THE INVERTEBRATES OF TEMPORARY RIVERS IN THE EASTERN CAPE, SOUTH AFRICA.

A thesis submitted in fulfilment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

GRAHAMSTOWN

by

Amanda Cloete Uys

November 1997

ERRATA

p13, para 2: delete the word 'two', and insert a comma after 'Eastern Cape', and the words 'Northern Province'.

p22, last line: Insert the following sentence -

'Data used for the calculation of taxonomic distinctness were in the form of percentage contribution to total'.

p23, 3rd line from bottom of para 1: 'infomation' should be 'information'.

P46, end of page: Insert the words 'Figure 2.1'.

p60, Table 2.6: Reference to King & Tharme should be dated 1993.

p80, end of line 4: Add 'in'.

p83: The arrow mentioned in the caption should be inserted vertically, with the tip facing the top of the page, to indicate flow direction.

p88, para 2: Insert before last sentence -

'Where less than 100 individuals of a taxon were present, these were counted and abundances recorded. Where over 100 were present, the abundance was assessed by counting the number of individuals present in randomly selected grids (marked on the sorting trays) and multiplying up to the total number of grids. '

p93, 2nd and 3rd lines: The references to Table 3.4 should be to Appendix 3.1.

p109, line 3: The reference should be to Table 3.9 and not 3.8. There was no Table 3.7 in this chapter.

p121: Delete para 1 (repetition).

p122, 4 lines from bottom: For 'upper site' read 'lower site'.

p135, caption for Appendix 3.1: 's - SIC' should read 'i - SIC'.

p139, footnote for Numerical Abundances: insert 'm*' before '= 101-1000'.

p143 para 3: 'thusfar' used twice in this para should be 'thus far'

p144, last two lines of para 1 should read:

'Examples of these are periodic flooding or spates (pulse disturbance), and drying (press disturbance)(Stanley and Fisher 1992, Sagar 1983).

p146, caption to Figure 4.2:

Hydrological phases are not shown as indicated in the caption. They are as follows:

May - Aug. 93	D (dry)	Jan. - May 95	F
Sep.- Oct. 93	O (onset)	Jun. - Jul. 95	NF
Oct.93 - Apr.94	F (flow)	Aug. 95 - Apr. 96	D
May - Jul. 94	NF (no flow)		
Aug. - Oct. 94	F		
Nov.- Dec. 94	NF		

p148 para 2 line 5: replace 'limits of detection' with 'ranges of detection'.

p186, after last sentence of para 1: Insert -

> 'Standardisation affects each individual variable in a data set. The mean of all the variables is subtracted and the resulting number is divided by the standard deviation.'

p191, line 1: 'Ph' should read 'pH'

p193, para 2, line 4: 'this clustered' should read 'this cluster'

p197, 4 lines from the bottom: Between 'affected' and 'number', insert 'by the'.

p198 Table 5.3a: The labels 'R' and '%SIG' which appear to the left of Table 5.3b data should also appear to the left of Table 5.3a data, in the equivalent position.

p199, Table 5.4: After the caption, insert -

> 'X represents presence only. Numbers represent the number of families found in each of the groups listed.'

p200, 2nd line under 'FLOW': 'Table 5.4' should read 'Appendix 5.2'

p200, 6th line under 'FLOW': 'Table 5.5' should read 'Table 5.6'

p205, Table 5.10: Delete one mention of each 'Ostracod' and 'Ceratophallus'.

p229, caption Figure 6.1: Insert -

> 'the Eastern Cape region of' between 'Map of' and 'southern Africa'

p230, line 1: 'diferent' should be spelt 'different'

p232, para 1: Delete last two lines of the paragraph.

p233, para 2 line 1: Should read 'This site is situated 2km downstream of UK1.'

p234, para 2, line 2: Delete hard return after 38 x 10^6m^3.

p239, line 2: 'measurment' should read 'measurement'

p248, middle para: Replace all mentions of Tables 6.4 and 6.5 with 'Appendix 6.2'.

p249, line 6: 'atration' should read 'abstraction'

p257, para 2, second last line: Delete text from 'mayflies' to end of paragraph.

p257 para 4 line 1: 'stie' should read 'site'

Chapter 7: Throughout this chapter, the Luvhuvhu and Letaba rivers are referred to as Mpumalanga rivers. They are in fact Northern Province rivers.

ABSTRACT

Temporary rivers in dryland regions are subject to highly variable and unpredictable rainfall and flow, and are considered unstable systems relative to perennial rivers of temperate zones. Little is known of the ecology of South Africa's temporary rivers, despite their abundance. The research presented focusses on the aquatic invertebrates inhabiting intermittently-flowing rivers in the 'arid corridor' of the Eastern Cape, South Africa. The major aims of the work were: to investigate which invertebrates inhabit these rivers, how the fauna is affected by environmental variability at various spatial and temporal scales, whether or not a characteristic fauna can be associated with these rivers or the hydrological phases which characterise them, and to establish to what extent faunal overlap occurs between different temporary rivers and between natural and modified temporary and perennial rivers. Research results indicate that the fauna of the Eastern Cape temporary rivers shows little structure at the scales of investigation, and that communities are generally non-equilibrial in character. The major forces shaping the biota are considered to be physical rather than biological, and the most important of these are: present and antecedent hydrological conditions and their duration; time of year; and biotope character, extent and heterogeneity. Three groups of fauna were identified as inhabitants of the temporary rivers: 'residents', 'facultative taxa' and 'opportunist colonists'. Taxa were tentatively allocated to these groups. Faunal resemblance was fairly high *in Eastern Cape temporary rivers at the level of family, but not at more detailed taxonomic levels. A comparison between faunas of temporary and perennial rivers in different regions of South Africa illustrated the influence of geographical location on diversity. Within regions, however, there was no indication that perennial rivers were more diverse than intermittent rivers. The relatively high diversities in temporary rivers in this study are attributed at least in part to the heterogeneity in surface water conditions over time. A conceptual framework envisioning a continuum between perennial and temporary rivers is proposed as a basis for ongoing research into these rivers. A supporting terminology for the range of river flow types in South Africa is presented.*

DECLARATION

In accordance with the regulations for the award of Doctorate of Philosophy, I declare that the work presented in Chapters 1-6 and 8 of this thesis is my own original work. Data from various studies of rivers in the Eastern Cape and Mpumalanga have been used for the purposes of comparison of river faunas in Chapter 7. Neither the whole, nor any other part of the thesis has been, is being, nor will be the subject for a higher degree from any other university.

Dedicated to my folks,
Beorn and Midge,
whose insanity I inherited

and, of course, to Harry.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF PLATES

ACKNOWLEDGEMENTS

This process was alway supposed to be as much about journey as destination. And what a journey! It has all sorts of analogies, generally of the 'running a marathon' variety. But more appropriately - after canoeing the Great Fish River Canoe Marathon recently, I wrote:

..'*in mastering the flow in big waters in a fragile boat, awareness of the Whole Picture becomes acute. River language is only understood by listening to the river, and not to stories about it. It is easy to forget that, as a scientist. Always thinking up theories about the subject instead of letting it tell its own tale. The Boat is steered most successfully in white waters by watching, watching, watching; by following the deepest channel, being part of the current, forgetting the human boundary. Falling out of the boat means you haven't forgotten properly! The complexity of fluid and the nature of its movement, the channel shape, the substratum character - all these have become sophisticated scientific disciplines, but they are so simply integrated in the boat, in the water, as just another part of the river..*'.

My first thank-you, then, must be to the River, for continuing to teach me its language when I'm quiet enough to hear. And, of course, for it's other great lesson - *Don't push the river!* (which mostly gets forgotten). If I do anything useful, it will be to make people aware of your secrets.

Now that it is too late to get out of this boat, I'm sure there must be someone I can blame ...

Prof. Jay O'Keeffe, my supervisor, was the instigator of this project. He recognised the necessity for this sort of research in SA many years before he found someone foolish enough to actually work in a dry river bed. Such Charm, Professor. It has been a great working alliance and friendship, and I owe much of my understanding of rivers (and people!) to you. Getting to this stage must be at least partly due to your well-known middle name - Jay 'It'll-be-fine' O'Keeffe. Thanks Boss.

My folks, Midge and Beorn, really deserve a doctorate themselves for their input into this project, particularly in the write-up stage when their garden cottage was my Hotel California, complete with pink champagne and ice. The value of families must Never be underestimated (those days before handing in the thesis ...). What you put up with, others would have run screaming from - in fact even river bugs could learn a great deal about 'resilience and resistance to disturbance' from you. And your proof-reading and paste-up skills must be legendary. It has been a very special time and if you think you're getting rid of me, forget it.

To Gary my fiancee and co-paddler, and to Max, thanks guys, A Lot. We really survived the Big Smoke like a three-legged pot. You kept saying 'keep it simple' and it was hard advice to follow, but really insightful. Enduring my topographical temperament was admirable, and I appreciated the space when I needed to tear someone's hair out (Very Wise Men). Thanks also for all the technical help and the support up in Joburg. Knowing you were there was what counted. There are many many more rivers out there, literally and figuratively, for us to explore, so let's do it. I'll make the tea from now on.

Dr Martin Villet should thank me for curing his insomnia by sending him reams of draft material which he patiently and assiduously scoured for scientific and grammatical credibility (Did you find any, Martin?). Your willingness to help and your rapid reading skills and cautious, critical discussions contributed in a major way to this thesis - thanks, Zomv, I owe you! Dr Carolyn Palmer also read several chapters of this thesis enthusiastically, and was most helpful in discussions on a range of topics. Thanks Tal, for your endless support over the past years, I'm never sure how you do it.

Kekere Soxujwa, my field assistant, apologised to God every time we netted bugs in the river (and in fact mentioned that I should be punished, if anyone). I'm sure I'm in for a bad time, if I ever make it to paradise. Keke - you were really the arms and legs of those fieldtrips and we learnt lots about that little river together, in Xhosa and in English. I really appreciated your energy and humour, and your skill at identifying those BUGS - I hope we'll be doing more fieldtrips together.

Margi Rogers and Gaye Youthed at the Institute for Water Research became my Grahamstown Mums - there aren't enough roses or chocolate cakes on the planet to express my thanks to you both for always being there and your endless running about. All I can say is "It won't happen again".

A couple of scientists became my Gurus from the early days of this research - Dr Mark Chutter must be thanked for his enthusiastic imparting of SASS4 and invertebrate identification skills - we had some great finds in the rivers of the Eastern and Southern Cape. Dr Andrew Boulton was regularly on the other end of the E-mail and was a great source of assistance, information and support. I hope we will work on these rivers together at some time in the future.

I am grateful to many people who assisted me with identifications of the bugs, and particularly to Dr Arthur Harrison for his tireless and cheerful identification of chironomids, which he himself likened to running a marathon. Dr Ferdy de Moor assisted with general identifications and cleared a corner in the Albany Museum for me for a few happy weeks. Mr Pat Reavell (University of Zululand) assisted identification of Hemipterans, Dr Koen Martins (Royal Institute of Natural Science, Brussels) with ostracods, Dr Nancy Rayner (University of Zululand) with copepods, Dr David Brown (London Natural History Museum) with snails, Dr Olaf Bistrom (Helsinki) with dytiscid beetles, Ms Gael Whitely and Ms Pat Caldwell (University of Natal, Pietermaritzburg) with dragonfly and damselfly larvae, Dr Rob Palmer (AfriDev Consultants, Mpumalanga) with blackfly larvae, and Dr Maureen Coetzee (SA Institute for Medical Research) with mosquitoes.

Another Big Thank You for my full tummy to all those who assisted with the project financially - particularly the Water Research Commission, from whom I received a two year fellowship, the Institute for Water Research, Grahamstown, who covered running costs of the project and more, and those other kind souls who know who they are.

The list really goes on and on ... I would like to mention a few of the people whose support, encouragement and technical assistance made this project such an Epic Adventure.

First, the family .. To my brother Chris for rigging up computers and modems and trying to turn me into a technocrat - a BIG thanks, Boet - the confuser didn't die on me once, and yours and Gina's support was way greater than machines - won't be forgotten. To my sister Sue and brother Gus for being Kind and Wise and Older and Funny, and There, always; and to their partners Mark and Sue for being robust enough to join the mad family. Thanks to all the little people - Stef, Nicks, Amy and Kara for their bright eyes and priceless artwork which was hung in my lab and recharged my 'bugging' batteries many times during the long microscope hours.

Now, my friends. Patsy Goetsch, my twisted sister, hauled me out of a tent within days of my arriving in Grahamstown, and invited me to stay in a real home for a few days. Three months later ... Well, Pats, nothing has changed, you've always been there and made me believe this PhD was possible - your friendship is second to none. Many poor delegates at meetings are going to have to encounter this 'Thelma and Louise' in action - very scary for the uninitiated. I trust we won't drive off the cliff when the cops find us.

My great friends Rat and Carol in the Big Smoke loaned me a printer and a spare room, fed me Gourmet Food and G&Ts, delivered a modem to my doorstep, and most-of-all, were there with big shoulders and fun and perspective on many occasions. Muchos gratsias amigos, Malawi, Malawi.

Father doctor Larry and his ridiculous hats caused havoc with my spiritual perspectives. Good one, Lar, you're the best. Lil kept the balance, kept the scientists singing, kept the lunacy alive, and gave the very best hugs in Grahamstown. Wild Sooze, a remarkable woman, materialised like a magic dove in 1996, and has continued to cast her spell on all of us, and now on the small Max. Here's to your own PhD, Sooze, and to plenty more long candlelit conversations. William 'Billy Bathgate' must be thanked for expanding my horizons by imparting anthropology, soccer, archery and alternative muzic philosophies (usually simultaneously), and by completing his thesis without a single sign of stress. A sad affair. Admit it wasn't as much fun. Dez Plant, my office-mate and fireside story man, inspired great notions of travel, gardening and scream-printing, along with a touch of dark humour. A fine vintage, Dr Weeks, you've got the t-shirt, now get the book! The Cathcart Streeters, Justerini, Bev and Goonie, are honoured for their respective skills - finding the edge of the universe, Being the edge of the universe, and collecting and analysing the edge of the universe (if it's a rock), but mostly for those great conversations while running ourselves ragged around Grahamstown. My neighbour Biscuits was always ready with tea and insight on current affairs and matters mathematical and philosophical. Thanks Wol. My Kenton-on Sea family, Bee, Ian and Lou, gave me oh-so much time and love and tolerance, and the very best sea view in the world - I hope I'll be back.

And to all of you I haven't mentioned .. but think of often, a luta continua and it's time to Party!

CHAPTER 1

INTRODUCTION AND OVERVIEW

'If you fall into a South African river, one of two things may happen:
you may pick yourself up and dust yourself off,
or you may find yourself swept out to sea ...'

Remark attributed to Professor D.C. Midgeley,
commenting on the variability of flow
in rivers of the region.

RHODES
UNIVERSITY
LIBRARY

1.1 THE BACKGROUND TO TEMPORARY RIVER RESEARCH

Dryland areas occupy about a third of the world's land-surface area (Thomas 1989). The dominant river types occurring in these areas are those which are temporary in nature, ceasing to flow and sometimes drying completely for some part of most years (Braune 1985, Williams 1988, Davies *et al.* 1990).

Many modern limnological concepts and principles had their origins in extensive research on aquatic ecosystems in the northern temperate regions, which occupy an area less than 20% the size of that occupied by arid, semi-arid, tropical and semi-tropical parts of the world (Williams 1988). Over a decade ago, W.D. Williams (1985) commented that the extent of limnological references to temporary waters was not in accord with their '*widespread occurrence and abundance, ecological importance, nor limnological interest*'.

In general, perennial temperate rivers are large, hydrologically stable, fresh-water systems with comparatively regular flow, low turbidities, and marked seasonality in environmental and biological factors. Arid and semi-arid zone temporary rivers may have features of both mesic and xeric systems (Walker *et al.* 1995). They are, however, hydrologically distinctive: flow is highly variable, the response to rainfall tends to be non-linear, and there may be a negative correlation between antecedent moisture and runoff - i.e. following a dry period, high runoff may occur (Molles *et al.* 1992, Davies *et al.* 1995). The fauna occupying these rivers is considered unstructured and physically-controlled (O'Keeffe *et al.* 1989, Davies *et al.* 1995).

Based on the physical and biological differences between the river types, Boulton and Suter (1986) and Williams (1987) cautioned against the extrapolation of concepts derived from the study of perennial lotic ecosystems to temporary river environments. The classic opinion paper on 'Limnological imbalances.., ' by W.D. Williams (1988) highlighted the necessity for a revision of many of long-held concepts in limnology, and encouraged awareness (by all limnologists) of the range and distribution of temporary lentic and lotic waters globally. Molles *et al.* (1992) attributed much of the high variability in arid and semi-arid zones to the

El Niño-Southern Oscillation (ENSO). Having studied the attributes of rivers in dryland zones, the authors suggested that research in arid and semi-arid areas should focus on the causes, effects and extent of all aspects of their inherent variability, in order to develop predictive powers for their apparently chaotic behaviour.

The insights of the aforementioned researchers, and many others, provided the basis for a new direction in limnological research - the investigation of the ecology of unpredictable, intermittent, turbid rivers of dryland zones, and the manner and extent to which they differed from the hydrologically stable, perennial, clear-water rivers of temperate North America and Europe. The capricious nature of temporary systems made them perfect subjects for the study of ecological concepts such as disturbance (e.g. Townsend *et al.* 1987, Grimm 1992, Hildrew and Giller 1992), the relative importance of biotic and abiotic factors in regulating faunal structure (e.g. Peckarsky 1983, Power *et al.* 1988), faunal succession (e.g. Fisher *et al.* 1982, Fisher 1990, Boulton and Lake 1992a) and patch dynamics (e.g. Townsend 1989). Studies contributing to the growth of the research field included those from Canada (Williams and Hynes (1976, 1977), Australia (e.g. Towns 1985, Boulton and Lake 1990, 1992a,b), and Arizona (Gray and Fisher 1981, Grimm and Fisher 1989, Valett *et al.* 1990, Boulton *et al.* 1992a,b; Stanley and Fisher 1992). Williams' (1987) book covering a number of the more important aspects of temporary waters, such as physical and abiotic features, biotic adaptations, colonisation patterns, and applied problems was a land-mark.

In recent years, research in this field has, of necessity, developed a more applied direction, taking cognizance of issues such as legislation and policies on river management and restoration (Boulton *et al.* in press), and the consequences of modifying temporary rivers, particularly regarding flow regulation which dampens the variability thought to drive these systems (e.g. Walker *et al.* 1995, Boulton *et al.* in press).

In semi-arid South Africa, virtually no long-term ecological research has been done on naturally temporary rivers, despite the recognition that a major proportion of river length is intermittent (Davies *et al.* 1993). High water demands in a dry region, and prevailing government policy regarding supply for all citizens (Department of Water Affairs 1997) has placed enormous pressure on the water resources by way of abstraction, interbasin transfers (IBTs), impoundments, and other developments. All of these modifications alter river regimes. Below the sites of impoundment and abstraction, naturally variable perennial flow may be regulated or transformed to intermittent in sections, while the import of water via IBTs can transform naturally temporary flow to perennial in the affected sections of a river. There are many examples of the alterations such modifications have made to flow regimes of South African rivers (e.g. Chutter 1971, Moore and Chutter 1988, O'Keeffe and de Moor 1988, Palmer and O'Keeffe 1990, Davies *et al.* 1992, Chutter and Heath 1993). As population increases and water demands grow, an increase in the rate of river manipulation is likely (see Davies *et al.* 1993, 1995). As the exploitation of South Africa's scarce water resources continues, more permanent rivers will become temporary, and more temporary rivers will be exploited.

While some work has been done to gauge the effects of some of these modifications (e.g. O'Keeffe and de Moor 1988, Moore and Chutter 1988, Chutter and Heath 1993), the lack of information on, and understanding of, the ecology of the range of naturally temporary South African rivers, and the manner in which they vary from naturally perennial rivers, provides little against which to judge the effects of temporary-to-permanent or permanent-to-temporary transformations. There is clearly, as Williams (1988) urged, a pressing need to expand our perception and understanding of temporary rivers and their functioning at an ecosystem level (e.g. Williams 1996).

For these reasons, the initiation of temporary river research in South Africa was necessary and overdue. Several projects, each concentrating on a different aspect of these systems, have been launched in recent years (e.g. Tharme 1995, Wishart *et al.* in prep., Gabriel pers. comm.). The study presented in this thesis forms a part of this field of endeavour. It focuses only on the 'surface' invertebrates of temporary rivers and thus does not include any work on, or reference to, the hyporheic zone (that between the epigean and groundwater zones). It is necessary at the outset to note that although the generic term used in the thesis is 'temporary rivers', a gradient in 'temporariness' exists, separating intermittent rivers (which flow for more time than they are dry) from ephemeral and episodic rivers (which are dry for the majority of the time). This subject is discussed in more detail in Chapter 2. The research presented here concentrates mainly on intermittent rivers.

1.2 CHARACTERISTICS OF TEMPORARY RIVERS

1.2.1 Hydrological features

In semi-arid and arid areas, high evaporation rates affect the conversion of rainfall to runoff, resulting in low mean annual precipitation to mean annual runoff (MAP:MAR) ratios of 8.6% for South Africa and 9.8% for Australia, in comparison to that of 65.7% for Canada and a world average of 48% (Davies *et al.* 1995). The coefficients of variation of annual flows in arid and semi-arid regions are, on average, more than four times greater than those from humid and temperate regions (Davies *et al.* 1994).

The flow regime forms the basis of most of the processes occurring in temporary rivers (Boulton *et al.* in press). Temporary rivers are characterised by highly variable discharge and extremes in drying or drought, and flooding (Braune 1985, Alexander 1985, Boulton and Suter 1986). In South Africa, where short-term cycles in flow are difficult to discern (Davies *et al.* 1995), and seasonality is often not distinct (in the more arid areas), another distinctive feature of temporary river flow is its unpredictability (Davies *et al.* 1995).

The drying process differentiates temporary rivers from perennial rivers in terms of both their fauna and their physico-chemical regimes. The effects of drying are influenced by the timing, duration and frequency of the drying event (Boulton *et al.* in press). Stanley and Fisher (1992), in their study of intermittency, suggested that in semi-arid areas, attention should be focussed on the phenomenon of drying as a natural disturbance and determinant of aquatic ecosystem state, and on the development of intermittent conditions. Stanley *et al.* (1997) maintained that first, and vital, step towards understanding the regulation of ecosystem function by drying was the documentation of water loss from streams. The authors also commented that the spatially heterogenous nature of drying rendered standard hydrological measurements (e.g. discharge) inadequate descriptors of the process. While consideration of the drying process has been integral to studies of temporary systems, interest has largely been centered on discharge events (flooding, spates) and the response of fauna to these.

1.2.2 The invertebrate fauna

The perception that the environmental adversity associated with temporary waters correlates with low species richness (e.g. Wiggins *et al.* 1980) has proved erroneous, with large numbers of invertebrate taxa (e.g. 200 to 260) reported in some studies of intermittent systems (Abell 1984, Williams 1987, Boulton and Suter 1986, Boulton and Lake 1992b).

Species from most of the major groups occurring in freshwater have been collected in these environments (e.g. Williams and Hynes 1976, 1977, Boulton and Lake 1992b). Taxa capable of inhabiting temporary lotic waters, and well represented in these environments in different parts of the world, include ephemeropterans, hemipterans, coleopterans, trichopterans, dipterans-particularly chironomids and tipulids, and molluscs (e.g. Williams 1988, Boulton and Lake 1992a, Williams 1996). Williams (1987) attributed the success of some of the groups found in temporary rivers (e.g. insects and mites) to their terrestrial evolution, suggesting that these animals may already be adapted to water loss, and that the environmental conditions regulating populations in permanent waters may as harsh as those in temporary ones.

Varying results have been reported concerning the overlap in fauna between temporary and perennial waters. Whereas the difference between the fauna of temporary standing waters and permanently flowing waters may be great, in temporary lotic waters the running water phase adds to the diversity of niches available (Williams 1987). Although little overlap was reported between the fauna of nearby temporary and permanent lotic waters in Canada (Williams and Hynes 1976), considerable similarity was reported in Australian temporary and permanent streams (Boulton and Suter 1986).

The question of what affects the composition, distribution and abundance of stream invertebrates is a key concern to stream ecologists (Hynes 1970). In unstable environments subject to unpredictable surface water conditions and habitat heterogeneity, the proximal controls on the fauna are considered to be physical in nature, with biological interactions acting at a lower intensity (Williams 1987, Power *et al.* 1988). A number of environmental variables may interactively (and possibly hierarchically) influence faunal character, including discharge, current velocity, light intensity, dissolved oxygen, pH, salinity, temperature, nutrient levels, and other variables (e.g. Boulton and Lake 1990, Feminella and Resh 1990, Schneider and Frost 1996).

The importance of interspecific interactions in regulating faunal structure may increase with a decrease in habitat heterogeneity and a resulting loss of food resources and trophic levels (Menge and Sutherland 1976). However, Williams (1987) commented that the coexistence of very similar dytiscid species in environments subject to ephemeral food resources may suggest just the opposite - a lowering of interspecific interactions in order to promote coexistence in a food-poor environment.

The duration of habitat or hydrological conditions (e.g. flow period) is associated with ecosystem stability and changes in faunal diversity (e.g. Boulton and Suter 1986, Grimm and Fisher 1989, Williams 1996). In environments subject to a highly variable and unpredictable flow regime, aquatic habitat (in the form of individual biotopes) persists for variable periods, and undergoes expansion and contraction (*sensu* Stanley *et al.* 1997) with the frequent changes in surface water. The advanced stages of habitat loss due to drying are associated with dramatic faunal losses (e.g. Grimm and Fisher 1989). However, where suitable refugia are available in the early stages of drying, fauna from the drying areas have been reported to relocate to these areas - for example, in the more temporary of two intermittent rivers, Boulton and Lake (1992a) found that fauna from drying riffles relocated to pool environments. As drying progresses, other instream refugia include drying sediments and the hyporheic zone (Boulton *et al.* 1992a). Somewhat like the 'opportunivore' feeders reported by Palmer (1991), certain taxa inhabiting intermittent rivers are clearly capable of behavioural flexibility and show opportunism in their ability to colonise a variety of substrata.

There are several measures of faunal response to environmental instability. The tendency of faunal composition to remain unchanged over time (persistence) or for species to coexist over long periods, both provide indices of faunal stability (see Townsend *et al.* 1987). Where abiotic factors cause reductions in - or local extinctions of - particular taxa, persistence of biota would rely on recolonisation, either actively by aerial adults, or passively by movement of larvae in drift (Townsend *et al.* 1987). Hildrew and Giller (1992) summarised a number of studies which reported community persistence over time despite environmental fluctuations and often dramatic disturbances. Two further measurable features of stability are the '*resistance*' of fauna to fluctuations or extremes in environmental variables (i.e. the ability to resist changes in the environment), and the '*resilience*' (or ability to recover) following disturbance (Fisher and Grimm 1988). Fisher (1990) recognised faunal succession as a major component of resilience.

Biota occupying highly variable environments subject to unpredictable extremes are considered to be unstructured and subject to continual recruitment and dispersal (Winterbourn *et al.* 1981, O'Keeffe *et al.* 1989). This lack of organisation is partially recognised in the concept of biological 'communities'. These have historically been viewed in one of two ways: either as tightly-organised, equilibrium-mediated units of interacting taxa, with distinctive and persistent species composition (e.g. Minshall and Petersen 1985), as in the River Continuum Concept (Vannote *et al.* 1980); or as more fluid entities - the random accumulation of individualistically arranged species or populations responding differently to environmental gradients, in which disturbance overwhelms interspecific interactions (Whittaker 1956, 1962, 1967, Rzoska 1978, Reice 1980, 1984, Winterbourn *et al.* 1981, Townsend *et al.* 1987, Resh *et al.* 1988). Cowie (1985) pointed out the irony that the perception of stream communities as 'well ordered entities that somehow aim to maximise their efficiency of energy utilisation' (Vannote et al. 1980) disregarded the fundamental role played by physical instability in determining faunal characteristics. This view is generally supported for the biota in rivers of highly variable environments. Reice *et al.* (1990) declared that many stream communities were in a state of *'perpetual recovery from frequent disturbances'* - and Hildrew and Giller (1992), citing Huston (1979), suggested that this might be called the 'clinging to the wreckage' model of community organisation, in which species were either entirely non-interactive, or the recurrence time of disturbances was too short to allow interactions to eliminate species. Hildrew and Giller (1992) maintained that stream communities 'track environmental conditions faithfully' and were fragile in the face of sustained perturbations.

1.3 CONSIDERATIONS IN THIS STUDY

The research presented here represents the initial stages of investigations into naturally and non-naturally temporary rivers in South Africa. The considerations in the planning of the research included a rationale for the research, the choice of a biological unit of study (vertebrates or invertebrates), the temporal and spatial scales at which the research should be conducted, the division of hydrological conditions in ecologically meaningful phases, and the discernment of criteria by which disturbance could be assessed in the system.

1.3.1 Rationale for the research

In South Africa, the lack of information regarding the range and functioning of a large proportion of our rivers provided ample motivation for the initiation of research. The gap in our knowledge was considered all the more serious in the context of increasing transformation of river flow regimes to cater for growing water demands. In the absence of information regarding naturally temporary river processes, it is impossible to quantify the ecological effects of the transformation flow regimes, and the consequences of such transformations can only be assumed to be ecologically damaging. The biological and management aspects of these issues provided the impetus for the research into temporary rivers reported in this thesis.

1.3.2 The choice of fauna

Invertebrates are the most diverse and well-studied group of animals inhabiting temporary rivers (see Williams 1987), and provide a range of responses to different conditions. Assemblages of invertebrates integrate the effects of environmental variability over time, thus providing a measure of observable impact, and reflecting overall ecological integrity (Plafkin *et al.* 1989). The low mobility of juvenile stages generally prevents movement away from the site even under adverse conditions (in comparison to fish, for example), so that assemblage structure at the site provides a true reflection of biotic response to local conditions. A further advantage is the generally short life-spans of invertebrates, which means that changes in local abundances and species ratios occur over short periods and are observable.

Difficulties in this choice of biota included the paucity of life-history information and systematic research on the majority of South African riverine invertebrates, and the desperate need for taxonomic revision of several of the groups.

Invertebrate fauna were identified to the lowest possible taxonomic level. Where taxa were identified only to higher taxonomic levels (e.g. Family), the taxa distinguished within that group were recorded as separate types (e.g. Hydrophilid A, Orthocladiinae A; e.g. Appendix 3.1). While this had the obvious effect of under-representing taxa identified at coarser taxonomic levels, the alternative of reducing all data to family-level would have resulted in a huge loss of information. The term 'equivalent taxa' was borrowed from King and Tharme (1994) to refer to the combination of taxonomic hierarchies used in analyses.

1.3.3 Temporal and spatial scales

'Scale of perception affects our viewpoint so that, at the extremes, all rivers are either the same, bearing water down the slope, or all are different, as no two streams have the same species complement at the same relative abundances' (Cummins *et al.* 1984, quoted by Hildrew and Giller 1992).

In order to develop a conceptual understanding of the structural and functional components of an aquatic ecosystem, and to describe any patterns in the system and the processes which generate them, it is necessary to have an appreciation of variation at different spatial and temporal scales (see Minshall 1988, Boulton and Lake 1992b). The spatial scales relevant to rivers vary over a number of orders of magnitude, from that of the microhabitat to that of the river catchment. The catchment can be easily resolved into a number sub-systems: Stanley *et al.* (1997), for example, focussed on four spatial scales - *reaches* (10^1 to 10^2m), *sections* (10^3m), *phases* (10^4m) and the entire drainage or catchment (in their case, 10^5m). Temporal scales of investigation, likewise, vary over an extensive range (e.g. seconds to years).

For the purposes of this study, it was considered necessary to investigate the variability in abiotic and biotic factors over a number of spatial and temporal scales. At the smallest scale (10^{-1}m), the biotope was selected as the unit of instream 'habitat'. Biotopes are those 'patches' within the river which exhibit similar substrata and physical or flow characteristics, and they are commonly described according to subjective criteria (Palmer *et al.* 1991). A number of biotopes identified by Chutter (1994) were used as the basis of random sampling for invertebrates, and two further biotopes appropriate to pools phases and drying conditions in the river were defined. Chutter's biotopes were marginal vegetation (MV), stones-in-current (SIC), stones-out-of-current (SOOC), and sand (SAND). The additional two biotopes were shallow pools (POOL) and drying substrata (DRG). Each of these was visually (subjectively) discernible, and full descriptions for each are provided in Chapter 3.

At a larger spatial scale, that of the river reach (10^1m), sampling sites were selected. The choice was either: i) to replicate sampling by selecting a few sites on two rivers and conducting intensive investigations at these localities over the period, following the methodology of Boulton and Lake (1990, 1992a,b) in their investigation of intermittent Australian streams; or ii) to choose two sites on a single river section for intensive investigation, and a number of sites on different temporary rivers in the region for sampling at a less rigorous ('survey' type) level. The strength of the former option was that it allowed rigorous assessment of variability between rivers over the full period of the study, thus generating a picture of the range of conditions and fauna characterising those systems. The latter option allowed a less rigorous but more extensive investigation of faunal variability both within and between rivers (a trade off of resolution for perspective). This option was more likely to show whether or not a characteristic regional 'intermittent river fauna' could be identified (Williams 1987). Because the study represented the first such work in the Eastern Cape region, the broadest possible picture of conditions in temporary rivers was desirable, without compromising the strength of the data set. For these reasons the second option was selected. Two sites were selected on the upper section of the Kowie River, a naturally temporary river in the Eastern Cape, for intensive investigation and analysis of the invertebrate fauna (Fig. 1.1, Chapters 3 to 5).

At a larger spatial scale (10^3m), a less intensive study of different temporary river regimes in the region was conducted. Four further sites were selected: one in the lower reaches of the Kowie River; an upper and a lower river site on the naturally temporary Bushmans River; and a single site on a small ephemeral tributary of the Great Fish River (Fig. 1.1). These and the upper Kowie River sites were surveyed at four-monthly intervals for a period of 20 months, and fauna was identified only to family level in all but two of these sampling events. An assessment of variability between the invertebrates of the different river regimes is presented in Chapter 6.

A further spatial component to the study allowed the assessment of variation between faunas of different temporary rivers in different regions, and of overlap in the faunas of temporary and permanent rivers from the same and from different regions (e.g. Williams and Hynes 1976, 1977, Boulton and Suter 1986, Williams 1987). Analyses of this nature are difficult, as variability can be attributed to regional influences, flow regimes, the effects of scale, differences in sampling design, etc, and a cautious and conservative approach was called for in analysis and interpretation of information. Data from a number of different invertebrate studies in the Eastern Cape and Mpumalanga (formerly Eastern Transvaal) areas were used. Four rivers with differing flow regimes in Mpumalanga, and three rivers in the Eastern Cape region, were included in the assessment. This is presented in Chapter 7.

The spatial scales over which variability could thus be assessed in the study were: within a reach (site), between reaches in the same section (upper river), between sections (upper and lower river), between rivers within a region (temporary rivers in the Eastern Cape), and between temporary and permanent rivers in two different regions (Eastern Cape and Mpumalanga).

Results of investigations into intermittent streams in Victoria, Australia, by Boulton and Lake (1990, 1992a,b) proved the value of long-term ecological research in measuring temporal variation in temporary rivers. On this basis, the full study was planned over a period of two and a half years (1993-1996). Within this period, smaller temporal units were selected for analysis of biotic and abiotic variability: within and between months over an eight month period (Chapter 3), and within and between midsummer periods in three consecutive years (Chapter 4).

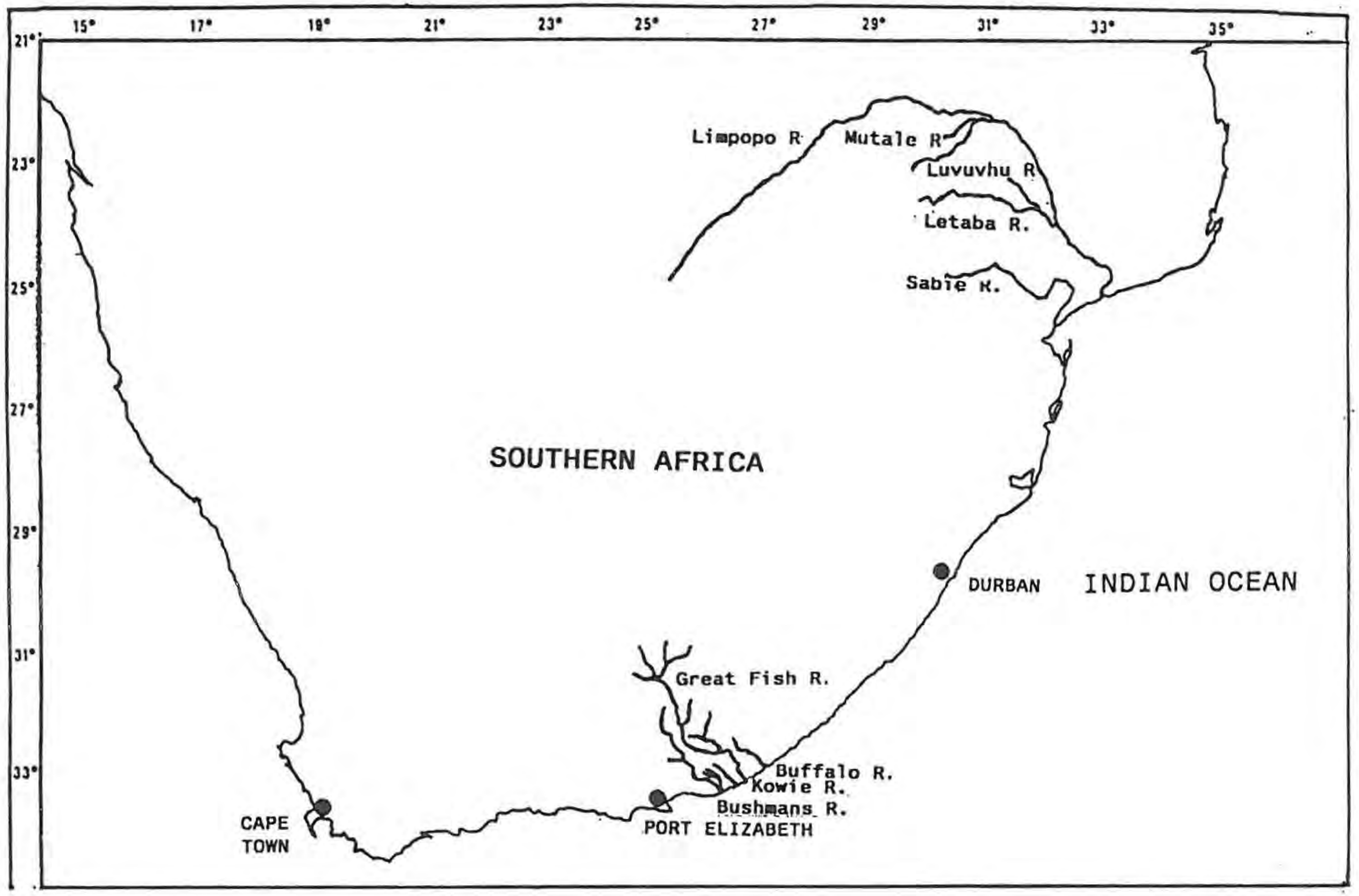


Figure 1.1 Map of South Africa showing the rivers included in this study.

1.3.5 Hydrological phases

In previous studies on temporary rivers, either biotic or abiotic factors have been used to discern a number of phases in a river. These assist in distinguishing which aspects of the flow regime are particularly relevant to the fauna (Walker *et al.* 1985). Traditionally, the phases have been discerned on the basis of empirical studies (*a posteriori*), and in the majority of cases this has been done subjectively, linking taxonomic composition to environmental conditions such as flow and season (e.g. Clifford 1966, Williams and Hynes 1976, Abell 1984, Grimm and Fisher 1992). Boulton and Lake (1990) identified cyclical sequences of five flow phases objectively, by multivariate ordination and classification of interactions among a number of abiotic variables. The authors later assessed the match between the flow phases and faunal groups which had been identified using multivariate methods, in order to ascertain whether particular flow phases were characterised by distinctive groups of invertebrates (Boulton and Lake 1992a).

For the purposes of this study, there was some justification for working in a reverse direction: that of discerning a set of hydrological phases at the outset of the study, and later determining whether or not these could be associated with particular biota or abiotic variables. The assumption was that the main force governing the distribution and abundance of fauna was the flow regime (Boulton *et al.* in press). Where seasonality in flow was distinct, seasons and their related hydrologies could generally be associated with particular fauna, as in Williams and Hynes' (1977) groupings of *'Fall-winter stream fauna'*, *'Spring pool fauna'*, and *'Summer terrestrial fauna'*. While seasonal air temperature patterns in the Eastern Cape were consistent from year to year (South African Weather Bureau data), seasonal trends in rainfall and flow were likely to be absent, according to reports of the erratic and unpredictable nature of rainfall in other catchments in the region. For example, monthly rainfall figures from an area in the Great Fish River catchment indicated that over the period between 1958 and 1976, the highest percentage of the mean annual precipitation (MAP) occurred in every month of the year except April and November (Davies *et al.* 1993). Taking this to be a feature of rivers of the Eastern Cape arid corridor, erratic and unpredictable rainfall would be reflected in hydrological variability, and the association of fauna with seasonally-mediated hydrological conditions in the river environment would not be possible.

On the basis of this reasoning, five hydrological phases were defined at the outset of the study (*a priori*), on the basis of what was known of intermittent river hydrology in the Eastern Cape region. Phases were initially identified according to surface-water characteristics only. Each was considered to represent sufficiently different surface aquatic conditions to have a ecological effect on the fauna present. They were: ONSET (lasting for a period of one month after recommencement of flow at the site), FLOW (stable continuous flow), NO-FLOW (following flow cessation, for the period that surface water was still continuous), POOLS (periods during which surface water was discontinuous and restricted to pools in the channel) and DRY (where there was no surface water at the site excepting in the form of rainpools). These phases were used to identify hydrological state throughout the study, and the frequency of change of phase was used as a criterion for disturbance in the river, as described in the following section.

1.3.6 The criteria for disturbance

'(A) species can be good at resisting either competition on one hand or disturbance and predation on the other, but it cannot be adept at resisting both kinds of stresses.' (Petraitis *et al.* 1989)

Disturbances have already been referred to in this chapter without proper explanation. Extreme or out-of-range events which significantly alter the faunal character of an environment are generally construed as stressors or disturbances (e.g. Sousa 1984, Resh *et al.* 1988, Fisher and Grimm 1988). In perennial lotic ecosystems, flow fluctuations are the most obvious sources of disturbance (Hildrew and Giller 1992). In temporary rivers, flow cessation and drying are additional disturbances (e.g. Stanley and Fisher 1992). Ecologists accept that disturbance is an important determinant of ecosystem structure, stability and process (Grimm 1992, Grimm and Fisher 1989, Boulton and Stanley 1995).

Resh *et al.* (1988), in a comprehensive review of the subject, defined disturbance in stream ecosystems as '*any relatively discrete event in time that is characterised by a frequency, intensity and severity outside a predictable range, and that disrupts ecosystem, community, or population structure and changes resources or the physical environment*'. Poff's (1992) assessment of this definition was that the 'predictability clause' introduced problems which limited the ability to identify, describe and discuss important aspects of disturbance in streams. Poff recommended that the definition of disturbance should be based on physical criteria (e.g. flows which caused bed movement) with clear ecological consequences (e.g. faunal or resource displacement) rather than on the response of the fauna. Grimm and Fisher (1992), similarly, maintained that a disturbance regime should be described by magnitude, areal extent, frequency and predictability of disturbances, and that such descriptors should be independent of their effects on the biota.

The definition of disturbance in terms of its effects (e.g. significant mortalities) is admittedly circular; but on the other hand it is difficult to answer the question '*when does an event constitute a disturbance?*' without reference to the outcome of the event (viz. the term can be only be used retrospectively). Odum (1975) expressed a similar sentiment eloquently: '*The term 'stress' has been widely used for both cause and effect, stimulus and response, or input and output. Although some authors worry about the dual use of this word, I view stress as comprising both input and output. One cannot have a response without a stimulus.*'.

Temporary rivers, and particularly those which lack seasonal cycles, are often subject to events and processes outside the 'predictable range' mentioned by Resh *et al.* (1988). In South Africa, temporary sections of rivers are often not gauged for flow, and the range of conditions may not even be known. Intermittent aseasonal river environments are event-driven and subject to constant and sometimes extreme fluctuations in hydrological and other physical conditions. In terms of the disruptions to ecosystem, resources and space referred to in the definitions of Resh *et al.* (1988) and Poff (1992), these systems are 'normally' or 'naturally' disturbed, something of a contradiction in terms!

In the case of the intermittent river which forms the focal point of this study, it was suspected that hydrological and physical changes were frequent, non-cyclical and non-sequential. The major sources of instability were presumed to be both hydrological 'events' (such as spates, onset of flow, and drying), and the *frequency and rate of change* in hydrological conditions (usually phases) in the river. These factors were capable of altering the character, extent and heterogeneity of the aquatic habitat and its resources, and were considered appropriate indices of the extent of disturbance to which the river was exposed.

1.4 STATISTICAL METHODS USED IN ANALYSIS OF FAUNAL DATA

Certain multivariate statistical methods were central to this research. The choice of techniques, the philosophy and statistical procedures underpinning them, and (where appropriate) their limitations, warrant consideration and discussion at this point in this thesis.

Multivariate statistical programs allow for the analysis of pattern and relationship in large sets of data comprising a suite of related or unrelated variables. The PRIMER (Plymouth Routines in Multivariate Ecological Research) software package was developed specifically for the study of community structure. All the methods adopted and developed within the package are based on conceptually simple, non-parametric statistical routines which distort data minimally and allow for transparent interpretation (Clarke and Warwick 1994). The package is convenient in that it encompasses the full suite of routines required for community analysis, including a number of techniques available in separate statistical packages such as BMDP, SPSS, SAS, CANOCO, and PATN. After review, discussion and trial of a number of different techniques and packages (e.g. BMDP, TWINSPAN, CANOCO), the PRIMER package was selected for the computation of all multivariate statistical procedures in this study.

Clarke and Warwick (1994) used the term 'community' to refer to any assemblage data and not necessarily to the structure thereof. They broadly categorised the stages in community analysis as:

1. Representation of communities by description and statistical summary;
2. Discrimination of sites on the basis of their biotic composition, in the framework of a null hypothesis of 'no difference between those sites or groups identified *a priori*;
3. Determination of levels of stress or disturbance, by attempting to define biological measures from the community data which are indicative of disturbed conditions; and
4. Linkage of biotic and environmental variables and examination of possible causality of any changes.

The three classes of techniques available for these sorts of analyses are univariate methods, which provide single indices for large counts (e.g. diversity index), distributional techniques, which summarise species counts and frequencies graphically, and multivariate methods, in which comparisons between two or more samples are based on similarity analyses (or the extent to which samples share taxa).

Analyses of faunal organisation at the various spatial and temporal scales were conducted in a stepwise fashion, as recommended by Clarke and Warwick (1994), though not all steps were necessarily included in the analyses:

1. Computation of univariate indices (e.g. diversity indices) for the data-set (1.4.1);
2. Computation of sample similarity (and triangular similarity matrices) using a coefficient of similarity (1.4.2);
3. Cluster analysis, in which samples are grouped or clustered on the basis of similarities between them, and presented in the form of a dendrogram (1.4.3);
4. Mapping or ordination of samples in two-dimensional space in such a way that the rank order of the distances between two samples agrees with the rank order of the matching similarities from the similarity matrix (1.4.4);
5. Analysis of similarity between groups of samples identified *a priori* (e.g. sites, times), for examination of the null hypothesis of 'no difference between groups' (1.4.6);

6. Association of biotic and abiotic variables to examine common patterns and trends between the two (1.4.7).

Although not a part of the community analysis 'sequence', the determination of percentage contribution of individual taxa to the similarity of samples in different clusters was used commonly (1.4.5). The procedures involved in each of the steps are described here.

