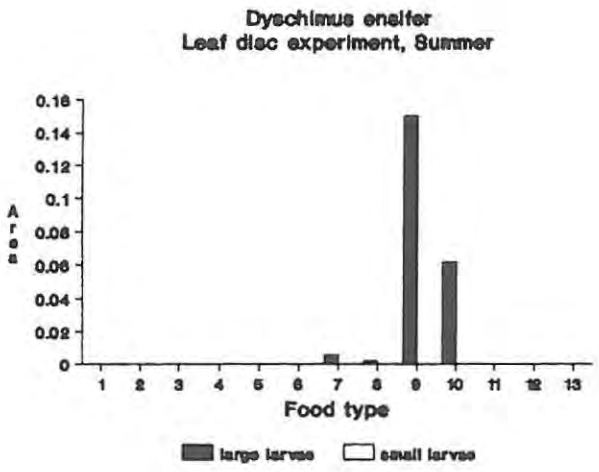


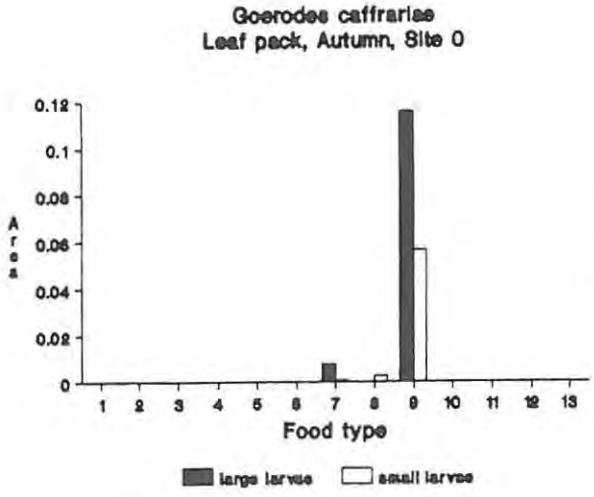
Dyschimus enaifer
Sediments, Autumn, Site 0

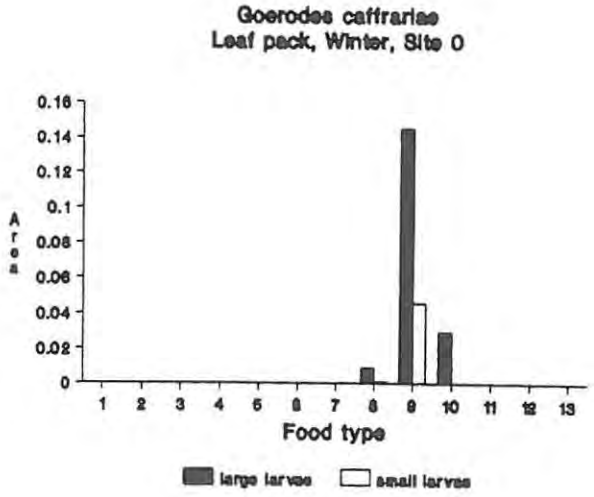


Dyschimus enaifer
Riffle, Summer, Site 0

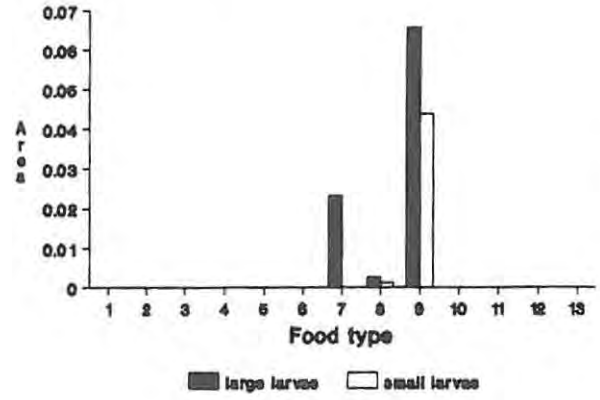



Dyschimus enalter
Leaf disc experiment, Summer
Area
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

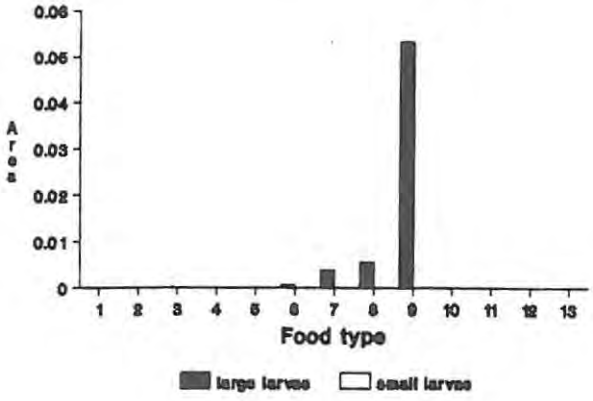

Goerodes caffrariae
Leaf pack, Autumn, Site 0
Area
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae


Goerodes caffrariae
Leaf pack, Winter, Site 0
Area
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13
Food type
large larvae
small larvae