1.4.1 Computation of univariate indices

Change in the structure of biological assemblages is commonly assessed using diversity indices. Because these incorporate measures of taxonomic richness and relative abundance into a single value, interpretation of what this statistic actually means is difficult (Ludwig and Reynolds 1988). Several measures of assemblage structure can be used to assist in the interpretation of data, following Clarke and Warwick (1994). One or more of these indices were included in faunal analyses in a number of chapters (Chs 3 to 7).

Taxonomic diversity was calculated using the Shannon Weiner diversity index (H'). This is formulated on the basis of what percentage of the total count of individuals each species (or lowest taxonomic unit) comprises. The equation for this index is:

$$H' = -\Sigma_i \, p_i(\log_2 p_i) \qquad \textbf{1.1}$$

where p_i is the proportion of the total count arising from the ith taxa (Clarke and Warwick 1994).

Taxonomic richness was computed using Margalef's index (d), which provides a measure of the number of taxa present for a given number of individuals (this reduces dependence on sample size). The index is computed using the equation:

$$d = (S-1)/\log N \qquad \textbf{1.2}$$

where S is the total number of taxa and N is the total number of individuals (Clarke and Warwick 1994).

Taxonomic evenness expresses how evenly the individuals present are distributed among the different species (or lowest taxonomic units). This was calculated using Pielou's evenness index (J'). The index ranges between 0 and 1, with 1 representing even distribution. Lower values represent dominance of individual taxa. The equation for the index is:

$$J' = H'(observed)/H'_{max} \qquad \textbf{1.3}$$

where H'_{max} is the maximum possible diversity which could be achieved if all taxa were equally abundant (Clarke and Warwick 1994).

Taxonomic distinctness provides a measure of the hierarchical level of diversity in a community (Warwick and Clarke 1995). In two faunal communities showing similar species diversity, one may comprise species which are closely related taxonomically (*less distinct*), while the other may comprise species which are less related taxonomically (*more distinct*). Warwick and Clarke note that *'for an ecologically meaningful measure of the taxonomic distinctness in a natural assemblage of organisms, or a sample of that assemblage, information on taxonomic level should clearly be utilised'*. Two indices apply: Δ, which is empirically related to the Shannon Weiner diversity index H', but includes a component of taxonomic separation; and Δ^*, which is a measure purely of taxonomic distinctness.

Warwick and Clarke (1995) base the calculation of the indices on a hierarchical taxonomic tree resembling a dendrogram, with nodes at various levels representing different taxonomic hierarchies (Family, genera, species, individuals). Branching increases towards the lower taxonomic levels. Path lengths between the different levels are weighted, so that a weighting between species from different branches of the dendrogram can be calculated. If x_i denotes the abundance of the *ith* taxon ($i = 1, ..., S$) and w_{ij} the 'distinctness weight' given to the path length linking species *i* and *j* in the hierarchical classification, then taxonomic distinctness Δ is defined as the average (weighted) path length between every pair of individuals, thus:

$$\Delta = \frac{\Sigma_{i<j} w_{ij} x_i x_j + \Sigma_i 0.x_i(x_i-1)/2}{\Sigma_{i<j} x_i x_j + \Sigma_i x_i(x_i-1)/2} \qquad \mathbf{1.4}$$

(where the null second term in the numerator is included to emphasise that the weight for the path linking individuals of the same species is taken to be zero). The taxonomic distinctness Δ^* is then defined as Δ divided by the value it takes when the hierarchical structure has the simplest possible structure (that of all species belonging to the same genus). It can also be defined as the average (weighted) path length, ignoring paths between individuals of the same species, so that

$$\Delta^* = \frac{\Sigma_{i<j} w_{ij} x_i x_j}{\Sigma_{i<j} x_i x_j} \qquad \mathbf{1.5}$$

where w_i (species within the same genus) is always set to unity for the sake of definiteness (Warwick and Clarke 1995).

All diversity indices but for the taxonomic distinctness indices were calculated using the DIVERS program with abundance data. Taxonomic distinctness indices were kindly calculated by Dr R. Warwick at Plymouth Marine Laboratories, using a recently-developed program not yet available in South Africa (Warwick and Clarke 1995).

1.4.2 Computation of sample similarity

Where possible in multivariate statistics, all taxa were included in statistical analyses, whether abundant or rare. It is common, in community ecology, to follow the recommendation of Gauch (1982) and select only taxa that represent less than 5 - 10% of the total count of individuals, to minimise distortion of subsequent clusters and groupings), It is maintained that analyses of such summarised data present a good picture of community trends. It was recognised early in the study that rarer taxa were the most numerous, and a 'true' picture of the community could not be attained by omitting them from analyses. This decision was supported by the statement of Clarke and Warwick (1994), that *'A view in which most of the emphasis is on the pattern of occurrence of rare species may be very different than one in which the emphasis is wholly on the handful of species that numerically dominate most of the samples. One convenient way of providing this choice, to match the biological imperatives whilst retaining desirable theoretical properties, is to restrict attention to a single similarity coefficient (such as that of Bray and Curtis, 1957), but allow a choice of prior transformation of data. A useful transformation continuum ranges through no transform, square root, fourth root, logarithmic, and finally reduction of the sample infomation to the recording of only presence or absence for each species: at the former end of the spectrum all attention will be focussed on the dominant counts, at the latter end on the rarer species'.*

As resemblance functions sought between samples were chiefly similarity and dissimilarity, taxonomic data was prepared in Q-mode as a *species x sample* matrix (Ludwig and Reynolds 1988). Once within-biotope variability had been quantified and assessed for a number of groups of replicates (Appendix 4.1), original data matrices were summarised by aggregating the data for the three replicate samples collected in a single biotope, to yield a single figure per taxon, representing its abundance in that biotope that month. These grouped replicates are hereinafter referred to as 'samples'. For coarser-resolution analyses, fauna collected in all biotopes at a site were aggregated to generate 'total samples' per site per month.

Faunal similarities were calculated between samples or total samples, using the non-correlation-based Bray-Curtis coefficient of similarity, which uses percentage similarity as a measure of resemblance (Bray and Curtis 1957, Ludwig and Reynolds 1988). The similarity between two samples, for example the *j*th and *k*th samples, S_{jk}, is defined as:

$$S_{jk} = 100 \left(1 - \frac{\Sigma^{p}_{i=1} \, y_{ij} - y_{ik}}{\Sigma^{p}_{i=1} \, (y_{ij} + y_{ik})} \right) \qquad \textbf{\textit{1.6}}$$

where y_{ij} represents the *i*th species in the *j*th sample, and y_{ik} the *i*th species in the *k*th sample (Clarke and Warwick 1994).

Triangular similarity matrices were generated using the CLUSTER program in PRIMER. Where resemblance between samples from separate biotopes was sought, data were standardised to account for different sampling techniques in each of the biotopes. Moderate square-root or more severe 4th-root transformations were used on abundance data to downweight the importance of more abundant taxa so that the (numerous!) less dominant taxa played some role in determination of similarity between samples (Clarke and Warwick 1994). Clustering and ordination techniques are based on similarity matrices.

1.4.3 Cluster analysis

The clustering method forms groups based on similarities among separate entities. Early clustering techniques produced overlapping groups, however recent methods generally produce hierarchical, non-overlapping groups, which are either 'nested' (one group included entirely within another, so that a single cluster eventually contains all samples), or mutually exclusive (have no members in common). Clustering methods work from the basis of a similarity matrix, and sucessively fuse samples into groups and the groups into bigger clusters, beginning with the highest similarities and gradually reducing the similarity level at which groups are formed (Ludwig and Reynolds 1988).

There are some limitations to this method. The indiscriminate use of cluster analysis was cautioned against by Cormack (1971), and more recently, de Queiroz and Good (1997) have levelled sterner criticism at the method. This deserves discussion as the technique has been used extensively in this thesis. de Queiroz and Good argue that the group-forming process in hierarchical cluster analysis is problematic in that the similarity relationships themselves rarely exhibit a nested hierarchical structure, despite having some nested component. As a result, these relationships are oversimplified by mathematical methods which are constrained to produce these sort of groupings. The authors argue that although groups can be delimited 'artificially' there may be no such structure inherent in the data. Further, the generation of mutually-exclusive groups in a dendrogram, as determined by some clustering procedure, does not mean that these groups are mutually exclusive in terms of their similarity relationships.

The clustering technique has proved useful in numerous studies over the past 20 to 25 years, and is considered a satisfactory technique when used to delineate groups of sites with distinct faunal structure, which does not imply that groups have no taxa in common (i.e. are mutually exclusive in the real sense; Clarke and Warwick 1994). While its limitations are well-known by practitioners, it is considered very useful when used in combination with an ordination technique (Prof. J. Field, pers. comm.). In their PRIMER manual, Clarke and Warwick (1994) advocate this combination of techniques, as concordance between the two representations strengthens '*the adequacy of both*'. The authors commented that where gradation in community structure across sites was evident, possibly related to a strong environmental gradient (e.g. pollution), ordination was a superior method of representation. In the data analyses presented in this thesis, the technique of clustering was backed by the techniques of ordination (1.4.4) and analysis of similarity (1.4.6) wherever possible. As a further measure of robustness, triangular similarity matrices were visually examined alongside dendrograms.

For the purposes of comparing the adequacy of each of the methods of clustering and ordination, and the match between the two, one or more arbitrary similarity values were selected on dendrogram and a line drawn through that value. All clusters forming to the right of the line were marked as 'Groups' and numbered.

These Groups were superimposed on the corresponding ordination, to check for agreement between the two results. This procedure was also convenient in that individual clusters could be referred to with ease.

King and Tharme (1994) noted that when using 'equivalent taxa' in analyses, as in this thesis, classification and ordination results should be viewed as relative rather than absolute. Clarke and Warwick (1994) recommended this in any event.

1.4.4 Mapping or ordination of samples

The ordination procedure summarises a high-dimensional data set in to low-dimensional space (1-3 axes) on the basis of triangular similarity matrices. Ludwig and Reynolds (1988) comment that the technique was developed in order to quantify the concept of vegetation as a continuum (Goodall 1954), and as such the product of ordination is not primarily one of categorisation or 'classification' of discrete groups as in cluster analysis, but rather a representation of gradients in the data (Ludwig and Reynolds 1988).

While ordination and clustering are complementary techniques, this fundamental difference in their underlying concepts reflects the discrepancy between the continuum and individualistic concepts (well represented by ordination) and the discrete organismic concept (well represented by clustering) already encountered in the discussion of the term 'community'.

The non-metric multidimensional scaling (MDS) technique of ordination was selected in preference to Principal Coordinates Analysis (PCoA), which is considered to have several limitations, particularly when dealing with highly heterogenous community sets (Ludwig and Reynolds 1988). The PCoA algorithm requires that a small number of taxa is used, and therefore data matrices have to be compressed, which represents loss of information about rarer taxa. MDS is a highly recommended technique (e.g. Kenkel and Orloci 1986), which is flexible and makes fewer assumptions about the form of the data and the inter-relationships of the samples than does PCoA, as it uses only rank order of dissimilarities using the most appropriate measure of (dis)similarity for the data. MDS is considered to provide a good link between the original data and the final picture, as it gives positions of samples relative to one another (Clarke and Warwick 1994). Its weakness lies in the fact that the algorithm weights large distances between samples most heavily, so that to distinguish structure within large clusters it may be necessary to ordinate the data within individual clusters separately.

Ordination is considered a useful representation of similarity relationships, but only where stress levels of the ordination are sufficiently low to facilitate accurate interpretation. Stress values range from 0 to 1, and increase with reducing dimensionality of the ordination. Stress less than 0.1 provides a good two dimensional representation of the data points, and is unlikely to lead to misinterpretation. Where stress levels are less than 0.2, the ordination still provides a useful representation of the data, but as they approximate 0.2, not too much reliance should be placed on the detail of the plot. Where stress levels exceed 0.3, the points on the plot are close to being arbitrarily placed in the two-dimensional ordination space (Clarke and Warwick 1994). Where stress levels of ordinations suggested satisfactory representation of sample relationships, ordinations were presented alongside dendrograms.

Ordinations were computed in the MDS program in PRIMER, and plotted using the CONPLOT program.

1.4.5 Contributions of individual taxa to similarities

The program SIMPER was used to discern the contributions of individual taxa to similarities between samples within each of the Groups discerned on a dendrogram (1.4.3). This program allows identification of a subset of taxa which are responsible for the similarities or dissimilarities between groups of samples. This gives some idea of which taxa are most indicative of the particular conditions defined by each group (in the event that there *is* an association between the two).

The use of this program required compression of data matrices, with the result that several 'Types' (e.g. Chironomini Types A,B,C..) were summarised into a single unit (e.g. 'Other' Chironomini'), which would then be represented for almost every sampling event. While this matrix compression had the effect of reducing 'real' diversity, cluster analyses of the data in these matrices produced very similar results to those produced using the full, detailed matrices. Information generated in this way by SIMPER was considered useful if interpreted with caution.

1.4.6 Analysis of similarity for examination of null hypotheses

This study possessed *a priori* defined structure between the different units of analysis, or 'groups', be these biotopes, sites, months, years, phases etc.. In order to interpret faunal differences between groups, it is necessary to demonstrate that there *are* statistically significant differences to interpret. A global test of the null hypothesis, H_o, that there are no differences between groups, requires the computation of a ratio of *variability between group means* to *variability within a group* (e.g. variability between sites to variability within sites).

A test which is analogous to the ANOVA (analysis of variance) procedure but designed for non-normally distributed data is ANOSIM (analysis of similarity; Clarke and Warwick 1994). This is based on the ranked similarity matrix underlying the ordination or clustering of samples, and is computed in the ANOSIM program in PRIMER. The examination of H_0 proceeds step-wise, firstly computing a test statistic with the equation:

$$R = (r_B - r_w) / (M/2) \qquad \mathbf{1.8}$$

where r_w is defined as the average of all rank similarities among replicates within sites, and r_B is the average of the rank similarities arising from all pairs of replicates between different sites. $M = n(n-1)/2$, where n is the total number of samples under consideration. R lies within the range (-1,1), and $R = 1$ only if all replicates within sites are more similar to each other than to *any* other replicates from different sites. Where global *R* is approximately zero, the null hypothesis is true (i.e. similarities within and between sites will be approximately the same on average). The importance of *R* lies, however, in whether or not it is *significantly* different from zero - Clarke and Warwick (1994) note that it is possible for *R* to be inconsequentially small, yet significantly different from zero in statistical terms.

The testing of significance involves an iterative process of recomputing the test statistic under permutations of the sample labels. Essentially, sample labels are randomly reassigned and all possible permutations of the samples are tested for the *R* statistic in a procedure explained by Clarke and Warwick (1994). Where the significance level generated is less than 5% for the observed *R*, the null hypothesis is rejected, and there is an indication that there are differences between certain of the groups that should be further explored.

Pairwise tests are then conducted between specific pairs of groups, which are extracted from the original matrix and subjected to a similar procedure to that already described for the global test. Thus it is possible to establish whether differences between two individual groups are significant or not.

1.4.7 Associations between abiotic and biotic variables

To investigate links between biotic data and univariate environmental variables, values for each abiotic variable were represented as symbols of varying sizes, and superimposed on the corresponding biotic ordination. A variety of different abiotic variables (relevant variables listed in individual chapters) were plotted separately in this way, using the MDS program with both biotic and environmental data. This provided a means of checking whether or not there were consistent differences in the abiotic variable between biotic clusters (groups); or of observing any smooth trends in an abiotic variable which matched the gradients in the biotic ordination (Clarke and Warwick 1994).

1.5 AIMS AND HYPOTHESES OF THE RESEARCH

The aims of this study were, firstly, to examine the spatial and temporal dynamics of the aquatic macroinvertebrates in an intermittent stream in the Eastern Cape over two years; secondly, to establish the extent to which findings could be generalised to other temporary rivers in and beyond the region; and thirdly, to establish the degree of overlap in faunal composition between temporary and permanent streams.

It was clearly necessary to contextualise temporary rivers within the broader picture of rivers in the country. To achieve this a conceptual framework for research was required, and alongside that, a systematic approach to the naming and description of the many flow types occurring along the perennial-temporary river continuum in South Africa. A subsidiary aim of the research was the synthesis of such a framework and terminology.

The key questions generated by the research aims were:

- Which invertebrates live in temporary rivers in the Eastern Cape region ?
- What is the variability in fauna of the upper Kowie River at various spatial and temporal scales ?
- How do flow and other abiotic variables vary over time and with different environmental conditions, and which of these factors influence the character of the invertebrate assemblages ?
- Which factors could be considered the *most important* in regulating invertebrate faunal character ?
- Do the five hydrological phases identified a *priori* represent ecologically meaningful 'units' - i.e. are they truly separable in terms of their biotic or physico-chemical attributes. Could a characteristic fauna be associated with any of the phases?

- What is the range and variability of invertebrates in different temporary rivers with different hydrological regimes within the Eastern Cape?

- How do the faunas of different temporary and perennial rivers (natural and modified) in different geographical regions of South Africa compare?

Further considerations in the research, which were not specifically tested for, were whether or not successional trends could be detected in the invertebrate fauna, to what extent resilience and/or resistance was demonstrated in response to perturbations; and over what period faunal recovery occurred.

One or more of these questions and considerations formed the basis of Chapters 3 to 7. The chief hypotheses arising out of the questions concerned the variability between the fauna at different spatial and temporal scales, i.e. within and between different biotopes, sites, rivers, regions, hydrological phases and times. It was hypothesized that at each of these scales there would be significant differences between the fauna of at least some of the units of the analysis (viz. between certain of the different biotopes, sites, temporary rivers etc.). Null hypotheses thus took the form 'H_0: there is no difference between the fauna of the different groups', where groups were the spatial units of the analysis, as identified *a priori*. Examination of the null hypotheses in this form was conducted with analysis of similarity, using the ANOSIM package in PRIMER, which is described in detail in Chapter 3. Where the null hypothesis was rejected, variability within a single unit (e.g. a site) over time was considered to be as great as variability between units (e.g. sites) over time (Clarke and Warwick 1994).

1.6 STRUCTURE OF THE THESIS

The research conducted for this doctoral thesis was prepared as a series of papers for publication in national or international peer-reviewed journals. Chapters 2 to 7 thus represent stand-alone documents. However, as the structure of the thesis preceded the preparation of individual papers, the order of the chapters reflects the examination of fauna at a hierarchy of spatial and temporal scales. Every attempt has been made to reduce repetition in methodology, site descriptions and general concepts by cross-referencing between chapters, however in many instances summary or change was inappropriate and would have had the effect of 'dissembling' the body of text in the chapter. Where it was possible to cross-reference, sections of the text referenced to are referred to as, for example, 'Section 1.6', or simply as '(1.6)'. Information regarding each separate paper and the authorship thereof is provided at the beginning of each chapter.

The conceptual framework for the study of temporary rivers in South Africa, and the supporting terminology for river flow types are proposed in Chapter 2. The three subsequent chapters deal with the intensive study of the upper Kowie River at various scales. Changes in the biotic and abiotic variables in the stream over an eight month period (i.e. within-year variation) are reported in Chapter 3. The variation in the invertebrate fauna of the upper Kowie River over three consecutive midsummer periods (i.e. between-year variation) is reported in Chapter 4. In Chapter 5, the value of hydrological phases in intermittent river studies is assessed, and the limits to the use of a biomonitoring technique in these systems is discussed.

Chapters 6 and 7 deal with faunal variability at larger spatial scales. The range of invertebrates found in different temporary rivers within the Eastern Cape region is described in Chapter 6, and faunal overlap between temporary and permanent rivers within and beyond the Eastern Cape is assessed in Chapter 7. The final chapter represents a synthesis and discussion of the outcomes of this research.

1.7 NOTES ON TERMS OF REFERENCE

Latin and common names:

Throughout this thesis, reference is made to individual taxa using both latin and common names.

'Habitat' vs. 'biotope':

Throughout this thesis, the term 'habitat' is used in a generic context, to describe the habitable aquatic or semi-aquatic environment at the individual site. The term 'biotope' refers to that subset of the habitat described by particular physical and surface water characteristics (e.g. substratum, flow).

REFERENCES

Abell, D.L. 1984. Benthic invertebrates of some Californian intermittent streams. *In*: S. Jain and P. Moyle (eds). *Vernal pools and intermittent streams.* University of California, Davis Institute of Ecology Publication No. 28. pp. 46-60.

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24:** 123-141.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology* **27**: 123-138.

Boulton, A.J. and Lake, P.S. 1992b. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* **27**: 99-121.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective. In: De Deckker P, Williams W.D. (eds). *Limnology in Australia.* pp486-96. Council for Scientifiic and Industrial Research, Dr W. Junk, Melbourne.

Boulton, A.J., Peterson, C.G., Grimm, N.B. and Fisher, S.G. 1992b. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* **73** (6) 2192-2207.

Boulton, A.J., Sheldon, F., Thoms, M.C. and Stanley, E.H. (in press). Problems and constraints in managing rivers with contrasting flow regimes. *In:* P.J. Boon, B.R. Davies, and G.E. Petts. *Global perspectives on river conservation: science, policy and practice'.*

RHODES UNIVERSITY LIBRARY

Boulton, A.J., Stanley, E.H., Fisher, S.G. and Lake, P.S. 1992a. Over-summering strategies of macroinvertebrates in intermittent streams in Australia and Arizona. *In:* R.D. Robarts and M.L. Bothwell (eds.). *Aquatic ecosystems in semi-arid regions: Implications for resource management.* NHRI Symposium Series 7, Environment Canada, Saskatoon.

Braune, E. 1985. Aridity and hydrological characteristics: Chairman's summary. *Hydrobiologia* 125:131-136.

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **22:** 325-349.

Chutter, F.M. 1971. Hydrobiological studies in the catchment of the Vaal Dam, South Africa. Part 1. River zonation and benthic fauna. *Internationale revue der gesamten Hydrobiologie* **55:** 445-494.

Chutter, F.M. 1994. The rapid biological assessment of stream and river water quality by means of the macroinvertebrate community in South Africa. *In:* M.C. Uys (ed). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94.

Chutter, F.M. and Heath, R.G.M. 1993. *Relationships between low flow and the river fauna in the Letaba River.* WRC Report No 293/1/93.

Clarke, K.R. and Warwick, R.M. 1994. *Change in marine communities: an approach to statistical analysis and interpretation.* Natural Environment Research Council, U.K. 144pp.

Clifford, H.T. 1966. The ecology of invertebrates in an intermittent stream. *Investigations of Indiana lakes and streams* **7:** 57-98.

Connell, J.H. and Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* **121:** 789-833.

Cormack, R.M. 1971. A review of classification. *Journal of Royal Statistical Series* **134:** 321-367.

Cowie, B. 1985. An analysis of changes in the invertebrate community along a southern New Zealand montane stream. *Hydrobiologia* **120**: 35-46

Cummins, K., Minshall, G.W., Cushing, C.E. and Peterson, R.C. 1984. Stream ecosystem theory. *Verhandelungen der Internationalen Vereinigung fur Theorestische und Angewandte Limnologie* **22:** 1818-1827.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1995. River and stream ecosystems in southern Africa: Predictably unpredictable. In: C.E. Cushing, K.W. Cummins, G.W. Minshall. *Ecosystems of the World 22. River and Stream Ecosystems*. Elsevier Publishers, Amsterdam. pp. 537-599.

Davies, B.R., Thoms, M.C., and Meador, M. 1992. The ecological impacts of inter-basin water transfers and their threats to river basin integrity and conservation. *Aquatic Conservation of Marine and Freshwater Ecosystems* **2:** 325-349.

Davies, B.R., Thoms, M.C. Walker, K.F., O'Keeffe, J.H. and Gore, J.A. 1994. Dryland Rivers: their Ecology, Conservation and Management. *In:* P.Calow and G.E. Petts (eds). *The Rivers Handbook.* Vol. 2. Blackwell Scientific, Oxford. Ch.25. pp.484-511.

Department of Water Affairs and Forestry. 1997. *White Paper on a National Water Policy for South Africa.*

de Queiroz, K. and Good, D. 1997. Phenetic clustering in biology: a critique. *The Quarterly Review of Biology* **72** (1): 3-30.

Feminella, J.W. and Resh, V.H. 1990. Hydrologic influences, disturbance and intraspecific competition in a stream caddisfly population. *Ecology* **71** (6) 2083-2094.

Field, Professor J. Personal Communication. Department of Zoology, University of Cape Town, South Africa.

Fisher, S.G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management* **14**: 725-736.

Fisher, S.G. and Grimm, N.B. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen der Internationale Vereiniging fur Theoretische und Angewandt Limnologie* **23:** 1183-1189.

Fisher, S.G., Gray, L.G., Grimm, N.B. and Busch, D.E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* **52:** 93-110.

Gabriel, Ms. M-J. Personal Communication. Department of Zoology, University of Pretoria, South Africa.

Gauch, H.G. 1982. *Multivariate analysis in community ecology.* Cambridge University Press, New York.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. *Australian Journal of Botany*. **2:** 304-324.

Gray, L.J. and Fisher, S.G. 1981. Postflood recolonisation pathways of invertebrates in a lowland Sonoran desert stream. *American Midland Naturalist* **106:** 249-257.

Grimm, N.B. 1992. Disturbance, succession and ecosystem processes in streams: a case study from the desert. *In:* P.S. Giller, A.G. Hildrew and D.G. Raffaelli (eds). *Aquatic Ecology: scale pattern and process.* Blackwell Science, U.K.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of North American Benthological Society* **8** (4): 293-307.

Grimm, N.B. and Fisher, S.G. 1992. Responses of arid-land systems to changing climate. *In:* P.Firth and S.Fisher (eds). *Climate change and Freshwater Ecosystems.* Springer-Verlag, New York. pp. 211-233.

Hildrew, A.G. and Giller, P.S. 1992. Patchiness, species interactions and disturbance in stream benthos. *In:* Giller, P.S., Hildrew, A.G. and Raffaelli, D.G. (eds). *Aquatic ecology: Scale, pattern and process.* Blackwell Science.

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113:** 81-101.

Hynes, H.B.N. 1970. *The ecology of running waters.* Liverpool University Press, Liverpool.

Kenkel, N.C. and Orloci, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies:some new results. *Ecology* **67:** 919-928.

King, J.M. and Tharme, R.E. 1993. *Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa.* Water Research Commission Report No. 295/1/94.

Ludwig, J.A. and Reynolds, J.F. 1988. *Statistical Ecology: A Primer on Methods and Computing.* John Wiley and Sons, Canada. 337pp.

Menge, B.A. and Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110:** 350-369.

Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* **7:** 263-288.

Minshall, G.W. and Petersen, R.C. 1985. Towards a theory of macroinvertebrate structure in stream ecosystems. *Archiv für Hydrobiologie* **104:** 49-76.

Molles, M.C.Jr., Dahm, C.N. and Crocker, M.T. 1992. Climatic variability and streams and rivers in semi-arid regions. *In:* R.D. Robarts and M.L. Bothwell (eds). *Aquatic ecosystems in semi-arid regions: Implications for resource management.* NHRI Symposium Series **7**: Environment Canada, Saskatoon.

Moore, C.A. and Chutter, F.M. 1988. *A survey of the conservation status and benthic biota of the major rivers of the Kruger National Park.* Report to the National Institute for Water Research, Council for Scientific and Industrial Research, Pretoria. 102pp.

Odum, E.P. 1975. Trends expected in stressed ecosystems. *BioScience* **35** (7)419-422.

Plafkin, J.L., Barbour, M.T., Porter, K.D., Gross, S.K. and Hughes, R.M. 1989. Rapid bioassesmentprotocols for use in streams and rivers: benthic macroinvertebrates and fish. US Environmental Protection Agency Report No. EPA/440/4-89-001. Assessment and Watershed Division, Washington, D.C.

O'Keeffe, J.H. and de Moor, F.C. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research and Management* **2:** 39-55.

O'Keeffe, J.H., Davies, B.R., King, J.M. and Skelton, P.H. 1989. The conservation status of southern African rivers. *In:* B.J. Huntely (ed.). *Biotic diversity in Southern Africa. Concepts and Conservation.* Oxford University Press, Cape Town. pp 276-299.

Palmer, C.G. 1991. *Benthic assemblage structure, and feeding biology of 16 macroinvertebrate taxa from the Buffalo River, Eastern Cape, South Africa.* PhD Thesis, Zoology Department, Rhodes University, Grahamstown. 257pp.

Petraitis, P.S., Latham, R.E. and Niesenbaum, R.A. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64** (4): 393-418.

Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* **11** (1): 86-92.

Power, M.E., Stout, R.J., Cusing, C.E. Harper, P.P., Hauer, F.R. Matthews, W.J., Moyle, P.B., Statzner, B, and Wais de Bagen, I. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* **7** (4): 456-479.

Reice, S.R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. *Ecology* **61:** 580-590.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz,M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. and Wissmar, R.C. 1988. The role of disturbance in stream ecology. *Journal of North American Benthological Society* **7** (4): 433-455.

Rzoska, J. 1978. *On the nature of rivers, with case histories from the Nile, Zaire, and Amazon.* Dr W. Junk publishers, The Hague.

Schlosser, I. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environmental Management* **14**: 621-628.

Schneider, D.W. and Frost, T.M. 1996. Habitat duration and community structure in temporary streams. *Journal of the North American Benthological Society* **15** (1): 64-68.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15:** 353-391.

Stanley, E.H. and Fisher, S.G. 1992. Intermittency, disturbance and stability in stream ecosystems. *In:* R.D. Robarts and M.L. Bothwell (eds). *Aquatic ecosystems in semi-arid regions: Implications for resource management.* NHRI Symposium Series 7, Environment Canada, Saskatoon.

Tharme, R. 1995. *Determination of the instream flow requirements of benthic macroinvertebrates, with particular reference to low flows.* PhD proposal. Department of Zoology, University of Cape Town, South Africa.

Thomas, D.S.G. 1989. The nature of arid environments. pp. 1-10 *In:* D.S.G. Thomas (ed.). *Arid Zone Geomorphology.* Belhaven Press, London, and Halsted Press, New York.

Towns, D.R. 1985. Limnological characteristics of a South Australian temporary strema, Brown Hill Creek. *Australian Journal of Marine and Freshwater Resources* **36:** 821-837.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society **8** (1): 36-50.

Townsend, C.R., Hildrew, A.G. and Schofield, K. 1987. Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* **56**: 597-613.

Valett, H.M., Fisher, S.G., Stanley, E.H. 1990. Physical and chemical characteristics of the hyporheic zone of a Sonoran Desert Stream ecosystem. *Journal of the North American Benthological Society* **9**: 201-205.

Vannote, R.L., Minshal, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.

Walker, K.F., Sheldon, F. and Puckridge, J.T. 1995. An ecological perspective on large dryland rivers. *Regulated Rivers* **11:** 85-104.

Warwick, R.M. and Clarke, K.R. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* **(129)** 301-305.

Whittaker, R.H. 1956. Vegetation of the great Smoky Mountains. *Ecological Monographs* **26:** 1-80.

Whittaker, R.H. 1962. Classification of natural communities. *Botanical Review* **28:** 1-239.

Whittaker, R.H. 1967. Gradient analysis of natural communities. *Botanical Review* **42:** 207-264.

Wiggins, G.B., MacKay, R.J. and Smith, I.M. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie (suppl.) **58:** 97-206.

Wishart, M., Uys, M.C., Gabriel, M-J, and Fowles, B. (in prep.). There is water but the river is dry: Temporary rivers in Southern Africa.

Williams, D.D. 1987. The ecology of temporary waters. Croom Helm Ltd., Kent/ Timber Press, USA.

Williams, D.D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society* **15** (4):634-650.

Williams, D.D. and Hynes, H.B.N. 1976. The ecology of temporary streams. I. The faunas of two Canadian streams. *Internationale Revue der gesamten Hydrobiologie* **61:** (6) 761-787.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue der gesamten Hydrobiologie* **62:** 53-61.

Williams, W.D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **125:** 85-110.

Williams, W.D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshwater Biology* **20:** 407-420

Winterbourn, M.J., Rounick, J.S. and Cowie, B. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Freshwater Resources* **15:** 321-328.

CHAPTER 2

THE CONTINUUM BETWEEN PERMANENT AND TEMPORARY RIVERS: A PROPOSED FRAMEWORK AND DESCRIPTIVE TERMINOLOGY FOR EARLY TEMPORARY RIVER RESEARCH IN SOUTH AFRICA.

This chapter has been published in the journal
Environment Management, 1977, Volume 21 no 4 pp. 517-531,
under the title: 'Simple words and fuzzy zones:
Early directions for temporary river research in South Africa',
under the joint authorship of M.C. Uys and J.H. O'Keeffe.
The paper is presented with minor modifications
which reflect recent developments and place the work
in the context of the rest of the thesis.

ABSTRACT

Although a large proportion of South Africa's rivers are non-perennial, ecological research into these systems has only recently been initiated. Consequently, there is little verified information about the ecological functioning of these rivers, or knowledge of how best to manage them. High water demands in a semi-arid region results in the flow of most perennial rivers being altered from permanent to temporary in sections, through impoundment, land-use changes, abstraction, etc. Conversely, sections of many temporary rivers are altered to perennial as a result of interbasin transfers (etc.), or may be exploited for surface water. Effective and appropriate management of these modifications must be based on sound scientific information, which requires intensified, directed research. It is anticipated that temporary river research in South Africa will (of necessity) be driven primarily by short-term collaborative efforts, and secondarily by long-term ecological studies. At the outset, a simple conceptual framework is required to encourage an appreciation of current views of the spatial and temporal dynamics of non-perennial rivers, and of the variability and unpredictability which characterise these systems. We adopt the view that perennial and episodic/ephemeral rivers represent either end of a continuum, separated by a suite of intermediate flow regimes. A conceptual diagram of this continuum is presented. In the absence of a functional classification for temporary rivers, a descriptive terminology has been systematically devised in an attempt to standardise definition of the different types of river regimes encountered in the country. Present terminology lacks structure and commonly-accepted working definitions.

2.1 INTRODUCTION

Temporary rivers are broadly defined as those in which surface flow ceases and surface water may disappear for some period of most years. They are the dominant river systems in arid and semi-arid zones (Boulton and Suter 1986). Intermittent flow is common in a large proportion of South Africa's rivers: Davies *et al.* (1993) estimated that over 44% of our total river length is naturally temporary. Despite the numerical importance of these systems, they remain poorly understood because research attention here has been directed primarily towards perennial river systems, as it has worldwide (see Williams 1988). Since the mid-1980s, limnologists have appealed for the urgent investigation of ecological pattern and process in temporary rivers (e.g. Braune 1985, Boulton and Suter 1986, Williams 1988, Davies *et al.* 1993).

In semi-arid, water-scarce areas such as South Africa, where distribution of the water resource and its flow is uneven (King *et al.* 1992), land-use changes, abstraction of water, relocation of water to areas of high demand, and water storage requirements has resulted in the transformation of flow regimes:

- from perennial with seasonal or variable flow to perennial with uniform or regulated flow below the point of regulation (i.e. a dampening of natural flow fluctuation),

- from perennial with seasonal or variable flow to regulated with intermittent flow below the point of regulation (through abstraction or impoundments), or

- from temporary with intermittent, variable flow to perennial with a dampening of flow fluctuations (through interbasin transfers; see Petitjean and Davies 1988).

The ecological effects of these and other modifications to our rivers are poorly understood and difficult to define because of a lack of contemporary and historical ecological data (Roux *et al.* 1994). Because little work has been done to gauge the impact of flow regime modifications on formerly temporary systems (e.g. O'Keeffe and de Moor 1988, Cambray 1991, Chutter and Heath 1993), the extent to which such ecosystems deviate from their former states cannot be assessed. Management of temporary rivers in the region must thus be largely based on unverified principles or presumption (see Armitage and Petts 1992).

The initiation of research into temporary rivers aligns South Africa with international research directives. The development of the field is, however, likely to be somewhat different from that in other countries, where much effort has been directed at longer-term ecological studies (e.g. Towns 1985, Boulton and Lake 1990, 1992a,b,c), and the consideration of theoretical ecological concepts such as disturbance, recovery, succession etc. (e.g. Grimm and Fisher 1989, Boulton *et al.* 1992a,b). Present government policies in South Africa have set equitable provision of water as a top priority (DWAF 1995). As a result, limnological research programmes are largely focussed on shorter-term issues concerning water supply, water quality, and protection or development of the water resource. Research is increasingly a cooperative and collaborative effort between scientists, managers, engineers, policy makers and catchment community representatives. Effective communication of ideas and information in this milieu is vital.

A coordinated national programme for the research of the country's temporary rivers is a desirable long-term aim. In the interim, we require a simple conceptual framework which will support the development of research ideas, and a common 'language' to ensure effective and unambiguous communication of research ideas and results in a multidisciplinary environment.

In addressing these requirements, the aims of this chapter are to present a conceptual framework to illustrate the range of temporary river regimes in South Africa and the influences on them, and to propose a supporting, systematic terminology for the description of river regimes in the country.

The conceptual framework presented is borne out of the notion that a hydrological gradient exists between the most perennial and most temporary of rivers (Williams 1987). Different river regimes are thus envisioned along a continuum. Flow regimes which are clearly distinct from each other and easily definable are considered to be points or 'epicentres' along the continuum. Flow regimes which are transitional or intermediate between these lie between the points, in a space we have termed the 'fuzzy zone'.

Table 2.1 The descriptions associated with different terms in ecological studies of temporary waters.

DESCRIPTOR TERM	EXPLANATION OF TERM IN LITERATURE	REFERENCE
TEMPORARY	Natural bodies of water which experience a recurrent dry phase of varying duration.	Williams 1987
	Rivers with relatively regular, seasonally intermittent discharge.	Boulton and Lake 1988, Davies and others 1994
	Rivers in which the entire bed dries.	Delucchi 1988
INTERMITTENT	Streams which flow only seasonally and usually drain semi-arid regions.	Bayly and Williams 1973
	Streams with relatively regular, seasonally intermittent discharge.	Williams and Hynes 1976, Towns 1985, Boulton and Lake 1988
	Natural bodies of water which experience a recurrent dry phase of varying duration.	Williams 1987
	Rivers which flow for 20-80% of the year.	Matthews 1988
	Rivers which only dry in parts.	Delucchi 1988
SEASONAL	Flow that occurs for more than half the year, every year, during the same season.	King and Tharme 1994
DRYLAND	The rivers of arid and semi-arid regions.	Davies and others 1994
EPHEMERAL	Streams which flow only seasonally and usually drain semi-arid regions.	Bayly and Williams 1973
	Rivers which flow less than 20% of the time.	Matthews 1988
	Rivers which run for short periods after rain has fallen high in their catchments.	Day 1990
	Rivers which flow only after strong rains have fallen over their catchments.	Jacobson and others 1995
EPISODIC	Rivers which only flow after unpredictable rainfall.	Bayly and Williams 1973
	Flow that only occurs after rainfall episodes; flow does not necessarily occur every year.	King and Tharme 1994
INTERRUPTED	Rivers which flow for less than 20% of the time.	Matthews 1988

The supporting terms of reference are presented in the form of a terminology which distinguishes different river regimes on the basis of known hydrological characteristics. The aims of this terminology are simply to encourage recognition of the range of non-perennial rivers in the country, to eliminate the noise created by inconsistent definition of terms in the literature (Table 2.1), and to generate easily interpreted, standardised working definitions to facilitate clear communication in this multidisciplinary field.

While this exercise in words may be considered pedantic, our experience is that the description of a river as a 'dryland'/ 'temporary'/ 'seasonal'/ 'intermittent'/ 'ephemeral' (etc.) system generates no more understanding of the dynamics of the river than that it ceases to flow at times. There is often no perceived difference between two or three descriptive terms, which could be effectively used to distinguish the types of temporary flow regimes encountered in semi-arid or arid zones. This exercise draws upon published river classification schemes, but should *not* be considered an attempt at classification itself, for reasons discussed in the following section.

2.2 THE CONTINUUM BETWEEN PERENNIAL AND TEMPORARY RIVERS

Classification exercises conventionally distinguish river 'types' by recognising geographical, geological, climatic or biotic boundaries between them, i.e. on the basis of the *outer* limits of features which characterise them (e.g. Hart and Campbell 1994). The conceptual framework developed here, in contrast, aims to discern different hydrological regimes according to the core characteristics or *inner* limits which typify them. The difference between the classification approach and our approach is illustrated in Figure 2.1.

As discussed, different hydrological regimes are represented by points or 'epicentres' on the continuum. The gradual change in hydrological character between adjacent epicentres is denoted by the space on the line between points, which is termed the 'fuzzy zone' in order to illustrate the transition in flow types between clearly definable hydrological regimes. The continuum is illustrated in

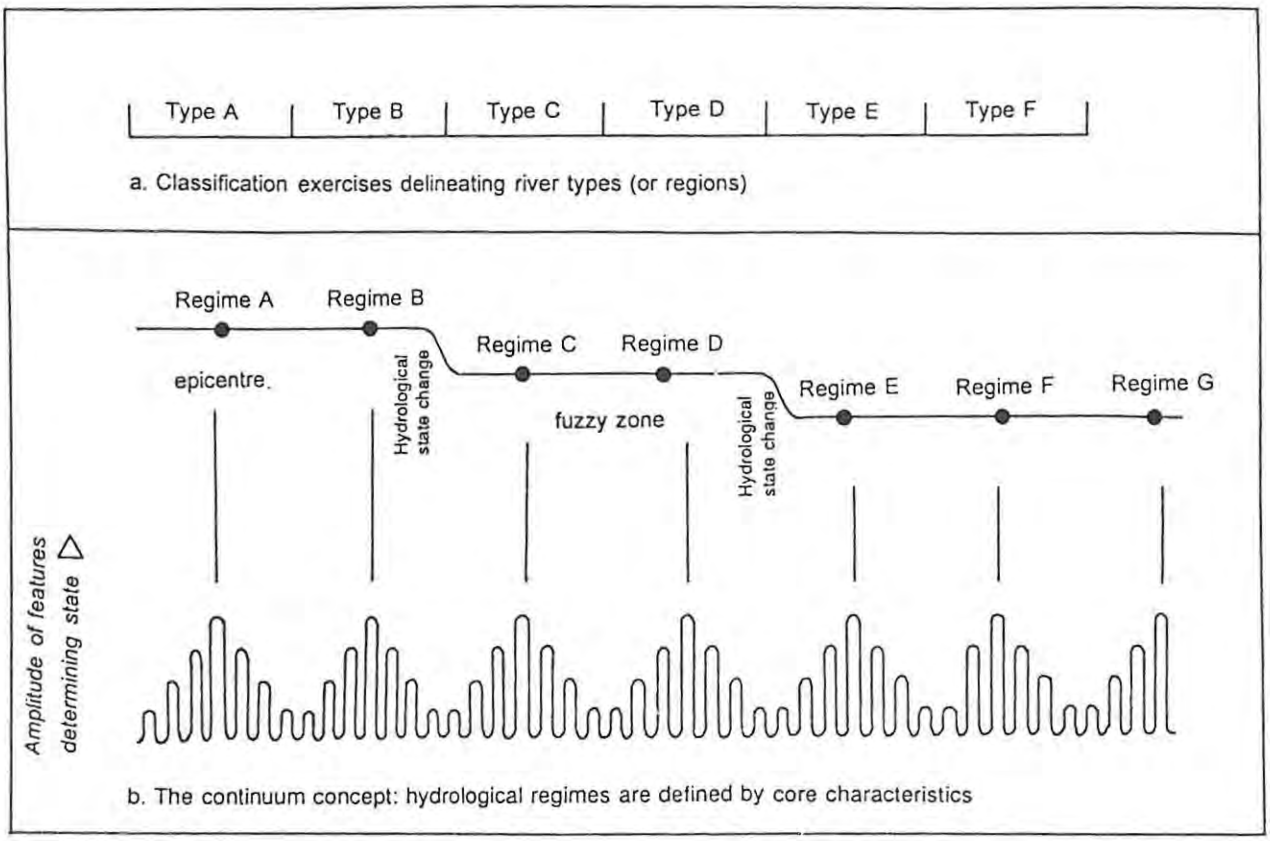


Figure 2.1 A graphic representation of the conceptual differences between classification exercises which delineate river types according to the outer limits of their characteristics, and the continuum concept, in which river regimes are defined by their core characteristics.

Two hydrological 'state changes' which may result in major biotic and abiotic changes in lotic systems, are represented as steps in the continuum: i) Where surface flow disappears but surface water is still present (pools etc.) in the majority of channel; ii) Where surface water disappears from the majority of the channel. The response and the rate of response of the biota to either of these state changes are major components of temporary river research (e.g. Boulton and Lake 1990, 1992 a,b,c).

The *x* and *y* axes of the continuum in Figure 2.2 represent gradients in flow intermittency, flow predictability, flow variability, faunal structuring forces, natural disturbance, and connectivity. These are described further.

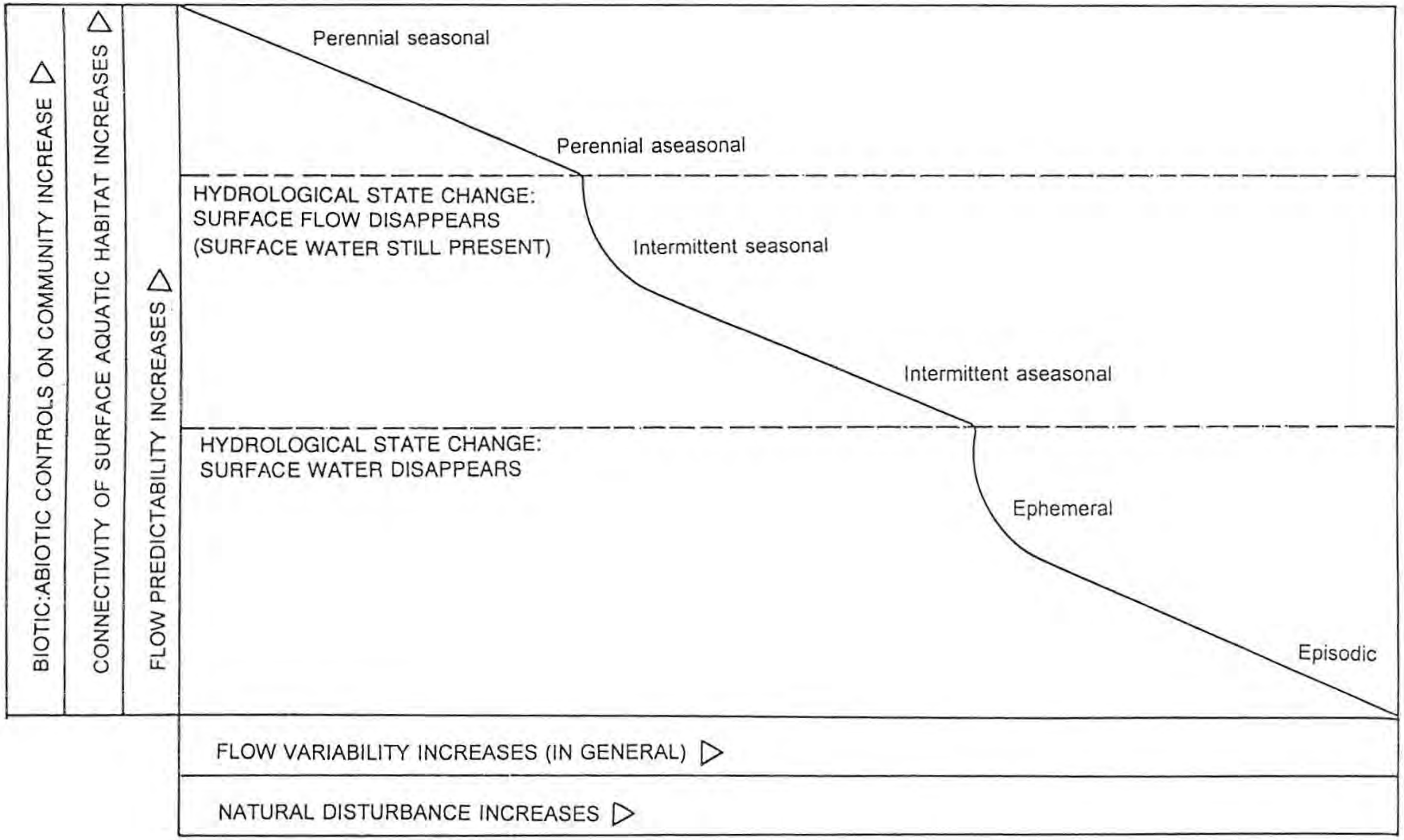


Figure 2.2 A conceptual illustration of the permanent-temporary river continuum, along which different river regimes are indicated. Two hydrological state changes are shown: one in which surface flow disappears (but some surface water is present), and one in which surface water disappears (or is absent) from the channel for long periods.

Flow intermittency (general increase towards the episodic state).

Flow predictability (general decrease towards the episodic state).

Flow variability as measured by the coefficient of variation of flow (CVF). In temporary rivers, 'high flow variability' indicates unpredictable periods of *intermittent or flashy flow* (i.e. periods of zero flow and/or drying), whereas in perennial streams 'high flow variability' denotes fluctuations in flow volume in a context of *continual flow*. The ecological consequences of loss of flow or surface water are clearly different to the effects of altered flow volumes (although not necessarily more extreme): Boulton (1989) comments that loss of water in temporary systems is *'probably the most influential environmental parameter affecting the aquatic biota'*.

CVFs in the country range from 0.33 (generally predictable perennial rivers in the Western Cape) to 2.58 (generally unpredictable temporary rivers of the north-west; King *et al.* 1992). Although CVF expresses variance as a percentage of the average (and averaging is considered meaningless in highly variable systems), it is effective in expressing *amplitudes* of variation. The likely extent, range and effects of flow variability on the river and its biota could best be ascertained by a long-term flow hydrograph, where available. If variability is considered in terms of CVF, there would be a general increase towards the episodic state.

Faunal structuring forces - the extent to which biotic and abiotic forces influence faunal assemblage character. It is generally accepted that as physical conditions become increasingly harsh, assemblage composition and species distribution are increasingly governed by abiotic rather than biotic factors (e.g. Peckarsky 1983, Williams 1987). However, Power *et al.* (1988) and Poff and Ward (1989) suggest that rather than adopt an 'either-or' approach, abiotic, biotic and other influences should be considered to be acting as multilateral controls on assemblage structure. Following this argument, this gradient is expressed as a ratio of biotic to abiotic controls (with a general increase in the ratio towards the perennial state).

Natural disturbance, as described in Chapter 1, increases in frequency towards the intermittent state, and in amplitude towards the episodic state.

Connectivity. This relates to the continuity or connectedness of flow or surface water, at the scale of interest. We take 'internal connectivity' to describe continuity of surface water or flow in a single river, and 'external connectivity' to describe the distance between a dry river bed and the closest source of surface water and aerial colonists. The scale at which connectivity is examined must be specified, and this makes it a difficult concept to measure but an important one to consider (Naiman 1992), particularly with respect to the biota. The connectivity of the surface aquatic habitat is considered here, with a general increase towards the perennial state.

The key considerations in establishing where a river regime fits along the continuum (i.e. which term would best describe its hydrology) are:

- ***Does flow stop, and if so, when and for what period of each year; how often and for what duration in a five year period?*** (See section on the issue of scale.) This will assess: intermittency of flow, predictability of flow, seasonality of flow, variability of flow.

- ***For how long does surface water persist?***
  This is of particular importance in relation to life history adaptations of the biota, and their resilience and resistance to disturbances (sensu Grimm and Fisher 1989).

- ***What is the connectivity of the system (at the scale of interest)?***

The limitations of the continuum should be recognised: Brierley (1994), while endorsing the concept, warned that '*interpretation of a river as intermediary between two or more styles may be no more than describing the system as a meaningless mean*'. To avoid this, 'fuzzy zones' should be seen as transitional (and dynamic) states between one and the next epicentre, rather than as average states.

2.3 STRUCTURING A TERMINOLOGY FOR TEMPORARY RIVER FLOW TYPES

2.3.1. The necessity for review and readjustment

In introducing a missing term into evolutionary science, Gould and Vrba (1982) reasoned that *'Terms in themselves are trivial, but taxonomies revised for a different ordering of thought are not without interest. Taxonomies are not neutral or arbitrary hat-racks for a set of unvarying concepts; they reflect (or even create) different theories about the structure of the world'.*

The organisation of the loose descriptive terminology for temporary rivers may, similarly, be a reflection of our present and developing ideas about these systems. Because of the lack of empirical studies on non-perennial rivers in South Africa, the scientific basis for the terminology is limited to what is known from a hydrological point of view, and to information derived from published classification schemes, as discussed later in the text. Our hope is that a revised 'lexicon' will assist in standardising definitions of the range of flow regimes encountered in the country, and in promoting common use and clear communication of descriptive terms in a multidisciplinary research environment. Poff (1992) comments that communication between scientists is often dependent on careful definition, and that *'this is certainly true in ecology, where many terms or phrases attempt to generalise across diverse systems and levels of organisation. ... Regardless of the underlying reasons, we may speak at cross purposes because definitional assumptions have not been adequately specified'.*

There is presently no structured terminology for temporary rivers in the international literature (see Section 2.4, Tables 2.1 to 2.7), and the somewhat haphazard use of descriptive terms has not yet been critically assessed. Although several comprehensive river classifications recognised a series of temporary river types (Tables 2.1 to 2.7), none of these systems was commonly adopted in South Africa (Uys 1994: 79-85). Eekhout (1994) began efforts to integrate certain of the local classifications into a single hierarchical system. With input from a group of local river experts, a three-tiered hierarchical classification of the country's rivers was developed over a number of years (Eekhout et al. 1996). This work forms the basis for the nationwide selection of sites for the South African Biomonitoring Program (SANBP), and the classification has thus been adopted by a large group of scientists in the country for this purpose.

At the first level, approximately 18 'bioregions' were distinguished for the country, based on broad historical distribution patterns of riverine invertebrates, fish and riparian vegetation. At the second level, at least 55 'sub-regions' were discerned by local experts on the basis of patterns of river zonation within bioregions. At the third level, one to six 'river types' per sub-region were distinguished in order to account for variation between rivers within a sub-region (Eekhout et al. 1996). Unfortunately, the majority of temporary rivers occurring in the 18 bioregions still represent unknown entities in terms of the fauna which occupy them, their flow regimes, and the physical and chemical changes which characterise them.

Scientists studying temporary rivers in South Africa and further afield have expressed an interest in a terminology which bridges this gap.

2.3.2 The present terminology for temporary rivers

The adjectives *temporary, intermittent, ephemeral, episodic, seasonal* and *interrupted* are commonly used to describe temporary river regimes. The variety of explanations for these terms renders the terminology somewhat abstruse and lacking in descriptive power and standard working definitions (see King and Tharme 1993 p.295).

Authors of ecological studies have commonly used few terms (e.g. *seasonal, intermittent* or *ephemeral)*, and have defined these loosely in terms of flow, drying and periodicity (e.g. Harrison 1966, Williams and Hynes 1976, Williams 1987, Delucchi 1988, Boulton 1989). Some authors (e.g. Bayley and Williams 1973) based their terminology on more complex criteria, e.g. flow predictability, which largely determined floral and faunal composition; community structure; and life history strategies of resident species. Several studies have referred to *intermittent* or *temporary* streams without explicit definition, but have qualified the term with an exact description of the flow regime of the river in question (e.g. Boulton and Lake 1990, 1992a,b; Brooks and Boulton 1991). Specificity has been the exception rather than the rule in studies. Matthews (1988) was among the few who attached probability ranges to definitions - for example, *intermittent* rivers were defined as *'those which flow for 20-80% of the time'*. Classification exercises have generated a plethora of new descriptive terms (Tables 2.1 to 2.7).

2.3.3 The limits of classification exercises in temporary rivers

It should be mentioned again that although the term 'taxonomy' has been quoted in reference to the broad process of reviewing and reordering ideas and terminology related to temporary rivers, we have avoided the term 'classification' for several reasons.

Classification relies on a synthesis and analysis of information relating to a range of individual entities to generate groupings based on shared or unshared characteristics (Platts 1980, O'Keeffe *et al.* 1994). Intermittency, variability and unpredictability in flow are among the characteristics shared by temporary rivers (e.g. Braune 1985, Davies *et al.* 1995). However, all three features - by their very nature - impede classification (Davies *et al.* 1993), which relies on multivariate procedures and the use of statistical averages (e.g. Joubert and Hurly 1994). The expression of variability and unpredictability is dampened and distorted by averaging, as central tendency does not exist, except over the long term (see Gould 1993). On the basis of this type of constraint, Davies *et al.* (1993) concluded that for temporary rivers, *'... any attempt at a rigid classification is self-defeating'*.

Although most classification schemes consider the full suite of flow regimes (perennial to temporary), there has been a sporadic recognition of the need to classify only temporary waters. Williams (1985) commented that *'no classification of temporary waters in temperate climates could be sufficiently comprehensive to cover the range of temporary waters in tropical and arid to semi-arid regions'*. Citing two previous classifications (those of Decksbach 1929, and Wiggins *et al.*

1980) as *'too specific to be of general interest'*, he proposed a more general, comprehensive classificatory scheme based on the determinants of the biology of temporary waters worldwide (i.e. degree of predictability, salinity, and extent to which waters occupy discrete basins or are associated with periodically flooding rivers). Six major types of temporary water body, Types A to F, were defined (Table 2.2).

Table 2.2 Williams' (1985) classification of global temporary waters.

	PREDICTABLY FILLED WATERBASINS	
Fresh	Discrete	Type A
	Associated with rivers	Type B
Saline		Type C
	UNPREDICTABLY FILLED WATERBASINS	
Fresh	Discrete	Type D
	Associated with rivers	Type E
Saline		Type F

Information on geology, geomorphology, geochemistry, climate, biotic composition and streamflow has been variously used to classify all rivers or delineate limnological/hydrobiological regions in South Africa (e.g. Harrison 1959, Agnew and Harrison 1960 a,b, Haines *et al.* 1988, Allanson *et al.* 1990, Eekhout 1994, Joubert and Hurly 1994, Wadeson and Rowntree 1994). None of these classification systems was put to common use. King *et al.* (1992) suggested that Harrison's (1959) hydrobiological regions should be assessed for this purpose, as they provided sufficiently fine-level resolution to allow detection of rivers with clear physical differences. The three-tiered hierarchical classification of South African rivers developed by Eekhout *et al.* (1996), has provided a sound basis for the division of the country's rivers into different bioregions, subregions and river types. The development and refinement of the classification will be an ongoing process linked to the implementation of the SANBP. Unfortunately, the SANBP was designed to monitor flowing rivers, so that even in the context of this classification, temporary river types are still not likely to be adequately described.

The geographical, hydrological and ecological attributes of temporary rivers in this country are too poorly known to make any sort of meaningful attempt at conventional classification. Furthermore, based on the comments of Davies *et al.* (1993), it seems unlikely that a conventional classification of these particular systems would be an appropriate exercise. Nonetheless, in devising a descriptive terminology for temporary rivers, we have borrowed from aspects of published classification schemes. Functional classification systems allow for extrapolation of information from known to unknown entities or situations (Joubert *et al.* 1993); and should be able to encompass broad spatial and temporal scales (Naiman *et al.* 1992). Where possible, both have been incorporated here.

Global and local classification exercises have grouped rivers based on their seasonal flow patterns and their flow characteristics (e.g. Haines *et al.* 1988, Poff and Ward 1989, Joubert and Hurly 1994). Temporary rivers can, similarly, be organised on the basis of their flow regime and the *extent* of their flow variability and unpredictability, although this may be hypothetical. These factors are largely determined by the climatic zone (and therefore the geographical area) in which the rivers occur.

For our purposes, river characterisations based on long-term streamflow data provide information of the effect of regional climatic influences on hydrology (thus satisfying the criteria of Davies *et al.* 1994); take account of the spatial and temporal patterns in the region's highly diverse river regimes; and make use of many of the parameters which are of particular interest in the study of temporary rivers, i.e. flow variability, flow predictability, duration of flow and no-flow, extent of intermittency, flood regime, etc.

Where temporary rivers are concerned, the limits of classifications based on streamflow data include: their use of statistical averaging (already discussed); the lack of information they provide on drying processes; and the paucity of long-term flow data for temporary rivers in the region, as efforts have been primarily directed at the gauging of permanent rivers. Walker *et al.* (1996) maintain that dryland rivers probably require long-term hydrographs (of the order of a hundred years) relative to those required by temperate zone rivers (of the order of ten years) to adequately demonstrate their range of temporal behaviour. This represents a constraint in the use of all the stream classifications using the streamflow approach, as neither real nor simulated hydrographs for temporary rivers are included in their analyses.

In establishing the terminology, and with these constraints in mind, three classifications already mentioned have been referred to: Haines *et al.* (1988), Poff and Ward (1989) and that of Joubert *et al.* (1993) and Joubert and Hurly (1994).

2.4 CLASSIFICATIONS OF RIVER REGIMES BASED ON STREAMFLOW

2.4.1 A Background

The first global classification of river regimes based on streamflow data was produced by Haines *et al.* (1988). Fifteen groups of rivers were generated by their exhaustive statistical treatment of the data (Table 2.3). Using long-term hydrographs, river groups were distinguished according to the season in which either narrow or broad flow peaks were likely to occur. For statistical reasons, non-seasonal streams were considered separately and were defined as those streams exhibiting uniform flow with mean monthly flows of 5-12% of the yearly average. In South Africa, many naturally temporary rivers are non-seasonal (hereinafter referred to as *aseasonal*), but have highly variable flow patterns and thus would not fit this definition.

One hundred and eighteen African rivers were included in the analysis by Haines *et al.* (1988). Six of the 15 groups which emerged were used by Haines *et al.* to describe rivers of southern Africa:

- Groups 12 and 13 (Moderate Winter and Extreme Winter) applied to Western Cape rivers;
- Groups 14 and 15 (Early Spring and Moderate Spring) to Southern Cape rivers, and
- Groups 5 and 6 (Moderate Early Summer and Mid Summer) to rivers in the central and eastern parts of the region.

Table 2.3 A global classification of river regimes, based on streamflow data from around the world (Haines *et al.* 1988).

DESCRIPTOR	EXPLANATION IN LITERATURE	REFERENCE
UNIFORM Group 1	Even flow regime with all months lying in the range of 5-12% of annual flow and no season with pronounced low or peak flow.	Haines, Finlayson and McMahon 1988
MID-LATE SPRING Group 2	A pronounced flow peak int he last two spring months which account for over 40% of total flow. A distinctive snowmelt pattern. N. Hemisphere	
LATE SPRING-EARLY SUMMER Group 3	A major peak beginning one month after Group 2 - peak flow in the last spring month and the first summer month. N. Hemisphere	
EXTREME EARLY SUMMER Group 4	Similar to Groups 2 and 3, occurring in regions with six sub-zero months. Spring thaw produces a massive flow. N. Hemisphere	
MODERATE EARLY SUMMER Group 5	A strong but broad flow peak in the early summer months, from which flow declines rapidly to a low level during late autumn, winter and early spirng. Some rivers of Group 5 derive their regime from high summer rains combined with a winter drought. Common in mid to eastern regions of southern Africa.	
MID-SUMMER Group 6	Strong late summer or early autumn peak combined with a winter low flow. Abundant early summer rains moderate and extend the peak flow period. Common in mid to eastern regions of southern Africa.	
EXTREME LATE SUMMER Group 7	Most rivers in the group derive their flow from intense late summer rainfall. Found only in the tropics.	
MODERATE LATE SUMMER Group 8	With a pronounced summer peak: displays an increasing influence of winter rainfall in its higher low-season flow, and often a minor peak in winter.	
EARLY AUTUMN Group 9	Strong peak flow period centred on early autumn; distinct though declining flow during winter.	
MID-AUTUMN Group 10	A moderate peak flow around early autumn; average flow in summer; low water in late winter and spring.	
MODERATE AUTUMN Group 11	Possessing a broad autumn peak flow; no distinct low flow periods.	
MODERATE WINTER Group 12	Very broad winter and early spring peak, and a distinct yet low summer flow (fairly even rainfall year-round). In southern Africa, western Cape rivers fall into Groups 12 and 13.	
EXTREME WINTER Group 13	Very strong winter and early spring flow which dwindles to a very low level during summer.	
EARLY SPRING Group 14	The largest regime class. Less winter flow than Group 12; which builds to a peak in early and mid-spring. Flow declines through summer before the beginning to build again in late autumn. In southern Africa, southern Cape rivers fall into Groups 14 and 15.	
MODERATE SPRING Group 15	No distinct low flow periods. Similar to Group 13 but importance of spring and autumn flows are reversed, and minor secondary autumn flow is likely to be absent.	

Poff and Ward (1989) produced a characterisation of streamflow variability and predictability, based on analysis of long-term daily streamflow records of 78 streams across the United States. Overall flow variability, flood regime patterns, and extent of intermittency were used to derive a set of summary statistics from the record of each stream. Hierarchical clustering generated nine groupings of rivers. Descriptions of each of these groups are based on flow and flood frequency (Table 2.4). Three categories of intermittency were recognised - *harsh intermittent, intermittent runoff* and *intermittent flashy.*

Table 2.4 A characterisation of streamflow variability and predictability based on streamflow data from 78 US streams (Poff and Ward 1989).

DESCRIPTOR TERM	EXPLANATION OF TERM	REFERENCE
INTERMITTENT	Three groups characterised by high variability and low predictability of flow.	Poff and Ward 1989
HARSH INTERMITTENT	Characterised by long periods of zero flow and by very low flow each year.	
INTERMITTENT FLASHY	Streams with a high frequency of floods which were moderately seasonal in their distribution.	
INTERMITTENT RUNOFF	These streams flood less frequently and less predictably than the former group (it was suggested this could be due to higher vegetational cover and less seasonal precipitation patterns).	
PERENNIAL	Six groups: these streams have no more than occasional zero flow days.	
PERENNIAL FLASHY	Characterised by a high frequency of nonseasonal flooding (arid to semi-arid regions)	
PERENNIAL RUNOFF	Flood less frequently and appear to be less influenced by subsurface flow than previous group (more densely vegetated, mesic regions)	
SNOWMELT	Flood predictably, but not necessarily every year. Low variability and high predictability of flow.	
SNOW+RAIN	Differ from previous group in their greater flood frequency, lesser (but still relatively high) flood predictability and lesser flow predictability.	
WINTER RAIN	Characterised by intermediate flood frequency and medium to high seasonality of flow and flooding.	
MESIC GROUNDWATER	Most constant of all groups over time (with respect to flow variation). Similar to the previous group streams, except this group floods relatively infrequently and less seasonally.	

The classifications of South African river flow regimes by Joubert *et al.* (1993) and Joubert and Hurly (1994) grouped rivers according to both seasonal flow patterns and flow characteristics, using two different statistical methods. The objective for Method One (using non-hierarchical cluster analysis and stepwise discriminant analysis) was to group most similar rivers, and for Method Two (using correspondence analysis and covariance biplots) was to produce river management regions.

The nine variables describing aspects of river flow used in their analyses included a coefficient of intra-annual variation, predictability indices, and average measures of zero-flow days. In analysis of flow characteristics, the results of both methods reflected three major flow regions around the country: a winter peak region, an aseasonal peak flow region, and a variety of different types of summer flow in the rest of the country, which were not geographically separable. In analysis of flow types, eight groups were discerned in Method One, each described by a different set of variables. These were separated into three main groups on the basis of perenniality of flow (Table 2.5). Overall, predictability of flow was not found to be high.

Table 2.5 The eight major groups and three supergroups produced in analysis of flow characteristics of South African Rivers (Joubert and Hurly 1994).

DESCRIPTOR TERM	EXPLANATION IN LITERATURE	REFERENCE
EXTREME SEASONAL	A. Predictable low/zero flow conditions	Joubert and Hurly 1994
MIXED	B. Long flood durations G. Unpredictable D. Strongly seasonal H. Unpredictable flow and floods	
PERENNIAL	C. Frequent floods E. Predictable infrequent floods F. Long intervals between floods	

The authors concluded that the use of variables describing flow characteristics could produce geographic regions, but not naturally in all areas - particularly those in which predictability of flow conditions was low.

We have adopted certain of the terms generated by this classification in our terminology, and refer also to the summary descriptions of river types prepared by Joubert and Hurly (1993; Table 2.6).

Table 2.6 Summary descriptions of South African river types as given by Joubert and Hurly (1993).

DESCRIPTOR TERM	EXPLANATION IN LITERATURE	REFERENCE
EPISODIC	Flow that only occurs after rainfall episodes; flow does not necessarily occur every year	King and Tharme 1994
EXTREME SEASONAL	Flow that usually occurs for less than half the year, every year, during the same season.	
SEASONAL	Flow that usually occurs for more than half the year, every year, during the same season	
QUASI-PERENNIAL-SEASONAL	Flow that in some years continues all years, but in other years ceases for anything from a few days to most of the year.	
FLASHY	Flow with frequent floods of short duration	
PERENNIAL	Flow that usually continues all year, every year	

The term 'seasonal', which is often used as a synonym for 'temporary', is used in a broader context to describe *seasonality of flow* (and flow volume) in both perennial and temporary rivers. The term 'aseasonal' is used in a similar but opposite way, and also applies to descriptions of temporary and permanent rivers.

2.5 A PROPOSED TERMINOLOGY FOR S.A. RIVER FLOW TYPES

The hazard of presenting a terminology for river flow types - particularly those of temporary rivers - is that yet another set of terms is introduced to further confound the literature. The intention here is rather to consolidate and organise the terms already in use in the literature, providing appropriate definitions of each in an attempt to standardise their usage. Where necessary, extended or modified terms are suggested.

RHODES UNIVERSITY LIBRARY

The terminology distinguishes different river regimes according to the hydrological features which, in the absence of a multivariate analytical approach, most simply facilitate characterisation of temporary river regimes. Where applicable and where possible, a number of factors were considered in the formulation of the terminology: approximate duration and periodicity of flow and no-flow phases, approximate time of year at which flow recommences, and the extent of variability and unpredictability in flow regimes within and between years (within a five-year timescale, to allow for an assessment of the effects of variability on river fauna; see Section 2.5.2).

The terminology is designed to give a staged, systematic description of river regimes, and should be applicable at various spatial scales (from river reach upward).

Three major hydrological states are recognised: where surface flow is present continually, where surface flow disappears but some surface water is present in the channel, and where surface water disappears from most of the channel. These are separated by the 'steps' on the continuum illustrated in Figure 2.2. Each flow type is described by a sequence of terms, with each successive term providing a more detailed description of the system. For example, flow in a particular perennial river may be described by any one of the terms in the following series: Perennial - Perennial seasonal - Perennial seasonal winter - Perennial seasonal winter moderate - etc., depending on how much is known of the flow regime.

A full sequence of terms provides a broad description of hydrological state (e.g. Perennial), a description of periodicity or seasonality of flow (e.g. Perennial seasonal); identification of the season in which flow is most likely to occur, in the case of seasonal rivers (e.g. Perennial seasonal winter); and an identification of the nature of flow, where information is available (e.g. Perennial seasonal winter moderate).

Although they are not strictly the subject of this paper, perennial river regimes form part of the continuum, and have thus been included in the terminology.

2.5.1 Qualifying between natural and modified flow regimes

As many South African rivers are not naturally temporary, but have become so as the result of either human activities (e.g. water abstraction, impoundment, catchment modification, etc.) or climatic changes, it is necessary that a terminology distinguishes between the natural and the modified state.

While the description of a river as 'modified temporary', for example, is acceptable, it describes an action to the river rather than the river itself, and is ambiguous - has the river been altered *to* temporary or *from* temporary? A more accurate description of the modified flow regime at a site includes both the former and the present state. In characterising a section of a naturally perennial river site currently exhibiting intermittent flow due to upstream impoundment, the description of flow may be: 'formerly perennial seasonal, modified to intermittent aseasonal'.

2.5.2 A question of scale

For a terminology to be *functional*, the population in question (rivers, in this case) must be described within spatial and temporal limits. Stevens (1994) gives the example that a 'lake' is a concept that has meaning for most people, however the definition does not address size (i.e. what are the limits on area and depth) or temporal fluctuation (i.e. if a lake dries up is it still a lake, was it a lake before the drought?), or discern natural lakes from constructed reservoirs.

Both the proposed terminology and the concept of the continuum could be applied at several temporal scales, either based on fixed time periods (i.e. 1, 5, 10, 50 or 100 year scales) or on variable time periods (i.e. intervals between various magnitude floods, as indicated by a long-term hydrograph). While a one-year period would be a useful scale for the consideration of management issues such as water releases from dams, the minimum period over which temporary rivers should be considered is five years, to accommodate for year-to-year variability. One river may dry only once in three years (e.g. Boulton and Lake

1992a), another may flow throughout one year and intermittently the next (see Joubert and Hurly 1994), and another may flow only once in four or five years.

To take adequate account of this unpredictability and variability, a double time-scale is attempted: the river flow type is considered first at the scale of a single year, after which the five year pattern is considered before characterising the flow regime (see terminology for a clearer working of this scale).

The spatial scale is similarly difficult to define: there is clearly a need to describe 'whole' rivers within regions, however natural variability and the extent of modifications results in the majority of rivers exhibiting more than one flow regime along its length. Which of these should then be used to describe the river? We suggest that the most dominant regime over the length of the river, as established empirically or using a long-term hydrograph, be used, and that zones or reaches with differing flow regimes be described separately. Thus, the *primary* spatial scale for the proposed terminology is the whole river.

The proposed terminology is presented here and summarised in Table 2.8. The continuum illustrated in Figure 2.2 assists in locating the approximate position of the flow regimes along the perennial-temporary gradient.

2.6 THE TERMINOLOGY

HYDROLOGICAL STATE: RIVERS WHICH FLOW CONTINUOUSLY (RARELY EXPERIENCE NO-FLOW CONDITIONS)

PERENNIAL

Flow throughout the year, all years.

Perennial seasonal

Seasonally predictable fluctuations in discharge. Flow variability low.

Perennial seasonal winter

Flow maximised over winter and early spring, diminishes over summer.

Perennial seasonal winter moderate: Elevated late winter and early spring flow, and a distinct yet lower summer flow. (Equivalent to Group 12, Haines *et al.* 1988; Group 3 Joubert and Hurly 1994; Fig. 2.3).

Perennial seasonal winter extreme: Very strong winter and early spring peak flow which dwindles to a low level during summer. (Equivalent to Group 13, Haines *et al.* 1988; Group 2, Joubert and Hurly 1994; Fig. 2.4).

Perennial seasonal spring

Lower winter flow than Perennial Seasonal Winter groups, with elevated flow in spring and in late autumn.

Perennial seasonal early spring

Less winter flow than Perennial Seasonal Winter groups. Flow peaks in early and mid-spring, declines through summer and is elevated again in late autumn (equivalent to Group 13, Haines *et al.* 1988).

Perennial seasonal moderate spring

Similar to previous group but the importance of spring and summer groups is reversed. No distinct low-flow period (equivalent to Group 15, Haines *et al.* 1988).

Perennial seasonal summer

Occur in summer rainfall regions: flow elevated over spring, summer and autumn months. Low flow over winter months.

Perennial seasonal summer moderate: Flow elevated over late spring and summer months with peaks in December, January, February. Flow declines in autumn, and declines further over winter months (equivalent to Group 5, Haines *et al.* 1988; Group 5, Hurly and Joubert 1994, Figure 2.5).

Perennial seasonal summer extreme: Strong late summer or early autumn peak combined with a winter low flow. Plentiful rainfall in early summer moderates and extends the peak flow period (equivalent to Group 6, Haines *et al.* 1988; Group 6, Joubert and Hurly 1994, Figure 2.6).

Perennial aseasonal

Climatic transition areas in which rainfall occurs throughout the year. Discharge is unpredictable year-round, as are discharge peaks. Flow is variable (Figure 2.7).

HYDROLOGICAL STATE CHANGE:
SURFACE FLOW DISAPPEARS BUT SOME SURFACE WATER REMAINS

TEMPORARY

Flow stops and surface water may disappear along parts of the channel either yearly or during two or more years in five. This is a covering term for the description of all the flow regimes encountered in this and the following hydrological state.

INTERMITTENT

Rivers which cease to flow and may dry along parts of their lengths for a variable period annually, or during two or more years in five. Flow may recommence seasonally, or highly variably, depending on climatic influences and predictability of rainfall in the area. An intermittent river may experience several cycles of flow, no flow and drying in a single year.

Intermittent seasonal

Rivers which exhibit seasonally-predictable intermittent flow. Surface flow disappears for a period of each year or some of the five years, and channel may be reduced to pools or may dry completely during the dry season. Flow commences in rainy season (earlier or later depending on extent of drying during dry months). Flow may be sustained or intermittent over wet season.

Intermittent seasonal summer

Predictable floods/recommencement of flow in spring-summer months. Surface flow disappears and the channel may dry in parts throughout the year, certainly during winter months.

Intermittent seasonal winter

Predictable floods/recommencement of flow in winter months. Surface flow disappears and the channel may dry in parts thoughout the year, certainly during summer months.

Intermittent aseasonal

Rivers which exhibit intermittent, unpredictable and highly variable flow within and between years in a five year period. Usually occur in climatic transition zones, semi-arid areas and marginal areas, e.g. southern African drought corridor. Although major rainfall and discharge events may be broadly seasonal, flow follows no distinct pattern and drying may occur in any season. Duration of flow, no flow and drying events is highly variable within and between years, depending on antecedent climatic conditions (Figure 2.8).

HYDROLOGICAL STATE CHANGE:
SURFACE WATER DISAPPEARS FROM THE CHANNEL FOR
SOME/ALL OF EACH YEAR, OR SOME YEARS IN A FIVE YEAR PERIOD

TEMPORARY

See previous description.

Ephemeral

Rivers which flow for less time than they are dry. Flow or flood for short periods of most years in a five year period, in response to unpredictable high rainfall events (Figure 2.9). Support a series of pools in parts of the channel.

Episodic

Highly flashy systems which flow or flood only in response to extreme rainfall events, usually high in their catchments. May not flow once in a five year period, or may flow only once in several years (Figure 2.10).

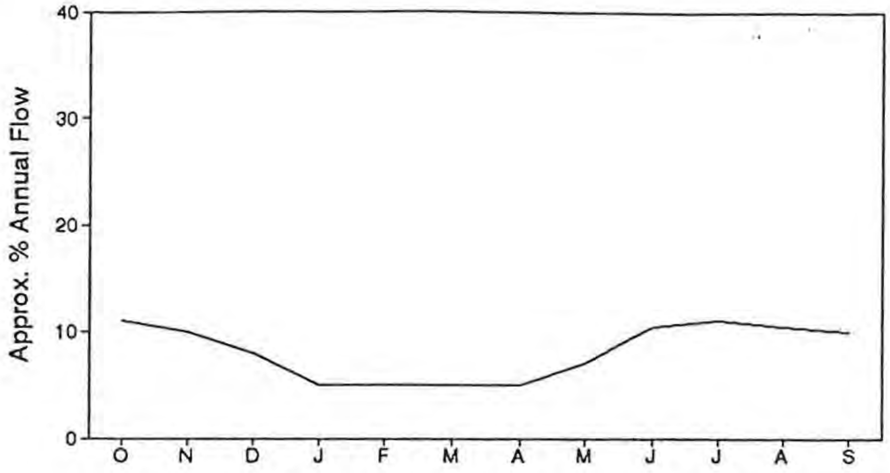


Figure 2.3 Perennial seasonal winter moderate: flow in a typical year (*Adapted from Joubert and Hurly 1994)*

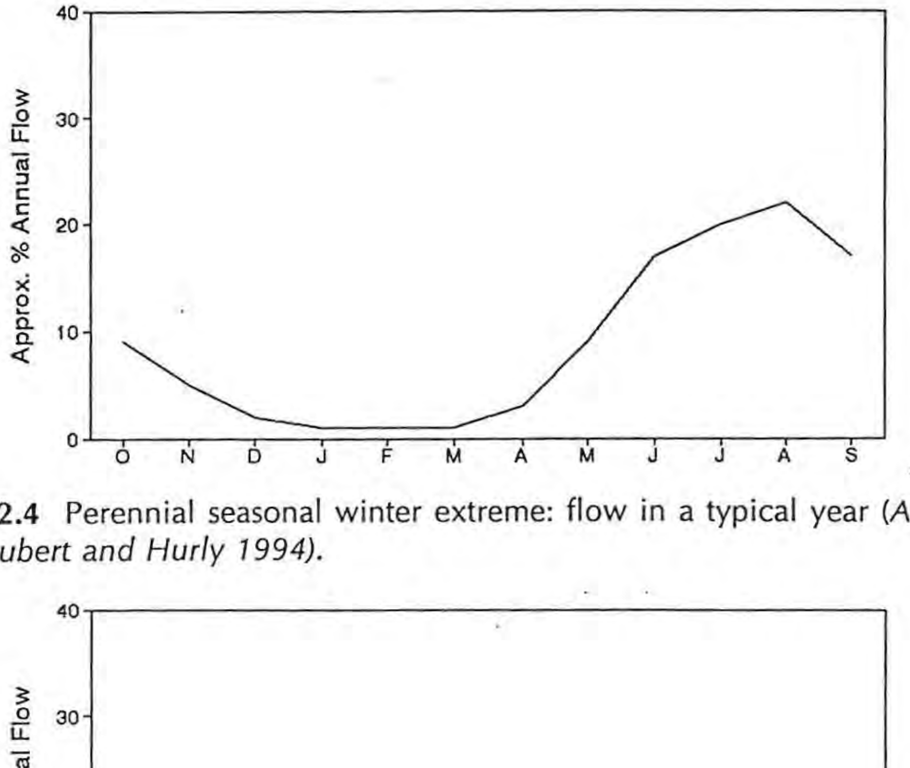


Figure 2.4 Perennial seasonal winter extreme: flow in a typical year (*Adapted from Joubert and Hurly 1994).*

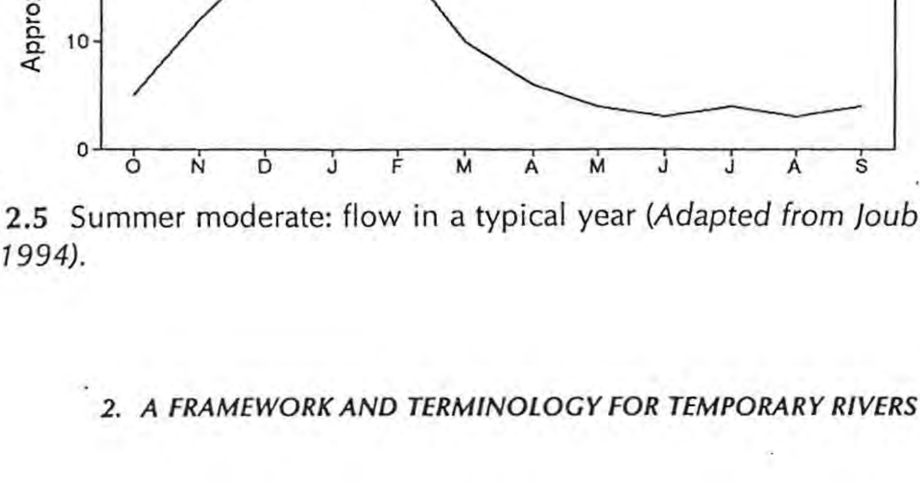


Figure 2.5 Summer moderate: flow in a typical year (*Adapted from Joubert and Hurly 1994).*

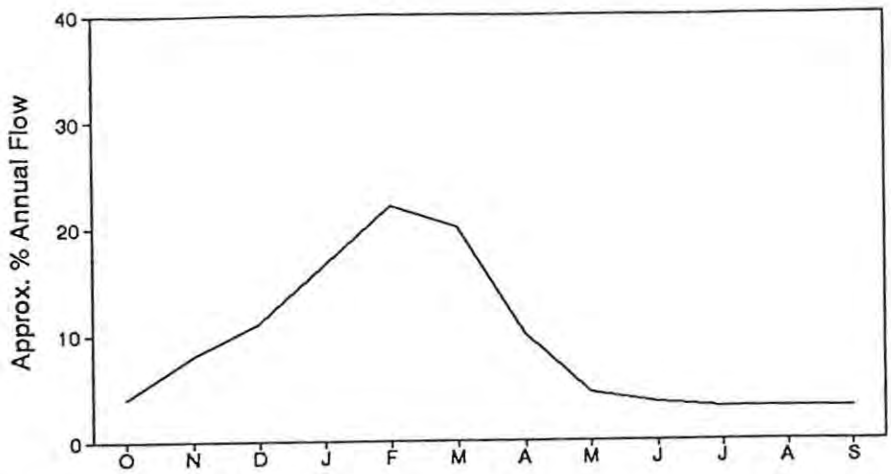


Figure 2.6 Perennial seasonal summer extreme: flow pattern in a typical year (*Adapted from Joubert and Hurly 1994*).

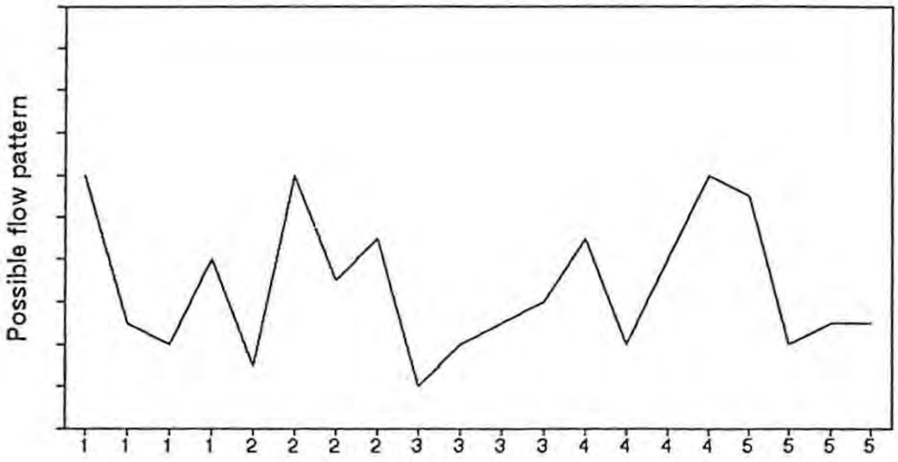


Figure 2.7 Hypothetical flow pattern in a perennial aseasonal river over a period of five years.

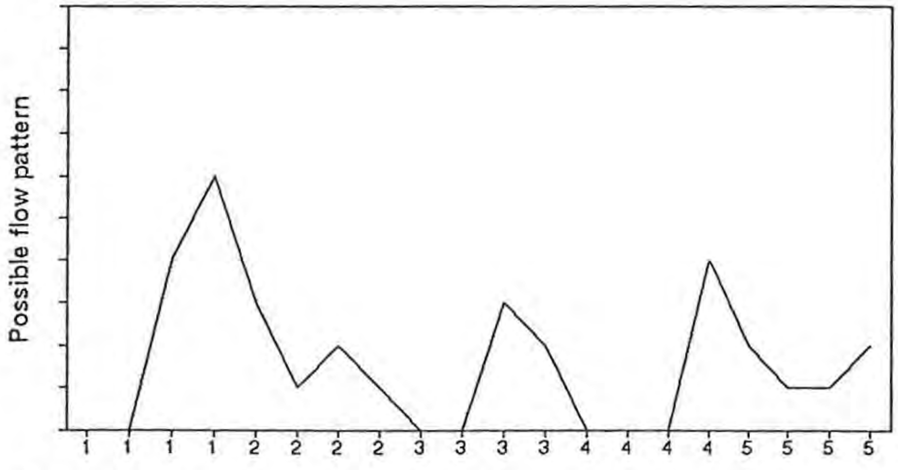


Figure 2.8 Hypothetical flow in an intermittent aseasonal river in a five year period.

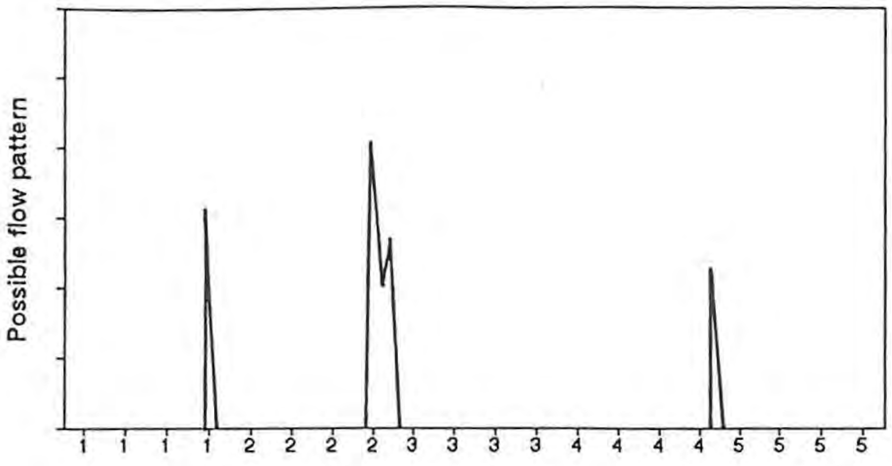


Figure 2.9 Hypothetical flow in an ephemeral river over a five year period.

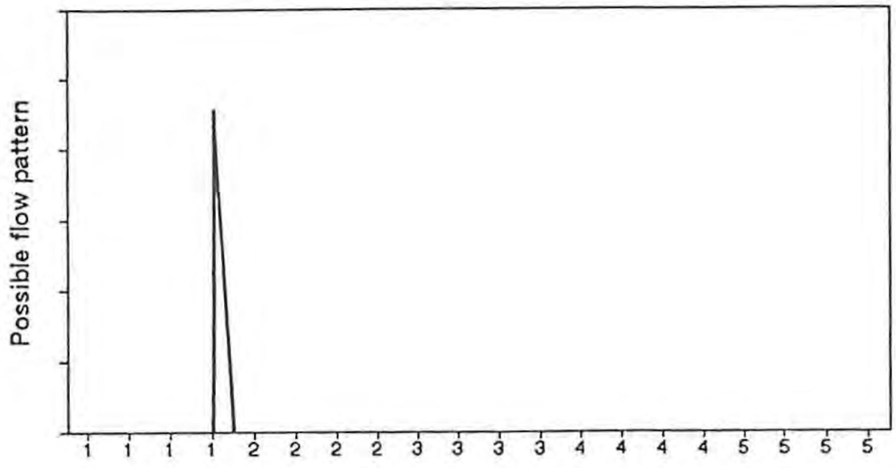


Figure 2.10 Hypothetical flow in an episodic river over a five year period.

Table 2.7 Proposed terminology for temporary and perennial flow types

PERENNIAL	PERENNIAL SEASONAL	PERENNIAL SEASONAL WINTER	Perennial seasonal winter extreme
			Perennial seasonal winter moderate
		PERENNIAL SEASONAL SUMMER	Perennial seasonal summer moderate
			Perennial seasonal midsummer
	PERENNIAL ASEASONAL		

TEMPORARY	INTERMITTENT SEASONAL	Intermittent summer
		Intermittent winter
	INTERMITTENT ASEASONAL	
	EPHEMERAL	
	EPISODIC	

2.7 CONCLUSION

In the absence of a functional river classification scheme for South African rivers, the conceptual framework of the perennial-temporary river continuum and the proposed terminology provide a first-level means of arranging, conceptualising and describing river regimes in the country. The conceptual framework is aimed at expanding perception of river types, and of encouraging a different view of the boundaries between the range of temporary and perennial rivers in South Africa. Although the process of refining the existing terminology in a systematic fashion was initially an exercise for the purposes of this study, there is clearly value in formulating standard working definitions for temporary rivers, at least those in South Africa. Accurate and unambiguous communication of information is as important as the information itself. Our terms are a preliminary attempt to encourage consistency in the use of terms, with the hope that this will improve information transfer between those involved in temporary river research.

REFERENCES

Agnew, J.D. and Harrison, A.D. 1960a. *South African hydrobiological regions. Exploratory survey to region L (Middle Veld region).* Report no 2. Project 6.8H. Internal report, National Institute for Water Research, Council for Scientific and Industrial Research, Pretoria.

Agnew, J.D. and Harrison, A.D. 1960b. *South African hydrobiological regions. Exploratory survey to region K.* Report no 3. Project 6.8H. Internal report, National Institute for Water Research, Council for Scientific and Industrial Research, Pretoria.

Allanson, B.R., Hart, R.C., O'Keeffe, J.H. and Robarts, R.D. 1990. Inland Waters of Southern Africa: an Ecological Perspective. *Monographiae Biologicae* **64**. Kluwer Academic Publishers, Dordrecht, 458pp.

Armitage, P.D. and Petts, G.E. 1992. Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. *Aquatic conservation: marine and freshwater ecosystems* **2:** 1-17.

Bayley, I.A.E. and Williams, W.D. 1973. *Inland waters and their ecology*. Longman, Melbourne.

Boulton, A.J. 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of Science*, Australia, **113:** 23-24.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective in P. De Deckker and W.D. Williams (eds.). Limnology in Australia. CSIRO/Junk Publications, Melbourne.

Boulton, A.J. and Lake, P.S. 1988. Australian temporary streams - some ecological characteristics. *Verhandlungen Internationale Vereiniging fur Theoretische und Angewandte Limnologie* **23:** 123-141.

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24:** 123-141.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* **27:** 99-121.

Boulton, A.J. and Lake, P.S. 1992b. Benthic organic matter and detritivorous macroinvertebrates in two intermittent streams in south-eastern Australia. *Hydrobiologia* **241:** 107-118.

Boulton, A.J. and Lake, P.S. 1992c. The macroinvertebrate assemblages in pools and riffles in two intermittent streams (Werribee and Lerdeberg Rivers, southern central Victoria). *Occasional Paper of the Museum of Victoria* **5:** 55-67.

Boulton, A.J., Peterson, C.G., Grimm, N.B. and Fisher, S.G. 1992a. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* **73** (6): 2192-2207.

Boulton, A.J., Stanley, E.H., Fisher, S.G. and Lake, P.S. 1992b. Over-summering strategies of macroinvertebrates in intermittent streams in Australia and Arizona *in* R.D. Robarts and M.L. Bothwell (eds) Aquatic ecosystems in semi-arid regions: Implications for resource management. NHRI Symposium Series 7, Environment Canada, Saskatoon.

Braune, E. 1985. Aridity and hydrological characteristics: Chairman's summary. *Hydrobiologia* 125:131-136.

Brierley, G.J. 1994. River reach analysis as a geomorphic tool for river classification. *In:* M.C. Uys (ed.), Classification of rivers and environmental health indicators. Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94. pp. 111-117.

Brooks, S.S. and Boulton, A.J. 1991. Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbance in an Australian temporary stream. *Australian Journal of Marine and Freshwater Research* **42**: 295-308.