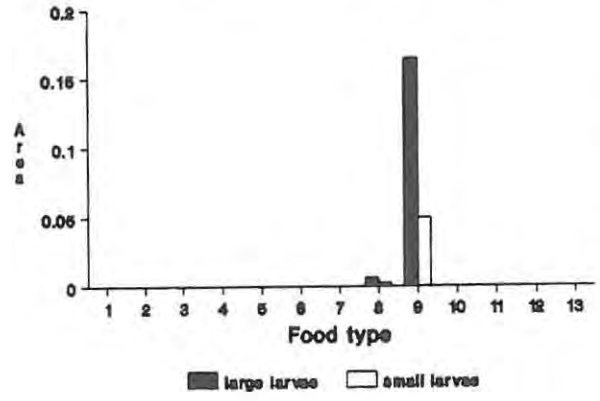
Goerodes caffrariae
Riffle, Summer, Site 0



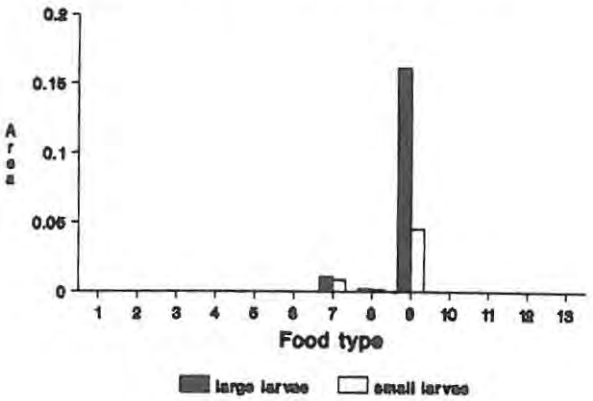
Goerodes caffrariae
Stony backwater, Spring, Site 0



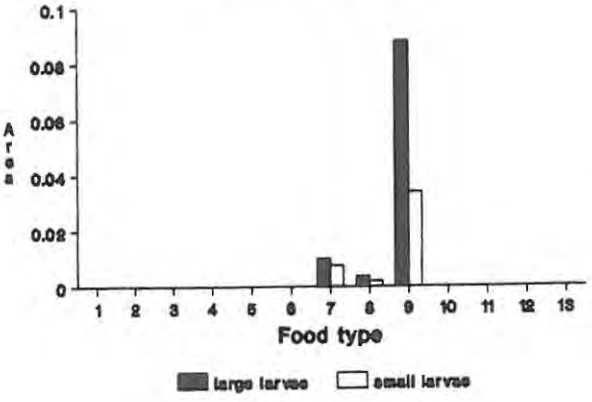
Goerodes caffrariae
Stony backwater, Summer, Site 0



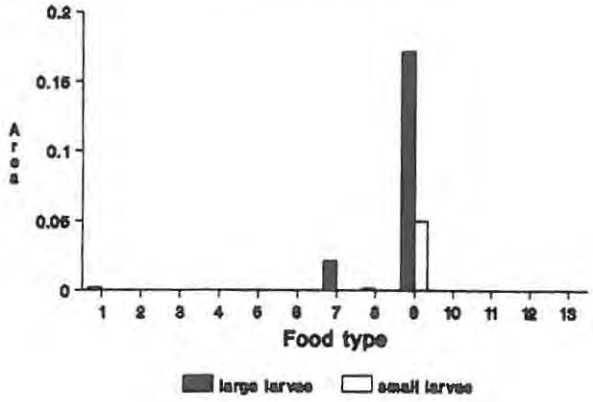
Goerodes caffrariae
Stony backwater, Autumn, Site 0

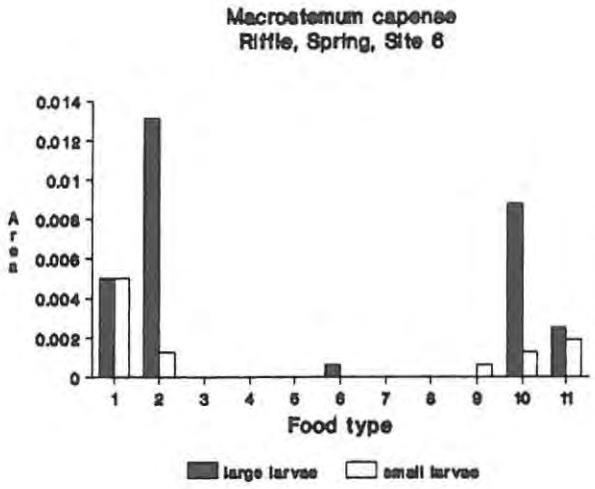


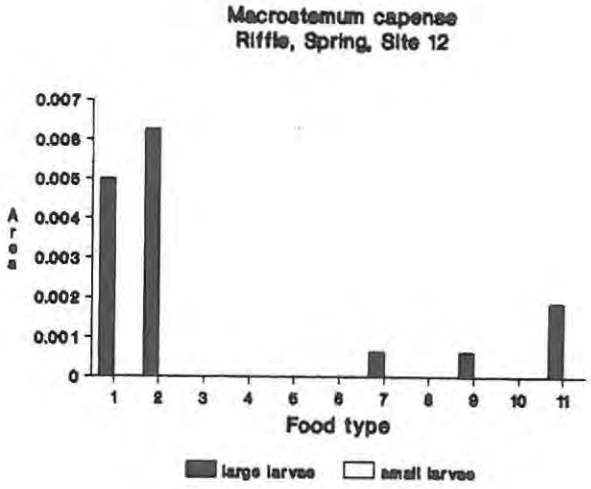
Goerodes caffrariae
Leaf pack, Spring, Site 0

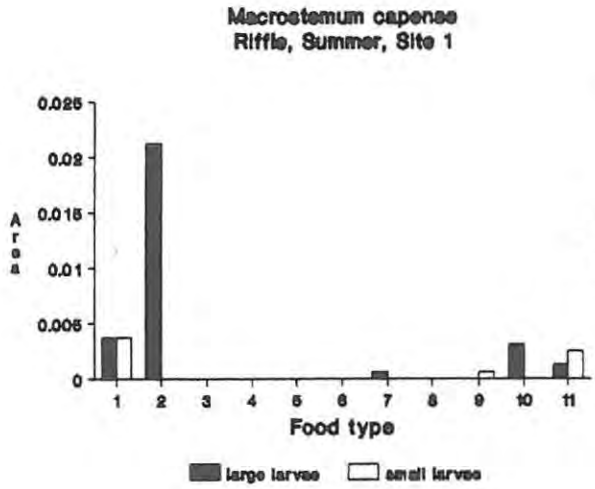


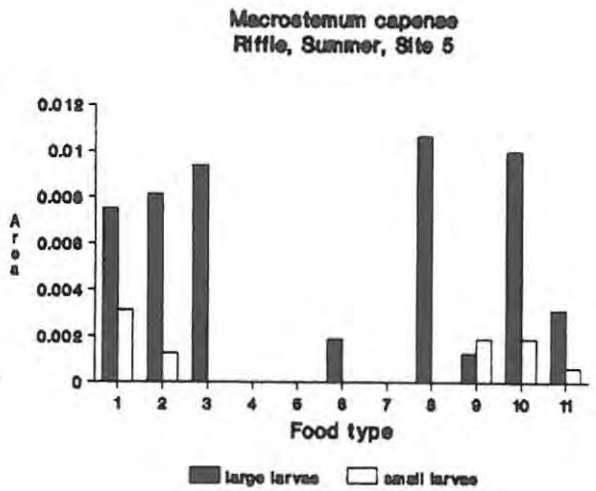
Goerodes caffrariae
Leaf pack, Summer, Site 0

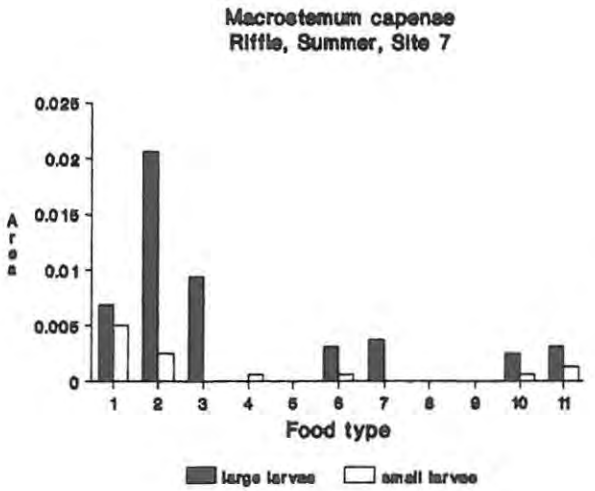


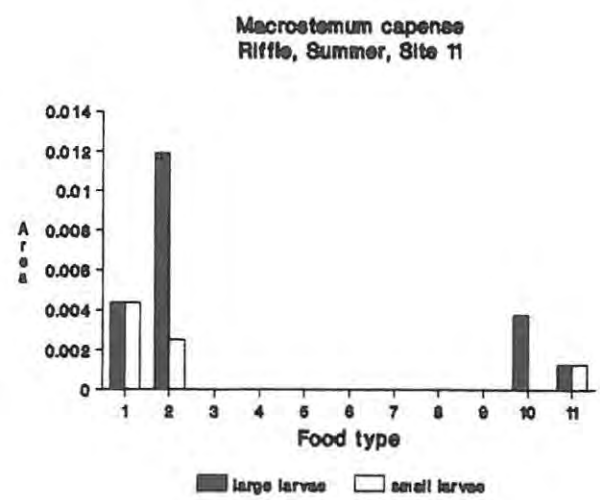

Macrostemum capense
Riffle, Spring, Site 6
Area
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Macrostemum capense
Riffle, Spring, Site 12
Area
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

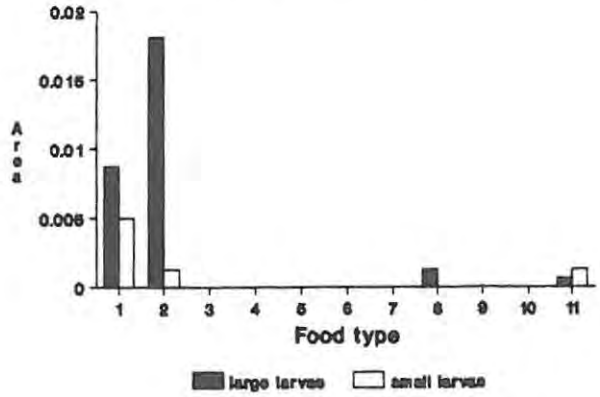

Macrostemum capense
Riffle, Summer, Site 1
Area
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Macrostemum capense
Riffle, Summer, Site 5
Area
0.012
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