Cambray, J.A. 1991. The effects on fish spawning and management implications of impoundment water releases in an intermittent South African river. *Regulated Rivers: Research and Management* **6:** 39-52.

Chutter, F.M. and Heath, R.G.M. 1993. *Relationships between low flow and the river fauna in the Letaba River.* Water Research Commission Report No 293/1/93.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* Water Research Commission Report No. TT62/93.

Davies, B.R., Thoms, M.C., Walker, K.F. O'Keeffe, J.H. and Gore, J.A. 1994. Dryland rivers, their ecology, conservation and management. *in* P.Calow and G.E. Petts (eds.). *The Rivers Handbook. Volume* 2. Blackwell Scientific Publications, Oxford.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1995. River and stream ecosystems in Southern Africa: predictably unpredictable. *In:* C.E.Cushing, K.W. Cummins and J.H. O'Keeffe (eds). *Ecosystems of the World 22: River and stream ecosystems.* Elsevier, New York.

Day, J.A. 1990. Environmental correlates of aquatic faunal distribution in the Namib Desert. *In:* M.K. Seely (ed.). *Namib ecology: 25 years of Namibian research.* Transvaal Museum Monograph No 7. Transvaal Museum Pretoria. pp. 99-107

Decksbach, N.K. 1929. Zur Classification der Gewasser vom astatischen Typus. *Archivs Hydrobiologica* **20:** 399-406.

Delucchi, C.M. 1988. Comparison of community structure among streams with different flow regimes. *Canadian Journal of Zoology* **66:** 579-586.

DWAF (Department of Water Affairs and Forestry). 1995. You and your water rights. *South African Law Review.*

Eekhout, S. 1994. A biotic classification of the rivers of South Africa. Pages 43-48 *In:* M.C. Uys (ed.) *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94.

Eekhout, S., Brown, C.A. and King, J.M. 1996. *National Biomonitoring Programme for Riverine Ecosystems: Technical considerations and protocol for the selection of reference and monitoring sites.* NBP Report Series No.3. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Gould, S.J. 1993. The median isn't the message. *In:* S.J. Gould. *Adam's navel and other essays.* Penguin, UK. pp.15-20

Gould, S.J. and Vrba, E. 1982. Exaptation: a missing term in the science of form. *Paleobiology* **8** (1): 4-15.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of North American Benthological Society* **8** (4): 293-307.

Haines, A.T., Finlayson, B.L. and McMahon, T.A. 1988. A global classification of river regimes. *Applied Geography* **8:** 255-272.

Harrison, A.D. 1959. General statement on the South African hydrobiological regions. *National Institute for Water Research Report* 1, Project 6.8H.

Harrison, A.D. 1966. Recolonisation of a Rhodesian stream after drought. *Archives Hydrobiologica* **62** (3) 405-421.

Hart, B.T. and Campbell, I.C. 1994. Ecological classification scheme for Australia. *In:* M.C. Uys (ed.). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94. pp. 87-100.

Jacobson, P.J., Jacobson, K.M. and Seely, M.K. 1995. *Ephemeral rivers and their catchments - sustaining people and development in Western Namibia.* Desert Research Foundation of Namibia, Windhoek. 160pp.

Joubert, A.R. and Hurly, P.R. 1994 Grouping South African rivers using flow-derived variables. *In:* M.C. Uys (ed.). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94. pp 27-42

Joubert, A.R. and Hurly, P.R. 1993. The use of daily flow data to classify South African rivers. *In:* King, J.M. and Tharme, R.E. (Main authors). *Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies For South Africa.* Water Research Commission Report No. 295/1/94. pp. 286-359.

King, J.M., de Moor, F.C. and Chutter, F.M. 1992. Alternative ways of classifying rivers in South Africa. *In:* P.J. Boon, P. Calow and G.E. Petts. River conservation and management. John Wiley and Sons Ltd. pp. 231-228.

King, J.M. and Tharme, R.E. 1993. *Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa.* Water Research Commission Report No. 295/1/94.

Matthews, W.J. 1988. North American streams as systems for ecological study. *Journal of the North American Benthological Society* **7** (4): 387-409.

Naiman, R.J., Ionzarich, D.G., Beechie, T.J. and Ralph, S.C. 1992. General principles of classification and the assessment of conservation potential in rivers. *In:* Boon, P.J., Calow, P. and Petts, G.E. (eds.). *River conservation and management.* Wiley, Chichester.

O'Keeffe, J.H. and de Moor, F.C. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research and Management* **2:** 39-55.

O'Keeffe, J.H., King, J., Eekhout, S. 1994. The characteristics and purposes of river classification. *In:* M.C. Uys (ed.). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94. pp. 9-18.

Peckarsky, B.L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. *in* Fontaine III, T.D. and Bartell, S.M. *Dynamics of lotic ecosystems.* Ann Arbor Science Publishers, Ann Arbor.

Platts, W.S. 1980. A plea for fishery habitat classification. *Fisheries* **5**(1): 2-6.

Petitjean, M.O.G. and Davies, B.R. 1988. A review of the ecological and environmental impacts of inter-basin water transfer schemes in southern Africa. Synthesis (Part 1) and international bibliography (Part 2). Occasional report no. 38. Ecosystems Programmes, Council for Scientific and Industrial Research, Pretoria.

Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* **11** (1): 86-92.

Poff, N.L. and Ward, J.V. 1989. Implications of streamflow variability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46:** 1805-1817.

Power, M.E. Stout, R. J., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Statzner, B., Wais de Badgen, I.R. 1988. Biotic and abiotic controls in stream and river communities. *Journal of the North American Benthological Society* 7 (4): 456-479.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. and Wissmar, R.C. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7 (4): 433-455.

Roux, D.J., Thirion, C., Smidt, M and Everett, M.J. 1994. *A Procedure for assessing biotic integrity in rivers - application to three river systems flowing through the Kruger National Park, South Africa.* Interim Report for Department of Water Affairs, No. N000/00/REQ/0894.

Towns, D.R. 1985. Limnological characteristics of a South Australian intermittent stream, Brownhill Creek. *Australian Journal of Marine and Freshwater Research* **36:** 821-37.

Uys, M.C. 1994. *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/ Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94.

Wadeson R.A. and Rowntree K.M. 1994. A hierarchical geomorphological model for the classification of South African river systems. *In:* M.C. Uys (ed.), *Classification of rivers and environmental health indicators. Proceedings of a joint South African/Australian workshop, Cape Town*. Water Research Commission Report No. TT 63/94. pp 49-67.

Walker, K.F., Sheldon, F. and Puckridge, J.T. 1995. A perspective on dryland river ecosystems. *Regulated Rivers Research and Management* **11:** 85-104.

Wiggins, G.B., Mackay, R.B. and Smith, I.M. 1980. Evolutionary and ecological strategies of animals in temporary pools. *Archiv für Hydrobiologie Supplement* **58:** 902-76.

Williams, W.D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **4** (125): 85-110.

Williams, W.D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshwater Biology* **20:** 407-420

Williams, D.D. 1987. *The ecology of temporary waters*. Croom Helm Ltd., Kent/ Timber Press, USA.

Williams, D.D. and Hynes, H.B.N. 1976. The ecology of temporary streams. I. The faunas of two Canadian streams. *Internationale Revue des gesamten Hydrobiologie* **61** (6): 761-787.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue des gesamten Hydrobiologie* **62:** 53-61.

CHAPTER 3

THE CHARACTER AND VARIABILITY OF THE INVERTEBRATE FAUNA OF THE UPPER KOWIE RIVER WITHIN A SINGLE YEAR

This chapter has been submitted as a paper to the journal Archiv für Hydrobiologie, with the title 'Invertebrate dynamics in an intermittent stream in the Eastern Cape, over a period incorporating several hydrological phases', under the joint authorship of M.C. Uys and J.H. O'Keeffe. The paper is currently in the review process. It has been substantially edited for the purposes of this thesis, to reduce repetition of concepts and methodologies already outlined (e.g. those relating to the multivariate statistics), and to maintain the theme and flow of the rest of the document.

ABSTRACT

Changes in the invertebrate fauna of an aseasonal intermittent stream in the Eastern Cape, South Africa, were investigated over a period of eight months, during which four distinct hydrological phases occurred. Faunal composition and numbers of taxa collected showed high variability over time and space. The diversity and stability of the biota increased with increasing duration of physical conditions, but in general the frequency of disturbance (rate of change of phase; unpredictable onset or cessation of flow and drying) was high and resulted in low similarities between the biota of different months. Physical forces apparently played the major role in shaping faunal assemblages, with three interacting variables considered to have the major effect: 1) present and antecedent hydrological conditions and their duration, 2) time of year, and 3) biotope or substratum character and availability. Significant differences were found between the biota of different biotopes, sites and months.

3.1 INTRODUCTION

The character and distribution of faunal assemblages in an aquatic environment are considered a function of several interacting variables, both physical and biological in nature. These include the flow regime, water quality, character and availability of substrata, local hydraulic conditions (at the scale of the biota), ecosystem productivity, distribution of food resources, biotic interactions, and the extent of disturbance and environmental variability to which the fauna is exposed (e.g. Minshall 1984, Statzner and Higler 1986, Poff and Ward 1989, Stanley and Fisher 1992, Ward 1992, Armitage *et al.* 1995, Wootton *et al.* 1996, Yule 1996). The degree to which one or several factors can be correlated with biotic organisation is dependent on the type of water body under consideration and the scale and resolution of the investigation (e.g. Downes *et al.* 1993).

Clear spatial patterns in faunal distribution have been reported in many stable, naturally perennial rivers, and - commonly - distinct, sometimes intergrading communities are associated with particular 'patches' - e.g. substratum types, biotopes, river zones, or hydraulic conditions (Vannote et al. 1980, review by

Minshall 1984, King *et al.* 1988, Yule 1996). Some authors have reported characteristic seasonal cycles in community structure and function (see King 1981, Hildrew and Giller 1992), while others have noted the absence of such temporal changes (King *et al.* 1988).

In temporary rivers and rivers with highly variable flow regimes, spatial patterns in faunal composition and distribution are less clear, and the global applicability of predictable longitudinal change in faunal composition (e.g. River Continuum Concept, Vannote et al. 1980) has been questioned following a number of Southern Hemisphere studies (e.g. Winterbourn et al. 1981, Bunn et al. 1986, Boulton and Lake 1988). In these environments, the relationship between aquatic habitat and faunal composition is mediated by interrelated factors, primarily hydrological conditions (Stanley et al. 1997), degree of temporariness (Boulton and Lake 1992a), duration of habitat, and disturbance frequency (Wiggins *et al.* 1980, Williams 1987, Hildrew and Giller 1992, Schneider and Frost 1996). Temporal variability in the fauna seems to show clearer form than does spatial pattern, at least in those temporary rivers with clear flow seasonality. Cyclical temporal changes in invertebrate assemblage composition were reported for seasonal intermittent streams in Victoria, Australia, although unpredictable disturbances in the form of flow cessation or floods temporarily disrupted these cycles (Boulton and Lake 1992b). Palmer *et al.* (1991) also reported clear temporal changes in the fauna of an intermittent headwater stream, despite the high overlap in species composition between habitats.

In intermittent rivers, habitat shift is rapid, and can involve a change from fast-flowing, well-oxygenated water to isolated pools in the channel (Chapman and Kramer 1991). These changes represent a continual expansion and contraction in the ecosystem (Stanley et al. 1997). Low habitat stability, high temporal variability in flow, and large fluctuations in rainfall all lead to reduced persistence of macroinvertebrates (e.g. Wallace *et al.* 1988, Boulton and Lake 1992 a,b). As discussed in Section 1.2.2, the concept of a well-ordered, energy-efficient stream 'community' is not appropriate to unstable and highly variable systems (Cowie 1985), and a more fitting view is that of an unstructured fauna subject to continuous recruitment and dispersal, comprising 'resident' and 'hardy opportunist' taxa (Davies *et al.* 1995) which exhibit rapid reproduction, short life-cycles, physiological adaptation (e.g. ability to resist desiccation), behavioural avoidance, or active relocation under adverse conditions (e.g. Grimm and Fisher 1989, Williams 1987).

In South Africa, virtually nothing is known about the invertebrates living intermittent rivers, and what factors are most important in regulating their presence, abundance and distribution. Research on the invertebrate fauna of temporary rivers elsewhere (e.g. Australia, Arizona, Canada) has provided perspective on the spatial and temporal dynamics of the fauna of temporary rivers relative to those of permanent rivers, but most of these studies have focussed on streams subject to seasonal patterns in drying and rewetting (e.g. Stehr and Branson 1938, Williams and Hynes 1976, 1977, Boulton and Lake 1990, 1992a,b, Boulton *et al.* 1992a, Williams 1985). The study reported here was concerned with *aseasonal* temporary river in the 'arid corridor' of the Eastern Cape region, South Africa. It took place over eight months, winter to midsummer (July 1994 to February 1995), during which time the river was characterised by highly variable and unpredictable hydrology. Several of the hydrological phases identified *a priori* (1.3) occurred, some more than once.

The aims of the study were:

- to investigate the invertebrate fauna occurring in different biotopes and reaches (sites) of the upper Kowie River section over the eight months
- to establish to what extent spatial and temporal patterns in invertebrate fauna could be detected over this period
- to investigate links between abiotic and biotic variables, and (along similar lines)
- to determine which factors were most important in shaping invertebrate faunal character in this section of the river.

Null hypotheses were framed in terms of 'no differences between groups', where different 'groups' were the spatial or temporal units distinguished *a priori* for each different level of analysis, as discussed in Section 1.4. The three groups were biotopes, sites and months of the study. The null hypotheses were thus:

H_0: That there is no difference between the invertebrate fauna of different biotopes within a site.

H_0: There is no difference between the invertebrate fauna of different sites.

H_0: That there is no difference between the invertebrate fauna of different months.

3.2 STUDY SITES

The Kowie River rises close to Grahamstown in the Eastern Cape, and flows approximately 60km to its mouth at Port Alfred (Fig. 3.1). Like many southern African rivers, it rises amongst hills rather than mountains (Harrison 1966), at approximately 700m above sea level. It is naturally temporary. The $652km^2$ catchment occurs within a vegetation biome described by Lubke and Van Wijk (1988) as *Subtropical Thicket* (dense woody vegetation comprising small trees with a closed canopy up to 3m high), with inland plant formations described as *Valley Bushveld* (succulent thicket which extends into the Coastal Grassland Zone). The river is underlain by rocks of the Bokkeveld group (characterised by dark shales and sandstones). Average yearly rainfall is approximately 650mm.

Two sites in the upper reaches of the river were selected for this study. In terms of the terminology presented in Chapter 2, this section of the river was described as 'intermittent aseasonal'. Both sites were located in uncultivated farmland, and upstream of major impacts.

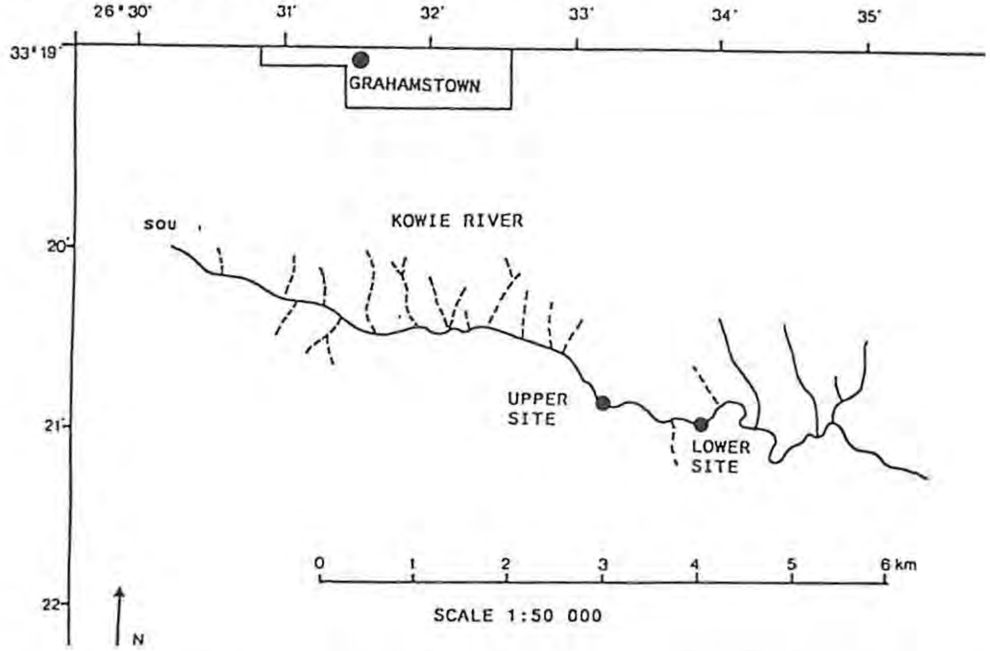


Figure 3.1 Map of the upper Kowie River, Eastern Cape. Also see Fig. 1.1.

3.2.1 **Upstream site, UK1** (26°33'11"E, 33°20'50"S)

This site was situated approximately 5km downstream of the spring-fed source of the river. Within 10 to 15m of the top end of the site, there was a vertical drop of a metre (which formed a cascade during flow), and a gradual drop of a metre over the ± 40m length. Width varied from 1 to 10m (during flow). The chief substratum was bedrock, overlain in places with boulders and a mosaic of rocks, cobbles and coarse sand (*sensu* modified Wentworth classification, Cummins 1962). The approximate distribution of these substrata is illustrated in Figure 3.2. The stream was dimly-lit due to heavy canopy cover provided by riparian trees. Upstream of UK1, a derelict concrete roadbridge had a slight damming effect. Within a week of flow cessation at UK1, there were discontinuities in surface water, and as drying progressed, a series of isolated pools with varying substrata remained in the channel (Plates 3.1-3.4).

3.2.2 **Downstream site, UK2** (26°33'50"E, 33°21'00"S)

This site was situated a kilometre downstream of UK1. There was virtually no gradient over its 30m length (during flow) and width varied from 3 to 10 metres. No bedrock was visible in the channel, and the chief substratum was mixed coarse and fine sands; with rocks, cobbles and stones occurring at the upper end of the site (Fig. 3.3). Sand may have entered the site via erosion of an abandoned track approximately 500m upstream. The right bank was steep and vegetated, and shaded the site throughout the year. The sloping left bank was covered with indigenous and exotic grasses, trees and shrubs. Following flow cessation, a large, persistent pool was left (Plates 3.6, 3.7) and marginal vegetation on the left bank was inundated until the mature pools phase.

3.3 HYDROLOGY OF THE STUDY SECTION

Four of the five hydrological phases (1.3.5) occurred during the eight month study - POOLS, ONSET, FLOW and NO FLOW. Certain of these occurred more than once. The greatest discharge recorded during the period was $0.08m^3s^{-1}$ (Fig. 3.4).

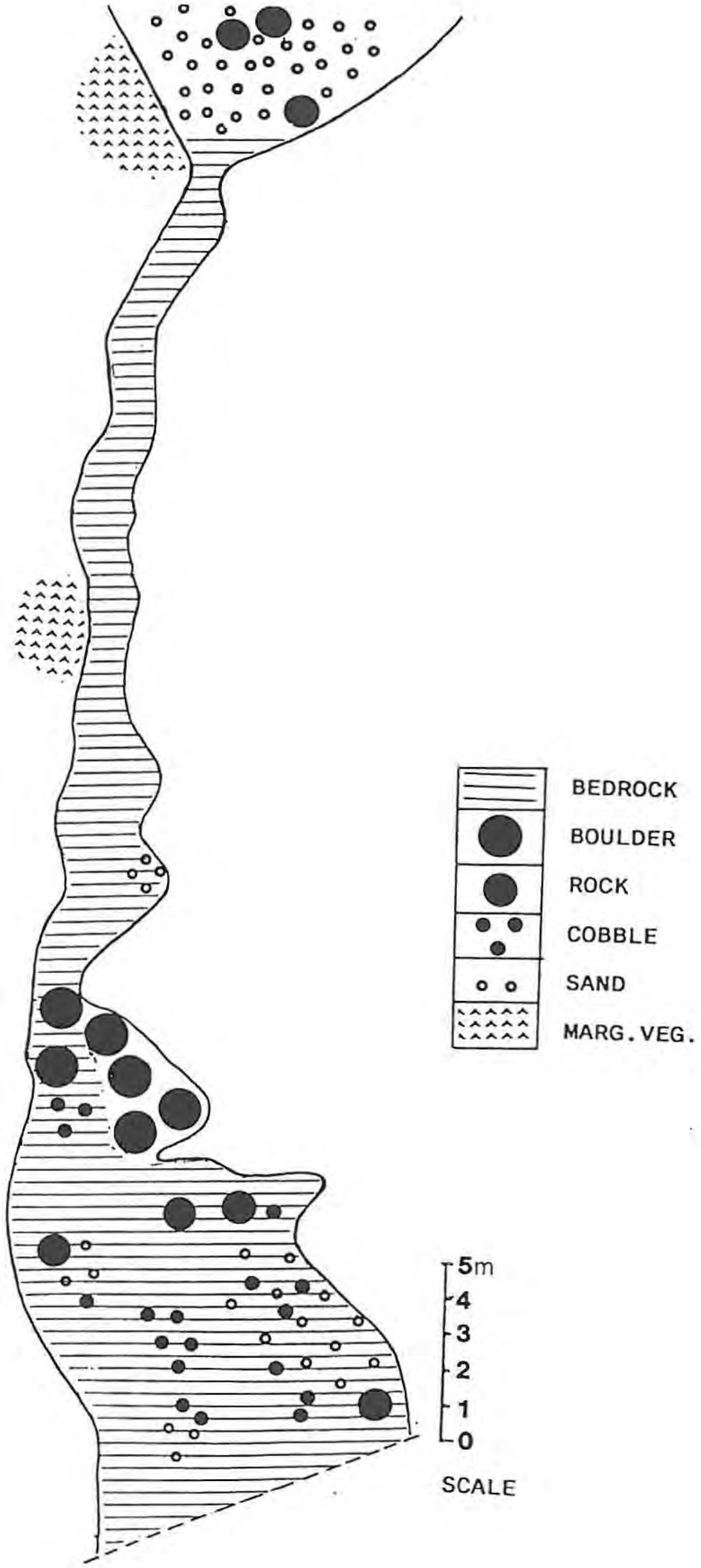
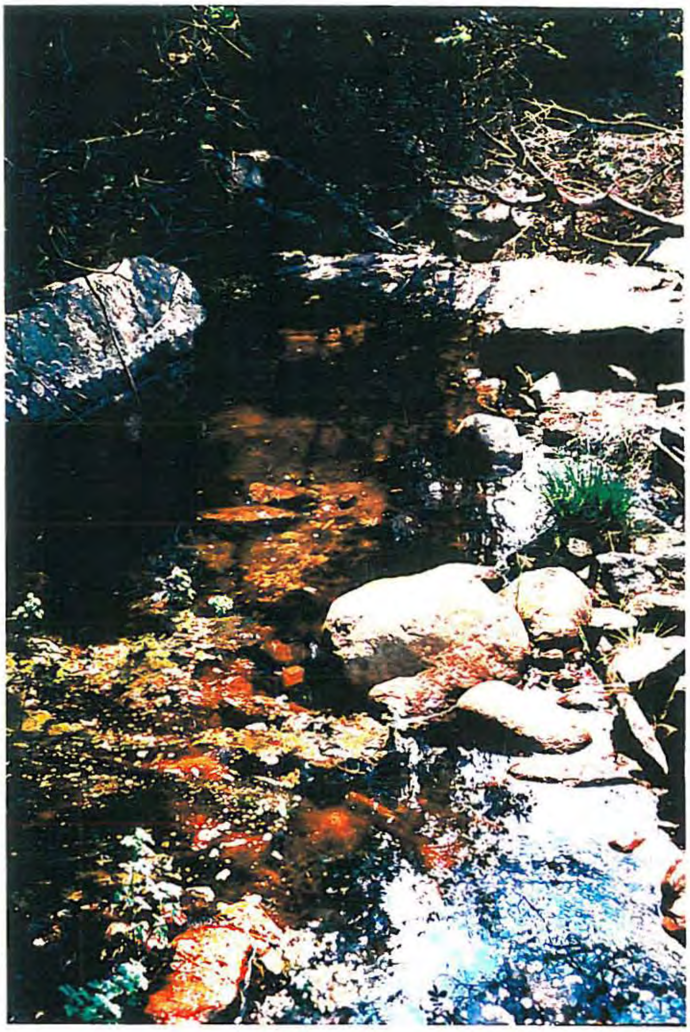
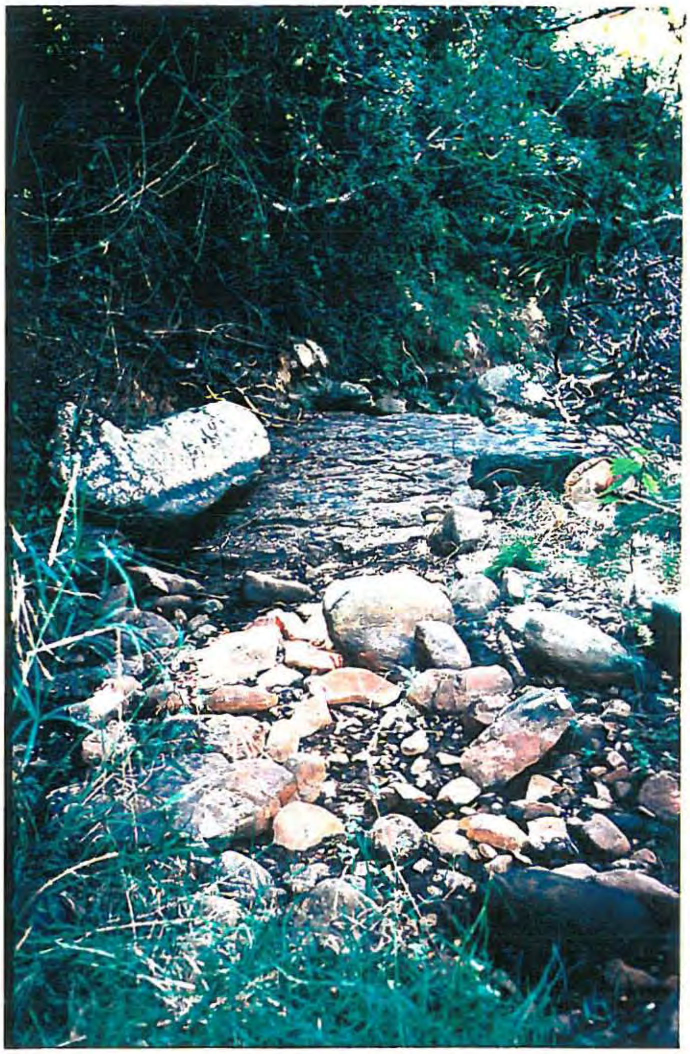


Figure 3.2 Longitudinal section of the upper site UK1, showing approximate channel shape and distribution of substratum types over its ±40m length, during periods of flow. Flow in the direction of the arrow.

3.1



3.2



3.3

PLATES 3.1 - 3.3
UPPER KOWIE RIVER,
SITE UK1

3.1 FLOW
3.2 NO FLOW
3.3 DRY

PLATES 3.5 - 3.8
UPPER KOWIE RIVER,
SITE UK2
(2pp overleaf)

3.5 ONSET/FLOW
3.6 NO FLOW
3.7 POOLS
3.8 DRY

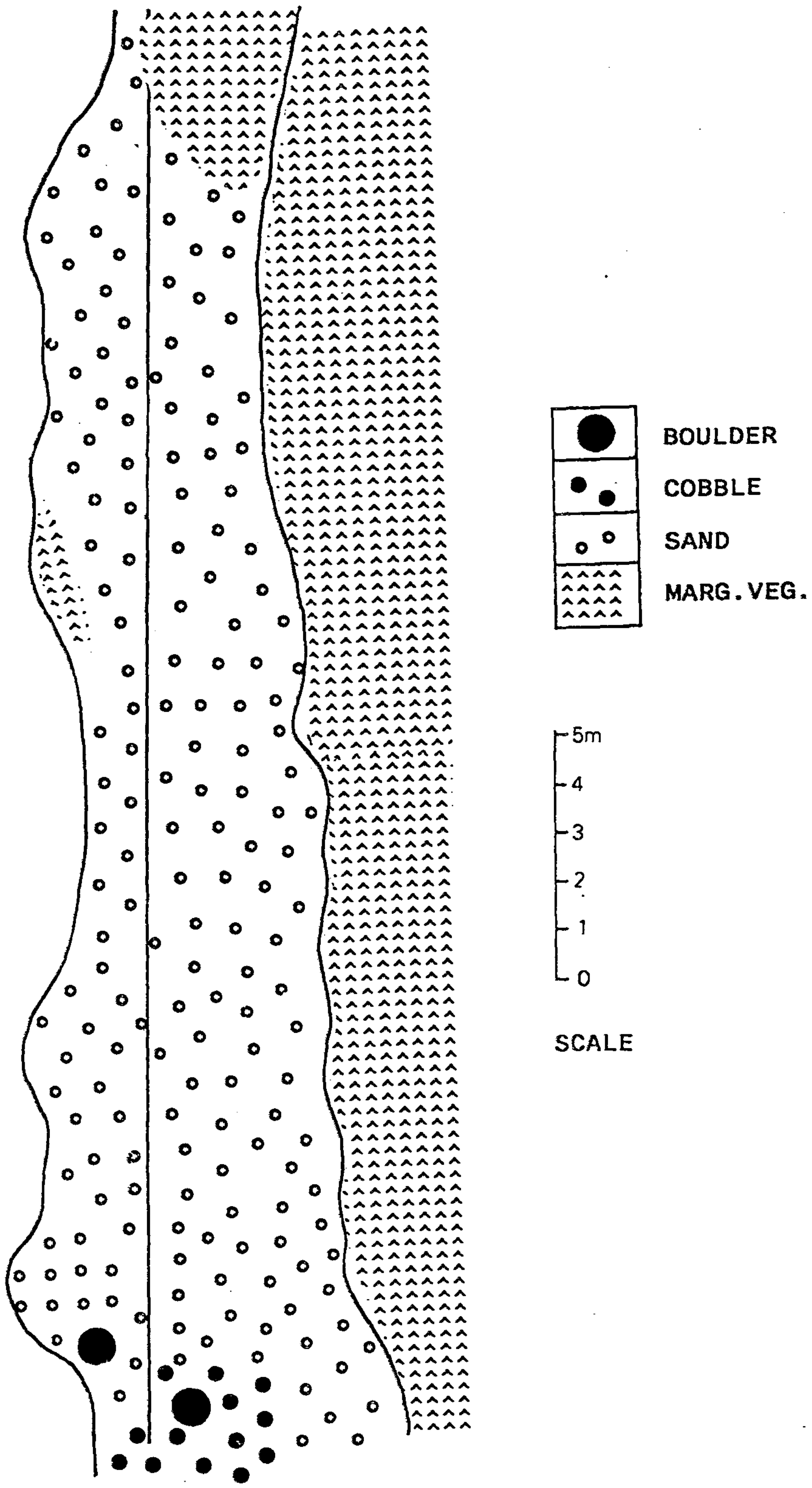


Figure 3.3 Longitudinal section of the lower site, UK2, showing approximate channel width and distribution of various substratum types along its ± 30m length, during periods of flow. (Flow in direction of arrow).

3.5

3.6

3.7

3.8

During the winter month of July, surface water was restricted to small bedrock pools at UK1 and a single large pool at UK2. Recommencement of flow occurred in August, and flow continued until October at low volumes (Fig. 3.4). Following cessation of flow in November, high summer temperatures resulted in rapid loss of surface water, and by the time of sampling only shallow pools remained at UK1, and the pool at UK2 had diminished in volume (though marginal vegetation was still inundated). By December, the upper site was virtually dry, with a few rainpools and several large damp areas covered with leaves and detritus. The pool at UK2 was the smallest it had been since the commencement of the study, with an extensive, damp 'littoral' zone covered with moss, drying algae and scattered leaves (see Plates 3.1 to 3.8).

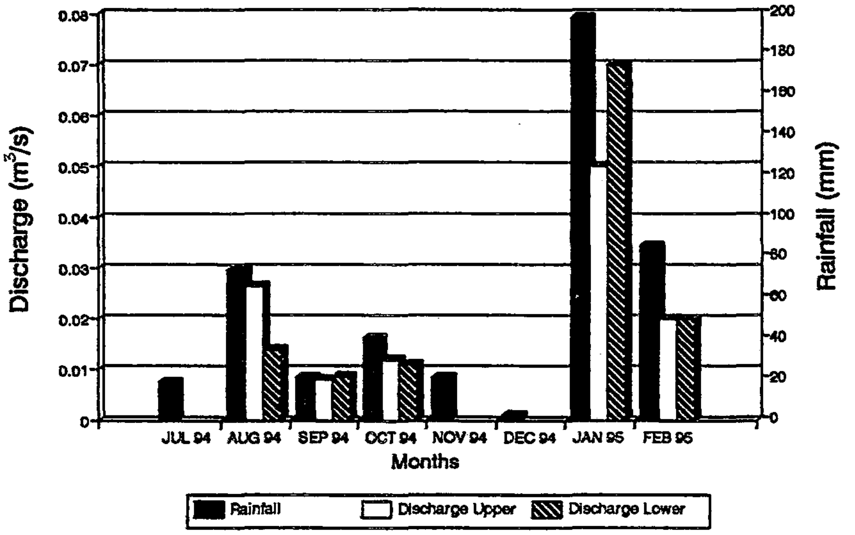


Figure 3.4 Discharge and rainfall at the upper Kowie River over the period of the study (*Rainfall data supplied by Grahamstown City Engineers, discharge values measured at each sampling occasion as described in Methods*).

3.4 METHODS

3.4.1 Sampling of invertebrates

Sampling for the period in question involved monthly trips to the two upper Kowie River sites. The choice of biotopes was described in Section 1.3.3. All five biotopes identified were sampled at some time of the study (when available): stones-in-current (SIC) or riffle areas, stones-out-of-current (SOOC), marginal vegetation (MV), sandy substrata (SAND), full pools where pool volume was too small to sample separate biotopes (POOL), and drying fringes of pools (DRG).

All biotopes except DRG were sampled using 100μm mesh-size nets, and where appropriate following Chutter's (1994) techniques. MV was sampled by sweeping the net once forwards and once backwards through one to two metres of vegetation, or what was available. SIC and SOOC were kick-sampled for a period of 30 seconds to 1 minute. SAND was sampled using a 25cm x 25cm Surber sampler. Shallow, low-volume pools (POOL) were sampled by sweeping a net several times back and forth through the pool, ensuring that mobile sediments were disturbed. Drying fringes of pools (DRG) were sampled using a 10cm length of 8cm diameter poly vinyl chloride (PVC) pipe. The corer was forced into the substratum to full depth (where possible), a square of aluminium sheeting was slipped in below the base of the corer, and the sample removed and inverted into a large sampling bottle. These samples yielded a volume of approximately 500cm^3. Three replicate samples were taken in each biotope. Invertebrate samples were stored in 70% alcohol and returned to the laboratory for sorting and identification to the lowest possible taxonomic levels (see Section 3.4.3). The invertebrate collection will be housed at the Albany Museum, Grahamstown.

Depth and current speed were recorded at each sampling point. Approximate percentage composition of the substratum was estimated visually in each of the biotopes sampled, for the following materials: bedrock, boulders, cobbles, coarse to fine sand, mud, filamentous algae, vegetation (submerged or emergent), detritus, and leaf-fall. Four numerical classes used in the estimation of percentage composition: 1 = 0-25%, 2 = 26-50%, 3 = 51-75%, 4 = 75-100%.

3.4.2 Measurement of abiotic variables

Several abiotic variables were measured at each site when surface water was present. All meters and their levels of resolution and accuracy are recorded here for completeness. Conductivity (mS.m^{-1}) was measured using an Electronic Scientific Instrumentation (ESI) M90 portable microprocessor-based meter, corrected to 25°C, with a resolution of 0.01 and an accuracy of ± 0.5%. pH was measured using an ESI M90 meter with a resolution of 0.01 and an accuracy of

± 0.01%. Water temperature was recorded in °C, using a glass and mercury thermometer. Oxygen concentration (ppm O_2) was read from a Hanna HI 9143 portable dissolved oxygen meter with automatic temperature compensation and corrected for altitude, with a resolution of 0.1 ppm and an accuracy of 1.5% of the full scale (0-19.9ppm or 0-100%). Where oxygen saturation exceeded 100%, a portable ESI dissolved oxygen meter with a range of 0-200%, a resolution of 1% and an accuracy of ± 1% was used. Dissolved oxygen readings were all converted to % oxygen saturation.

During periods of flow, an A.Ott flow meter with a 50mm propeller (0.25mm pitch) was used to measure current speed (rpm) at fixed intervals across a predetermined section of the river. Meter readings for each interval were converted to current speeds ($m.s^{-1}$) using a standard conversion formula. The depth (m), current speed ($m.s^{-1}$) and width (m) of each measured interval were multiplied to calculate discharge ($m^{-3}.s^{-1}$) for each interval of the section. These discharge values were summed across the channel to provide an estimate of total discharge.

3.4.3 Data analysis

Data preparation

The identification of fauna to various taxonomic levels, and the reference to 'equivalent taxa' following King and Tharme (1994) was discussed in Section 1.3.2. For the purposes of this study, faunal abundances were recorded in three categories: **1** = 1-10 individuals, **2** = 11-100 individuals, **3** = > 100 individuals. This is almost equivalent to a log transformation of abundance data, one of the methods of transformation recommended by Clarke and Warwick (1994) for assessment of similarity.

Where possible, all taxa were retained for analyses, for reasons discussed in Section 1.4.2. This rendered the use of large data sets complex and unwieldy (see Appendix 5.1 where a 100-sample matrix was used in clustering). The similarity between replicate samples taken within a biotope was tested for in the analyses conducted in Chapter 4. Results of cluster analysis (Appendix 4.1) indicated that in, general, similarity between replicates (*within biotopes*) was higher than that between biotopes within and between months, and, acknowledging the trade-off between ease of interpretation and resolution, these replicates were pooled for analyses so that each biotope was represented by a single 'sample' (within-biotope variability, although of interest, was not one of the aims of this investigation). This procedure was eventually followed in the majority of analyses.

MULTIVARIATE STATISTICS

Non-parametric, multivariate statistics were performed using programs in the PRIMER software package (Clarke and Warwick 1994), as described in Section 1.4.

Calculation of similarity

Faunal similarities were calculated between samples or total samples, using the Bray-Curtis coefficient of similarity, as described in Section 1.4.2.

Cluster analysis

The use and limitations of the clustering method was discussed in some detail in Section 1.4.3. Hierarchical agglomerative clustering with group-average linkage was performed on pooled replicates (hereinafter referred to only as 'samples') from each biotope and each month, using the CLUSTER program in PRIMER.

The combination of clustering and ordination is considered an effective way of checking for the adequacy of each and their mutual consistency, as discussed in Section 1.4.3. For this purpose, and for the convenience of describing individual groups of samples, an arbitrary similarity value was selected on the dendrograms produced, and a line was drawn through that value. All clusters formed to the right of the line were marked as 'Groups'. These Groups were also entered into in the SIMPER program to calculate contributions of individual taxa to group similarities (see 1.4.5).

Ordination

Ordinations were computed in the MDS program, as described in Section 1.4.4. Ordinations were plotted using the CONPLOT program in PRIMER.

Contributions of individual taxa to similarities

The program SIMPER was used to discern the contributions of individual taxa to similarities between samples within Groups. This procedure was described in Section 1.4.5.

Examination of null hypotheses

This study possessed *a priori* defined structure between the different groups or units of analysis (biotopes, sites, and months). Null hypotheses were examined using analysis of similarity (ANOSIM program), as described in Section 1.6.

Samples from 1) individual biotopes, 2) individual sites and 3) individual months of the study were tested for significant differences. In examination of differences between biotopes, data from each site were tested separately, as inter-site differences in fauna of individual biotopes may have complicated results. Global *R* values and significance levels were calculated, and pairwise tests were computed in order to establish whether there were significant differences between different pairs of biotopes. In the case of months, the global *R* value and its significance was calculated per site, however pairwise tests were not possible as the low numbers of replicates per site per month (3 to 4 biotopes) resulted in few permutations (e.g. 10 for 3 samples), under which conditions it was impossible to establish significance below 10% (Field pers. comm., Clarke and Warwick 1994). Thus, for analysis of between-month differences, samples from both sites were pooled, and a global test of *R* and pairwise tests were conducted to show differences between total fauna per month.

Associations between abiotic and biotic variables

To investigate links between biotic data and univariate environmental variables, values for each abiotic variable were represented as symbols of varying sizes (scaled according to value), and superimposed on the corresponding biotic ordination. Each the abiotic variables measured was plotted separately in this way, using the MDS program with both biotic and environmental data, as described in Section 1.4.7. The environmental variables tested were: water temperature, conductivity, dissolved oxygen, pH, discharge, depth in biotope, current speed in biotope, and percentage composition of bedrock, rock, cobble and sand in the substratum (each tested individually).

3.5 RESULTS

3.5.1 Abiotic variables

During flow months, discharge varied from 0.008m^3.s^{-1} to 0.07m^{3}s^{-1} (Table 3.1). Water temperature fluctuated between a winter low of 11.1 °C and a summer high of 26°C (Table 3.2). Dissolved oxygen values ranged from less than 20% saturation (winter POOLS) to over 100% saturation (generally during FLOW phases). Conductivity varied between 16 and 47mS.m^{-1}, and pH was circumneutral, ranging from 6.7 to 7.4 (Table 3.2).

Table 3.1 Details of hydrological phases and biotopes sampled over the study.

Month	Hydro. phase	Biotopes sampled Upper site *	Biotopes sampled Lower site
JUL 94	POOLS	mv,sooc,sand	mv,sooc,sand
AUG 94	ONSET	mv,sic,sooc	mv,sic,sooc
SEP 94	FLOW	mv,sooc,sand,drg	mv,sooc,sand
OCT 94	FLOW	mv,sooc,sand,drg	mv,sooc,sand
NOV 94	POOL	drg,pool	mv,sooc,sand
DEC 94	POOL	drg,pool	drg,pool
JAN 95	ONSET	mv,sic,sooc	mv,sic,sooc
FEB 95	FLOW	mv,sic,sooc	mv,sic,sooc

*mv=marginal veg., sooc=stones-out-of-current, sic=stones in current, drg=drying, pool=whole pool

Table 3.2 Physico-chemical conditions in the river over the study period.

MONTH	HYDRO. PHASE	TEMPERATURE (°C)		DISSOLVED OXYGEN (%)		EC (mS/m)		pH	
Site:	Both	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
JUL 94	POOL	16.1	11.1	18	12	16.1	43.2	7.1	6.8
AUG 94	ONSET	13.3	14.4	25	93	37.1	38.0	6.8	6.9
SEP 94	LOW FLOW	14.3	14.2	60	100	35.0	40.0	7.3	7.3
OCT 94	LOW FLOW	17.0	18.0	90	125	33.8	42.3	7.3	6.7
NOV 94	NO FLOW	15.4	16.0	85	118	46.4	47.0	6.9	7.0
DEC 94	POOLS	16.9	19.2	71	112	36.2	50.3	7.2	7.3
JAN 95	ONSET	22.3	26.0	124	102	27.9	30.9	7.1	7.1
FEB 95	FLOW	21.3	21.9	102	120	28.3	30.5	7.4	7.4

3.5.2 Invertebrate diversity

Number of taxa and taxonomic composition varied widely at the different spatial and temporal levels of investigation (Tables 3.3, 3.4). Altogether, over 200 taxa were identified in the upper Kowie River over the period of the study (Table 3.4). Abundances were generally low, with less than ten individuals of a taxon occurring in a sample. Total number of taxa collected in a month varied from 13 to 53, with the greatest number occurring at the upper site UK1 during the second month of flow in September, and the least at the upper site during the winter POOLS phase of July 1994. Month by month changes in diversity are reported in the following section.

3.5.3 Faunal composition in individual months and biotopes

The fauna collected at each of the sites is discussed on a month-to-month, and biotope-to-biotope basis in this section. While some statistical results are included, it is chiefly descriptive in nature and somewhat extensive and arduous (!), but serves to fulfil one of the major aims of this thesis, the documentation of the invertebrate fauna of the upper Kowie River. The information reported here is also *discussed* at some length in Section 3.6.3. Results of statistical analyses are presented in following sections.

Individual months:

July (winter POOLS)

During July, water temperatures were low and oxygen saturation was below 20% at both sites. Salinity was particulary low at UK1 (Table 3.1). The three biotopes sampled at UK1 during July (MV, SOOC, SAND) yielded a total of 13 taxa, the majority of which were found in MV. These included hydracarina, *Anisops* sp. adult notonectids, *Leptocerus* sp. leptocerids, gyrinids, tabanids, and chironomids (Appendix 3.1). Chironomid genera collected were generally common inhabitants of standing or slow-flowing water (e.g. *Polypedilum, Procladius, Chironomus*).

Table 3.3 Number of 'equivalent taxa' (*sensu* King and Tharme 1994) collected in individual biotopes each month over the period of the study.

Month	Biotope	Total Taxa	
		Upper	Lower
JUL. 1994	MV	9	16
POOLS	SOOC	6	18
	SAND	5	8
	TOTAL	*13*	*32*
AUG. 1994	MV	13	19
ONSET	SIC	10	5
	SOOC	4	2
	TOTAL	*23*	*24*
SEP. 1994	MV	12	14
LOW-FLOW	SOOC	20	8
	SAND	11	26
	DRG	33	
	TOTAL	*53*	*40*
OCT. 1994	MV	14	27
LOW-FLOW	SOOC	19	7
	SAND	18	13
	DRG	6	
	TOTAL	*45*	*40*
NOV. 1994	MV		32
NO-FLOW	SOOC		23
	SAND		10
	DRG	4	
	DRG	6	
	POOL	32	
	TOTAL	*38*	*53*
DEC. 1994	DRG	7	24
POOLS	POOL	11	20
	POOL	13	21
	POOL	8	
	TOTAL	*25*	*41*
JAN. 1994	MV	24	27
ONSET	SIC	5	19
	SOOC	9	5
	TOTAL	*34*	*42*
FEB. 1994	MV	22	25
FLOW	SIC	11	19
	SOOC	17	20
	TOTAL	*37*	*46*

Table 3.4 Shade matrix showing the taxa which contributed to the majority of similarity in each of the nine groups, as determined by SIMPER. Taxa which contributed to up to 95% of similarity in each of the groups. Abundances of taxa in the various samples are marked as '1' (1-10), '2' (11-100), or '3' (101-1000). Taxa contributing to group similarity are shaded.