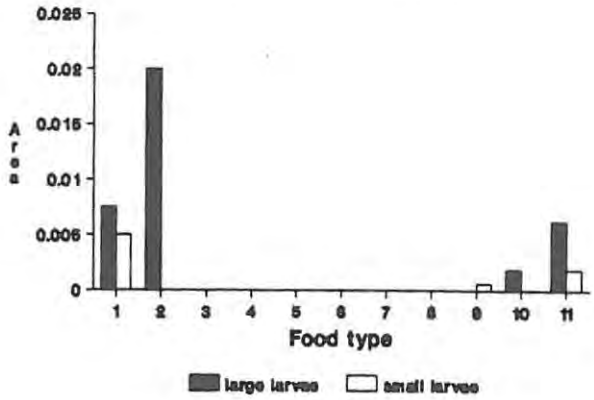

Macrostemum capense
Riffle, Summer, Site 7
Area
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Macrostemum capense
Riffle, Summer, Site 11
Area
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

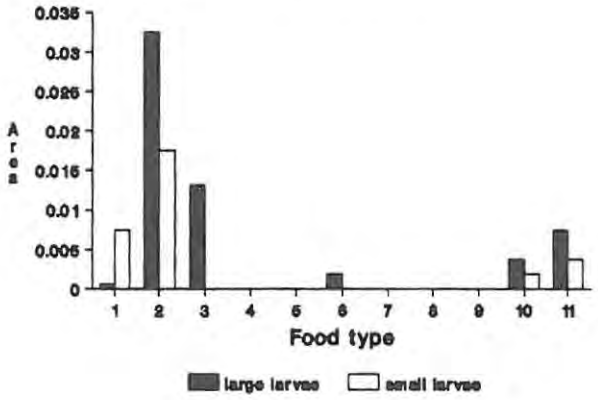
Macrostemum capense
Riffle, Summer, Site 12



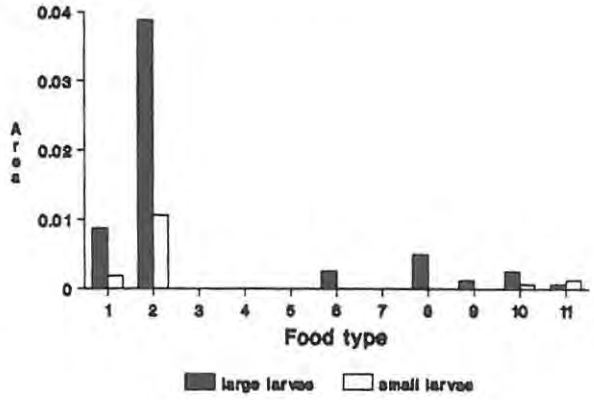
Macrostemum capense
Riffle, Summer, Site 13



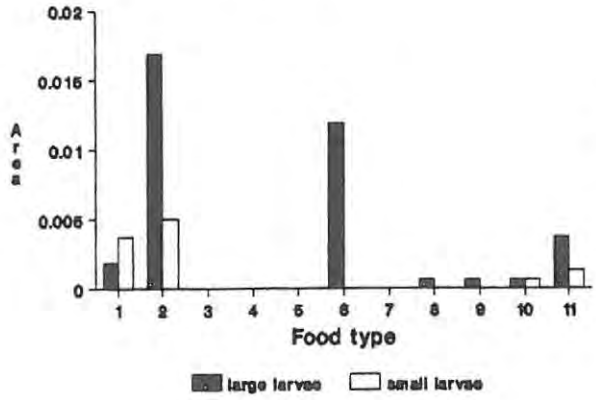
Macrostemum capense
Riffle, Autumn, Site 6



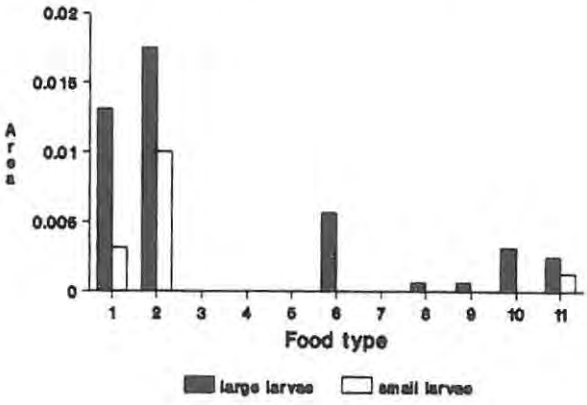
Macrostemum capense
Riffle, Autumn, Site 12