Family	Subfamily	Genus / species	Gp1		Gp2			G2	Gp3		Group 4							Group 5													Gp 6		Group 7							Group 8									Group 9					
		No. of samples in group:	2		3			1	2		7							13													2		7							9									6					
Chironomid pupa		*Cricotopus pupa*		1																																																		
Chironomidae	Orthocladiinae	Krenosmittia sp.		1																																																	
Chironomidae	Tanytarsini	"Other" Tanytarsini	1	2	1	1	1					1		1				1	1		1	2	2	2					2	2							1	1			2	1													
Chironomidae	Tanypodinae	"Other" Tanypodinae			1		1	1	1		1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1		2	2			1					2	1		2									1				
Veliidae		*Microvelia sp.*							1	1								1															1	1	1	1			1		1													
Ostracoda		"Other" Ostracoda	1					1		1							1									2				1					2		2		1				1											
Chironomidae	Orthocladiinae	*Limnophyes natalensis*		2								1	1		1		1																																				
Baetidae		*Afroptilium pulchrum*											1		1							1																															
Gyrinidae		*Dineutus grossus*									1			1					1											1				1								1												
Chironomidae	Tanypodinae	*Ablabesmyia sp*												1	1	1											1													1	2													
Chironomidae	Chironomini	*Polypedilum sp.*					1		1	2	1	1	1		1	1	3	1	1	1	1	1	2	2			2	1	2	2	1					1	2	1	1	1	2	1	2	1	1	1	1			1		1	1	1
Chironomidae	Tanypodinae	*Procladius sp*									1		2	1	2	1		1	1	1			2	1													2			2	2	1	1	1		1		2						
Tipulidae						1					1									1			1	1			1			1								1							1			1						
Dytiscidae		*Philaccolus lineatoguttatus*										1						1					1			1						1			1																			1	
Chironomidae	Chironomini	Other chironomini																1	2			2			1	2			2	1									1																
Chironomidae	Diamesinae	*Harrisonina petricola*																1		1																																	
Simuliidae		*Simulium nigritarse*																	1		2																																
Simuliidae		*Simulium hargrimedusae*																				1		2																													
Chironomidae	Orthocladiinae	Other orthocladiinae	2	1				1											1		2	2	1	1	2	1		2		2		2																						
Chironomidae	Tanytarsini	*Rheotanytarsus sp.*	2							1								3	2	1	3	1	1	2	1	1	1	2	1	1						1		1													1		
Copepoda		Copepoda																								1		1		1	1	1			2	1	1	1			1	1				1					1		
Hydracarina		Hydracarina	1	1																1							2			2						1	1	1	1											1				
Dytiscidae		*Laccophilus lineatus*			1							1						2				1	1			1						1	1	1	1	2	1	1	1	1		1		1	1			1						
Libellulidae		*Orthetrum sp*															1		1			1												1		1				1		1		1	1	1			1			1
Hydroptilidae		*Oxyethira sp.*	1																			1	2									1	1	1	1				1													
Belostomatidae		*Diplonychus capensis*																1													1			1	1	1	1															
Cladocera		Cladocera																									1				1	1	1		1											1						
Corduliidae		*Syncordulia sp.?*									1																				1		1		1																	
Hydrometridae		*Hydrometra ambulator*																														1	1	1			1			1												
Lymnaeidae		*Lymnaea columella*						1																							1	1	2	1	1		2				1										
Coenagrionidae		*Pseudagrion sp.*	1																													1			1							1				1						
Corixidae		*Micronecta sp.*																			1								1			1	1						1	1													
Culicidae		*Anopheles sp.*		1				1														1								1	1		1		1	1		1			1	1	1		1	1							
Dytiscidae		Other larvae	1																		1				2					2	1							1			1		1		1								
Notonectidae		*Anisops sp.*								1											1								1			1	1			1	1	1	1	1	1					1	1						
Ostracoda		*Paracypretta syngramma*																															2										3		1						1
Caenidae		*Austrocaenis sp.*																									1								1				1		1	1		1		2						
Gomphidae		*Notogomphus sp.*																									1					1							1	1		1	1				1						
Chlorolestidae		*Chlorolestes sp.*																			1													1						1	1	1			1							
Corixidae		*Sigara sp.*																	1		1								1							1		1				1											
Chironomidae	Tanypodinae	*Clinotanypus sp*																																				1	2		1	1	1									
Chironomidae	Tanytarsini	*Tanytarsus sp.*														1	1		1			1	2			1			1							1		1	1	1	1	1	1	1	1		1	1					
Chaoboridae		*Chaoborus sp.*																											1											1				1	1							
Baetidae		*Baetis harrisoni*	1																																					1		1		1	1	1						
Coenagrionidae		*Enallagma sp*																																						1		1				1						
Corixidae		*Sigara meridionalis*																																	1					1		1				1						
Sphaeriidae		*Pisidium sp.*																																						1	1	1	1	1	1		1					
Dytiscidae		*Copelatus sp.*									1					1														1										1			1			1						
Annelida		Oligochaeta																	1																			1			1		1			2	1	1	1	1	1	1
Planorbidae		*Ceratophallus sp.*																	1											1	1			1	1		2	1				1	1	1			1				1		1
Ceratopogonidae		*near Bezzia*										1		1					1			1	1		1		1		1							1				1		1		1			1	1	1	1		1	
Dytiscidae		Other dytiscids															1							1						1	1	1	1																1	1				

At UK2, 32 taxa were collected, of which 18 were found in SOOC and 16 in MV (Table 3.3). The assemblage at this site included developing *Afroptilum* sp. baetids, *Anax* sp. aeshnids, *Notogomphus* sp. gomphids, adult hemiptera (*Diplonychus, Anisops, Micronecta* spp.), dytiscid and hydrophilid adults, and lymnaeid snails (*Lymnaea columella*). Chironomid taxa similar to those found at UK1 were collected (Appendix 3.1).

August (ONSET)

Flow recommenced during August. Oxygen concentrations were elevated at both sites, though only to 25% at UK1 (Table 3.2). An increase in number of taxa was recorded at UK1 (13 to 23) and a decrease at UK2 (32 to 24; Table 3.3). At the upper site, colonists included adult dytiscids and hydrophilids, which were usually collected in areas out of direct flow. The chironomid pupae in the samples had the effect of increasing total number of taxa at the upper site, as pupae representing different genera were recorded as separate taxa. Several of the chironomid genera which had been present in July (e.g. *Ablabesmyia, Procladius, Larsia*) were absent, although some reappeared in subsequent months during low flow or no flow conditions (Appendix 3.1).

At the lower site, MV yielded 19 taxa and SIC only 5 (Table 3.3). Taxa absent from UK2 samples included oligochaetes, *Afroptilum pulchrum* baetids, corduliid and gomphid dragonfly nymphs, ecnomid trichopterans, dytiscids, ceratopogonids, and several chironomid genera (e.g. *Polypedilum, Ablabesmyia, Clinotanypus, Procladius, Chironomus, Cryptochironomus*).

September and October (low FLOW)

Faunal diversity increased substantially at both sites during the spring month of September, when flow was slightly reduced relative to that of August (Tables 3.1, 3.3). The highest number of taxa were recorded at UK1, where 53 taxa were collected in contrast to the 23 of the previous month. At UK2, total numbers of taxa rose from 24 to 40 (Table 3.3). Oxygen saturation increased to 60% at UK1 and to 100% at UK2, and all other abiotic variables measured remained fairly stable (Table 3.2).

Flow was slightly raised by the time of sampling in October, the third consecutive summer month of flow (Table 3.1). Oxygen concentrations were close to 100% at both sites, and water temperature had increased to around 17°C (Table 3.2). During this month, total taxa decreased slighly at the upper site (from 53 to 45) and remained stable at the lower site.

Over these two months of stable summer low-flow conditions, the juvenile stages of adult colonists such as mayflies, damselflies, dragonflies, and dytiscids were collected at the lower site (Appendix 3.1). At the upper site, the immature stages of most of these groups of insects appeared only during November (Appendix 3.1). Corixids, hydrometrids, gerrids, and veliids were common occupants of the upper river from September onwards, particularly in areas out of flow. *Oxyethira* sp. hydroptilids and *Leptocerus* sp. leptocerids were collected at UK1, and *Dyschimus ensifer* pisullid trichoptera occurred at both sites. Coleoptera were chiefly represented by dytiscid adults and larvae, with hydrophilids appearing in greater numbers during November and December.

November (NO FLOW)

Flow ceased early in November and by the time of sampling, few pools remained at the upper site. Salinity was slightly elevated at both sites, but was still below $50mS.m^{-1}$, and oxygen saturation remained close to 100% (Table 3.2). At the upper site UK1, only drying substrata (DRG) and isolated, shallow pools (POOL) could be sampled, as the rapid loss of surface water had resulted in the drying of MV and areas of stones and cobbles. The reduction in total taxa was slight (45 to 38). Baetid nymphs were collected for the first time in this study at this site, in POOL samples. Taxa which were absent from included hydracarinids, *Oxyethira* sp. and *Leptocerus* sp. trichopterans, *Sigara* sp. corixids, and several chironomid genera (Appendix 3.1).

At the lower site, loss of surface water was more gradual because of the large volume of the single pool that remained after flow cessation (Plate 3.6). SOOC, SAND and MV were sampled. The total number of taxa had increased to 53 from the previous month's yield of 40. Additional animals included ostracods, oligochaetes, baetid and caenid nymphs, *Macromia* sp. corduliids, *Orthetrum* sp.

libellulids, corixid and notonectid genera, dytiscid and hydrophilid adults and larvae, gyrinids, chaoborids, certain orthoclad and tanypod chironomids, and several gastropods which had not been previously collected at the site (*Ferissia* sp. ancylids, *Bulinus forskalii* physids and *Pisidium* sp. sphaeriids; Appendix 3.1).

December (POOLS)

High midsummer air temperatures caused substantial evaporation of surface water, and by mid-December, all pools were substantially reduced in volume. Dissolved oxygen had decreased to 71% at the upper site, but was maintained at over 100% at the lower site where there was prominent algal growth. Water temperature was raised at the lower site, but pH remained close to neutral. The highest conductivity for the study (50.3mS.m^{-1}) was recorded at UK2 (Table 3.2).

Biotope diversity had diminished at both sites such that only full pools (POOLS) and fringing drying areas (DRG) could be sampled. Pools were shallow, and their bedrock or sandy substrata were overlain with plentiful organic matter. Oxygenation occurred as a result of surface air movement and algal photosynthesis, particularly at the lower site.

Despite the stability in abiotic conditions, total numbers of taxa decreased from 38 to 25 at the upper site and from 53 to 41 at the lower site. Upper site samples yielded microcrustaceans, crabs, hardy mayfly nymphs (*Baetis harrisoni*, *Afrocaenis* sp.), libellulid dragonfly nymphs (*Orthetrum* sp.), a few chironomid genera (*Procladius*, *Polypedilum*, *Tanytarsus*), culicids, and mollusc genera (*Burnupia*, *Ceratophallus* and *Pisidium*). Adult coleoptera were absent and hemiptera were represented only by corixids (*Arctocorisa meridionalis*).

Most of these taxa occurred at the lower site, where additional animals included oligochaetes, gomphid dragonfly nymphs (*Notogomphus* sp.), damselfy nymphs (*Pseudagrion* sp., *Ennallagma* sp., *Chlorolestes* sp.), notonectid hemiptera (*Anisops* sp.), ecnomid trichoptera, dytiscid genera (*Copelatus*, *Hyphydrus*, *Laccophilus*), hydrophilid adults and larvae; chironomid, ceratopogonid, tabanid, tipulid and chaoborid larvae, and *Ferissia* sp. limpets.

January (ONSET) and February (FLOW)

Sampling occurred in early January, approximately two weeks after major rains had caused recommencement of flow in the upper river. Highest discharge values for the study were recorded (Table 3.1). Water temperatures and dissolved oxygen were high, and conductivity had decreased somewhat at both sites (Table 3.2). Faunal diversity in early January was raised relative to that of December. Numbers of taxa and faunal composition remained relatively constant, however, over January and February (Table 3.3, Appendix 3.1), which were characterised by stable flow.

In January, *Cloeon* sp. baetids were collected for the first time during the study. *Notogomphus* sp. gomphids and *Ennallagma* sp. coenagriids, which had been collected during December, were absent. The diamesid chironomid, *Harrisonina petricola*, which has only been collected in temporary mountain streams (Harrison 1978), were only collected during this and a previous ONSET phase. Chironomini were represented only by *Polypedilum* and *Zavreliella* species, however large numbers of *Rheotanytarsus* sp. were collected in the SIC biotope in both January and February. Several Orthocladiinae and Tanypodinae were also collected (Appendix 3.1). Snails were absent from the upper site, but ancylids, lymnaeids, physids and planorbids were collected at the lower site, mostly in MV.

Individual biotopes:

Marginal vegetation (MV)

Up to 24 taxa were collected in MV at UK1, and up to 32 at UK2 (Table 3.3). Typical residents of MV included copepods, ostracods, *Leptocerus* caddis, hemipterans, dytiscid adults and larvae, chironomids and molluscs (Appendix 3.1). During the first three months of the study (late winter to early summer, under POOLS, ONSET and FLOW conditions), other taxa collected included hydracarinids, corduliid dragonflies and chlorolestids damselfly nymphs and hydroptilid caddisflies. During the summer months of October, November, January and February, fauna common to samples included cladocerans, hydrophilid beetles, *Laccophilus* sp. dytiscids, and *Microvelia* sp. veliids.

Stones in current (SIC)

This biotope was sampled only during ONSET and early FLOW phases. It occupied a small area at both sites (see Figs. 3.2 and 3.3), and was 'ephemeral' in nature due to erratic and often low flow. Generally, less than 20 taxa were collected in SIC (Table 3.3). Common taxa in SIC during stable flow months included baetid mayflies (*Baetis* sp.), chironomids (Tanypodinae and *Polypedilum*, high abundances of *Rheotanytarsus*), and simuliids (*Simulium adersi*). Other regular occupants of the SIC biotope were ostracods, *Potamonautes* sp. crabs, hydracarinids, corixids, and various chironomids.

Stones-out-of-current (SOOC)

Again, large variance was recorded in number of taxa collected in this biotope over the study (Table 3.3). Common taxa in SOOC samples included ceratopogonids (*Bezzia* sp.) and chironomid genera. Less common animals included oligochaetes, microcrustacea, crabs, mayflies (*Afroptilum pulchrum*, *Cloeon* sp. during low-flow), developing *Notogomphus* sp. gomphids and *Chlorolestes* sp. chlorolestids, corixids, gerrids, veliids and notonectids, *Ecnomus* sp. and *Oxethira* sp. trichopterans, dytiscids, culicids, tipulids, and *Bulinus forskalii* and *Ceratophallus* sp. gastropods (Appendix 3.1).

Sandy substrata (SAND)

Commonly, less than 20 taxa were recorded in the SAND samples (Table 3.3), and these were commonly dominated by chironomids. Other taxa collected in SAND included microcrustaceans, hydracarinids, *Afroptilum* sp., *Baetis* sp. and *Austrocaenis* sp. mayflies, *Syncordulia* sp. corduliids, *Notogomphus* sp. gomphids, dytiscid larvae, hydrophilid adults and larvae, and tipulid larvae. Abundances were low for all taxa except chironomids. Predaceous *Polypedilum* spp., which are morphologically adapted to burrowing in shifting sand, were numerically dominant (>100 individuals) in all but one sample.

Drying substrata (DRG)

Material from the drying fringes of the river or pools (DRG) was only sampled following flow cessation in November and December (Table 3.3). Where the biotope was largely dry, few taxa and only one or two individuals per taxon were collected, e.g. between 4 and 8 at UK1. However, when DRG was sampled in areas which were still damp, or in which water content was high, as during December, many taxa were collected (24 at UK2; Table 3.3). The greatest number of taxa (33) was, however collected at UK1 in September, when drying areas adjacent to the wetted channel (in which there was low flow) still had a high water content. Taxa collected in damp samples included ostracods, hydracrinids, collembolans, several dragonflies including *Notogomphus* sp. and *Orthetrum* sp., few corixids and notonectids (possibly stranded), adult and larval dytiscids, ceratopogonids, chaoborids, several hydrophilid larvae, tipulids, and abundant chironomids. Drier samples were generally dominated by chironomids, but *Laccophilus lineatus* and *Philaccolus lineatoguttatus* dytiscids, ceratopogonids, culicids, *Ferrissia* sp., *Ceratophallus* sp. and *Lymnaea columella* and *Pisidium* sp. molluscs were also found in small numbers in samples.

3.5.4 Cluster analysis of samples from individual biotopes

Hierarchical agglomerative cluster analysis based on the similarities between samples from all biotopes indicated generally low similarity between different samples, with major clusters forming below 40% (Fig. 3.5). A line was drawn at the point of 20% similarity, for the purposes of describing groups of samples and for checking the adequacy of the clustering, as described in Section 1.4.3. Clusters to the right of the line were labelled Groups 1 to 9. The invertebrates responsible for the majority of similarity in a group were calculated in the program SIMPER (Table 3.4).

Group 1 comprised only SIC samples from flow periods. The only animal restricted to Group 1 was the orthoclad chironomid *Krenosmittia* sp. (Appendix 3.1). Group 2 comprised SIC and SOOC samples from both sites during August (ONSET). Major contributors to similarites within the group were 'Other Tanytarsini' and 'Other Tanypodinae' respectively. For reasons given in Section 1.4.5, the over-representation of these groups was expected, and their contributions to similarity were not restricted to Group 2.

Two flow samples taken in SOOC at the lower site clustered in Group 3. July, August, September and October samples from UK1 and UK2 clustered to form

Group 4, representing POOLS, ONSET and FLOW phases. The majority of samples were collected in the SAND or SOOC biotopes, with only two MV samples in the group. Fauna contributing to the majority of Group 4 similarity included the orthoclad *Limnophyes natalensis* (associated with damp soil or wet moss in streams), the baetid *Afroptilum pulchrum*, the chironomid *Ablabesmyia* sp. (Tanypodinae), and several other common chironomids (Tables 3.4, Appendix 3.1).

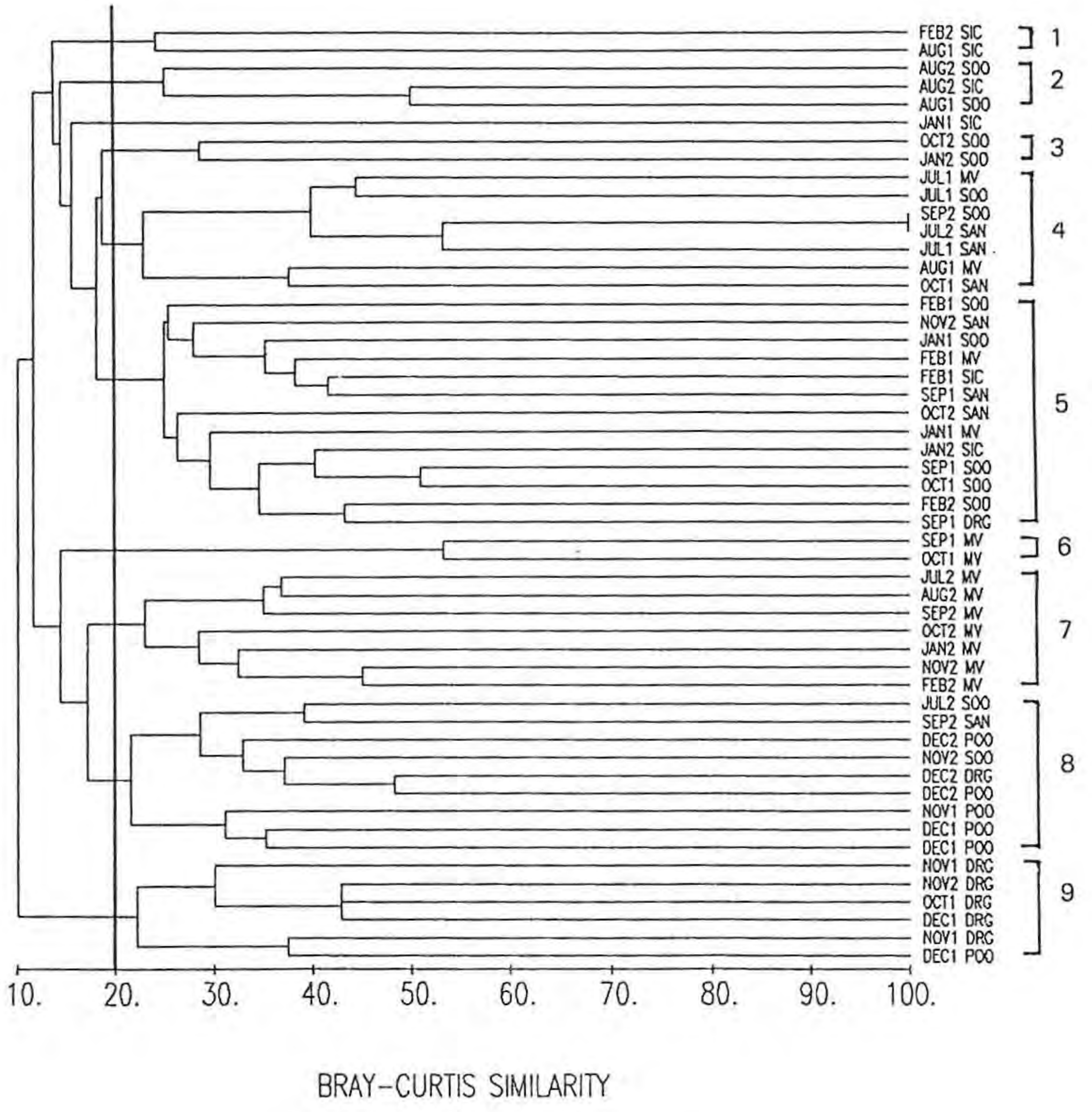


Figure 3.5 Dendrogram for hierarchical cluster analysis of monthly samples from individual biotopes for the period of the study. Samples grouping at greater than 20% similarity are labelled Groups 1-9. Abbreviations of the format: Month-site Biotope (e.g. FEB2 SOOC sample taken in February at UK2, in stones-out-of-current).

The samples in Group 5 were collected at both sites and (except one) during summer months when similar total discharge values were recorded (September, October, January, February; Table 3.1). 'Other' Orthocladiinae, 'Other' Tanypodinae, *Rheotanytarsus* sp. and *Polypedilum* sp. accounted for most of the similarity of the group. Other contributors included the diamesid chironomid *Harrisonina petricola*, 'Other' Chironomini, *Philaccolus lineatoguttatus* dytiscids, and tipulids (Table 3.4).

Two upper-site MV samples from October and November (FLOW and NO FLOW) were linked in Group 6, and the full complement of lower-site MV samples from between July and February clustered in Group 7. In the latter group, *Laccophilus lineatus* dytiscids, *Anisops* sp. notonectids, belostomatid hempiterans, copepods, cladocerans, *Polypedilum* sp. chironomids and corduliid nymphs accounted for the majority of similarity (Table 3.4). Lesser contributors included hemipterans, dystiscid and hydrophilid beetles, lymnaeid and sphaeriid snails, and libellulid and coenagriid nymphs (Table 3.4).

Group 8 included all but one of the POOL samples taken during the study, as well as individual SOOC, SAND and DRG samples. All but one sample were collected during November or December. Chironomid genera were largely responsible for the similarities in this group, with *Procladius*, *Tanytarsus*, and *Polypedilum* and *Clinotanypus* species explaining over half of similarity. *Austrocaenis* sp. mayflies, *Laccophilus lineatus* dytiscids, *Notogomphus* sp. gomphids and chaoborids accounted for a further proportion of similarity (Table 3.4).

All but one of the samples in Group 9 were collected in the damp/drying (DRG) areas fringing small pools. Most of this cluster comprised upper-site samples. Taxa which accounted for the majority of the similarity included *Polypedilum* sp. chironomids, oligochaetes, *Ceratophallus* sp. planorbids, *Bezzia* sp. ceratopogonids, 'Other' dytiscids, and *Orthetrum* sp. libellulids (Table 3.4).

3.5.5 Ordination of samples from individual biotopes

MDS ordination of the biotic data produced a high stress (0.26) two dimensional map, indicating that it could not be considered an entirely reliable representation of the relationships between samples (Clarke and Warwick 1994). It was, however, required as a template for testing the association of biotic and abiotic variables (Section 3.5.8), and was thus included here. Groupings determined on the dendrogram (Fig. 3.5) were superimposed onto the data points on the ordination. Some overlap occurred between the positions of Groups 1 to 9, as was expected with the high stress levels (Fig. 3.6).

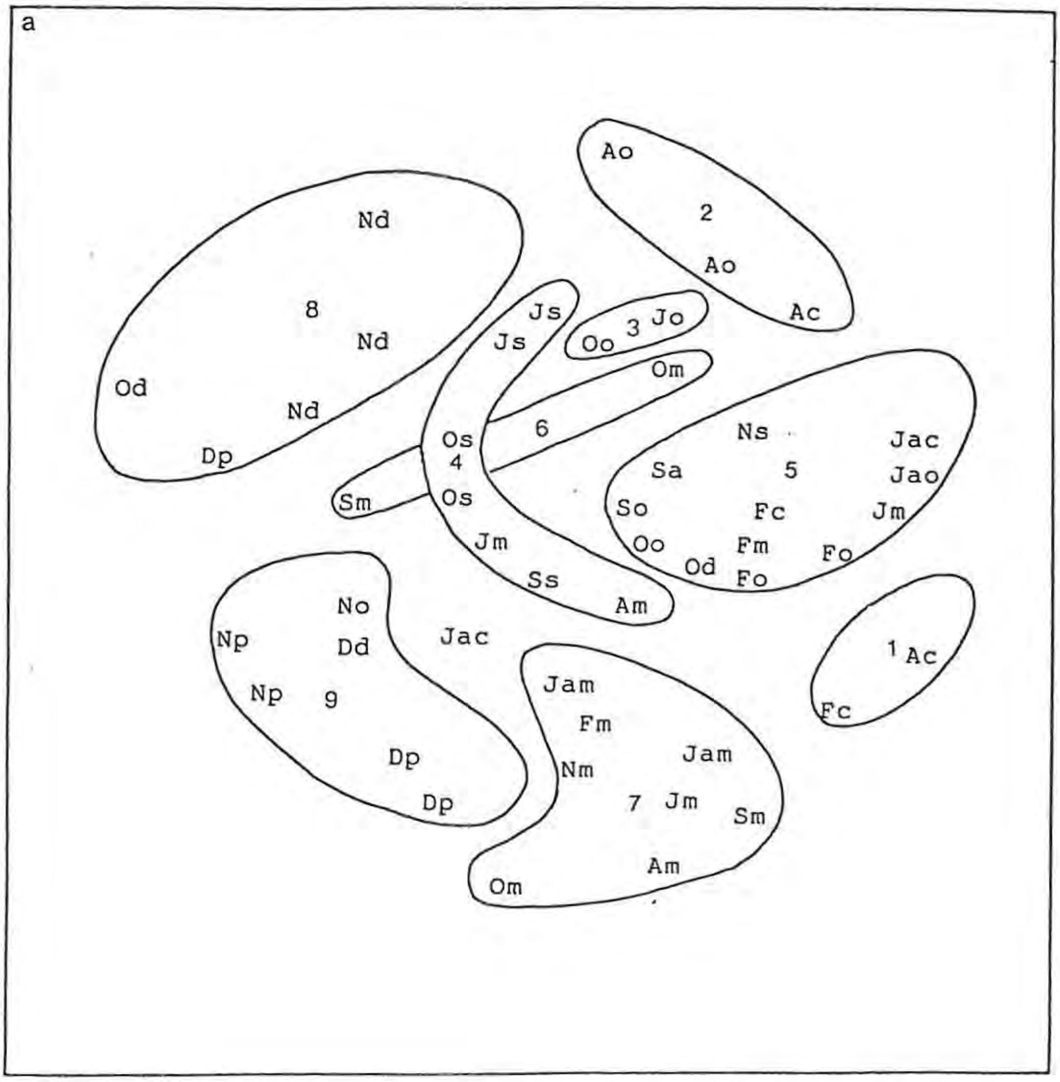
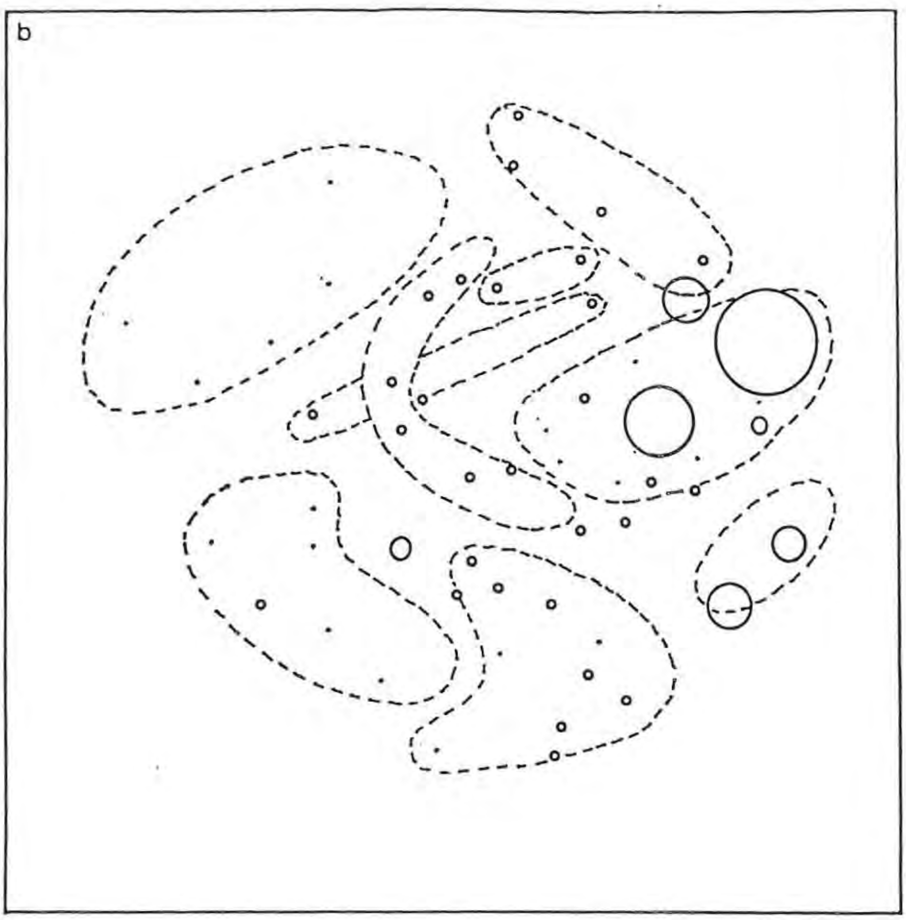
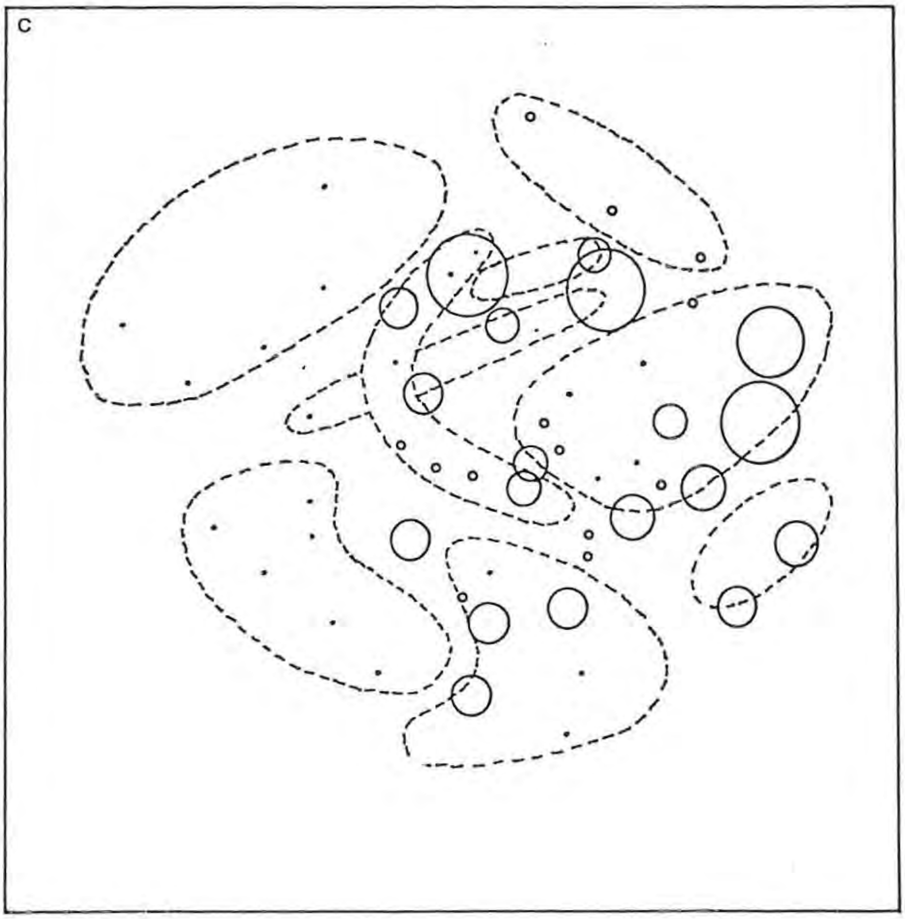


Figure 3.6 a) MDS ordination based on Bray Curtis similarities of total monthly samples for the 8 month study period. Groups 1 to 9 are superimposed and labelled. First letter: J-July, A-August, S-September, O-October, N-November, D-December, Ja-January, F-February. Second letter: M-MV, C-SIC, O-SOOC, P-POOL, D-DRG. Note the sample 'JaC' belongs to Group 5 (omitted for clarity). ***Overleaf:*** b) - c) The same MDS ordination with superimposed circles of increasing size with increasing value of b) current speed in biotope and c) % of cobbles and stones in the substratum.


b


c

3.5.6 Cluster analysis of total monthly samples

Taxa occurring in all biotopes at a site were aggregated into 'total' samples for each month, in order to check whether patterns in faunal similarities emerged at a coarser resolution. Only presence/absence data were used. Cluster analysis based on Bray Curtis similarities between samples indicated that faunal resemblances were again low, with major clusters occurring between 20% and 30%. Clusters to the right of the line drawn through the 23% similarity level were labelled Groups 1 to 3 (Fig. 3.7). The contributions of individual taxa to similarity were not determined for these data.

Group 1 represented samples from July, August and September (POOLS, ONSET and FLOW phases), all but one of which were collected at UK2. Samples from October, November and December (FLOW, NO FLOW and POOLS phases) from both sites clustered in Group 2. Fauna from UK1 and UK2 paired off for January and February in Group 3. These two couplets grouped, suggesting a relatively high overall similarity between fauna of the two months.

3.5.7 Ordination of total monthly data

Ordination of total monthly samples generated a lower-stress (0.18) two-dimensional representation of similarities than the previous ordination. When groupings discerned on the dendrogram (Fig. 3.7) were superimposed over the ordination points, Groups 1 to 3 were clearly in agreement with those formed in cluster analysis, and were positioned approximately equidistant from one another (Fig. 3.8).

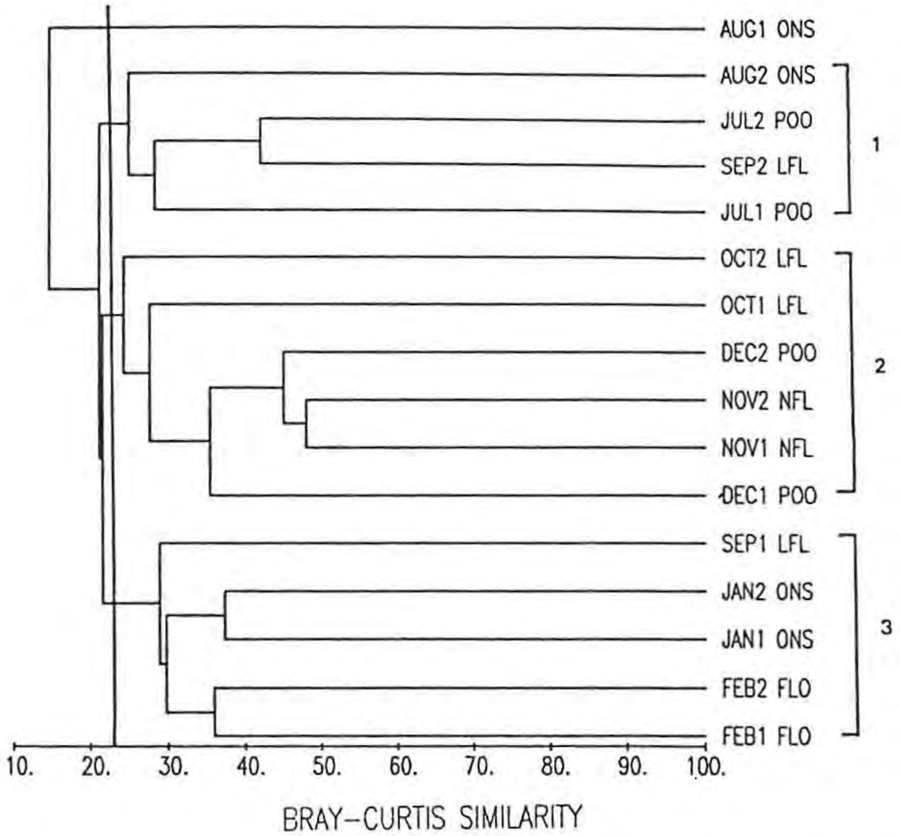


Figure 3.7 Dendrogram for hierarchical cluster analysis of total monthly samples. Groups 1-3 were discerned at over 23% similarity level. Abbreviations record month, site, and hydrological phase (e.g. 'Aug2 ONSET' refers to total sample from August at UK2, during the ONSET phase).

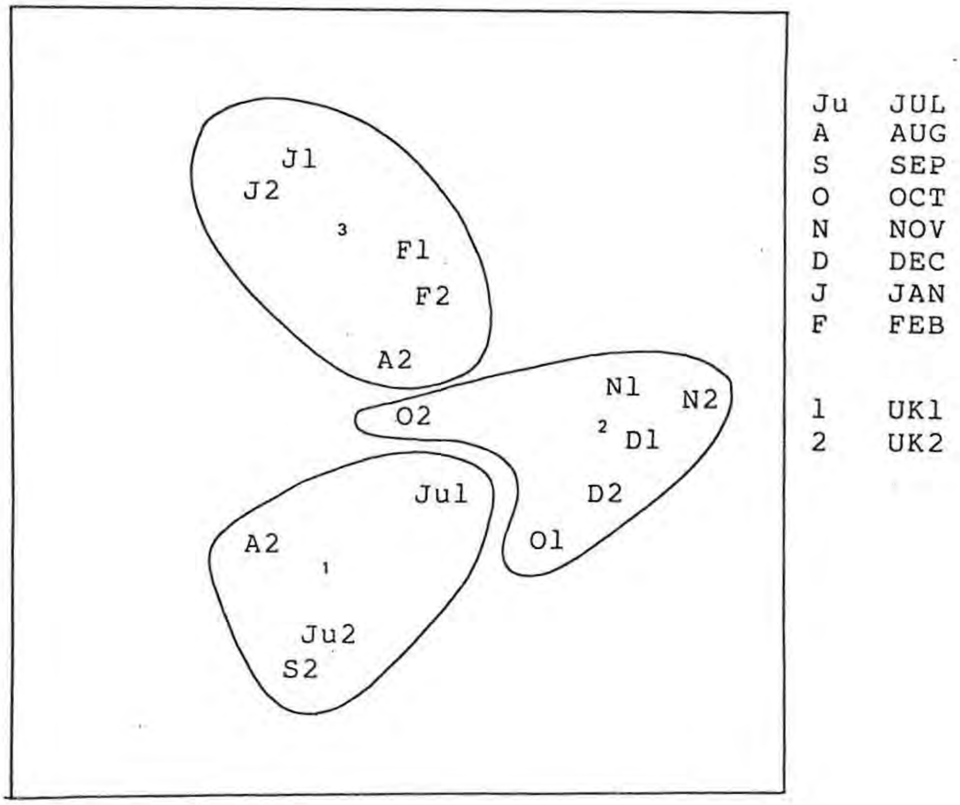


Figure 3.8 MDS ordination of total monthly samples (Stress = 0.18), showing the relative positions of Groups 1 - 3.

3.5.8 Testing of null hypotheses with analysis of similarity

Faunal differences between biotopes at the upper site UK1

This analysis generated a global *R* of 0.35, at a significance level of 0.0%, at which the null hypothesis of 'no differences between biotopes' could be rejected. This indicated that there were significant faunal differences between at least some of the biotopes. Pairwise tests indicated which biotopes differed significantly in terms of their fauna (Table 3.5).

Table 3.5 Results of pairwise tests in the ANOSIM of fauna from different biotopes at the upper site, UK1. The R value and significance value (%) for each pair of biotopes is given. Sites which were significantly different in terms of their fauna are highlighted. SOC - stones out of current, SND - sand.

	MV	SIC	SOC	SND	POOL
SIC	**0.56** **1.2**				
SOOC	0.13 16.9	0.09 34.5			
SAND	0.05 34.5	0.59 10*	0.04 7.1		
POOL	0.14 20	**1.0** **2.9**	**0.55** **0.5**	**0.84** **2.9**	
DRG	**0.4** **1.7**	**0.71** **1.8**	**0.35** **2.8**	0.32 12.5	**0.54** **2.4**

* Due to low numbers of samples for one or both of these biotopes, only 10 permutations were possible in this test, so that the smallest significance level possible was 10%, and the null hypothesis could only be rejected at 10% (Clarke and Warwick 1994).

Faunal differences between biotopes at lower site UK2

The global *R* generated was 0.295, at a significance level of 0.3%. Thus the null hypothesis of 'no difference between biotopes' could be rejected for UK2. Pairwise tests indicated which biotopes differed significantly (Table 3.6).

Faunal differences between months at UK1 and UK2

The global R generated in this ANOSIM was 0.352, and the significance level 0%. This nullified the H_0 of 'no differences between fauna of different months'. The results of pairwise tests are given in Table 3.8.

Table 3.6 Results of pairwise tests in the ANOSIM of fauna from different biotopes at the lower site, UK2. The R value and significance value (%) for each pair of biotopes is given. Sites which were significantly different in terms of their fauna are highlighted. SOC - stones out of current, SND - sand.

	MV	SIC	SOC	SND	POOL
SIC	**0.57** **0.8**				
SOOC	**0.37** **0.1**	0.06 30			
SAND	**0.81** **0.3**	0.29 8.6*	-0.13 80		
POOL	**0.58** **2.8**	-0.04 60	-0.07 50	0.5 6.7	
DRG	**0.66** **2.8**	-0.83 70	-0.02 44	0.66 6.7	-0.5 100

* *Due to low numbers of samples for one or both of these biotopes, only 10 permutations were possible in these tests, and the smallest significance level possible was 10%. Thus in these pairs the null hypothesis could only be rejected at 10% significance (Clarke and Warwick 1994).*

3.5.9 Association of abiotic and biotic variables

Several of the abiotic variables measured (e.g. current speed, depth, substratum type) were specific to particular biotopes and sampling dates, and could not be averaged for the site. It was thus necessary to use samples from individual biotopes (rather than total monthly samples), for all eight months, to test for correlations between abiotic and biotic variables. Thus the ordination of 'all samples' (Fig. 3.6a) formed the template for the superimposition of abiotic data.

Table 3.8 Results of pairwise tests in the ANOSIM of fauna from different months at both sites, where global $R = 0.352$, at a significance level of 0%. The R value and significance value (%) for each pair of biotopes is given. First site in each of the pairs is underlined. Sites which were significantly different in terms of their fauna are highlighted. (Triangular matrix not used in presentation due to number of samples).

SAMPLE PAIR		PHASES	R	SIGNIFICANCE %
JULY,	**AUGUST**	**POOLS, ONSET**	**0.43**	**1.1**
	SEPTEMBER	FLOW	0.130	11.2
	OCTOBER	**FLOW**	**0.28**	**1.9**
	NOVEMBER	**NO FLOW**	**0.42**	**0.5**
	DECEMBER	**POOLS**	**0.53**	**0.1**
	JANUARY	**ONSET**	**0.34**	**1.7**
	FEBRUARY	**FLOW**	**0.81**	**0.2**
AUG.,	**SEPTEMBER**	**ONSET, FLOW**	**0.22**	**4.1**
	OCTOBER	**FLOW**	**0.36**	**0.9**
	NOVEMBER	**NO FLOW**	**0.66**	**0.1**
	DECEMBER	**POOLS**	**0.76**	**0.1**
	JANUARY	**ONSET**	**0.44**	**0.4**
	FEBRUARY	**FLOW**	**0.76**	**0.2**
SEP.,	OCTOBER	FLOW, FLOW	0.08	18.1
	NOVEMBER	**NO FLOW**	**0.19**	**3.7**
	DECEMBER	**POOLS**	**0.33**	**0.7**
	JANUARY	ONSET	-0.003	49.5
	FEBRUARY	**FLOW**	**0.32**	**0.6**
OCT.,	NOVEMBER	FLOW, NO FLOW	0.11	15.4
	DECEMBER	**POOLS**	**0.27**	**2.4**
	JANUARY	ONSET	0.15	10.4
	FEBRUARY	**FLOW**	**0.59**	**0.1**
NOV.,	DECEMBER	NO FLOW, POOLS	-0.01	45.7
	JANUARY	**ONSET**	**0.24**	**2.7**
	FEBRUARY	**FLOW**	**0.53**	**0.2**
DEC.,	**JANUARY**	**POOLS, ONSET**	**0.35**	**0.5**
	FEBRUARY	**FLOW**	**0.85**	**0.1**
JAN.,	FEBRUARY	ONSET, FLOW	0.21	5.2

Of the 14 abiotic variables superimposed in turn on this biotic ordination (Figs. 3.6b - d), only current speed (Fig. 3.6b) and percentage distribution of stones and cobbles in the sample substratum (Fig 3.6c) showed trends in common with those of the biotic ordination. Current speed in the biotope showed a gradient from left to right in the ordination, with the position of intermediate values corresponding with Groups 4, 6 and 7 (mainly low-FLOW samples), and the maximum current speed values corresponding with the position of Group 5 (mainly FLOW samples). The gradient in percentage distribution of cobbles and stones corresponded with the positioning of Group 1 (SIC samples), Group 3 (SOOC samples) and Group 5 (flow samples from various biotopes) on the biotic ordination. Smaller proportions of cobbles and stones corresponded to the Group 8 (POOL samples) and Group 9 (DRG samples).

3.6 DISCUSSION

3.6.1 Environmental variability

The variability in timing, extent and duration of rainfall over this period was reflected in the hydrology of the upper Kowie. The occurrence of four hydrological phases, some more than once, within a period of eight months illustrated of the sort of hydrological variability commonly associated with temporary streams (e.g. Davies *et al.* 1995).

The change in character, extent, availability and heterogeneity of habitable aquatic or semi-aquatic substrata verified the views of Stanley *et al.* (1997) that *'streams are spatially dynamic systems that undergo cycles of expansion, contraction and fragmentation'* and that *'change in ecosystem size is a fundamental, defining feature, not only of desert streams, but also of all stream and river ecosystems'*.

Whereas the amplitudes in physico-chemical variables are often extreme in temporary streams (e.g. Williams 1987), and even in small streams in temperate environments (e.g. Townsend *et al.* 1987), most physical and chemical variables other than flow remained fairly stable over time. Low oxygen saturation was recorded only during two months of the study. The narrow ranges in these variables suggested that they were unlikely to exert a major influence on faunal character over time. Tests of the association between abiotic and biotic variables reflected this, with only two variables, current speed in biotope and the percentage distribution of cobbles in the substratum, showing an association with biotic form. The physical constancy of headwater streams has been commented on elsewhere (Stanford and Ward 1983), although this included reference to flow constancy.

3.6.2 Numbers of Taxa

Over two hundred taxa were identified in the upper Kowie River over the period of this study. Boulton and Lake (1992b) recorded over 250 invertebrate taxa in their study of four sites on two intermittent rivers in Australia. They commented that in comparison with the number of taxa reported from other temporary river studies (quoting, for example, Stehr and Branson 1938, Harrison 1958, 1978, Clifford 1966, Williams and Hynes 1976, 1977, Towns 1985), these assemblages were species-rich. Other studies in which species richness had been of the same order of magnitude were also quoted, e.g. Abell (1984) recorded 250 taxa, Gray (1981) recorded 104, and Wright *et al.* (1984) recorded 156. Boulton and Lake (1992b) acknowledged the hazards of comparing between studies in this way, and these problems are recognised and discussed further in Chapter 7. Nonetheless, this sort of comparative information provides at least a coarse-resolution indication that species richness in the upper Kowie River was relatively high.