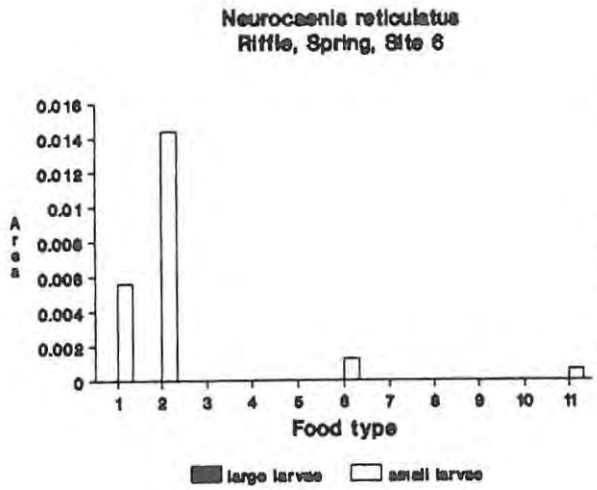


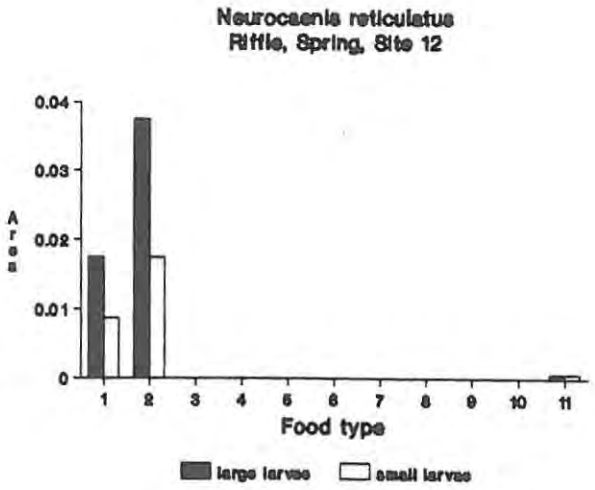
Macrostemum capense
Riffle, Winter, Site 6

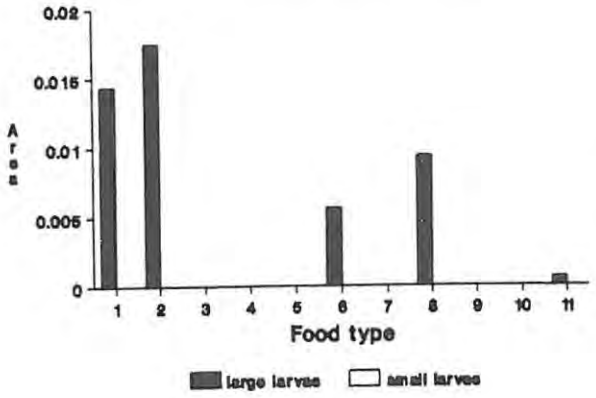


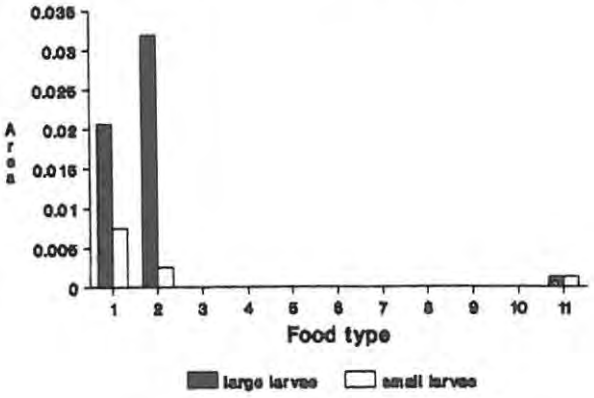
Macrostemum capense
Riffle, Winter, Site 12

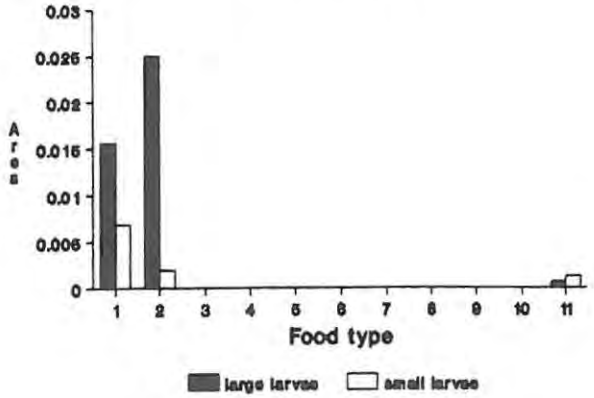


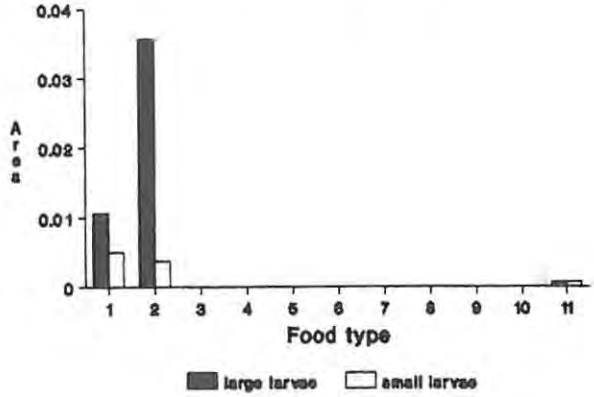

Neurocaenis reticulatus
Riffle, Spring, Site 6
Area
0.016
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Neurocaenis reticulatus
Riffle, Spring, Site 12
Area
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

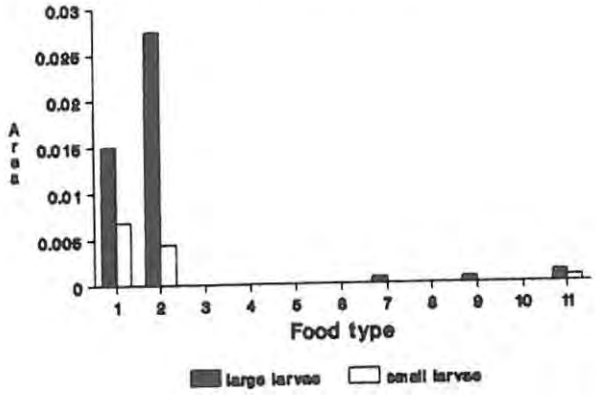

Neurocaenis reticulatus
Riffle, Summer, Site 2b
Area
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Neurocaenis reticulatus
Riffle, Summer, Site 7
Area
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

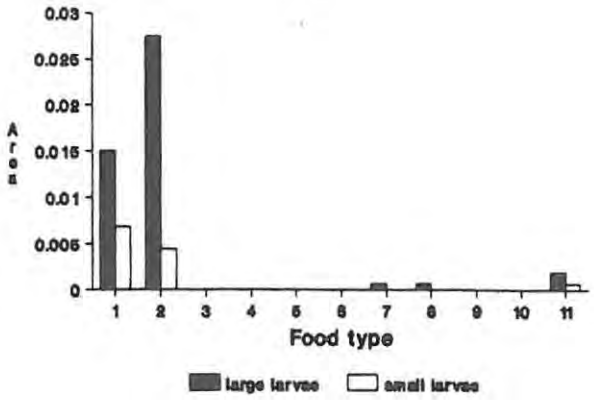

Neurocaenis reticulatus
Riffle, Summer, Site 11
Area
0.03
0.025
0.02
0.015
0.01
0.006
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae


Neurocaenis reticulatus
Riffle, Summer, Site 12
Area
0.04
0.03
0.02
0.01
0
1 2 3 4 5 6 7 8 9 10 11
Food type
large larvae
small larvae

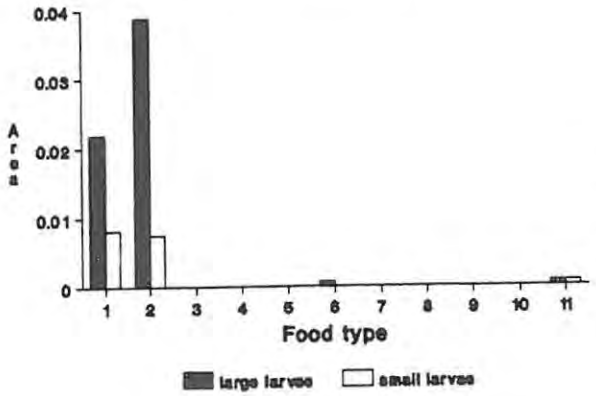
Neurocaenis reticulatus
Riffle, Summer, Site 13



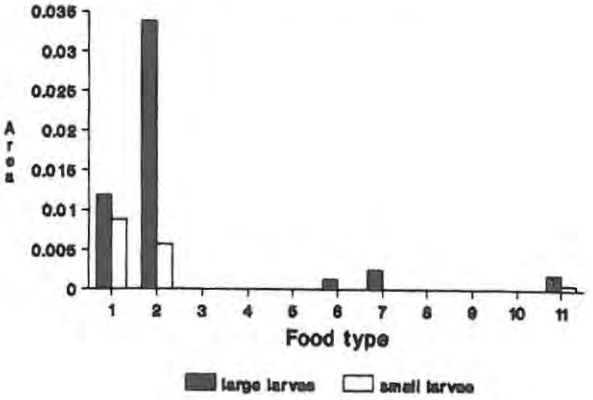
Neurocaenis reticulatus
Riffle, Autumn, Site 6



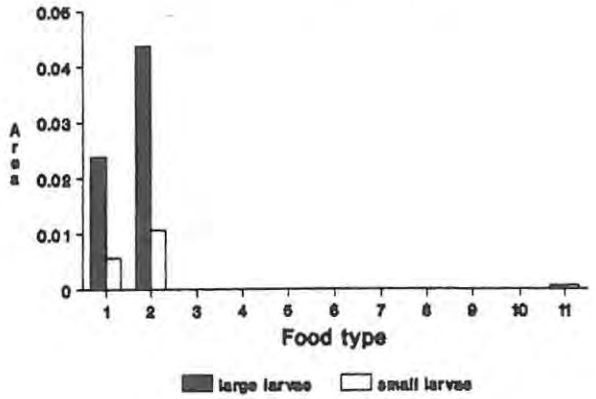
Neurocaenis reticulatus
Riffle, Autumn, Site 12