While habitat stability and duration is associated with increasing diversity (e.g. Schneider and Frost 1996), disturbance in the upper Kowie - symbolised by the rate of change of hydrological phases (see 1.3.6) - resulted in a suite of different hydraulic and substratum conditions in the river over time. Each of these represented a habitable 'patch' to some element of the total fauna. Viewed at different spatial and temporal scales, the river represented a complex mosaic of conditions to which a variety of fauna may be attracted at different times. The variability underlying this 'mosaic' seemed at least in part accountable for the overall taxonomic diversity reported at these sites (e.g. Boulton and Lake 1992a).

Maintenance of species diversity is generally associated to some extent with disturbance, where disturbances are viewed as events which prevent a system from reaching equilibrium, and diversity as *'the result of a balance between the frequency of disturbances that provide opportunities for species to recolonise, and the rate of competitive exclusion, which sets the pace of species extinctions within patches'* (Petraitis *et al.* 1989). [Processes such as 'competitive exclusion' and 'species extinctions' are liable only to be factors in the late POOLS stages, where space and food are limiting factors, and predaceous fauna such as dytiscids, dragonflies, and tanypod chironomids make up a large proportion of the fauna].

Equilibrium hypotheses assume species composition to be at equilibrium and unchanging. Non-equilibrium theories operate from the premise that species composition is rarely stable, and that high diversity is maintained only when composition is continually changing (Connell 1978). The low similarities between upper Kowie River samples at all scales of analysis, and the relatively high numbers of taxa indicate that the fauna was non-equilibrial, though the notion of 'maintenance of high diversity' in such communities was only applicable over the longer term. The most suitable description of the diversity of this fauna came from Grassle and Sanders (1973), who distinguished between *'long-term, equilibrium, or evolutionarily high diversity (which is) a product of past biological interactions in physically stable, benign environments'*, and *'short-term, non-equilibrium, or transient high diversity induced by unpredictable physical or biological perturbations or stress resulting in biological "undersaturation of the environment"'*.

In rivers subject to high variability, where communities may fit the description of non-equilibrial, short-term studies are likely to provide only partial information regarding the biota. The full picture required is a time-integrated, multicomponent one, and 'mapping the mosaic' requires long-term ecological research, sufficient to accommodate hydraulic and seasonal cycles, if these are detectable. Boulton and Lake (1992b) recommend studies of up to 2 years.

3.6.3 A description of the fauna over the eight month period

As one of the major aims of this research was a description of the aquatic invertebrates inhabiting the upper Kowie River, this rather extensive and arduous section represents a deviation from discussion based on quantitative findings, and provides a qualitative account of the general character of the invertebrate fauna over the study period. Later sections deal with faunal variability at the various scales of examination, and the major factors influencing faunal character.

A month-by-month account of the fauna

During the winter month of July, pools had been present in the channel at both sites for over a month. The low number of taxa collected at the dimly-lit upper site was attributed chiefly to the low oxygen saturation (18%), and to the decreasing volume of individual pools. Most of the chironomid taxa collected were resilient to low oxygen conditions. While the cumulative effect of several months of low air temperatures could have had an adverse effect on diversity, thermal regime is one of the few factors in an aseasonal temporary river which is structured and predictable from year to year, and it is likely that biota are adapted to its fluctuations (see Sweeney 1984).

With the onset of flow in August, faunal diversity increased at the upper site and decreased at the lower site (although a similar number of taxa were collected at the two localities). During this period, certain aerial adults may have relocated to more suitable environments: this was suggested by the absence of several dytiscid and hemipteran taxa in this and subsequent FLOW samples [reflecting the preference of these groups for lentic conditions (Williams and Feltmate 1992)].

Stable low-flow conditions in the spring month of September and the early summer month of October created agreeable conditions for the arrival of aerial colonists at the lower site, where nymphs of mayflies, damselflies and dragonflies were collected. At the upper site, hatching of many of these taxa was apparently delayed until November. Harrison (1978), working in a seasonal, temporary South African stream, reported that juvenile ephemeropterans, odonates, trichopterans and dipterans were generally derived from eggs laid by adults soon after flow resumption. While this corresponded with our findings, resumption of flow in the Kowie River was not necessarily into a dry channel, and eggs or juveniles may have already been present in pools.

Representatives of hemipteran families which favour fringe habitats or quieter waters (corixids, hydrometrids, gerrids, veliids) were common in marginal vegetation from September onwards, during low flow. Stehr and Branson (1938), studying an intermittent stream in Ohio, also reported that these families built up their populations during the spring months. Hydrophilid beetles, which generally prefer quiet waters (McCafferty 1981), were noticeably sparse until the NO-FLOW and POOLS phases of November and December.

During November, flow cessation and high summer temperatures resulted the exposure of MV, SOOC and SAND at the upper site. Decrease in faunal diversity was attributed to the loss of flow, and at least in part, to contraction of available habitat. At the lower site, the persistence of water in MV over several months was associated with a relatively persistent (stable) fauna, and steadily increasing diversity, which was maximised in November. Additional fauna collected at this site were chiefly those favouring standing water or pond-type environments (Williams and Feltmate 1992, McCafferty 1984).

By the time of sampling in December, pool size had diminished further, and no MV was available for sampling at the lower site. The lack of gyrinids and other surface-dwelling taxa (e.g. gerrids, veliids, hydrometrids) at both sites may have been partially attributable to this reduction in biotope, but may also have been a sampling artifact - these highly mobile, air-breathing taxa were generally observed close to, if not at, both sites during POOLS phases. *Ferrissia* sp. limpets, which are characteristic of stagnant waters and capable of modifying their shell in anticipation of a need to aestivate (Brown 1980), were collected at the lower site during December.

During the midsummer month of January 1995, when flow had resumed, *Cloeon* sp. baetids were collected for the first time in this study. As these were not early instars they may have been transported to the site in drift. The diamesid chironomid, *Harrisonina petricola*, which inhabits temporary mountain streams (Harrison unpubl.), appeared in lower-site samples during this and a previous ONSET phase only. These chironomids are not commonly found, and have only been collected in intermittent streams close to the source, in clean water flowig over bedrock, as they were in this study. That they were found only during ONSET may indicate that they were transported to the site in drift, or may that they were outcompeted by other biota with increasing duration of flow. Chironomini were represented only by *Polypedilum* spp. and *Zavreliella* sp. Large numbers of *Rheotanytarsus* sp., which are common inhabitants of running waters, were found in the SIC biotope in both January and February. Other Tanytarsini found only during January and February were *Stempellinella* sp. which are only recorded from other Eastern Cape streams in Harrison's (Website) checklist of Southern African chironomids.

Several of the Orthocladiinae and Tanypodinae associated with slow-flowing or running water were present in January and February samples. The absence of molluscs from the upper site during this period may have been related to the preference of many of these families for quiet-water environments which were lacking at this site during flow. At the lower site, the plentiful marginal vegetation provided this sort of 'lentic' environment.

Fauna of individual biotopes

Stones in current (SIC)

Typical SIC taxa included simuliids (*Simulium adersi*), baetid mayflies (*Baetis* spp.) which cope well with currents (Williams and Feltmate 1992), and chironomids (Tanypodinae, *Polypedilum spp.*, large numbers of *Rheotanytarsus sp.* and Orthocladiinae). Harrison (1978), reporting on faunal succession in a seasonal intermittent stream in the Western Cape, South Africa, noted that soon after onset of flow the community was dominated by *Simulium ruficorne*, which was replaced during the course of winter by *Simulium adersi*. The absence of this type of 'simple succession' was conspicuous in the Kowie River, and could possibly be attributed to the *aseasonality* of flow in this section of the river.

No stoneflies were collected in this or any other biotope during this eight month period, and during the full study, few were collected, despite conditions favourable to them [stony substrata in cool, well-oxygenated water (McCafferty 1981)]. Williams (1996) also commented on the scarcity of this group in temporary waters, and noted that stoneflies seem less able to dealt with standing water conditions than with drought, and survive drought only in running water habitats. Active stonefly larvae cannot withstand desiccation (Hynes 1976) which is a constant threat in an aseasonal intermittent river. Plecoptera are not, however, absent from intermittent rivers by any means - Boulton and Lake (1992c) listed this group as relatively 'species rich' in seasonal intermittent Australian streams.

Hydropsychid trichopterans were also absent from SIC samples during the study period. A few individuals were collected in MV only during February when flow was stable (Appendix 3.1), and in low numbers at other times (usually late summer flow periods). Harrison (1978) remarked on the 'conspicuous absence' of this family in temporary streams in the Western Cape, and the family was not included in the taxonomic list for the Australian intermittent streams studied by Boulton and Lake (1992).

Stones out of current (SOOC)

The arbitary grouping and lack of faunal cohesion between SOOC samples reflected the changing character of this biotope over time. For instance, areas sampled as SOOC during low flows may have been sampled as SIC during raised flows. With adequate flow, interstices between stones or cobbles are kept relatively clear by the action of the current. As flow slows, silt and organic matter is deposited in interstices, creating new microhabitats. Following flow cessation, epilithic algal growth and further accumulation of detritus in and around these areas again altered the character of the microenvironment, providing ample shelter and food resources.

Following flow cessation, invertebrates tended to relocate to suitable refugia: the appeal of the SOOC environment to invertebrates was evident during November (NO-FLOW), when numbers of taxa inhabiting SOOC tripled relative to those of October. The presence of *Rheotanytarsus* sp. filter-feeding tanytarsines commonly associated with running water, was probably due to their abundance in this area during flow. *Ablabesmyia* sp., which - unlike other Tanypodinae - are generally associated with lotic conditions, was also collected in SOOC, possibly for similar reasons. The presence of these rheophilic species during a no-flow period may provide some insight into behavioural adaptations in diminishing-water conditions. Williams and Feltmate (1992) noted that the 'littoral zone' of lentic waters was exposed to wave action, and in that sense resembled a running stream. They collected the larvae of many lotic insects in this zone, including the chironomid genera *Polypedilum, Tanytarsus, Procladius* and *Ablabesmyia*. While these authors were primarily referring to large water-bodies, this phenomenon of 'splashing' was observed at the edge of shallow pools in the upper Kowie, particularly where there were surface breezes.

During October, low flow was insufficient to create a SIC biotope. SOOC was sampled in an area recently exposed to flow, which explains the relatively high numbers of simuliids (*Simulium hargreavsi/medusaeforme*) collected. Members of this family (usually *Simulium nigritarse*) were sometimes collected over a month after flow cessation, in areas of shallow water exposed to light breezes. This is not an uncommon finding (de Moor, pers. comm.).

The planorbids *Bulinus forskalii* and *Ceratophallus* sp. were collected in SOOC: these genera have a robust accessory gill which allows for respiration in lower-oxygen water, and for longer submersion than other families such as lymnaeids. They are also capable of aestivation under adverse conditions (Brown 1980). *Pisidium* sp. sphaeriids, which occur in waterbodies varying in volume and permanence, were typically collected in SOOC, POOLS and DRG. These gastropods feed on dead and decaying organic matter and the periphyton community on submerged surfaces (Appleton unpubl.).

Marginal vegetation (MV)

The fauna of this biotope lent interesting perspectives to the consideration of 'stability' in a highly variable environment, and it is discussed more fully in later sections. Generally, over half the total number of taxa at the site occurring in MV (except during September at the upper site). A glance at Appendix 3.1 illustrates the importance of MV at the lower site particularly, where it formed an extensive 'boundary' between the aquatic and terrestrial environment.

The animals collected commonly in the restricted sections of narrow belt of MV at the upper site included leptocerid tichopterans, *Laccophilus lineatus* and *Philaccolus lineatoguttatus* dytiscids, and *Polypedilum* sp. and Tanypodinae chironomids (Appendix 3.1).

At the lower site, this biotope was favoured by a wide variety of taxa which show a general preference for slow-moving or still water conditions: microcrustaceans, hydracarinids, corduliid and coenagriid nymphs, belostomatids, corixids, hydrometrids, notonectids, microveliids, hydroptilid caddis-larvae, dytiscid and hydrophilid adults and larvae, chironomids, culicids, and lymnaeid, physid and planorbid snails.

Sand (SAND)

Although mobile sand-beds are considered poor habitats (Ward 1992, Williams and Feltmate 1992), during periods of reduced or no-flow, coarse sandy substrata represented a more stable environment. With deposition of silt (during flow) and organic matter (during all phases) on this sandy surface, the food resources were also enhanced - Tarzwell (1936) reported an almost eleven-fold increase in faunal diversity in silt-rich sand relative to clean sand.

Sandy substrata became increasingly important during periods of diminishing surface water. Sandy-bottomed pools served as refugia, providing food (in the form of algae and detritus) and cover to the biota, many of which relocated to this environment from drying biotopes. This movement of animals from exposed areas to pools was also reported in one of the streams studied by Boulton and Lake (1992b). During November, when drying had commenced, predaceous *Polypedilum* chironomids, which are morphologically adapted to burrowing in shifting sand, were numerically abundant in all but one sample - this genus is common in fine and medium sands and is known to dominate the fauna (Shadin 1956 quoted by Ward 1992).

Pools (POOL)

While receding surface water in November and December posed a threat to developing larvae, pools also provided a buffered environment offering shelter and plentiful food (algae, leaves, detritus). Algal growth during summer (mainly at the lower site) contributed to the retention of high dissolved oxygen, and was clearly favoured as a source of food and shelter by early instar baetid mayflies. The relatively high numbers of *Procladius* and *Chironomus* chironomids collected were indicative of the high silt content of the sand (Williams and Feltmate 1992).

Commonly, taxa such as mayflies were collected in damp leaf-packs on the sand or in the detritus fringing the pools. This fringe area was otherwise occupied by oligochaetes, microcrustaceans, gomphids, dytiscids, hydraenids, tipulids and tabanids, some of which burrowed into the top few centimetres of the sand, or sheltered beneath partially-embedded rocks or stones.

Drying beds were colonised by an assortment of terrestrial fauna, referred to by Boulton and Suter (1986) as the 'cleanup crew'. These were generally edge-dwellers: frogs, ants, spiders, amphipods, adult diptera, beetles, bugs, and snails, which took advantage of the damp microclimate and scavenged on dead or dying individuals or emerging imagoes (cf. Stehr and Branson 1938); grazed on exposed algal mats (e.g. snails), or may have laid eggs in damp, decaying organic material (cf. Williams 1987).

Drying (DRG)

The high disparity in total taxa between the faunally-rich and faunally-depauperate DRG samples was due mainly to the high water content of the former samples, but also to the heterogenous character of this biotope. Because sampling was not restricted to a particular type of drying substratum, the material collected as DRG varied both in its composition and its water and oxygen content. These and other variables would have affected the faunal complement of the sample.

In September at the upper site, drying substrata occurred within metres of the slow-flowing section of the stream. Fauna collected from the drying substratum were probably those taxa unable to relocate to the lotic environment, or those which could withstand the drying environment. The high number of taxa in DRG in December could be related to the reduction in diversity in the adjacent pools. Fauna may have been stranded at the pool edge as the water evaporated, or may have relocated to a more habitable environment at the fringe (close to the 'splash' zone referred to earlier).

Drying beds were colonised by an assortment of terrestrial fauna, referred to by Boulton and Suter (1986) as the 'cleanup crew'. These were generally edge-dwellers: frogs, ants, spiders, amphipods, adult diptera, beetles, bugs, and snails, which took advantage of the damp microclimate and scavenged on dead or dying individuals or emerging imagoes (cf. Stehr and Branson 1938); grazed on exposed algal mats (e.g. snails), or may have laid eggs in damp, decaying organic material (cf. Williams 1987).

3.6.4 Faunal differences between individual biotopes

Cluster analysis and ordination of samples suggested that, on the whole, similarities between the fauna of different biotopes at a site were low. Analysis of similarity proved significant differences between the fauna of some of the biotopes at each site, indicating that in general, faunal variability between biotopes was greater than variability within a biotope over time (Clarke and Warwick 1994).

At UK1, approximately 50% of the biotope pairs were significantly different. Faunal overlap was a therefore a feature of the other 50% of biotope pairs. Significant differences were indicated between biota collected in DRG and that from all other biotopes. This difference was probably related to the small numbers of taxa collected in DRG, rather than to faunal composition of samples, as all animals collected were found in other biotopes during the study.

The significant difference between POOL and SOOC and SAND faunas at UK1 was attributed to the lack of sandy-bottomed pools in the majority of the site. Fauna from SIC also differed substantially from that collected in MV and POOLs. This was partly due to the absence of rheophilous species in MV and POOLs, but also suggested that when SIC dried, fauna from this biotope did not relocate to pools. At UK1, areas of SIC were separated by a vertical 1m bedrock 'step' in the channel (cascade during flow) from areas in which persistent pools were situated. This may have represented a barrier to the movement of fauna downstream into pool refugia.

At UK1, in contrast, there was no significant difference between the faunas of SIC and POOL. This site was virtually level, favouring movement of invertebrates from one to another part of the site both during periods of plentiful surface water and when drying commenced. Overlap in the faunas of SIC, SOOC, SAND, POOLS and DRG is indicated by the lack of significant differences between these biotopes (the significance of SAND,POOL and SAND,DRG differences was uncertain). At this site, the relocation of animals to suitable refugia during drying was further shown when drying commenced in December. Only the POOL and DRG biotopes were sampled this month, and only ten taxa had been lost since the previous month when MV, SOOC and SAND were still under water and available as biotopes. Of the taxa collected during December, over half were found in DRG, which was sampled on the damp, sandy fringes of the small pool.

The fauna collected in MV at the lower site was, however, distinctive, as illustrated by its significant difference from that of all other biotopes, and also in the results of cluster analysis of individual samples. This biotope represented a plentiful food source and a sheltered environment, and it supported a rich fauna. The large proportion taxa were those preferring either shallow water or lentic conditions (e.g. hemipterans, microcrustaceans, odonates, coleopterans, molluscs). Significance of difference was thus attributed to the high taxonomic richness of individual MV samples relative to that of samples from other biotopes, the frequency of occurrence of taxa in samples, and the relatively stable composition of the fauna over time - as illustrated by the grouping of all MV samples from this site in cluster analysis.

3.6.5 Faunal differences between sites

Results indicated significant differences between the fauna of UK1 and UK2 over the eight month period. In general, the lower site was more taxon-rich than the upper site. Several factors may have contributed to this. The large, open channel at the upper site had high visibility to potential colonists due to its lack of canopy cover and the high reflectivity of the single large pool or channel. The upper site was shaded by riparian trees and thus less visible to aerial colonists. At the lower site, gradual surface water loss occurred, and a single, large, deep pool with relatively homogenous substratum (coarse to fine sand overlaid with organic material and algae) remained. At the upper site, in contrast, the channel was generally narrow and bedrock dominated, and its topography reduced invertebrate access from one to another area of the site in periods of no flow. Flow cessation resulted in several shallow, isolated, low-volume pools in the channel. These had varying substratum characteristics (usually bedrock, overlain with a combination of coarse sand, stones, leaves, and other organic matter). Probably the most significant cause of elevated taxonomic richness at the lower site, however, was the broad strip of marginal vegetation along the left bank. As discussed, the duration of this biotope was long, and the stability of such a micro-environment within the context of a continually-changing macro-environment, favoured an increase in diversity and stability of its fauna. While the majority of taxa occurred at both sites during some part of the study, the higher frequency at the lower site was probably due to the structurally diverse marginal vegetation.

The group in which the most conspicuous differences were seen was the molluscs. It was thought that the scarcity of many of these families at the upper site (relative to the lower site) may, at least during the months of diminished surface water, be linked with the presence of reddish flocculant precipitates of iron salts at the site. These result from the deposition of ferric hydroxide by certain iron-reducing bacteria, and are considered an indirect effect of low oxygen tension (Brown 1980), which was not necessarily the cause in the upper Kowie. Brown (1980) remarked that snails are rare in the presence of these precipitates, and that this may be due either to oxygen shortage, or to a reduction in food supply caused by the adverse effect of colloidal iron on the growth of algae (quoting Van Someren 1946).

3.6.6 Faunal differences between months of the study

Most months differed significantly in terms of their total fauna (that collected at UK1 and UK2), and the null hypothesis of 'no difference between months' was rejected. Thus in general, faunal variability within a month (e.g. between biotopes, sites) was less than variability between months of the study. Of the seven 'pairs' of months which did not differ significantly, four comprised consecutive months: September and October (low FLOW), October and November (low FLOW and NO FLOW), November and December (NO FLOW, POOLS) and January and February (ONSET, FLOW). These results were borne out to some extent in cluster analysis and ordination of total monthly samples from each site. Major groupings here were July, August, September; October, November, December; and January, February. These groupings represented fauna collected in:

- consecutive months;
- similar times of the year (e.g. late winter/spring/early summer; midsummer; late summer);
- periods of similar biotope heterogeneity and availability;
- similar hydrological conditions.

3.6.7 Factors affecting faunal character

Based on these results, there appeared to be three major influences on the character (or 'form') of the invertebrate fauna in the river at any time: present and antecedent hydrological conditions and their duration; time of year; and biotope or substratum heterogeneity and character. In keeping with the view of Minshall and Minshall (1978), it is presumed that the factors regulating faunal composition may act syncronously, in a hierarchical fashion, but their order of operation may vary from one species to another.

The role of each of the influencing variables is discussed in turn (although they should not be viewed as truly separable).

Present and antecedent hydrological conditions

The frequency of change in hydrological conditions in the upper Kowie resulted in individual phases lasting for only one to two months, which was considered insufficient time for distinctive groups of taxa to develop to characterise that hydrology. Groupings of adjacent months with similar hydrological characteristics, as discussed in the previous section, indicated that surface water conditions were a vital determinant of faunal character. However, the character of the fauna present 'now' in the river (present conditions) can only be comprehensively understood in the context of conditions in the channel prior to this time. For instance - flow recommencement (ONSET) may be preceded by dry conditions, or by pools in the channel. The fauna present under the two different scenarios would probably show some differences. This is examined in Chapter 5.

Similarly, the duration of conditions plays a major role in shaping faunal character. Schneider and Frost (1996) suggested that pond assemblages were structured by random processes, life-history characteristics and biotic interactions, but that the relative importance of these processes depended on duration of habitat. This would apply particularly in an aseasonal river in which seasonal environmental cues such as air temperature provide no warning of impending conditions, or how favourabile the environment is for breeding or development.

In the upper Kowie River, duration of conditions affected total fauna in one of two ways: when conditions were maintained in a *relatively* stable state, with gradual rather than abrupt physical changes (e.g. low FLOW to NO FLOW from September to November), the general tendency was for numbers of taxa and compositional stability to increase. However, with rapidly changing conditions, as in those periods when surface water diminished and variability in substratum or biotopes was lost (as during December), sharp decreases in taxonomic richness were recorded.

The changes associated with reductions in pool volume, all of which could affect fauna adversely, are loss of habitat, space constraints for the invertebrates ('saturation' of the habitat and increase in competitive interactions), predation, pressure on the food resource, organic enrichment, and changes in water chemistry - e.g. decreased dissolved oxygen due to high summer temperatures, etc. In the Kowie River, water chemistry remained fairly stable throughout the study, and was probably not related to this loss of taxa. Oxygen saturation was high even during the late POOLS stage, although this was associated with photosynthesis of algae, and oxygen tension may have been low nocturnally. Faunal losses due to death, emergence, relocation of aerial adult forms, or physiological avoidance of conditions were probably due mainly to reduction of habitat and to the numbers of predaceous taxa (e.g. odonates, dytiscid beetles, hempiterans) in the pools. The high numbers of fauna found (possibly stranded) in the adjacent drying substrata (DRG) at the lower site during December also hinted that the increased *rate* of surface water loss due to high evaporation may have been another contributing factor.

Prevailing hydrological conditions influenced the clustering of several groups of samples. In analysis of similarity of fauna from individual biotopes, clusters formed at over 20% similarity suggested that during the NO-FLOW/POOLS and ONSET/early FLOW phases of midsummer, hydrological conditions played a major role in shaping faunal character. In one of the groups (Group 5, Fig. 3.5a), the samples were all collected during flow conditions, and flow and time of year were the governing factors. Rheophilic simuliids *S.nigritarse* and *S.hargreavsii / medusaeforme* contributed to similarities in this group only (at a low percentage), further endorsing this view. Substratum character was also a contributing factor, as the majority of samples were collected in SIC and SOOC. In general, five of the nine groups were dominated by samples from flow periods, and four comprised samples from drying periods.

Taxa which accounted for the majority of the sample similarity in the group of DRG samples were either typical of fringe environments, or adept at using behavioural mechanisms (e.g. burrowing) to avoid desiccation at the surface: *Polypedilum* sp. chironomids, oligochaetes, *Ceratophallus* snails, *Bezzia* ceratopogonids, dytiscids, *Orthetrum* sp. libellulid nymphs, and nematodes.

Time of year

The splitting of July, August and September samples from midsummer samples taken in November and December and those taken in January and February was clearly not due to hydrological factors alone (as similar hydrological conditions applied to some of the samples in each of the three groups). In contrast to the midsummer samples, which appeared to group in relation to the prevailing hydrological conditions, fauna from consecutive months of late winter-spring-early summer showed resemblances *despite* the changes in hydrology. Further, fauna collected in the winter POOLS phase of July was more similar to that collected during the two consecutive months (in which hydrological conditions were totally different), than to that collected in the summer POOLS phase of December. This may be attributable to life history characteristics of the fauna in the winter POOLS fauna (e.g. only one breeding period in a year, or univoltinism). This dissimilarity indicated that time of year should be incorporated into the concept of hydrological phases (e.g. winter POOLS, summer POOLS). Because of high inter-annual variations in rainfall and hydrology, it would, however, still not be possible to predict the occurrence of particular taxa in particular months of the year, and it is unlikely that there would be a fauna *typical* to any particular month or season (this is examined further in Chapter 4). Time of year could only strengthen predictive power in that expected fauna for a single phase would differ at various times of the year (e.g. fauna from summer FLOW phases would be expected to differ from fauna from winter FLOW phases). This concept is further developed in Chapter 5.

Biotope or substratum character and availability

In general, results suggested that biotope specificity was low and - for certain taxa - overlap in composition between biotopes was relatively high, to some extent corresponding with findings in other rivers subject to highly variable or intermittent discharge (e.g. Palmer *et al.* 1991).

In cluster analysis of all samples, two out of nine groups were dominated by MV samples, one by POOL samples, and one by DRG samples. The last of these was to be expected, as DRG usually represented extreme conditions, and as drying progressed, only particular fauna were capable of inhabiting it. The relatively high similarity of samples from MV at the lower site indicated a degree of faunal stability in this biotope relative to the other biotopes, and suggested that some sort of faunal succession was occurring in MV which may not be apparent at the larger scale. Taxa contributing to similarity in MV were typical of slow-moving waters: the dytiscid *Laccophilus lineatus*, *Anisops* sp. notonectids, belostomatids, corixids, gerrids, veliids, libellulids (*Orthetrum* sp.) and coenagriids, copepods, cladocerans, and chironomids (*Polypedilum* and *Rheotanytarsus*).

The influence of biotope heterogeneity and the nature of available biotopes on faunal diversity has already been mentioned (3.7.1). Contractions of habitat (*sensu* Stanley *et al.* 1997) and loss of biotope heterogeneity resulted in faunal losses, while expansion of habitat and increase in number of available biotopes generally effected increases in faunal diversity, as seen between October and January. Following flow cessation in November, and the loss of MV, SOOC and SAND as aquatic biotopes at UK1, numbers of taxa decreased by 29% and further losses were recorded as pool size diminished. At the lower site, contraction of aquatic habitat was gradual, and high numbers of taxa were collected in November, but loss of fauna occurred when MV was exposed. Resumption of flow in January 1995 caused expansion of aquatic habitat and increases in numbers of taxa were recorded at both sites within two weeks.

3.7 CONCLUDING POINTS

- Significant differences were found at all scales of this investigation: between the fauna of different biotopes, different sites, and different months.

- The factors which seemed to have the greatest effect on the character of the faunal character were thought to be:
    - present and antecedent hydrological conditions and their duration,
    - time of year, and
    - biotope or substratum character and availability.

REFERENCES

Abell, D.L. 1956. *An ecological study of intermittency in foothill streams of central California.* PhD thesis, University of California, Berkeley, USA.

Appleton, Professor C. Unpublished Key to South African Gastropods. Department of Zoology and Entomology, University of Natal, Pietermaritzburg, South Africa.

Armitage, P.D., Pardo, I. and Brown, A. 1995. Temporal constancy of faunal assemblages in 'mesohabitats' - application to management? *Archiv für Hydrobiologie* **133** (3) 367-387.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* **27:** 99-121.

Boulton, A.J. and Lake, P.S. 1992b. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology* **27:** 123-138.

Boulton, A.J. and Lake, P.S. 1992c. Benthic organic matter and detritivorous macroinvertebrates in two intermittent streams in south-eastern Australia. Hydrobiologia **241:** 107-118.

Boulton, A.J. and Lake, P.S. 1992d. The macroinvertebrate assemblages in pools and riffles in two intermittent streams (Werribee and Lerderberg Rivers, southern central Victoria). *Occasional Papers from the Museum of Victoria* **5:** 55-67.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams: an Australian perspective. *In:* De Deckker, P., and Williams, W.D. *Limnology in Australia*. pp. 313-329. CSIRO/ Dr W. Junk, Melbourne and Dordrecht.

Brown, D.S. 1980. *Freshwater snails of Africa: and their medical importance.* Taylor and Francis Ltd., London.

Bunn, S.E., Edward, D.H, and Loneragan, N.R. 1986. Spatial and temporal variation in the macroinvertebrate fauna of streams of the Northern Jarrah Forest, Western Australia: Community structure. *Freshwater Biology* **16:** 67-91.

Chapman, L.J. and Kramer, D.L. 1991. Limnological observations of an intermittent tropical dry forest stream. *Hydrobiologia* **226:** 153-166.

Chutter, M. 1994. The rapid biological assessment of stream and river water quality by means of the macroinvertebrate community in South Africa. *In:* M.C. Uys (ed). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94.

Clarke, K.R. and Warwick, R.M. 1994a. *Change in marine communities - an approach to statistical analysis and interpretation.* Plymouth Marine Laboratories, Bournemouth.

Clifford, H.T. 1966. The ecology of invertebrates in an intermittent stream. *Investigations of Indiana lakes and streams* **7:** 57-98.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199:** 1302-1310.

Cowie, B. 1985. An analysis of changes in the invertebrate community along a southern New Zealand montane stream. *Hydrobiologia* **120:** 35-46.

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist* **67:** 477-504.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* Water Research Commisssion Report No. TT62/93.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1995. River and Stream Ecosystems in southern Africa: Predictably unpredictable. pp. 537-599 *In:* C.E. Cushing, K.W. Cummins, and G.W. Minshall. *Ecosystems of the World 22: River and Stream Ecosystems.* Elsevier, New York.

de Moor, F. (Pers. Comm.) Aquatic invertebrate section, Albany Museum, Grahamstown, South Africa.

Downes, B.J., Lake, P.S. and Schreiber, E.S.G. 1993. Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organisation. *Freshwater Biology* **30:** 119-132.

Grassle, J.F. and Sanders, H.L. 1973. Life histories and the role of disturbance. *Deep Sea Research* **20**: 643-659.

Gray, L.J. 1981. *Recolonisation pathways and community development of desert stream macroinvertebrates.* PhD thesis, Arizona State University, Tempe, Arizona, USA.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* **8:** (4) 293-307.

Harrison, A.D. (unpublished). Taxonomic information relating to the family Chironomidae in Southern Africa.

Harrison, A.D. 1978. Freshwater invertebrates (except molluscs). *in:* M.J.A. Werger and A.C.van Bruggen (eds). Biogeography and ecology of southern Africa. *Monographiae Biologicae* **31:** 1139-1152.

Harrison, A.D. 1966. Recolonisation of a Rhodesian stream after drought. *Archiv für Hydrobiologie* **62:** 405-421.

Harrison, A.D. 1958. Freshwater invertebrates (except molluscs). *In:* Werger,M (ed.). Biogeography and ecology of Southern Africa. W.Junk Publishers, The Hague.

Hildrew, A.G. and Giller, P.S. 1992. Patchiness, species interactions and disturbance in the stream benthos. *in:* P.S. Giller, A.G. Hildrew and D.G. Raffaelli (eds). *Aquatic Ecology: scale, pattern and process.* The 34th Symposium of the Brititsh Ecological Society with the American Society of Limnology and Oceanography, University College, York. Blackwell Science.

King, J.M. 1981. The distribution of invertebrate communities in a small South African river. *Hydrobiologia* **83:** 43-65.

King, J.M. and Tharme, R.E. 1994. *Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa.* Water Research Commission Report No. 295/1/94.

King, J.M., Day, J.A., Hurly, P.R., Henshall-Howard, M-P., and Davies, B.R. 1988. Macroinvertebrate communities and environment in a southern African mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **45:** 2168-2180.

Lubke, R.A. and Van Wijk, Y. 1988. Terrestrial plants and animals: terrestrial plants and coastal vegetation. *In:* R.A. Lubke, F.W. Gess and M.N. Bruton (eds.). *A field guide to the Eastern Cape Coast.* A Wildlife Society Handbook.

McCafferty, W.P. 1981. *Aquatic Entomology.* Jones and Bartlett Publishers, Boston.

Menge, B.A. and Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110:** 350-369.

Minshall, G.W. 1984. Aquatic insect-substratum relationships. *in:* V.H. Resh and D.M. Rosenberg (eds.). *The ecology of aquatic insects.* Praeger, New York.

Minshall, G.W. and Minshall, J.N. 1978. Microdistribution of benthic invertebrates in a rock mountain (USA) stream. *Hydrobiologia* **55** (3): 231-249.

Palmer, C.G., O'Keeffe, J.H. and Palmer, R.W. 1991. Are macroinvertebrate assemblages in the Buffalo River, Southern Africa, associated with particular biotopes? *Journal of the North American Benthological Society* **10:** 349-357.

Pennak, R.W. 1953. *Freshwater invertebrates of the United States.* The Ronald Press Company, New York.

Petraitis, P.S., Latham, R.E. and Niesenbaum, R.A. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* **64** (4): 393-418.

Poff, N.L. and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46:** 1805-1817.

Power, M.E., Jean Stout, R., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Statzner, B., and Wais de Bagen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *Journal of North American Benthological Society* **7** (4): 456-479.

Schneider, D.W. and Frost, T.M. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* **15** (1): 64-86

Shadin, V. I. 1956. Life in Rivers. *Juzni preznih vod SSSR* 3: 113-256. (in Russian)

Stanford, J.A. and Ward, J.V. 1983. Insect species diversity as a function of environmental variability and disturbance in stream ecosystems. *In:* J.R. Barnes and G.W. Minshall (eds). *Stream ecology: the application and testing of general ecological theory.* pp. 265-278. Plenum Press, New York.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. 1997. Ecosystem expansion and contraction in streams. *BioScience* 47 (7): 427-435.

Stanley, E.H. and Fisher, S.G. 1992. Intermittency, disturbance and stability in stream ecosystems. *In:* R.D. Robarts and M. implications for resource management. NHRI Symposium Series 7, Environment Canada, Saskatoon.

Statzner, B. and Higler, B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* **16:**127-139.

Stehr, W.C. and Branson, J.W. 1938. An ecological study of an intermittent stream. *Ecology* **19**: 294-310.

Sweeney, B.W. 1984. Factors influencing life-history patterns of aquatic insects. *In:* Resh, V.H. and Rosenberg, D.M. *The ecology of aquatic insects.* Praeger Publishers, New York.

Tarzwell, C.M. 1936. Experimental evidence on the value of trout stream improvement in Michigan. *Transactions of the American Fisheries Society* **66:** 177-187.

Towns, D.R. 1985. Limnological characteristics of a South Australian intermittent stream, Brown Hill Creek. *Australian Jounal of Marine and Freshwater Research* **36:** 821-837.

Townsend, C.R., Hildrew, A.G. and Schofield, K. 1987. Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* **56:** 597-613.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. and Cushing, C.E. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130-137.

Van Someren, V.D. 1946. The habitats and tolerance ranges of *Lymnaeae (Radix) caillaudi*, the intermediate snail host of liverfluke in East Africa. *Journal of Animal Ecology* **15:** 170-197.

Wiggins, G.B., Mackay, R.B. and Smith, I.M. 1980. Evolutionary and ecological strategies of animals in temporary pools. *Archiv für Hydrobiologie* Suppl. **58**: 902-76.

Williams, W.D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologgia* **125:** 85-110.

Williams, D.D. 1987. *The ecology of temporary waters.* Croom Helm Ltd., Kent/ Timber Press, USA.

Williams, D.D. and Feltmate, B.W. 1987. *Aquatic insects.* CAB International, UK.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue der Cesamten Hydrobiologie* **62:** 53-61.

Williams, D.D. and Hynes, H.B.N. 1976. The ecology of temporary streams. I. The fauna of two Canadian streams. *Internationale Revue der Gesamten Hydrobiologie* **61:** 761-787.

Winterbourn, M.J., Rounick, J.S. and Cowie, B. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* **15:** 321-328.

Wootton, J.T., Parker, M.S. and Power, M.E. 1996. Effects of disturbance on river food webs. *Science* **273:** 1558-1560.

Wright, J.F., Hiley, P.D., Cooling, D.A., Cameron, A.C., Wigham, M.E. and Berrie, A.D. 1984. The invertebrate fauna of a small chalk stream in Berkshire, England, and the effect of intermittent flow. *Archiv für Hydrobiologie* **99:** 176-177.

Yule, C.M. 1996. Spatial distribution of the invertebrate fauna of an aseasonal tropical stream on Bougainville Island, Papua New Guinea. *Archiv für Hydrobiologie* **137:** 227-249.

APPENDIX 3.1

List of taxa collected during each month at the upper Kowie River. Each letter represents the biotope in which the animal was collected: m - MV, s - SIC, o - SOOC, A - SAND, p - POOL, and d - DRG. The size of letters represents the abundance category, e.g. m = 1-10, M = 11-100, and M* = 101-1000.

	UPPER SITE, UK1								LOWER SITE, UK2							
	JUL	AUG	SEP	OCT	NOV	DEC	JAN.	FEB	JUL.	AUG	SEP	OCT	NOV	DEC	JAN.	FEB.
HYDROZOA																
Hydra sp.																
NEMATODA						d		o				d			o	
OLIGOCHAETA				d	d	dp			o			d	o	pP	i	
CRUSTACEA																
CLADOCERA			s						m	m	m		m	p	m	
COPEPODA			m	m	p	p						Ms	o		m	
Calanoida																
Other			ms	m	d				m				mo			m
OSTRACODA																
Paracypretta syngramma						p						M		p		
Candonopsis sp						p										
Cypridopsis sp.												s				
Ilyodromus viridulus												m				
Physocypria cf capensis						p						m			m	
Pseudocandona gr geratsi							m								m	
Ostracoda A				s									mo			mi
Ostracoda B													m			
Ostracoda C							i	o			m		m			m
Ostracoda E			d	s				o			m					
Ostracoda F															o	
DECAPODA																
Potamonautes sp.							i	m						dp	m	mio
ARACHNIDA																
HYDRACARINA		i	D	d								mS	m		mi	mi
INSECTA																
COLLEMBOLA			d			d										
EPHEMEROPTERA																
BAETIDAE																
Afroptilum pulchrum									s		o					o
Baetis latus								m								i
Baetis harrisoni					p	p								dp		i
Baetis sp. indet.								m					s			
Cloeon sp.								O							m	
Demoulinia complex													m			
CAENIDAE																
Afrocaenis sp.						p					s		mos	dP		
ODONATA																
AESHNIDAE																
Aeshna sp.																

	UPPER SITE, UK1								LOWER SITE, UK2							
	JUL	AUG	SEP	OCT	NOV	DEC	JAN.	FEB	JUL.	AUG	SEP	OCT	NOV	DEC	JAN.	FEB.
AESHNIDAE																
Anax sp.									o	m						
CORDULIIDAE																
Macromia sp.								o					ms			m
?Syncordulia sp.		m							m		m		m			
GOMPHIDAE																
Notogomphus sp									mo		s		os	dp		
LIBELLULIDAE																
Orthetrum sp			o		dp	p	m					m		dp	mi	
Other							m									
COENAGRIONIDAE					p									dp		
Pseudagrion sp.										m			m	dp		i
CHLOROLESTIDAE																
Chlorolestes sp.					p	p						m	o	d		o
LESTIDAE																
Lestes sp.													o		m	m
HEMIPTERA																
BELOSTOMATIDAE																
Diplonychus capensis								m	m			m	m		m	m
CORIXIDAE																
Arctocorisa meridionalis					p	p						m				
Micronecta citharistia							m						mo			
Micronecta sp.			d						mo	m	s					o
Sigara meridionalis					p								m	dp		
Sigara sp.			d										mo		i	mo
HEBRIDAE																
Hebrus sp.			od													
GERRIDAE																
Gerris swakopensis										m		mo	m			mi
HYDROMETRIDAE																
Hydrometra ambulator					p					m	m	m				m
NAUCORIDAE																
Limnogonus sp.							o					m				
MESOVELIDAE																
Mesovelia sp.			o									m				
NOTONECTIDAE																
Anisops gracilis					p											
Anisops limpida														p		
Anisops ?aglaia													m			
Anisops sp.	m		d		p	p			mo	m	s		m	p	m	mo
Enithares sp.							o									
PLEIDAE																
Plea pullula												m				
VELIIDAE																
Microvelia venustissima																
Microvelia sp.							m		m	m	ms	mo			o	m
TRICHOPTERA																
ECNOMIDAE																
Ecnomus sp.							m		o					d		

	UPPER SITE, UK1								LOWER SITE, UK2							
	JUL	AUG	SEP	OCT	NOV	DEC	JAN.	FEB	JUL.	AUG	SEP	OCT	NOV	DEC	JAN.	FEB.
DIPTERA																
CERATOPOGONIDAE																
near Bezzia			od	od	d	d		o			so		mos	p	i	
CHAOBORIDAE																
Chaoborus sp.			d		p	p										
CHIRONOMIDAE																
CHIRONOMINI																
Polypedilum sp.	ms	mo	mOS	OS*d	dp	dp	m	mi	so		So	mSo	MOs	dp	miO	mo
Chironomus sp.	ms			S					o		s			p		
Cryptochironomus sp.									so		o					
Microchironomus sp.											s					
Zavreliella sp.															m	
Other Chironomini			Sd				om	MO								mO
TANYTARSINI																
Cladotanytarsus sp.						p	m								m	
Rheotanytarsus sp.			osd	O	d		M*o	Ml*o				s	mS		io	mlo
Stempellinella sp.							m									
Tanytarsus sp.			od	Os	p	p	m		o		s	sd	mo	dpp	i	m
Other Tanytarsini	o	mlo	OSD	O	p		m	mi		io	s		m		m	io
DIAMESINAE																
Harrisonina petricola							m								i	
ORTHOCLADIINAE																
Chaetocladius sp.											s					
Coryoneura sp.				o												
Krenosmittia sp.		i														
Limnophyes sp.							i					s		p		
Limnophyes natalensis		ml		s					s		o					
Mesocricotopus sp.												s				
Nanocladius sp.											s	s				
Parametriocnemus sp.				O											m	
Pseudosmittia sp.													s			
Rheocricotopus sp.				o											i	
Cricotopus sp.														d		
Other orthocladiinae		i	od	Mo			io	mlo					S			io
TANYPODINAE																
Ablabesmyia dusoleili				s												
Ablabesmyia sp	so								so		So	s				
Clinotanypus sp									o		S		o	dp		
Conchapelopia							m	m								
Paramerina sp				os	p				o						mi	
Procladius sp	mso		O	o	p	p	m	m	SO		SO		Mo	dP	i	
Tanypus sp.																
Larsia sp	mo			OS			m		o			o	O	dp		
Other Tanypodinae	mso	mo	OD	osd			mio	mio	ms	i	So	so			mi	mo
CHIRONOMID PUPAE																
Cricotopus sp.		i														
Rheocricotopus sp.											s					
Polypedilum sp.											s				i	
Chironomus sp.		o														
CULICIDAE																
Anopheles sp.		i	o	m	dp	p				m		mo	mo	d		m
PSYCHODIDAE		m		s								s				

	UPPER SITE, UK1								LOWER SITE, UK2							
	JUL	AUG	SEP	OCT	NOV	DEC	JAN.	FEB	JUL.	AUG	SEP	OCT	NOV	DEC	JAN.	FEB.
HYDROPTILIDAE																
Oxyethira sp.			o	O						m	ms	m	m			i
HYDROPSYCHIDAE																
Cheumatopsyche afra								m								
LEPTOCERIDAE																
Leptocerus sp.	m	m	Md	mos											m	i
PISULLIDAE																
Dyschimus ensifer			M	M												
COLEOPTERA																
DYTISCIDAE																
Copelatus caffer		m		m	p							m				
Copelatus sp.		m		ms	p									pp		
Hydaticus ?capicola												m				
Hydaticus servillianus											s					
Hydrochus sp.									m							
Hyphydrus distinctus					p								m	d		
Hyphydrus signatus					p				o							
Hydrovatus brownei									m							
Laccophilus lineatus		m	o	m	p		M	o	mo	mi	m	M	m	dp	m	mo
Laccophilus sp.					d				m							
Lelodytes evanescens												m				
*Philaccolus lin.**		m	o	m		d	m	o			m					
Other dytiscids			md	m			om		m	m		d				
DYTISCID LARVAE																
Colymbetinae				s												
Dytiscinae																
Hydroporinae					p						s					
Hydaticus sp.				s							m					
Hydryphus sp.			d			p							o m		m	
Larva C								o								i
Larva K								O								mO
Larva M																m
Larva X			M	m	p	p								d		
ELMIDAE																
Stenelmis sp.																
GYRINIDAE																
Aulonogyrus caffer					p											
Dineutus grossus	mo		d		p			m		m						
Aulonogyrus sp.																
Other			s		p			i					o			i
HALIPLIDAE																
Haliplus sp.																
HELODIDAE																
Helodidae larva							m			m						
HYDRAENIDAE																
Ochthebius andronius												m				
HYDROPHILIDAE																
Amphiops sp.		m											o			
Hydrobius sp.					p									p		
Hydrochus sp.										M						
Other hydrophilids		mi	d	s		dp	m		m	m	m		m	p		mi
Hydrophilid larvae			d	s										p	m	

	UPPER SITE, UK1								LOWER SITE, UK2							
	JUL	AUG	SEP	OCT	NOV	DEC	JAN.	FEB	JUL.	AUG	SEP	OCT	NOV	DEC	JAN.	FEB.
SIMULIIDAE																
Simulium alcocki								m								
Simulium nigritarse								ml								
Simulium ruficorne								mi								
Simulium adersi																i
Simulium hargr/med **				O												o
TABANIDAE										i				p	i	
TIPULIDAE	m		od	o						o		s		p	mi	
MOLLUSCA																
GASTROPODA																
ANCYLIDAE																
Burnupia sp.			m		p	p						m				
Ferissia sp				m	p									dp	m	
LYMNAEIDAE																
Lymnaea columella									O	m	m	Mo	m	d	m	
PHYSIDAE																
Bulinus forskalii													o		m	
Bulinus sp.												m				
PLANORBIDAE																
Ceratophallus sp			m	m	d	p					m	m	o	dp	Mi	m
PELECYPODA																
SPHAERIIDAE																
Pisidium sp.					p	p						d	o	dp		

CODES: M=MV, S=SAND, I=SIC, 0=SOOC, D=DRG, P=POOL
NUMERICAL ABUNDANCES: m=1-10, M=11-100, =101-1000

* *Philaccolus lineatoguttatus*

** *Simulium hargreavsi/medusaeforme*

CHAPTER 4

THE VARIABILITY IN THE INVERTEBRATE FAUNA OF THE UPPER KOWIE BETWEEN CONSECUTIVE YEARS

This chapter is currently in press in the
Journal of the South African Society of Aquatic Sciences (SASAQS).
The title of the paper is 'Variability in the invertebrate fauna
of an intermittent stream over three consecutive midsummer periods',
under the joint authorship of M.C.Uys and J.H. O'Keeffe.
Certain changes have been made for the purposes of the thesis -
chiefly, the removal of repetition, additional
discussion, and continuation of the theme of different
spatial and temporal levels of investigation in the study.