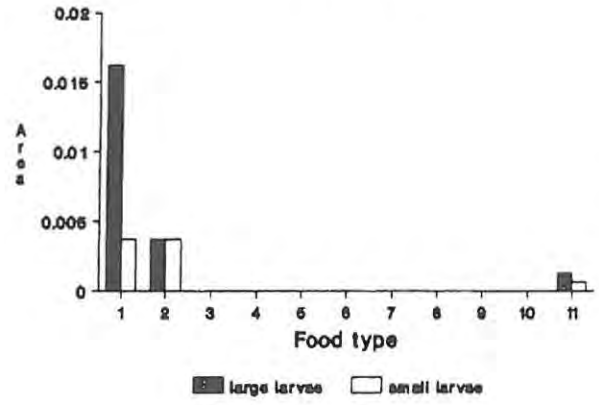
Neurocaenis reticulatus
Riffle, Winter, Site 6



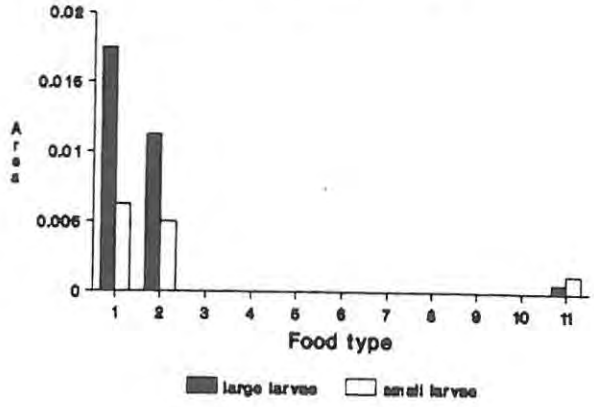
Neurocaenis reticulatus
Riffle, Winter, Site 12



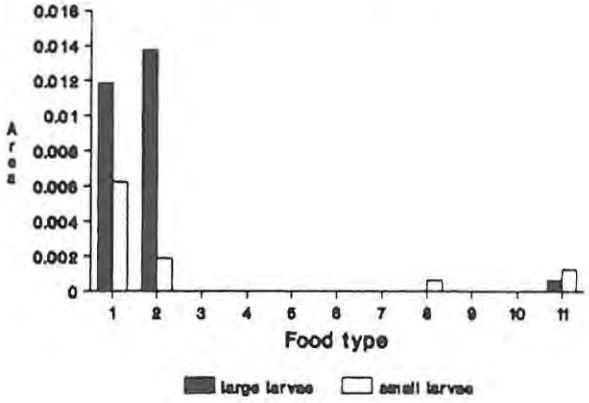
Pseudocloeon maculosum
Riffle, Spring, Site 12



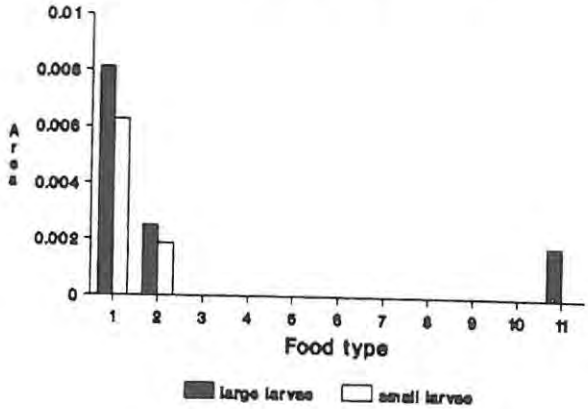
Pseudocloeon maculosum
Riffle, Summer, Site 12



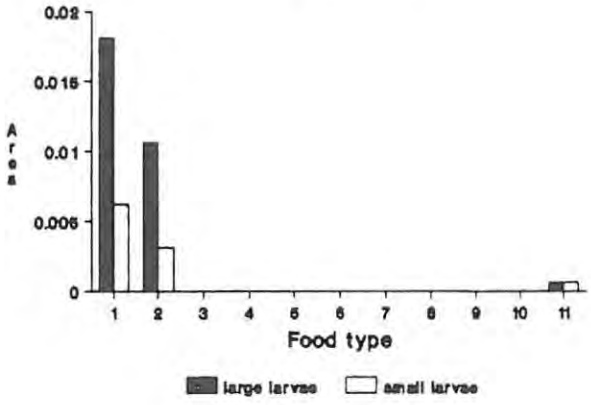
Pseudocloeon maculosum
Riffle, Summer, Site 13



Pseudocloeon maculosum
Riffle, Autumn, Site 12



Pseudocloeon maculosum
Riffle, Winter, Site 12



ADDENDUM

BENTHIC ASSEMBLAGE STRUCTURE, AND THE FEEDING BIOLOGY OF SIXTEEN MACROINVERTEBRATE TAXA FROM THE BUFFALO RIVER, EASTERN CAPE, SOUTH AFRICA.