ABSTRACT

Intermittent aseasonal rivers are exposed to unpredictable and highly variable rainfall and hydrology, which can have considerable effects on fauna at different scales. Spatial and temporal dynamics in the aquatic invertebrate fauna of an aseasonal intermittent river in the Eastern Cape, South Africa, were studied over three consecutive midsummer periods, to investigate whether any cyclical patterns were detectable. There was high variability in taxonomic composition both within and between years. Faunal abundances were generally low, and spatial distribution highly heterogenous. Values of most of the abiotic variables measured (excluding discharge) remained within narrow ranges over the study period. Only current speed in individual biotopes could be linked to biotic organisation. Fauna collected during similar hydrological conditions showed greatest resemblances, rather than those collected during the same months or within the same year. The erratic nature of rainfall and flow was viewed as disruptive to biota, inhibiting linear or cyclical development of juvenile fauna, and indicating that the concept of faunal succession in highly variable aseasonal environments should be re-examined. Despite the apparent lack of structure in the biota at the majority of scales, invertebrate assemblages showed consistently high taxonomic evenness (demonstrating a lack of dominance by individual taxa), and taxonomic distinctness (the degree to which individuals in a sample are taxonomically related) fluctuated minimally. These elements of unity within the greater picture of disorganisation suggest that some thought could be given to the application of mathematical models such as chaos theory to the study and management of aseasonal temporary rivers.

4.1 INTRODUCTION

The relative importance of abiotic and biotic factors in the structuring of faunal assemblages changes with differing environmental conditions (Power *et al.* 1988). It is generally acknowledged that in unstable, unpredictable environments, the primary determinants of ecosystem structure and function are physical rather than biological in nature (e.g. Williams 1987, Fisher and Grimm 1991). It has also been recognised that the relative contributions of abiotic and biotic factors to faunal structure are regulated by the *extent* of variability in a system (Poff and Ward 1989), and that an appreciation of the bilateral or multilateral controls on assemblage structure (in preference to an 'either-or' approach) is important (Power *et al.* 1988).

Variability itself is viewed over a variety of scales, and recognition of the gradients within variability is important. For example, at the largest scale, Brown (1985) distinguished between living and non-living systems on the basis of the variability characterising the former as compared to the latter. When Davies *et al.* (1995) referred to all southern African rivers, perennial and otherwise, as characterised by variability and unpredictability, they were expressing a generalist and comparative view (i.e. semi-arid zone rivers in general, in relation to temperate North American perennial rivers); and their perspective was a long-term (> 10 year) one. The authors associated this high variability in lotic environments with faunas which possibly comprised *'hardy opportunists, able to exploit suitable habitats between catastrophic floods and droughts, and with quiescent and/or avoidance/escape, life history stages necessary to survive the harsher episodes'*.

Scaling down somewhat, and bearing in mind the perennial-temporary river continuum presented in Chapter 2, the spatial and temporal gradients within variability itself should be recognised. For example, the environmental changes (or disturbances) affecting perennial river fauna are of a different frequency, magnitude and duration to those affecting temporary river fauna. Likewise, while southern African rivers *in general* tend to lack pronounced seasonality (Davies *et al.* 1995), the *extent* to which seasonality is lacking also varies along the perennial-temporary river continuum. This gradient in seasonality, and the effects thereof, was inferred by Allanson *et al.* (1990) in their suggestion that it would be useful to distinguish between four river types in South Africa: perennial rivers, seasonal rivers (equivalent to 'temporary' rivers, Ch. 2) in the summer rainfall area, seasonal rivers in the winter rainfall area, and intermittent rivers (equivalent to 'intermittent'or 'ephemeral' rivers, Ch.2). They noted that a distinction between seasonal rivers in summer and winter rainfall areas was important, because the implications of no flow during summer (period of maximum biological activity) were more serious than those of no flow during winter. *Intermittent* rivers, on the other hand, were *'as likely to flow during one season as another, and the stochastic nature of their flow regimes overrides any seasonal influences on the biota'*. The gradient in seasonality even in different types of temporary rivers was implicit.

The apparent lack of seasonality in flow in the upper Kowie motivated the study reported in this chapter. In intermittent seasonal rivers in Victoria, Australia, Boulton and Lake (1990) had used multivariate techniques to identify a series of five cyclical, sequential flow phases which correlated with changes in faunal composition. It was not known whether similar cycles in abiotic or biotic elements would be detectable in an *aseasonal* intermittent river.

Thusfar in this thesis, significant variation in the invertebrate fauna of the upper Kowie River has been reported at the spatial scales of the biotope and the reach (site), and at the temporal scale of individual months (Ch. 3). This study examined faunal variation at the temporal scale of the year, or - more specifically - contrasted the fauna occurring in three consecutive midsummer periods. On the basis of findings thusfar, it was hypothesized that the biota would be affected by unpredictable changes in hydrological conditions, and that there would be a significant difference between the fauna of the various years. The null hypothesis was thus H_0: there are no differences between the invertebrate fauna of midsummer periods within three consecutive years.

Aquatic macroinvertebrate samples collected in the upper Kowie River during three midsummer periods (November, December, January 1993-1996) were analysed. The midsummer period was selected because if surface water and flow were present, air and water temperatures would make it an optimal time for colonisation and breeding of aerial opportunist taxa and for the hatching and early development of juveniles. The *extent* (or range) of changes in hydrological conditions, and the effect on the fauna was sought.

Further considerations in this study were whether or not successional trends in invertebrate fauna were detectable despite the lack of predictable flow; and which environmental factors exerted the greatest influence on faunal character.

The criteria for disturbance discussed in Section 1.3.6 should be reiterated here. The chief sources of instability in the Kowie River were presumed to be significant alterations in surface water conditions (e.g. flow cessation, drying) and the *frequency of change* of the hydrological phases identified in Chapter 1. These factors were considered appropriate criteria for the recognition of disturbance in this study. It is useful to observe two types of disturbance: acute 'pulse' events such as flash floods or volcanic eruptions (*sensu* Bender *et al.* 1984), and extended 'press' disturbances, which have a far smaller impact, may occur more often, and are often anthropogenic in nature (Boulton and Stanley 1995). Examples of these are periodic flooding or spates (pulse), and drying (press; Stanley and Fisher 1992, Sagar 1983).

4.2 STUDY SITE

Samples from a single reach on a section of the upper Kowie River were analysed. The river is described in Section 3.2. The upper section is characterised by unpredictable onset and cessation of flow, and drying, fitting the description of an 'intermittent aseasonal' river type (Chs 2, 3).

Of the two sites studied intensively for the thesis (3.2), the downstream site UK2 was selected for the purposes of this study. A brief description is given here (full description in Section 3.2.2; see also Plates 3.5 to 3.8).

The site was a low-gradient, depositional section 30 to 50m in length and up to 10m in width. The chief substratum was coarse to fine sand, much of which may have originated from upstream bank erosion adjacent to a disused farm road. The right bank was overhung by a steep, vegetated bedrock bank, which shaded the stream for most of the day throughout the year. The left bank was heavily vegetated with a strip of indigenous and exotic grasses, and further up the slope, by deciduous trees and shrubs. Following flow cessation and surface water loss, a single large pool remained in the channel. This was apparently the most persistent water in this section of the river. The grassed left bank comprising the marginal vegetation biotope, remained inundated until the late pool stages.

4.3 HYDROLOGICAL CONDITIONS OVER THE 3 MIDSUMMER PERIODS

Rainfall for the period May 1993 to May 1996 (Fig. 4.1), and discharge for the same period, as measured on the upper Kowie (Fig. 4.2) are described briefly. Average annual rainfall for the Grahamstown district, in which the upper Kowie River occurs, is approximately 680mm, somewhat higher than that of the Kowie River catchment (650mm). Rainfall gauged in this district by the South African Weather Bureau (SAWB) has been used in this study, as regular trips to the upper Kowie to record rainfall were not possible.

1993

Although above-average rainfall was reported for the Grahamstown area in 1993 (943mm), the majority of the rain fell in the last three months of the year. Surface water was absent in the upper reaches of the Kowie from May to October. A heavy downpour (165mm) in late September caused the onset of flow. Peak rainfall in December (331mm) caused a spate in the river. Rainfall and flow were reduced by January 1994. The hydrological phase represented by all three months of the first midsummer period (1993/4) was FLOW.

1994

Total rainfall in 1994 was again above average (880mm). Low-flows persisted in the upper Kowie River between January and the winter month of June 1994, when flow ceased and the onset of drying caused discontinuity in surface water. Water at the site gradually diminished to a single large pool which persisted until rainfall in late August (118mm) caused the onset of flow.

Lack of significant rainfall in September and October again resulted in flow cessation in early November, and the commencement of drying. High summer air temperatures accelerated the drying process, and by mid-November water at the site was reduced to a large pool. The pool margins had receded further by mid-December 1994. High rainfall in late December (271mm) resulted in the recommencement of flow. The second midsummer period (1994/5) was characterised by the NO FLOW phase in November, the POOLS phase in December, and the ONSET phase in January.

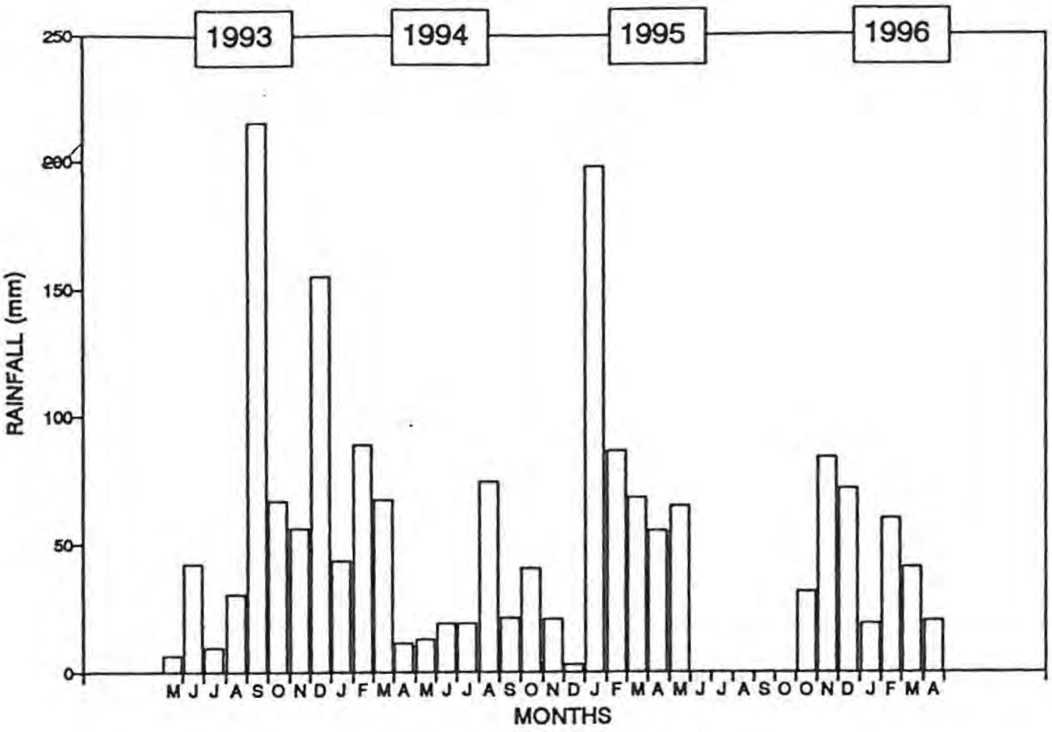


Figure 4.1 Rainfall in the Grahamstown District over the period May 1993 to May 1996, incorporating the three midsummer periods. (*Rainfall data supplied by Grahamstown City Engineers*)

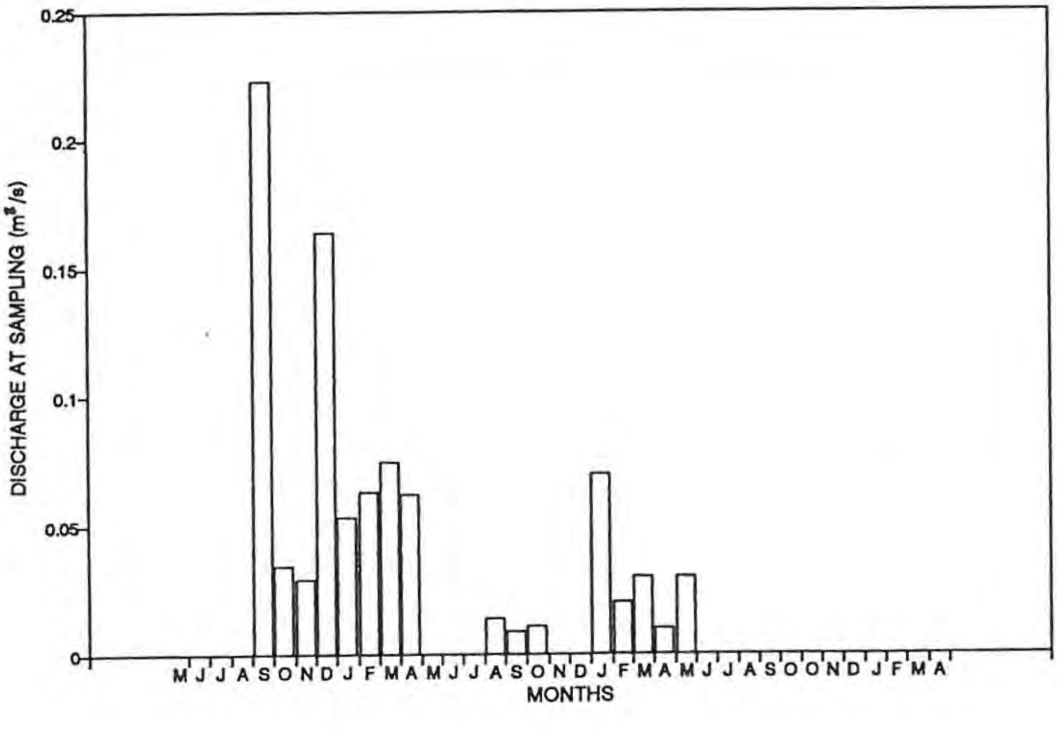


Figure 4.2 Discharge in the upper Kowie River over the period May 1993 - May 1996, as measured in the river at monthly intervals. Hydrological phases are indicated: D-DRY, O-ONSET, F-FLOW, N-NO FLOW, P-POOLS.

1995

Just-below average rainfall was recorded in 1995 (644mm). Flow persisted in the upper reaches of the river from January until May. Over the winter period (June-August), surface water was confined to one or more pools in the channel. Low precipitation in the spring and summer months (September-December) of 1995 served merely to maintain or increase the volume of the pool in this section of the river. No flow was recorded during the period. The third midsummer period (1995/6) thus represented only the POOLS phase.

1996

Sufficient rain fell during January 1996 to swell the pool at the site so that marginal vegetation was inundated with water.

4.4 METHODS

Sampling of invertebrate fauna involved monthly trips to the Kowie River site. As procedures followed in sampling trips were almost identical to those described in detail in Section 3.4, they have been extensively summarised here.

4.4.1 Sampling of invertebrates

The biotopes sampled for aquatic macroinvertebrates were the four identified by Chutter (1994) and described in Section 3.4.1: stones-in-current (SIC), stones-out-of-current (SOOC), marginal vegetation (MV) and sandy substrata (SAND); and the two identified for the purposes of this study: the full pool (POOL), and, when surface water was absent altogether, drying substrata fringing the pool (DRG). Sampling methods used were the same as those described in Section 3.4.1.

Three replicate samples were taken in each biotope. Depth and current speed were recorded at each sampling point. Approximate percentage composition of the substratum was recorded for the following materials: bedrock, boulders, cobbles, sand (coarse to fine), submerged / aquatic / floating vegetation, detritus, and leaf-fall. The four numerical classes used in the estimation of percentage composition were 1=0-25%, 2=26-50%, 3=51-75%, 4=75-100%.

4.4.2 Measurement of abiotic variables

Several abiotic variables were measured at the site when surface water was present. All procedures and instruments used were the same as those described in Section 3.4.2. Briefly, the variables measured were temperature, salinity as electrical conductivity ($mS.m^{-1}$), pH, and oxygen saturation (%). During periods of flow, discharge was computed as cross-sectional area times current velocity measured with an A. Ott flow meter (50mm propeller).

Water samples were collected in clean plastic bottles and filtered through Whatman 47mm glass microfibre filters before being stored on ice. On return to the laboratory, samples were analysed for Ammonia, Nitrate, Nitrite and Soluble Reactive Phosphorus (SRP), using a Hach DR/2000 Direct Reading Spectrophotometer. Limits of detection for nutrients were: Ammonia 0-0.50$mg.l^{-1}$ NH_3-N; Nitrate 0-4.5$mg.l^{-1}$ NO_3^--N; Nitrite 0-0.300$mg.l^{-1}$ NO_2^--N; and Soluble Reactive Phosphorus (SRP) 0-2.50 $mg.l^{-1}$ PO_4^{3-}.

4.4.3 Data analysis

Preparation of data

Taxa were identified to the lowest possible taxonomic levels, which resulted in a number of different taxonomic levels in the final data sets. Taxa in this format were referred to as 'equivalent taxa' as described in Section 1.3.

As within-biotope variability was not sought, data sets were simplified by pooling replicates for each biotope. While this was undesirable and represented a loss of information, it was considered necessary due to the inclusion of all taxa in analyses. The combination of this universal inclusion and large data-sets of individual replicates resulted in unwieldy similarity matrices, cluster analyses and ordinations, which were 'noisy' and too complex to interpret (e.g. Appendix 5.1). On average, the variability within biotopes was less than that between biotopes in a single month (see cluster analyses in Appendix 4.1), under which conditions pooling of data was considered permissible (Radloff, pers. comm).

Abundance data from the three replicates collected in each biotope were thus pooled so that each taxon per biotope per site was represented by a single number.

STATISTICAL ANALYSES

Univariate and non-parametric multivariate statistics were computed using programs from the PRIMER package (Clarke and Warwick 1994) on double-root transformed, standardised abundance data, as described in Section 1.4.

Diversity indices

Diversity indices are described (with equations) in Section 1.4.1. A number of indices were computed. These are prefixed with the term 'taxonomic' rather than 'species' (e.g. 'taxonomic diversity') because of the multiple levels to which taxa were identified. All indices were calculated on the basis of abundance data from grouped replicates ('samples').

Taxonomic diversity: using the Shannon Weiner diversity index (H', Equation 1.1);
Taxonomic richness: using Margalef's index (d, Equation 1.2);
Taxonomic evenness: using Pielou's evenness index (J', Equation 1.3)
Taxonomic distinctness: with the Δ and Δ^* indices (Equations 1.4, 1.5).

Faunal similarity

Faunal similarity was calculated in the CLUSTER program, using the non-correlation-based Bray-Curtis coefficient of similarity (1.4.3). Two sets of analyses were performed:

- the first using abundance data from individual biotopes and months, with the three replicates grouped - these were referred to as 'samples',
- the second using aggregated data from all biotopes for each month, which generated a total abundance figure for each taxon for the month - this was referred to as the 'total sample'.

Cluster analysis

Hierarchical agglomerative cluster analysis with group-average linking was performed on the Bray-Curtis similarity matrices using the CLUSTER program, as described in Section 1.4.3. Dendrograms for the clustering were generated using the program DENPLOT.

Ordination

Ordinations based on similarity data were performed using non-metric multidimensional scaling (MDS and CONPLOT programs), as described in Section 1.4.4.

Contribution of individual taxa to similarity

The program SIMPER was used to examine the contribution of individual taxa to the Bray-Curtis similarity measures within a group or cluster of samples, as described in Section 1.4.5.

Analysis of similarity for examination of null hypothesis

The ANOSIM procedure was used to examine whether or not there were significant differences between the fauna of the three midsummer periods ('groups'). Samples from individual biotopes from each three month periods (9 or more replicates) were used as data for each of these three groups. The ANOSIM procedure is described in Section 1.4.6.

Association between biotic and abiotic data

To investigate links between biotic data and univariate environmental variables, the multivariate summary of the biotic data (MDS ordination) was used as a template. Values for each abiotic variable were represented as symbols of varying sizes, and superimposed on the corresponding biotic ordination. Each abiotic variable was plotted separately in this way, using the MDS procedure with both biotic and abiotic data, as described in Section 1.4.7.

4.5 RESULTS

4.5.1 Abiotic variables

As the site studied and the upstream reaches were minimally affected by human activities, it was assumed that abiotic parameters were influenced chiefly by natural processes, and to some extent by non-recent upstream impacts (see site description).

Despite the variability in rainfall and hydrological conditions in the river between the three midsummer periods (Figs 4.1, 4.2), most of the abiotic variables measured during the wet phases remained within fairly narrow ranges for the period (Tables 4.1 and 4.2). Water temperature fluctuated between 18°C and 27°C, oxygen saturation between 85% and 125%, electrical conductivity between 16.5 and 50.3 $mS.m^{-1}$, and pH between 6.4 and 7.6.

Ranges in nutrient concentrations were broader, varying over orders of magnitude, with Ammonia (as NH_3-N) varying between 0.04 and 0.48 $mg.l^{-1}$, Nitrate (as NO_3^- -N) between 0.09 and 0.4 $mg.l^{-1}$, Nitrite (as NO_2^- -N) between 0 and 0.27 $mg.l^{-1}$, and Soluble Reactive Phosphorus (as PO_4^{3-}) between 0.09 and 1.2 $mg.l^{-1}$.

4.5.2 Diversity and composition of fauna

First midsummer period, 1993-1994: FLOW phase

The number of taxa collected in individual biotopes and in different months varied substantially during the first midsummer phase of 1993-4 (FLOW). The number of taxa, taxonomic richness and taxonomic diversity were at their lowest during December 1993 during peak flows, and at their highest for the study in January 1994, when flow levels had decreased (Table 4.3).

In November, two months after the commencement of flow into a dry channel, 45 taxa were collected in MV, 22 in SIC and 11 in SAND. Taxonomic richness at the site was bolstered by the fauna collected in MV (Table 4.3). The total

Table 4.1 Values of abiotic variables measured monthly at site UK1 on the upper Kowie River, over the three midsummer periods (October included for antecedent conditions).

PERIOD	PHASE	DISCHARGE (m^3/s)	WATER TEMP.(C)	% OXYGEN SAT.	EC (mS/m)	pH
1993-4						
October	ONSET	0.02	21.5	106	45.1	6.8
November	FLOW	0.05	18.7	81	40.3	6.4
December	FLOW	0.17	24.5	95	33.3	6.4
January	FLOW	0.05	21.0	98	22.6	6.6
1994-5						
October	FLOW	0.01	18.0	125	42.3	6.7
November	NO FLOW	0.00	16.0	118	47.0	7.0
December	POOLS	0.00	19.2	112	50.3	7.3
January	ONSET	0.07	26.0	102	30.9	7.1
1995-6						
October	POOLS	0.00	18.9	106	26.6	7.4
November	POOLS	0.00	27.0	103	16.5	7.3
December	POOLS	0.00	24.2	85	30.1	7.4
January	POOLS	0.00	23.0	103	39.8	7.6

Table 4.2 Nutrient concentrations recorded for site UK1 on the upper Kowie, monthly over the three midsummer periods.

	93/4			94/5			95/6		
(mg/l)	Nov.	Dec.	Jan.	Nov.	Dec.	Jan.	Nov.	Dec.	Jan.
Ammonia (as NH_3-N)	0.48	0.51	0.06	0.17	0.07	0.00	0.08	0.07	0.04
Nitrate (as NO_3^--N)	0.09	0.20	0.20	0.30	0.41	0.30	0.21	0.02	0.02
Nitrite (as NO_2^--N)	0.00	0.01	0.01	0.00	0.01	0.01	0.02	0.27	0.27
Phosphorus (as PO_4^{3-}) (reactive)	1.20	0.22	0.04	0.08	0.15	0.17	0.27	0.11	0.80

RHODES UNIVERSITY LIBRARY

Table 4.3 Various univariate community indices for the upper Kowie River, computed on abundance data from samples collected in available biotopes.

	TOTAL TAXA	TAXON. RICHNESS *d*	TAXON. DIVERSITY *H'*	TAXON. EVENNESS *J'*	TAXON. DISTINCTNESS *Delta* Average (Std.Deviation)	TAXON. DISTINCTNESS *Delta**
NOVEMBER 1993						
TOTAL	**47**	**7.41**	**2.96**	**0.77**	**3.656 (0.39)**	**4.476 (0.39)**
SIC	22	4.98	2.42	0.78		
MV	45	7.46	2.99	0.79		
SAND	11	2.4	1.72	0.72		
DECEMBER 1993						
TOTAL	**37**	**6.52**	**2.74**	**0.76**	**2.57 (0.39)**	**3.405 (0.38)**
SIC	20	3.96	1.8	0.60		
MV	10	2.67	2.22	0.97		
SAND	18	3.69	2.04	0.71		
JANUARY 1994						
TOTAL	**83**	**12.2**	**3.8**	**0.86**	**3.645 (0.51)**	**4.08 (0.42)**
SIC	25	5.11	2.84	0.88		
MV	64	9.62	3.57	0.86		
SAND	14	3.5	2.02	0.77		
NOVEMBER 1994						
TOTAL	**61**	**8.39**	**3.56**	**0.87**	**3.49 (0.55)**	**4.39 (0.26)**
MV	37	5.96	3.18	0.88		
SAND	7	1.34	1.6	0.82		
SOOC	50	7.43	3.42	0.87		
DRG	7	1.59	1.78	0.92		
DECEMBER 1994						
TOTAL	**41**	**6.34**	**3.31**	**0.89**	**3.46 (0.5)**	**4.01 (0.51)**
MV	28	4.81	3.08	0.93		
POOL	19	3.3	2.54	0.86		
DRG	19	4.73	2.62	0.89		
JANUARY 1995						
TOTAL	**47**	**8.37**	**3.5**	**0.91**	**3.68 (0.28)**	**4.35 (0.21)**
SIC	23	5.05	2.79	0.89		
MV	28	5.54	3.03	0.91		
SAND	14	3.69	2.52	0.95		
NOVEMBER 1995						
TOTAL	**40**	**6.59**	**2.87**	**0.78**	**3.56 (0.29)**	**3.95 (0.38)**
POOL	18	3.58	2.5	0.86		
POOL	32	5.69	2.69	0.78		
DRG	9	2.82	1.99	0.90		
DECEMBER 1995						
TOTAL	**47**	**7.33**	**3.04**	**0.79**	**3.95 (0.24)**	**4.69 (0.22)**
POOL	40	6.47	2.86	0.78		
POOL	20	4.19	2.54	0.85		
DRG	7	1.86	1.66	0.85		
JANUARY 1996						
TOTAL	**59**	**9.54**	**3.19**	**0.78**	**3.78 (0.17)**	**4.38 (0.27)**
POOL	22	4.39	2.22	0.72		
POOL	28	5.26	2.48	0.74		
MV	40	7.81	3.15	0.86		

complement of 47 taxa was numerically dominated by ostracods, dytiscid adults, planorbid and lymnaeid snails, simuliids (*S. nigritarse)* and culicids (Appendix 4.2). Other groups present included mayflies, dragonflies, gyrinids, gerrid and hydrometrid hemipterans and chironomids. Taxonomic evenness reflected a relatively uniform distribution of individuals among taxa (Table 4.3).

During December's peak flows, the total number of taxa decreased to 37 and the indices of taxomomic richness, diversity and distinctness also showed a slight decrease (Table 4.3). Taxonomic evenness was not affected. MV yielded 10 taxa, SIC 20, and SAND 18. Chironomini and simuliids were common in samples. Additional taxa included *Oxyethira* sp. hydroptilids, *Orthetrum* sp. libellulids, *Sigara* sp. corixids, *Amphiops* sp. hydrophilids, Tanypodinae, Tanytarsini and Orthocladiinae (Appendix 4.2). Many of the animals which had been present in November's samples were absent from these samples (e.g. culicids, physids, caenids, corduliids, libellulids).

Many of the invertebrates absent from December's samples were present again during January, when flow had diminished and stabilised. In total, January's sample yielded 83 taxa, more than double the number collected in December. Of these, 64 were collected in MV, 25 in SIC and 14 in SAND. Certain of the taxa collected in December were still present (e.g. crabs, baetids), and dominant groups in the samples were odonates, hemipterans, hydrophilid beetles, Chironomini and certain Tanytarsini.

Taxa common to all three months in 1993/4 midsummer included oligochaetes, *Paracypretta syngramma* ostracods, *Cloeon* sp. baetids, *Simulium nigritarse* blackflies, Tanytarsini (type B), chironomid pupae, *Ceratophallus sp.* planorbids and *Lymnaea columella* lymnaeids (Appendix 4.2).

Second midsummer period - 1994-1995: POOLS and ONSET phases

The early POOLS phase of November 1994, one month after flow cessation, yielded a total of 61 taxa. Of these, 50 were collected in SOOC, 37 in MV, 7 in SAND and 7 in DRG. Taxonomic diversity was slightly elevated relative to that of the previous November (FLOW phase). Taxonomic evenness, approaching the value of 0.9 for all biotopes, suggested a close-to-even spread of individuals between taxa present, and a lack of species dominance (Table 4.3). Δ and Δ^* values revealed similar taxonomic distinctness to that of the previous midsummer, with values suggesting taxonomically distinct assemblages (a spread of species through different taxonomic groups). Typically-rheophilic taxa (e.g. simuliids) were absent, however nymphal instars of baetid and caenid mayflies, lestid and coenagriid damselflies, and corduliid and gomphid dragonflies were present in low numbers. The balance of fauna comprised mobile forms such as dytiscid, corixid and notonectid adults, and groups typical of lentic conditions, such as ostracods and gastropods (Appendix 4.2).

By December 1994 (late POOLS), the volume of pools had diminished and the number of taxa collected had decreased to 41: 28 from MV, 19 from the POOL biotope, and 19 from DRG. Water temperature was below 20°C, EC was within the narrow range of its values for the three periods, and dissolved oxygen levels were greater than 100% (Table 4.1). Taxonomic evenness approached a high value of 0.9, and taxonomic distinctness was comparable to that of the previous month, but marginally higher than that of the previous December (Table 4.3). Several of the taxa which had been collected in November 1994 samples were absent, including *Baetis* sp. and *Demoulinia* complex mayflies, several odonates and hemipterans, and hydroptilid trichopterans (Appendix 4.2). *Baetis harrisoni* and *Austrocaenis* sp. nymphs were present in low numbers, together with predaceous coenagrionid, chlorolestid and libellulid odonate nymphs, oligochaetes, several chironomid genera, tabanid larvae, and several molluscs (*Ferrissia* sp., *Lymnaea columella, Pisidium* sp. and *Ceratophallus* sp.).

High rainfall caused the onset of flow in late December 1994. Within two weeks, 47 taxa were collected, of which marginal vegetation yielded 28 taxa, SIC 23 and SAND 21 (Table 4.3). Taxa present in these flow samples included ostracods, lestids, *Sigara* sp. corixids, *Cloeon sp.* baetids, *Orthetrum* sp. libellulids, dytiscid and hydrophilid larvae, tipulids, and molluscs (Appendix 4.2). Slight increases in the indices of taxonomic diversity, evenness and distinctness were recorded (Table 4.3).

Taxa which persisted in the river throughout the midsummer months of 1994-1995 were oligochaetes, *Potamonautes* sp. crabs, *Austrocaenis* sp. caenids, *Anisops* sp. notonectids, *Laccophilus lineatus* dytiscids, *Bezzia* type ceratopogonids, orthoclad chironomids, *Ferrissia* sp. ancylids, *Lymnaea columella* lymnaeids, *Ceratophallus* sp. planorbids and *Pisidium* sp. sphaeriids.

Third midsummer period - 1995-1996: Late POOLS

Flow had ceased and drying commenced between July and August 1995, and pools which remained in the channel persisted through this third midsummer period. Short bursts of rainfall were insufficient to cause flow, but maintained or increased pool volume during November and December, causing inundation of marginal vegetation in January. Other abiotic conditions were relatively stable over the period (Tables 4.1 and 4.2).

The substantial increases in taxonomic richness and diversity were an illustration of the increase in total number of taxa collected: 40 during November, 47 during during December, and 59 during January. Taxonomic evenness was lower than that of the previous midsummer period, although still close to 1, and there was no change in taxonomic distinctness (Table 4.3, Appendix 4.2). During November, POOLS yielded 18 and 32 taxa respectively, and DRG 9. During December, POOLS yielded 20 and 40 taxa, and DRG 7. MV contributed 40 taxa and POOLS 28 and 22 taxa to January's total (Table 4.3).

Microcrustaceans and chironomid taxa were numerically abundant in November's samples, and other common taxa included mayflies, dytiscid adults and larvae, and sphaeriid bivalves. Hemipterans and odonates were sparse in comparison with the previous November's fauna (Table 4.3). During December, a similar fauna was collected in the pool, and additional taxa included cladocerans, ancylid snails (*Ferrissia* sp.), ecnomid trichopterans, gomphids, and a variety of hemipterans (Appendix 4.2). January's samples yielded several additional taxa including decapods, mayflies, libellulids, helodid and hydrophilid beetles, and lymnaeid snails (Appendix 4.2). Taxa collected in all three months of this midsummer period included oligochaetes, ostracods, *Austrocaenis* sp. mayflies, *Sigara* sp. corixids, *Anisops* sp. notonectids, hydrophilid larvae, ceratopogonids, chironomids, culicids, and sphaeriid snails.

4.5.3 Cluster analysis and ordination of samples from individual biotopes

The dendrogram for hierarchical cluster analysis of pooled replicates (hereinafter referred to as 'samples') from individual biotopes and all months of the study is presented in Figure 4.3.

Faunal similarities were, on average, low between sample groups, with the majority of clusters forming between 20 and 35%. A line was drawn through the similarity point of 20%, and clusters occurring to the right of the line were marked as Groups 1 to 7 (Fig. 4.3). Samples from the midsummer FLOW phase of 1993/4 were clustered in Groups 1 to 3, together with a few additional samples from November 1994. Samples collected in the second midsummer phase, which represented NO FLOW, POOLS and ONSET phases, were scattered through the dendrogram, with the NO FLOW samples grouping with samples from the 93/94 midsummer FLOW phase samples (Group 2); and the POOLS and ONSET samples grouping with the POOLS phase samples from 95/96 (Group 5). Two further samples clustered in Group 4. Samples from the third period, 1995/6, were clustered in Group 5 (with samples from the previous year), and in Groups 6 and 7 (Fig. 4.3).

MDS ordination based on similarities between samples from individual biotopes generated a high stress (0.26) representation due to low sample resemblances seen in clustering. This indicated that it could not be considered an entirely reliable representation of the relationships between samples (Clarke and Warwick 1994). Groups 1 to 7, as discerned on the dendrogram, were superimposed on the ordination points. Although there is little distance between samples, there is a gradient between sample groups representing FLOW conditions (Groups 1 and 2) and those representing NO FLOW, POOLS and ONSET conditions (Groups 3, 4 and 5). The groups are presented in Figure 4.4a for the purposes of comparing the biotic ordination with abiotic variables (Fig. 4.4b, see Section 4.5.7).

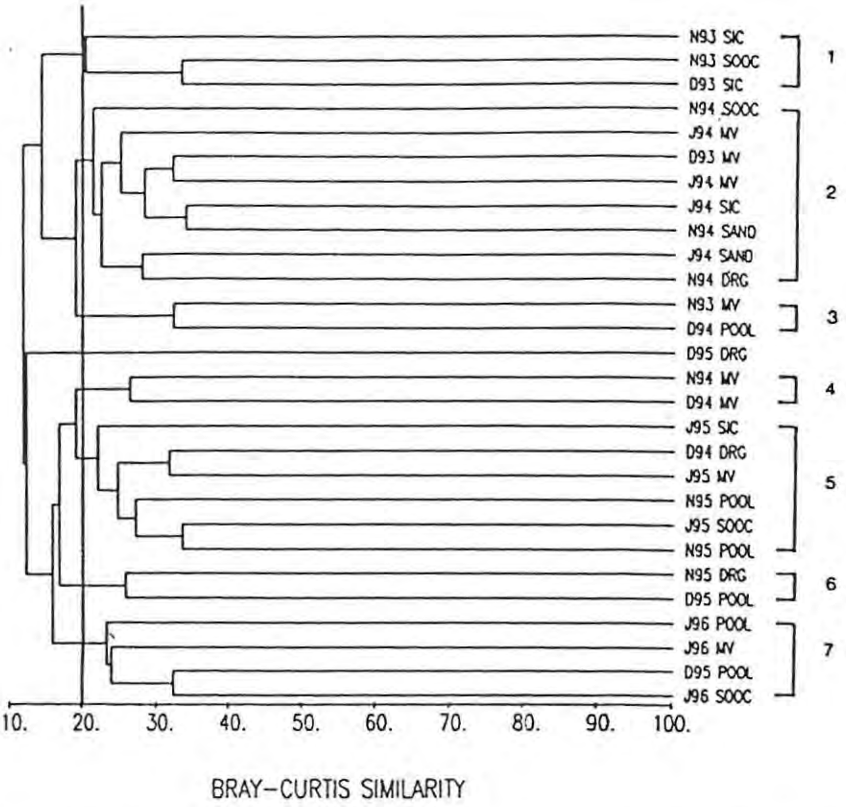


Figure 4.3 Dendrogram for hierarchical cluster analysis of monthly samples from all biotopes for the three midsummer periods, based on Bray-Curtis similarities, which were calculated on standardised, double-root transformed data. Groups to the right of 20% similarity are labelled 1 to 7. N-November, D-December, J-January. SIC - stones in current, SOOC - stones out of current, SAND - sandy substrata, POOL - shallow pools, DRG - drying fringes.

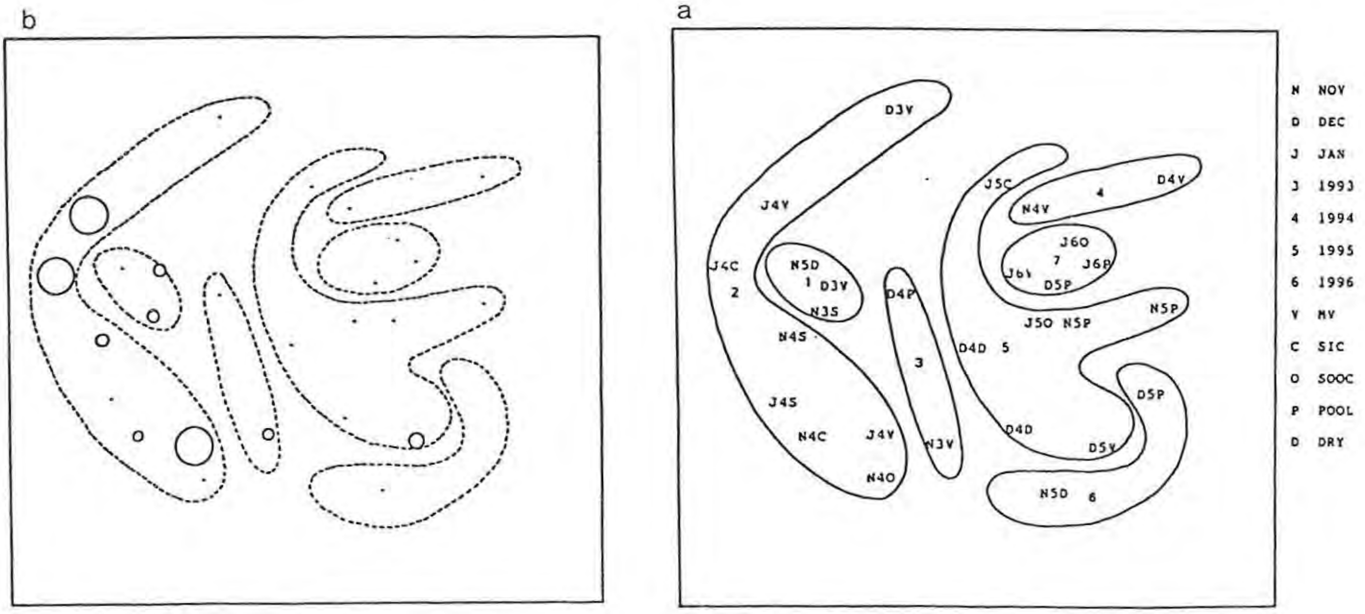


Figure 4.4 a) Ordination based on Bray Curtis similarities of monthly samples (Stress – 0.26). Data were standardised and double-root transformed. b) Same ordination with scaled symbols representing increasing values of current speed in individual biotopes.

4.5.4 Cluster analysis and ordination of total monthly samples

Cluster analysis of total (aggregated) samples from each month (Fig. 4.5) generated three major groupings, all at less than 50% faunal similarity. Clusters to the right of the line drawn through the 30% similarity point were designated Groups 1 to 3. Samples from the FLOW period of November 1993 to January 1994 clustered together in Group 1. Samples from December 1994 (late POOLS) and January 1995 (ONSET) coupled in Group 2. The greatest overall faunal similarity was that of Group 3 samples, collected in November 1994, November and December 1995, and January 1996 (NO FLOW and POOLS phase samples).

Ordination of total samples from each month using MDS produced a low stress (0.12) map of the relative positions of sample groups (Fig. 4.6), with a clear spatial gradient between samples collected in established flow conditions (Group 1) and those collected in onset and in non-flow conditions (Groups 2,3).

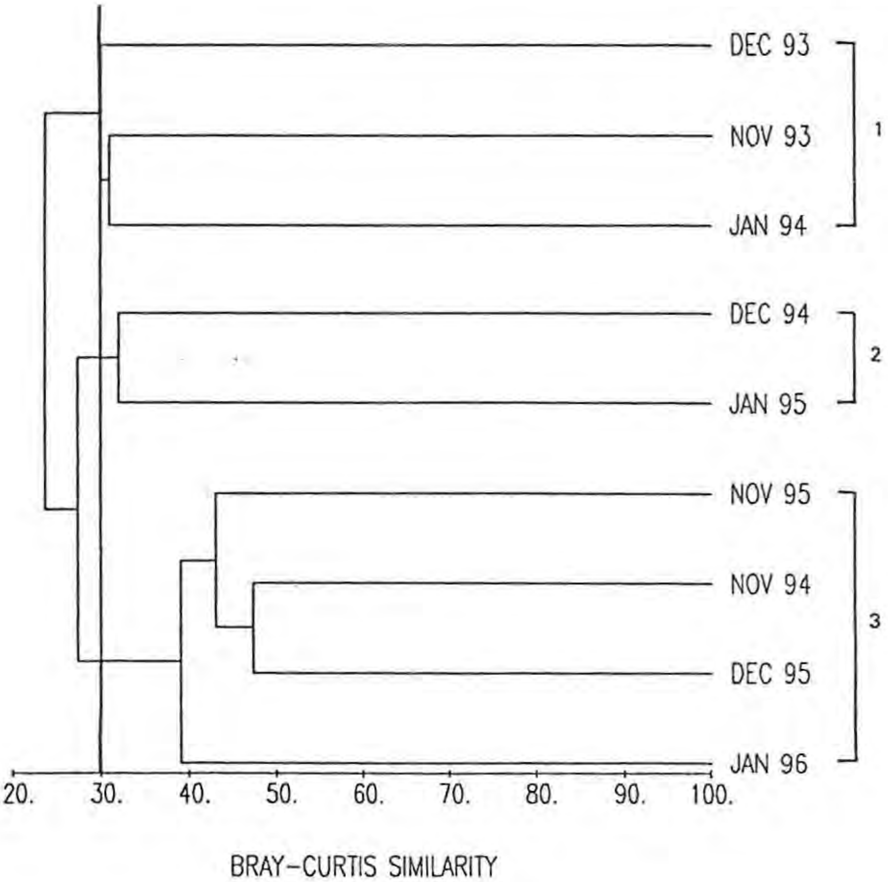


Figure 4.5 Dendrogram for hierarchical cluster analysis of total monthly samples for the three midsummer periods, using aggregated data from all biotopes sampled.

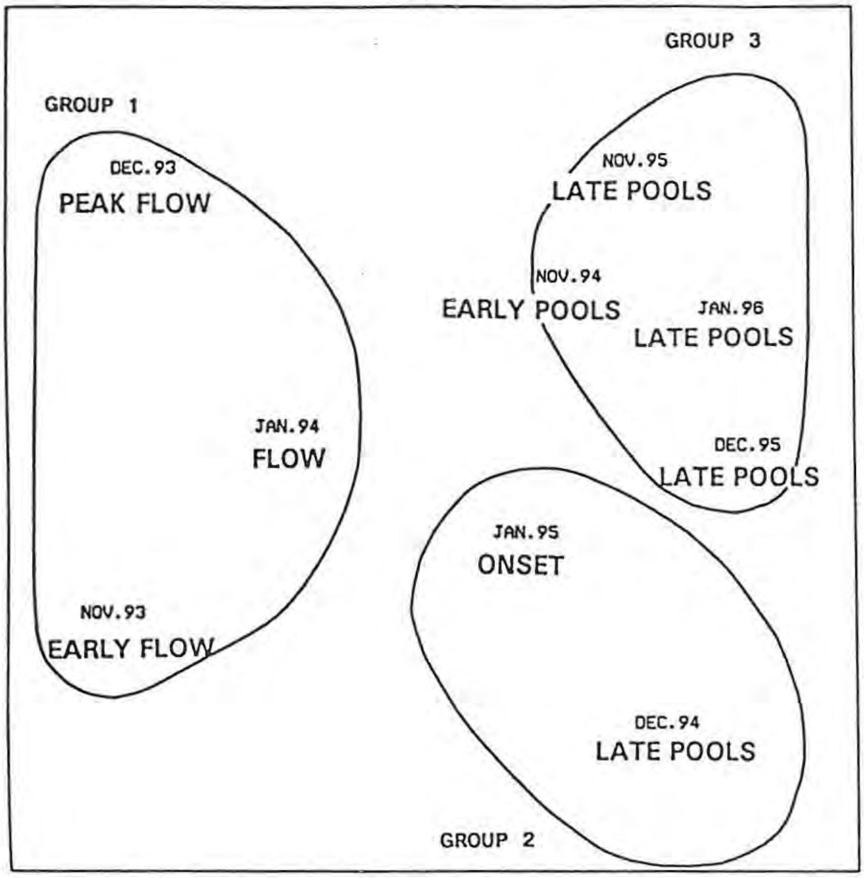


Figure 4.6 MDS ordination of the nine total monthly samples for the three midsummer periods, based on Bray Curtis similarities between samples.