Carolyn Gay Palmer

p. 24 Paragraph 2, line 8 should read:
2) problems with gut content analysis as a method for ascertaining FFGs;

p. 53 In Fig. 3.1a the sites referred to at Level 4 should be Site 6 and Site 12, not Site 2 and Site 3.

p. 79 For clarity, the first sentence in paragraph 2 should be rephrased:
For all food choice experiments: 1) at the final observation time, both the number of larvae present in each compartment and the number feeding, were totalled for the five replicates, and recorded; and 2) 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.

p. 92-96 The FFGs referred to here, on p. 148, p. 167, and elsewhere in this thesis have been defined as follows:

a) Filterers
  i) passive (net) - feed on seston which is moved by a current, using silk nets,
  (setal) - feed on seston which is moved by a current, using body parts,
  ii) active - resuspend deposits which are filtered using silk nets or body parts,

b) Collectors
  i) gatherers - use structures other than setae to remove lightly attached, or loosely deposited organic material,
  ii) brushers - use setae to remove lightly attached, or loosely deposited organic material,
  iii) scrapers - have structural adaptations which allow them to feed on tightly accreted material.

c) Shredders - feed on allocthonous leaf material, and have leaf fragments as the dominant material in the foregut.

With the exception of the shredder definiton, and the distinction between net and setal passive filterers, these are the definitions given by McShaffrey and McCafferty (1988), which appear on p. 114-115.

These definitions provide an essential basis for the allocation of macroinvertebrates to FFGs. However, they do not necessarily make the procedure easy since several methods are necessary to gather the information needed to assign an organism to a FFG. Even when an organism is assigned to one or more FFGs it is only done so with a greater or lesser degree of certainty, depending on the flexibility of feeding behaviour.

Methods which are useful in assigning organisms, with their specific advantages and disadvantages include:

1. Observation: Observation of feeding can be achieved at several levels. Field observation using goggles provides useful data on the habitat in which the organism feeds. It provides an indication of the resource used as food, and if the organisms are big enough, provides information on the mechanism of feeding. Where visibility allows, it is a useful initial procedure. Laboratory observations using a modified dissecting microscope provide excellent information on the general mechanism of feeding, but do not enable descriptions of the sequential movements of the various mouthparts. Videomacroscopy is the most refined, but most technically difficult and expensive observational method. It was not used in this study, but it can provide detailed information on the interaction of the various mouthparts and enables a precise and accurate description of the mechanism of feeding. Of these methods, only field observations indicate the food ingested in the river.

2. Gut content analysis: This method, though time consuming, does provide sound information on the food ingested in the field. The limitations of gut content analysis are dealt with in section 1.8.2 (p. 25). This method allows the positive recognition of shredders, but not of other FFGs.

3. Morphology: The morphology of the mouthparts can be described using both light and electron microscopy. Details of the structure of the mouthparts provide valuable information on the possible mechanisms of feeding. In all cases, since these observations are static, mechanisms should be confirmed by observation and the foods ingested ascertained using gut content analysis.

4. Food Choices: In this study food choice experiments were the least satisfactory approach. If used, it should be ensured that the foods chosen are available, and are ingested, in the field.

Since the definitions of FFGs require the use of a combination of methods, not all of which were possible for all species in this study, the taxa from the Buffalo River were assigned to FFGs with varying degrees of certainty:

Taxon	FFG	Methods Used	Confidence
Baetis harrisoni	gatherer	2,3	b
Pseudocloeon maculosum	active filterer	2,3	b
Cloeon africanum	gatherer	2,3	b
Centroptilum excisum	gatherer	2,3	b
Choroterpes elegans	brusher	1,2,3	a
Choroterpes nigrescens	brusher	1,2,3	a
Afronurus harrisoni	scraper/brusher	1,2,3	a
Neurocaenis reticulatus	active/	2,3	b
	passive filterer	1,2,3	a
Caenidae sp. A	gatherers	1,2,3	a
Caenidae sp. B	gatherer/	2,3	b
	passive filterer	2,3	b
Cheumatopsyche afra	net filterer	1,2	a
Macrostemum capense	net filterer	1,2	a
Adenophlebia auriculata	brusher	1,2,3,4	a
Dyschimus ensifer	shredder	1,2, 4	a
Goerodes caffrariae	shredder	1,2,	a
Afronemoura spp.	shredders	1,2	c

Where:

1 - observation
2 - gut content analysis
3 - morphology
4 - food choices

a - confident
b - uncertain because of limited methods
c - confident for adults, some juveniles fall in a different FFG

p. 153 - 155

Sample numbers (n) for Fig. 6.2 are given in the text p. 153 & 155.

The data presented in Figs. 6.3 and 6.4 (p.157) are the result of two classification procedures. The same set of 156 samples was classified on the basis of the presence, absence, and abundance of 1) 119 taxa, and 2) 10 FFGs. There is a very clear similarity in the pattern of classification generated. The samples were not in exactly the same sequence, and the number of samples in the various groups was not identical, but the similarity of the two classifications was nevertheless striking.

Typographical and spelling corrections:

p. 80 The morphology of the mouthparts of A. auriculata was investigated using scanning electron microscopy (SEM).
p. 97 Delete a (5 lines from bottom)
p. 138 Fig. 6.5 should be Fig. 6.6 (12 lines from bottom)
p. 167 assign (line 14)
p. 168 variability (line 5)
p. 171 Appalachian (line 12)
p. 171 Yasuna (5 lines from bottom)