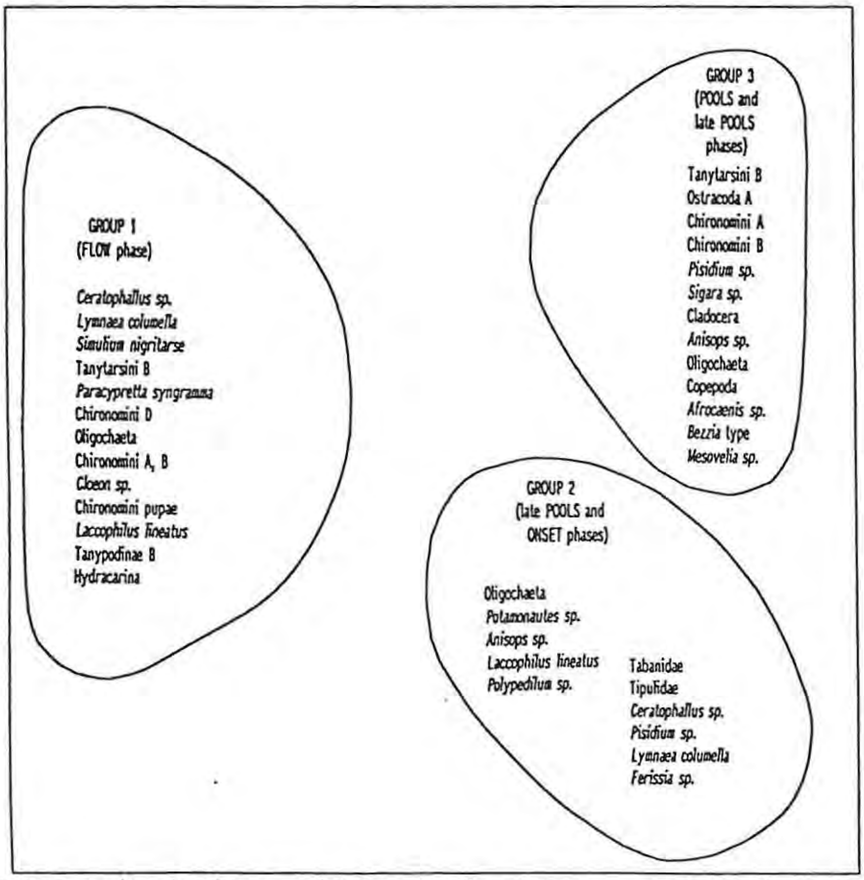


Figure 4.7 Individual taxa which contributed to approximately 75% of similarity within each group, as calculated using SIMPER (for Groups 1 and 3) and by visual inspection of data (Group 2).

4.5.5 Contributions of individual taxa to group similarities

Taxa which contributed to the majority of similarity in groups of total samples (only up to 70%, for the sake of brevity), as discerned by SIMPER, are superimposed on the MDS ordination of these samples (Fig. 4.7).

4.5.6 Analysis of faunal similarity for testing of null hypothesis

The ANOSIM procedure tested for significant differences between the three midsummer periods. Global *R* value for the test was 0.301, at a significance level of 0.0% at which the null hypothesis could be rejected. Pairwise tests, to examine whether individual years differed significantly from one another, showed that each of the midsummer periods was significantly different from the others (Table 4.4).

Table 4.4 Results of pairwise tests conducted to test for significance of difference between 'groups', in this case midsummer periods. Where the value of R is less than 1, at a significance of less than 5%, significant difference is indicated.

SAMPLE PAIR	R	SIGNIFICANCE %	SIGNIFICANTLY DIFFERENT
93/4 and 94/5	0.29	0.3	YES
94/5 and 95/6	0.49	0.0	YES
95/6 and 96/7	0.16	3.9	YES

4.5.7 Linking of biotic and abiotic variables

The MDS ordination of all samples from all biotopes (Fig. 4.5a) yielded a poor 2-dimensional representation of sample clusters (Stress = 0.26). However, as certain of the abiotic variables (e.g. current speed, depth, percentage composition of the substratum) were measured in individual biotopes, it was necessary to superimpose abiotic data onto this ordination rather than that of the total (aggregated) monthly samples.

The abiotic variables tested in this way were oxygen saturation, pH, EC, water temperature, current speed in the biotope, depth of the biotope, percentage composition of the substratum (cobbles, sand, gravel, algae, leaves all tested separately), and concentrations of Ammonia, Nitrate, Nitrite and Soluble Reactive Phosphorus. Of these, only current speed in individual biotopes showed any trend in common with the biotic ordination, with maximum values positioned in the vicinity of Group 1 (Fig. 4.4b).

4.6 DISCUSSION

4.6.1 Environmental variability

While the majority of abiotic variables remained fairly stable from year to year, rainfall and discharge showed the considerable fluctuations characteristic of semi-arid environments (e.g. Braune 1985). This variability, while disallowing the development of cyclicity in flow phases and biotic assemblage structure reported by Boulton and Lake (1990), seemed to be the very fabric of the upper Kowie River ecosystem.

The *relatively* narrow range of values reported for most of the environmental variables (other than rainfall, discharge, and current speed in biotopes), and the lack of association between these and the biotic data probably relates to the realtively stable 'internal' conditions in the aquatic environmentin the presence of sufficient surface water, relative to the inconstancy of the 'external' conditions and the biota. Relatively high nitrate concentrations (up to 0.4 mg/l) may have been attributable to groundwater inputs (*cf.* Porter 1975, cited by Dallas and Day 1993), but this was not tested for. While phosporus concentration in streams is affected by flow and duration of surface water (Dallas and Day 1993), inconsistency in soluble reactive phosphorus (as PO_4^{3-}), and high concentrations in certain months (> 1mg/l) are difficult to explain, other than from natural riparian organic inputs, and considering the lack of present-day farming activity or any other anthropogenic inputs upstream of the site.

4.6.2 Effects of hydrological variability on invertebrate fauna

The significant differences between the fauna of each of the three midsummer periods indicated that faunal variability within a midsummer period was less than that between periods. However, despite the variability in diversity and species richness both within and between years, and the low overall similarity levels indicated in cluster analysis, the grouping of samples from similar phases pointed to the primary role of hydrological conditions in regulating faunal character. Groupings further indicated some element of cohesion in the biota of FLOW periods and non-flow periods. It appeared that fauna from the ONSET phase was more likely to resemble that of the POOLS phase (which generally preceded onset conditions) than that of the FLOW phase (which generally followed the ONSET phase).

At a finer scale, current speed in individual biotopes clearly contributed to the separation between samples from the FLOW phase of midsummer 1993/4 and those from the ONSET and POOLS phases (Figs 5a,b).

From our results and observations, where surface water conditions persisted (at the scale of the channel or a single biotope), generating some degree of stability over time, a gradual increase in faunal diversity could result, as in the POOLS phase of November to January 1995-6 (and further examples in Section 3.6). Williams (1987) and Boulton and Suter (1986) found, similarly, that in temporary streams, species richness appeared to increase with increasing duration of surface water or flow.

Events such as peak flows or spates, which may be construed as disturbances (e.g. Poff 1992) had the potential to cause notable reductions in taxa, as demonstrated by the decreases in taxonomic richness and diversity during these conditions in December 1993. In this case, the disturbance was apparently related to the *rate* and *extent* of change in hydrological conditions. Number of taxa present recovered to over double pre-spate levels within a month (Table 4.3). Harrison (1966), Boulton and Lake (1992b), and Grimm and Fisher (1989) reported similarly rapid recovery of fauna in intermittent or ephemeral streams, which Boulton and Lake (1992b) attributed to rapid recolonisation rates and short life cycles. The ability of a fauna to recover from disturbance (*resilience, sensu* Grimm and Fisher 1989) in this way was considered by Boulton and Lake (1992b) to be a more important factor in faunal persistence than the ability of fauna to resist or deflect disturbance (*resistance, sensu* Grimm and Fisher 1989).

While the initial onset of flow into an almost-dry channel in late December 1994 may have caused a reduction in fauna (uncertain as samples were not taken at the time of the onset), within two weeks of flow recommencement, samples yielded a greater number of taxa than that found in the pre-onset samples. A 30% similarity between the invertebrates collected in pre- and post-onset samples (Fig. 4.4) suggested that at least a third of the taxa collected in December and January were shared. The implication is that the rapid faunal recovery may, for at least a portion of the fauna, have involved a combination of both resilience and resistance.

The resetting effect of unpredictable high flows in this environment (Poff 1992), and the small timeframe for the establishment of a more diverse fauna, lends weight to the suggestion of Davies *et al.* (1994) that in semi-arid environments, events such as floods should not be considered disturbances in the sense of 'aberrant phenomena', but should rather be viewed as important cues for dynamic ecosystem changes.

4.6.3 A consideration of succession in an intermittent aseasonal river

Succession - the sequential replacement of species groups over time to culminate in a climax community (Odum 1971) - is a generally accepted ecological concept. Boulton and Lake (1992), working on seasonal intermittent streams, proposed that where seasonal environmental factors such as rainfall, discharge, temperature, pH, etc. governed change in assemblages, succession adopted a cyclical pattern. This - unlike 'classical' succession - was non-linear, and lacked the development of a climax community. The authors referred to Reynolds' (1988) use of the term *'seasonal periodicity'* to describe this process of community change.

In the upper Kowie River, rainfall and discharge are aperiodic over the short term ($<$ 10 years), showing only broad seasonal trends over time (South African Weather Bureau database). No consistent patterns emerged in the fauna from year to year of this study, and the term 'seasonal periodicity' would probably not describe faunal change well. The low similarity in biota within and between months and years suggested a lack of faunal persistence, probably resulting from the frequency of disturbance (or change of phase, Section 1.3.6). Hildrew and Giller (1992) noted that recovery from small-scale disturbance was 'legendarily fast' in stream invertebrates, and that recolonisation of disturbed patches of stream bed was complete well within a generation time of the animals in question. They continued that '*Different arrival and departure rates of individuals of different species may produce sequences of dominant species at different times after disturbance (Downes and Lake 1991), but these changes do not constitute succession'*. While it is not possible to make inferences based on the data available, it appears that, on the whole, both linear and cyclical succession in upper Kowie fauna was disallowed by frequent destabilisation of aquatic habitat.

4.6.4 Identification of colonists, facultative taxa, and residents

Williams and Hynes (1977) associated three groups of fauna with the temporary streams they studied. The first group comprised permanent stream forms which were not particularly adapted to life in temporary rivers, but could withstand short dry periods. The second group included those facultative taxa which occurred in both lentic and lotic waters, and the third group consisted of aquatic invertebrates highly adapted to, and often restricted to, temporary rivers. These three groups are adopted here: the first as 'opportunist colonists', the second as 'facultative taxa' and the third as 'residents'.

Fauna of the first two groups generally consist of highly mobile, aerial taxa which colonise the river when conditions are suitable for breeding and for development of juvenile forms. Whereas facultative taxa may remain in the stream during more the more adverse conditions (e.g. loss of surface water and early stages of drying), the colonists are less tolerant of such conditions and may relocate to more favourable environments. The process of colonisation was described by Sheldon

(1984) as the *'sequence of events that leads to the establishment of individuals, populations, species, or higher taxa in places from which they were, however temporarily, absent'* (the author notes that this definition excludes the alternative to colonisation, which is persistence in dormant, resistant life-cycle stages). Adult requirements (e.g. for specific breeding conditions) can restrict successful colonisation, and larval requirements (e.g. adequate and appropriate food, and cover) can reduce the number of successful colonists. Gray and Fisher (1981), working in a desert stream, found that most colonists arrived in the system as adults.

Following Sheldon's (1984) definition, 'opportunist colonists' were distinguished as taxa which were absent from the stream for some period of time, due to relocation rather than physiological avoidance (e.g. aestivation). Adult colonists were generally distinguished either on the basis of their observed presence or that of their juvenile forms. Taxa regarded as opportunist colonists are listed in Table 4.5.

Long-lived aquatic adult members of Coleoptera and Hemiptera disperse widely and tend to persist for some time in the colonised habitat, with or without reproducing (Sheldon 1984). Many representatives of these orders are suited to the second group of temporary river fauna, which comprises facultative taxa found in both lentic and lotic environments.

All the coleopterans and hemipterans listed are capable of inhabiting a temporary river such as the Kowie during all but the driest periods, when they may relocate. Because both groups utilise atmospheric oxygen, reduced oxygen concentration in pools would not be a limiting factor. The taxa listed all prefer quiet freshwater habitats or the wet fringes thereof (McCafferty 1981), and are seldom present in areas of swiftly moving water.

Fauna of the third group may be referred to as 'residents' of the temporary river environment. These animals generally have low mobility and are capable of withstanding the capricious environment of temporary rivers by virtue of their low habitat specificity and/or their mechanisms of behavioural or physiological adaptation to adverse conditions (e.g. drying). In the upper Kowie River, a number of taxa could be allocated to the category of residents. In the case of these invertebrates, temporary absence from the river is an indication of dormancy in

Table 4.5 The three groups of taxa in the upper Kowie River, distinguished on the basis of findings in this study .

OPPORTUNIST COLONISTS	**FACULTATIVE TAXA**	**RESIDENTS**
EPHEMEROPTERA	ODONATA	OSTRACODA
Baetidae	Libellulidae	COPEPODA
Baetis sp.	*Orthetrum sp.*	CLADOCERA
Chloeon sp.	Gomphidae	OLIGOCHAETA
Demoulinia comp.	*Notogomphus sp.*	
Caenidae		DIPTERA
Austrocaenis sp.	COLEOPTERA	Chironomidae
	Dytiscidae	Tipulidae
ODONATA	*Laccophilus sp.*	Ephydridae
Aeshnidae	*Hyphydrus sp.*	Tabanidae
Aeshna sp.	Hydrophilidae	
Anax sp.	*Amphiops sp.*	GASTROPODA
Coenagrionidae	Gyrinidae	Ancylidae
Pseudagrion sp.	*Dineutus grossus*	*Ferrissia sp.*
Lestidae	Hydraenidae	Lymnaeidae
Lestes sp.	*Ochthebius andronius*	*Lymnaea columella*
		Planorbidae
TRICHOPTERA	HEMIPTERA	*Ceratophallus sp.*
Hydroptilidae	Corixidae	
Oxyethira sp.	Hydrometridae	PELECYPODA
Hydropsychidae	Notonectidae	Sphaeriidae
Cheumatopsyche sp.		*Pisidium sp.*
DIPTERA	?TRICHOPTERA	
Simuliidae	Ecnomidae	
Simulium spp.	*Ecnomus sp.*	

some resting state. The reappearance of these taxa following dormant periods does not make them colonists, according to Sheldon's (1984) definition of the term.

The presence of residents adds a dimension of stability to the biota, as these taxa are probably responsible for any pattern which exists. However, our findings do not correspond entirely with those of Williams and Hynes (1977), who found that in terms of the most abundant taxa, the species composition of the river could be considered stable despite the instability of the environment. Firstly, in the Kowie River, most abundant taxa were often opportunist colonists, occupying the river only when conditions were suitable to them (e.g. *Simulium* spp.) - these could not be seen as stabilising influences. Secondly, although at coarse taxonomic levels the abundance data may indicate that certain families or orders of invertebrates (e.g. ostracods, chironomids) consistently comprised a large proportion of the total fauna, at the level of tribe, genus or species, there was a *constant shift* in composition for many groups (e.g. dytiscids, hydracarinids, chironomids). Thus, while resilience and/or resistance may characterise certain families, giving the impression of stability, individual genera or species in these groups may exhibit highly specific preferences for particular hydraulic conditions or resource environments.

4.6.5 Possible alternative approaches in the investigation of intermittent rivers

In the sense that many temporary river systems are aperiodic, it is tempting to view them in the context of modern mathematical concepts which take account of the complexity inherent in dynamic systems. 'Chaos' is a mathematical concept of predicting unpredictability. The theory holds that in a non-linear (or non-equilibrial) world, order, system and pattern are often absent at the most commonly-applied scales, but that the seemingly chaotic or unpredictable behaviour may be underlain by structure at other (usually smaller) scales (see Naiman *et al.* 1988). So-called chaotic systems can give rise to turbulence and coherence at the same time (Gleick 1988). The quest for obvious pattern is often an inappropriate one, particularly in highly variable systems (see Brown 1985).

Although application of chaos models is not possible without large, long-term data sets, the principle of chaos is witnessed at a superficial level in the combination of both disorganisation and unanimity in the results of this study. Disorder is evident in the considerable variability in taxonomic composition over various spatial and temporal scales, and the resultant paucity of faunal structure. Unity, however, is shown to some extent in the consistently high taxonomic evenness and taxonomic distinctness of the fauna (with few outliers). High taxonomic evenness (>0.7) was a consistent feature of the biota, and dominance of individual taxa was thus negligible. Taxonomic distinctness, as measured by the Δ and Δ^* indices also remained consistently high (i.e. species or genera were, in general, not closely related, but belonged to several different families, or orders).

4.7 CONCLUDING POINTS

- Lack of seasonality in rainfall and flow in this semi-arid zone river resulted in highly variable and unpredictable hydrological conditions between midsummer periods.
- Significant differences were recorded in the fauna of the three midsummer periods.
- While hydrological conditions and faunal composition fluctuated widely, taxonomic evenness and distinctness values remained consistently high.
- Assemblage structure was unstable at most temporal and spatial scales, however those invertebrate taxa capable of withstanding the majority of physical conditions in the system (residents) provided a consistent 'base' for the invertebrate complement.
- Of all the abiotic variables tested for an association with biotic form, only 'current speed in the biotope' showed trends which matched those evident in the biota.
- Greatest faunal similarities were generally found between samples collected in the same hydrological conditions. Hydrology was considered the primary faunal structuring force in the upper Kowie River.

REFERENCES

Allanson, B.R., Hart, R.C., O'Keeffe, J.H. and Robarts, R.D. 1990. Inland Waters of Southern Africa: an Ecological Perspective. *Monographiae Biologicae* **64**. Kluwer Academic Publishers, Dordrecht, 458pp.

Bender, E.A., Case, T.J. and Gilpin, M.E. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* **65:** 1-13.

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24:** 123-141.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* **27**: 99-121.

Boulton, A.J. and Lake, P.S. 1992. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology* 27:123-138.

Boulton, A.J. and Stanley, E.H. 1995. Hyporheic processes during flooding and drying in a Sonoran Desert stream. II. Faunal dynamics. *Archiv für Hydrobiologie* **134:** 27-52.

Boulton, A.J., Peterson, C.G., Grimm, N.B. and Fisher, S.G. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* **73** (6): 2192-2207.

Boulton, A.J., Spangaro, G.M. and Lake, P.S. 1988. Macroinvertebrate distribution and recolonisation on stones subjected to varying degrees of disturbance: an experimental approach. *Archiv für Hydrobiologie* **113:** 551-576.

Braune, E. 1985. Aridity and hydrological characteristics: Chairman's summary. *Hydrobiologia* **125:** 131-136.

Brown, A.C. 1985. Variability in biological systems. *South African Journal of Science* **89:** 308-309.

Chutter, M. 1970. Hydrobiological studies in the catchment of the Vaal Dam, South Africa. Part 1. River zonation and the benthic fauna. *Internationale revue der gesamten Hydrobiologie* **55:** 445-494.

Chutter, M. 1994. The rapid biological assessment of stream and river water quality by means of the macroinvertebrate community in South Africa. *In:* M.C. Uys (ed). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town.

Water Research Commission Report No. TT 63/94.

Clarke, K.R and Warwick, R.M. 1994. *Change in Marine Communities: An approach to Statistical analysis and interpretation*. Natural Environment Research Council, U.K. 144pp.

Dallas, H.F. and Day, J.A. 1993. *The effect of water quality variables on riverine ecosystems: a review*. Water Research Commission Report no. TT61/93.

Davies, B.R., Thoms, M.C., Walker, K.F. O'Keeffe, J.H. & Gore, J.A. 1994. Dryland rivers, their ecology, conservation and management. *in:* P.Calow & G.E. Petts (eds). *The Rivers Handbook. Volume 2*. Blackwell Scientific Publications, Oxford.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems*. WRC Report no. TT 62/93.

Fisher, S.G. and Grimm, N.B. 1991. Streams amd disturbance: are cross-ecosystem comparisons useful. *In:* J.Cole (ed.) *Comparative analyses of ecosystems: Patterns, mechanisms, and theories*. Proceedings of the Thirdy Cary Conference in Ecosystem Science. Springer-Verlag, New York, NY.

Gleick, J. 1988. Chaos: making a new science. Heinemann, London.

Gray, L.J. and Fisher, S.G. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *The American Midland Naturalist* **107:** 58-72.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of North American Benthological Society* 8(4) 293-307.

Harrison, A.D. 1966. Recolonisation of a Rhodesian stream after drought. *Archiv für Hydrobiologie* **62** (3) 405-421.

Hildrew, A.G. and Giller, P.S. 1992. Patchiness, species interactions and disturbance in the stream benthos. *In:* P.S. Giller, A.G. Hildrew and D.G. Raffaelli (eds). Aquatic ecology: scale, pattern and process. Blackwell Science.

Ludwig, J.A. and Reynolds, J.F. 1988. *Statistical Ecology: A primer on methods and computing*. John Wiley and Sons, Canada. 337pp.

McCafferty, W.P. 1981. *Aquatic entomology. The fisherman's and ecologist's illustrated guide to insects and their relatives*. Jones and Bartlett Publishers, Boston.

Naiman, R.J., Décamps, H., Pastor, J. and Johnston, C.A. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* **7:** 289-306.

Odum, E.P. 1971. *Fundamentals of Ecology*. W.B. Saunders Co., London. 574pp.

Palmer, C.G. and O'Keeffe, J.H. 1991. Are macroinvertebrate assemblages in the Buffalo River, South Africa, associated with particular biotopes? *Journal of North American Benthological Society* **10** (4): 349-357.

Poff, N.L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* **11** (1): 86-92.

Poff, N.L. and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Science* **46:** 1805-1817.

Porter, K. 1975. *Nitrogen and phosphorus: Food production, waste and the environment.* Anne Arbor Science Publishers Inc., Michigan, United States. 372 pp.

Power, M.E., Jean Stout, R., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Statzner, B., and Wais de Badgen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *Journal of North American Benthological Society* **7** (4): 456-479.

Radloff, Dr S. Personal Communication. Department of Statistics. Rhodes University, Grahamstown, South Africa.

Reynolds, C.S. 1988. The concept of ecological succession applied to seasonal periodicity of freshwater plankton. *Verhandlung Internationale Vereinigung fur Theoretische und Angewandte Limnologie* **23:** 683-691.

Sheldon, A.L. 1984. Colonisation dynamics of aquatic insects. *In:* V.H. Resh and D.M. Rosenberg. The Ecology of Aquatic Insects. Praeger, New York.

Stanley, E.H. and Fisher, S.G. 1992. Intermittency, disturbance and stability in stream ecosystems. *In:* R.D. Robarts and M. Bothwell. *Aquatic ecosystems in semi-arid regions: implications for resource management.* NHRI Symposium Series 7, Environment Canada, Saskatoon.

Warwick, R.M. and Clarke, K.R. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* **(129)** 301-305.

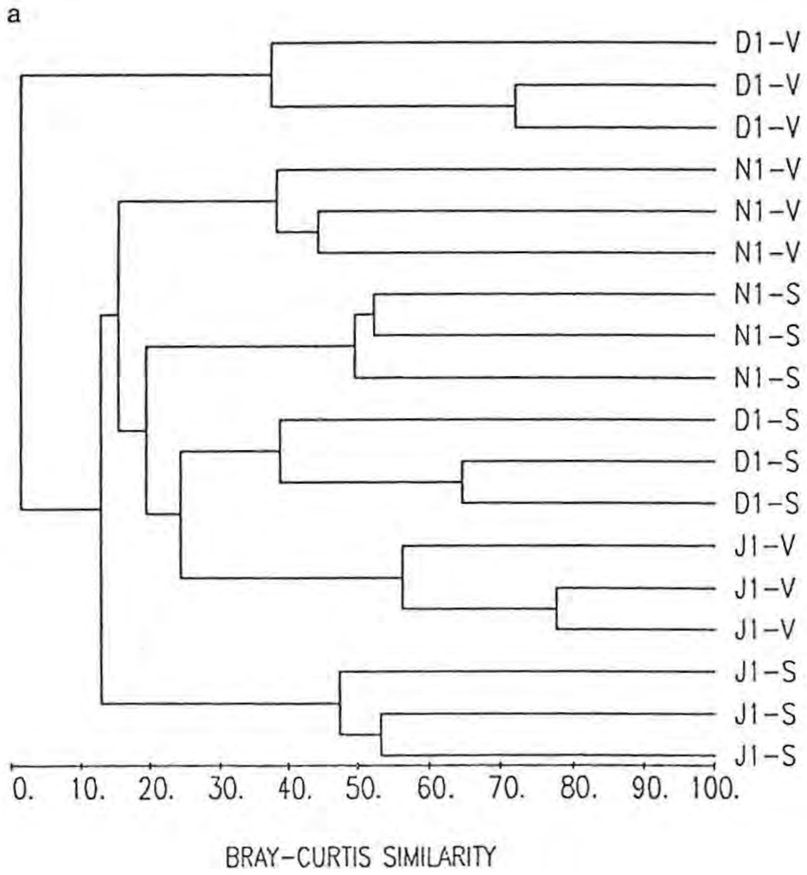
Williams, D.D. 1987. *The ecology of temporary waters*. Croom Helm Ltd, Kent, UK. 193pp.

Williams, W.D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **125:** 85-110.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *International Revue der Gesamten Hydrobiologie* **62:** 53-61.

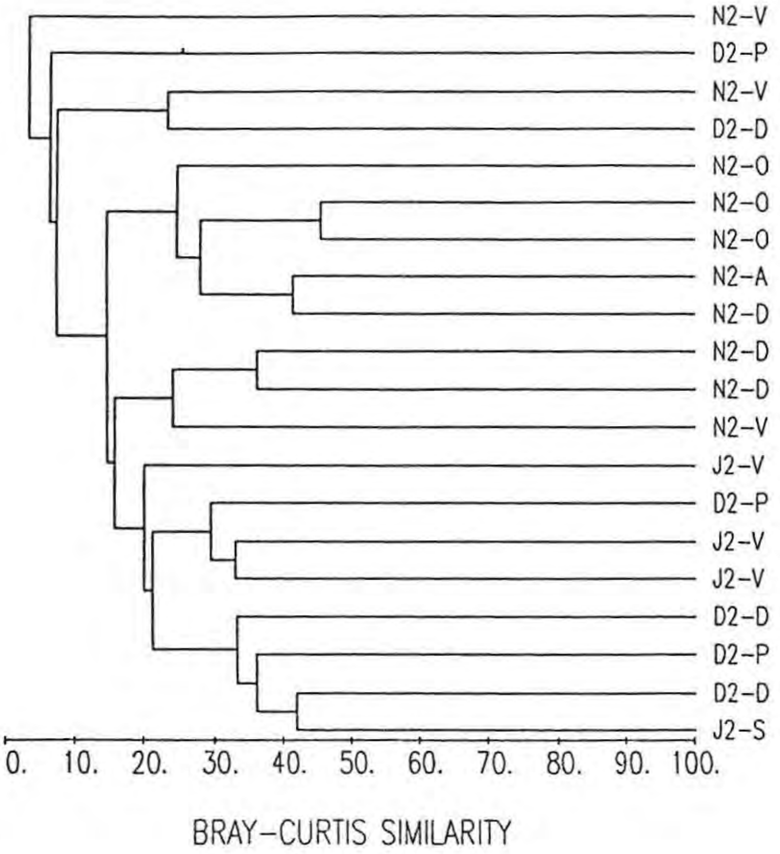
APPENDIX 4.1

a) - c) Cluster analyses based on Bray Curtis similarities between individual replicates within a biotope. a) November 1993 - January 1994; b) November 1994 - January 1995; c) November 1995 - January 1996. On average, replicates from single biotopes clustered as more similar to one another than those from different biotopes [particularly in (a)]. Variability within a biotope was thus lower than that between biotopes, indicating that pooling of replicates was acceptable (although not necessarily desirable) for the purposes of calculating similarity functions.

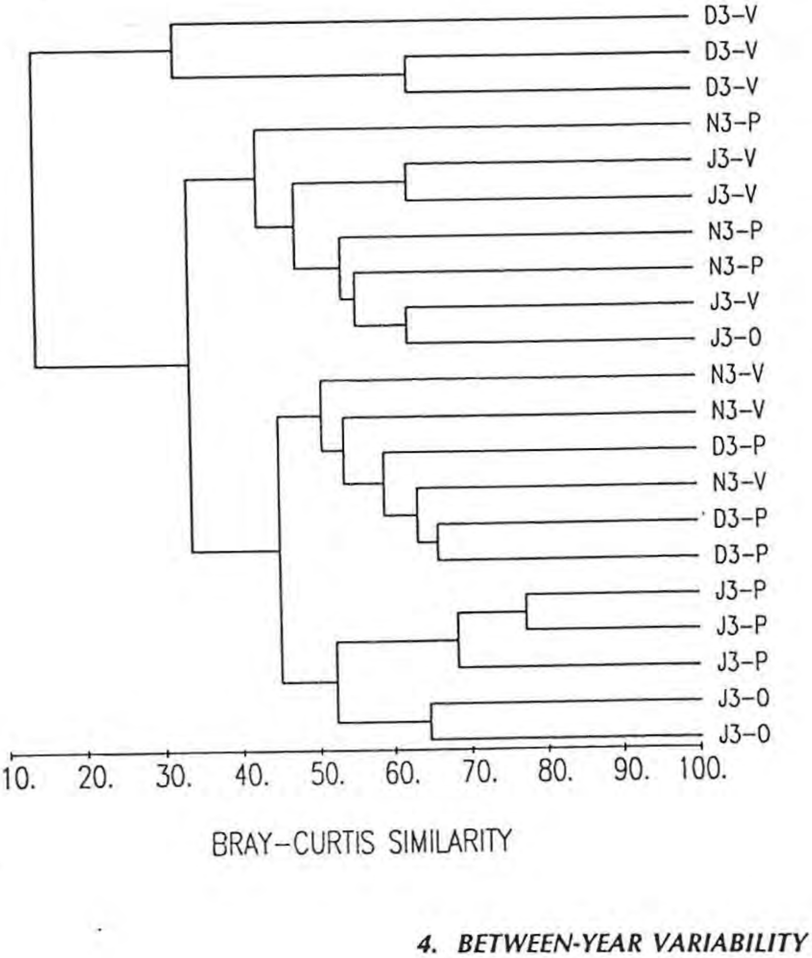


N - NOV D - DEC J - JAN
1 - SITE UK1
V - MARGINALVEGETATION
S - STONES IN CURRENT

b


N2-V
D2-P
N2-V
D2-D
N2-O
N2-O
N2-O
N2-A
N2-D
N2-D
N2-D
N2-V
J2-V
D2-P
J2-V
J2-V
D2-D
D2-P
D2-D
J2-S
0.
10.
20.
30.
40.
50.
60.
70.
80.
90.
100.
BRAY-CURTIS SIMILARITY

c


D3-V
D3-V
D3-V
N3-P
J3-V
J3-V
N3-P
N3-P
J3-V
J3-O
N3-V
N3-V
D3-P
N3-V
D3-P
D3-P
J3-P
J3-P
J3-P
J3-O
J3-O
10.
20.
30.
40.
50.
60.
70.
80.
90.
100.
BRAY-CURTIS SIMILARITY

APPENDIX 4.2

Taxonomic list indicating the percentage proportion of individual taxa in monthly samples over the study periods. (Taxa which comprised less than 1% of the total were omitted, so that column totals are generally less than 100).

		'93-'94			'94-'95			'95-'96		
		N	D	J	N	D	J	N	D	J
		93	93	94	94	94	95	95	95	96
ANNELIDA										
Oligochaeta	Oligochaeta A	1	0	1	1	5	7	2	3	2
	Oligochaeta B	0	0	0	0	0	5	0	0	0
CLADOCERA		0	0	0	4	0	0	0	15	9
COPEPODA		0	0	0	10	0	4	6	0	10
OSTRACODA	*Paracypretta syngramma*	3	0	0	0	0	0	0	0	0
	Candonopsis sp.	2	0	0	0	0	0	0	0	0
	Ilyodromus viridulus	1	0	2	0	0	0	0	0	0
	Paracypretta syngramma	19	0	1	0	1	0	0	0	0
	Pseudocandona gr geratsi	0	0	0	0	0	4	0	0	0
	Ostracoda A	0	0	0	7	0	0	12	2	16
	Ostracoda B	0	0	0	5	0	0	2	2	0
	Ostracoda C	0	0	0	1	0	6	0	14	0
	Ostracoda D	8	0	1	0	0	0	0	0	0
	Ostracoda X	0	0	4	2	0	0	0	0	0
DECAPODA	*Potamonautes sp.*	0	0	0	0	2	3	0	2	1
HYDRACARINA	Hydracarina A	0	0	0	0	0	0	0	1	0
	Hydracarina F	0	0	0	0	0	1	0	0	0
	Hydracarina G	0	0	0	0	0	1	0	0	0
	Hydracarina H	0	0	0	0	0	1	0	0	0
	Hydracarina I	0	0	0	0	0	1	0	0	0
	Hydracarina X	2	0	2	0	0	0	0	0	0
COLLEMBOLA		1	0	0	0	0	0	0	0	1
EPHEMEROPTERA										
Baetidae	*Baetis harrisoni*	0	0	0	0	1	0	0	0	0
	Baetis sp.	0	1	7	0	0	0	0	0	0
	Cloeon sp.	0	2	0	0	0	2	0	0	0
	Demoulinia complex	0	0	0	1	0	0	1	0	0
Caenidae	*Afrocaenis sp.*	0	0	0	2	2	0	1	0	5
ANISOPTERA										
Aeshnidae	*Aeshna miniscula*	0	0	1	0	0	0	0	0	0
	Aeshna sp.	0	0	2	0	0	0	0	0	0
Corduliidae	*Macromia sp.*	1	0	0	3	0	0	0	0	1
	Syncordulia sp.	0	0	0	1	0	0	0	0	0

		'93-'94			'94-'95			'95-'96		
		N	D	J	N	D	J	N	D	J
		93	93	94	94	94	95	95	95	96
Gomphidae	*Notogomphus sp.*	0	0	0	1	0	0	0	1	3
Libellulidae	*Orthetrum sp. B*	0	0	1	0	2	0	0	2	0
	Orthetrum sp. C	0	0	0	0	0	4	0	0	0
ZYGOPTERA										
Coenagriidae	*Enallagma sp.*	0	0	0	0	1	0	0	0	0
	Pseudagrion sp.C	0	0	1	0	0	0	0	0	0
	Pseudagrion sp.X	0	0	3	0	1	0	0	0	0
Chlorolestidae	*Chlorolestes sp.A*	0	0	0	0	1	0	0	0	0
	Lestes sp.A	0	0	0	1	0	1	0	0	0
HEMIPTERA										
Belostomatidae	*Diplonychus sp.*	0	0	0	1	0	0	0	0	0
Gerridae	*Gerris swakopensis*	0	0	5	0	0	0	0	0	0
	Rhagodotarsus sp.	0	0	5	0	0	0	0	0	0
Hydrometridae	*Hydrometra ambulator*	3	0	1	0	0	0	0	0	0
Naucoridae	*Laccocoris sp.*	0	0	2	0	0	0	0	0	0
Notonectidae	*Anisops sp.A*	0	0	5	1	1	1	0	5	2
	Anisops sp.B	0	0	1	0	0	0	0	0	2
	Anisops sp.C	0	0	0	0	0	0	0	0	4
	Enithares sp.A	0	0	1	0	0	0	0	0	0
TRICHOPTERA										
Hydroptilidae	*Oxyethira sp.*	0	0	1	2	0	0	0	0	0
Ecnomidae	*Ecnomus sp.*	0	0	0	0	1	0	0	0	1
COLEOPTERA										
Dytiscidae adults	*Hyphydrus ?distinctus*	0	0	0	1	1	0	0	0	0
	Hyphydrus sp.	0	0	0	1	0	0	0	0	0
	Laccophilus lineatus	0	0	0	1	4	3	0	6	0
	Laccophilus sp.	0	0	0	1	0	0	0	0	0
	Dytiscid B	0	0	0	0	0	0	0	1	0
	Dytiscid X	3	0	1	1	2	0	0	0	0
Dytiscidae larva	Hydroporinae A	0	0	0	0	0	0	0	1	0
	Laccophilus sp.	0	1	0	0	0	1	0	4	0
	Dytiscidae larva B	0	0	0	0	0	0	1	0	0
	Dytiscidae larva D	0	2	0	0	0	0	0	0	0
	Dytiscidae larva G	0	0	0	0	0	1	0	0	0
Elmidae	Elmidae	0	0	0	0	5	0	0	0	0
Gyrinidae adults	*Dineutus sp.*	0	0	1	1	0	0	0	0	1
Gyrinidae larva	Gyrinid larva A	0	0	1	0	0	0	0	0	0
	Gyrinid larva C	0	0	1	0	0	0	0	0	0

		'93-'94			'94-'95			'95-'96		
		N	D	J	N	D	J	N	D	J
		93	93	94	94	94	95	95	95	96
Hydraenidae adult	*Ochthebius andronius*	1	0	0	0	0	0	0	0	0
Hydrophilidae	*Amphiops sp.*	3	0	1	0	0	0	0	0	0
adults	*Hydrobius sp.*	0	0	0	0	3	0	0	0	0
	Hydrochus sp.	1	0	0	0	0	0	0	0	0
Hydrophilidae	Hydrophilid larva A	0	0	0	0	1	0	0	0	0
larvae	Hydrophilid larva B	0	0	0	0	0	1	0	0	0
	Hydrophilid larva C	0	0	0	0	2	0	0	1	0
DIPTERA										
Ceratopogonidae	Bezzia type	1	0	0	2	3	1	2	0	1
Chironomid pupa	Chironomid pupa A	0	1	0	0	0	1	0	0	0
Chironomidae larvae										
Chironominae	*Chironomus sp.*	0	0	0	0	2	0	0	0	0
	Cryptochironomus linderi	0	0	1	0	0	0	0	0	0
	Kiefferulus sp.	0	0	0	0	1	0	0	0	0
	Polypedilum sp.	0	0	0	0	9	6	0	0	0
	Zavreliella sp.	0	0	0	0	0	2	0	0	0
	Chironomini A	0	1	3	8	0	2	12	2	5
	Chironomini B	0	18	4	2	0	0	10	3	2
	Chironomini C	0	0	0	0	0	0	0	0	0
	Chironomini D	0	2	7	3	0	9	0	0	0
	Chironomini E	0	0	2	0	0	0	0	0	0
	Chironomini F	0	0	0	0	0	1	6	0	0
	Chironomini G	0	9	0	0	0	0	2	0	0
	Chironomini H	0	0	0	0	0	0	1	0	0
	Chironomini I	0	0	0	0	0	0	0	0	0
	Rheotanytarsus sp.	0	0	1	0	0	0	0	0	0
	Tanytarsus sp.	0	0	0	0	9	0	0	0	0
	Cladotanytarsus sp.	0	0	0	0	0	4	0	0	0
	Tanytarsini A	0	0	0	0	0	1	0	0	1
	Tanytarsini B	0	1	2	7	1	2	16	8	14
	Tanytarsini C	0	2	0	0	0	0	0	0	0
	Tanytarsini D	0	0	0	2	0	0	0	0	0
	Tanytarsini E	0	0	0	0	0	0	0	0	0
	Tanytarsini F	0	0	0	0	0	0	0	0	0
	Tanytarsini G	0	0	0	0	0	1	0	0	0
	Tanytarsini X	0	0	0	4	0	0	0	0	0
Tanypodinae	*Ablabesmyia dusoleili*	0	0	0	0	3	0	0	0	0
	Clinotanypus sp.	0	0	0	0	2	0	0	0	0
	Larsia sp.	0	0	0	0	2	0	0	0	0

		'93-'94			'94-'95			'95-'96		
		N	D	J	N	D	J	N	D	J
		93	93	94	94	94	95	95	95	96
Tanypodinae	Paramerina sp.	0	0	0	0	0	5	0	0	0
	Procladius sp.	0	0	0	0	8	0	0	0	0
	Tanypodinae A	0	0	0	0	0	0	10	0	0
	Tanypodinae B	2	1	0	1	0	3	3	0	0
	Tanypodinae C	0	1	0	0	0	0	0	0	0
	Tanypodinae D	0	0	0	0	0	0	0	0	0
	Tanypodinae E	0	0	0	0	0	0	0	0	0
	Tanypodinae F	0	0	0	0	0	0	0	0	0
	Tanypodinae G	0	0	0	0	0	0	0	0	0
	Tanypodinae H	0	0	0	0	0	0	0	0	0
	Tanypodinae I	0	0	0	0	0	3	0	0	0
	Tanypodinae X	0	0	0	2	0	0	0	0	0
Orthocladiinae	*Limnophyes sp.*	0	0	0	0	0	0	0	0	0
	Coryneura sp.	0	0	0	0	0	0	0	0	0
	Cricotopus sp.	0	0	0	0	0	0	0	0	0
	Parametriocnemus sp.	0	0	0	0	0	2	0	0	0
	Orthocladiinae A	0	12	0	0	0	0	0	0	0
	Orthocladiinae B	0	0	0	0	0	0	0	0	0
	Orthocladiinae C	0	0	0	0	0	0	0	1	0
	Orthocladiinae D	0	2	0	0	0	0	0	0	0
	Orthocladiinae E	0	0	0	0	0	0	0	0	0
	Orthocladiinae F	0	0	0	0	0	0	0	0	0
	Orthocladiinae G	0	0	0	0	0	0	0	0	0
	Orthocladiinae I	0	0	0	0	0	1	0	0	0
	Orthocladiinae J	0	0	0	0	0	0	1	0	0
	Orthocladiinae X	0	0	1	5	1	0	0	0	0
Ephydridae		0	0	1	0	0	0	1	0	0
Sciomyzidae		2	0	0	0	0	0	0	0	0
Simuliidae	*Simulium nigritarse*	1	27	0	0	0	0	0	0	0
	Simulium vorax	0	0	1	0	0	0	0	0	0
	Simulium sp. X	2	0	1	0	0	0	0	0	0
Tabanidae		0	0	0	0	2	1	0	0	0
Tipulidae		0	0	0	0	0	3	0	0	0
GASTROPODA										
Ancylidae	*Ferissia sp.*	0	0	0	1	5	4	0	0	2
Lymnaeidae	*Lymnaea columella*	8	3	4	0	2	1	0	2	0
Physidae	*Bulinus forskalii*	3	0	3	0	0	1	0	0	0
	Ceratophallus sp.	15	6	12	1	1	9	0	0	0
Sphaeriidae	*Pisidium sp.*	0	0	0	1	9	3	3	3	6

CHAPTER 5

ASSESSING THE VALUE OF DEFINING HYDROLOGICAL PHASES IN AN INTERMITTENT ASEASONAL RIVER FOR THE PURPOSES OF RESEARCH AND MANAGEMENT

This chapter was written specifically for the purposes of this thesis, to examine the question of whether or not particular hydrological phases could be characterised by individual taxa or groups of taxa. As a result of the findings in Chapters 3 and 4, a number of further considerations related to hydrological phases arose.

ABSTRACT

The possibility of an association between hydrological phases and characteristic faunal assemblages was investigated for the upper Kowie River. Each of the five phases identified ***a priori*** *was subdivided into a number of sub-phases, based on the recognition that hydrological conditions and their effects on the fauna could not be viewed in isolation from antecedent conditions and time of year. These two auxilliary influences were the basis on which twelve sub-phases were distinguished. The idea of sub-phases was considered a valuable extension to the concept of hydrological phases on account of the differences demonstrated in faunal composition between certain sub-phases representing the same phase. Significant differences were also demonstrated between the faunas of approximately half of the sub-phases, and between most of the phases (excluding the NO FLOW phase). On the basis of these results, it was inferred that a 'core' group of taxa present in most of the phases must be distinct and identifiable. Taxa occupying such core groups in each of the phases were proposed, on the basis of data presented here and in previous chapters. A simple predictive model could be based on the concept that hydrological 'units' (phases/sub-phases) have a characteristic fauna, or are at least characterised by indicator species. More long-term information regarding the natural invertebrate fauna of temporary rivers would, however, be required before such a model could be developed and used with any confidence.*

5.1 INTRODUCTION

Studies of within- and between-year variability in the invertebrate fauna of the Kowie River indicated that the major influences on faunal character were physical rather than biological in nature. More specifically, alongside hydrology, two of the determinants of biotic structure were considered to be present and antecedent hydrological conditions, and time of year (Chs 3 and 4).

It is useful to be able to identify the spatial or temporal 'units' of relevance in a river with expected groups of fauna for the purposes of research, environmental assessments, predictions and management applications (e.g. calculation of instream flow requirements; see Armitage et al. *1995). Commonly, these 'units' comprise physical* ***biotopes*** *(e.g Palmer et al. 1991),* ***substratum types*** *(e.g. Minshall and Minshall 1978),* ***river zones*** *(e.g. Vannote et al. 1980), and* ***seasons*** *(e.g. Williams and Hynes 1976, 1977). Fauna characterising such areas or periods are, of course, also characteristic of the relevant hydrological conditions.*

Research results presented in previous chapters suggested that in the upper Kowie River, it was generally not possible to link particular fauna with these spatial or temporal 'units' of this nature. Temporal changes in the invertebrates of the upper Kowie were associated primarily with unpredictable rainfall and hydrology, rather than with seasonal environmental cues (e.g. air temperature, water temperature). While time of year was judged an important influence on faunal character, it was not possible to link distinct times of the year (e.g. seasons) with expected taxa (Ch. 3).

In general, the spatial distribution of fauna was governed by availability and heterogeneity of aquatic habitat (biotopes) in an unstable environment. Substratum *preferences* of invertebrates were most apparent during stable flow conditions. Although it was shown that variation between biotopes was greater than variation within biotopes over time (3.5.8), the association of particular groups of taxa with individual biotopes in such a variable environment was not simple, as continual expansion and contraction of the aquatic ecosystem (*sensu* Stanley et al. *1997) and loss of biotope heterogeneity resulted in movement of invertebrates between biotopes. Where a biotope lasted long enough to favour stability in the fauna (e.g. marginal vegetation at the lower site, see Section 3.6), it may have been feasible to identify a characteristic fauna (but for those conditions only!).*

As hydrology was evidently the primary driving variable in faunal organisation, the next avenue of investigation was whether or not characteristic fauna could be associated with particular hydrological 'units' such as those identified at the outset of the study (1.3.5). The purpose of the analyses presented here was to investigate this possibility, as part of the long-term research on the invertebrates of the upper Kowie River. It was hypothesized that each hydrological phase was *of a sufficiently different character to have an effect on faunal composition and diversity. The first null hypothesis for this study was therefore that there was no faunal difference between the different hydrological phases.*

Previously, surface water conditions in temporary rivers have been assigned to categories a posteriori, either subjectively on the basis of faunal composition (e.g. Abell 1984, Williams and Hynes 1976, Clifford 1966) or objectively, by multivariate ordination and classification of interactions among a number of environmental variables, to generate a predictable (cyclical) series of phases (Boulton and Lake 1990a). At the outset of this study, five hydrological phases were discerned *a priori*, on the basis of what was known of intermittent river hydrology in the Eastern Cape region (see 1.3.5). Phases were initially identified according to surface-water characteristics only, and each different phase represented a 'state change' in the river, as discussed previously (1.3.5). The phases described were: ONSET (lasting for a period of one month after recommencement of flow at the site), by which stage it was anticipated that substantial faunal recovery would have occurred), FLOW (continuous surface flow), NO-FLOW (following flow cessation, for the period that surface water was continuous), POOLS (periods during which surface water was discontinuous and restricted to pools in the channel) and DRY (where there was no surface water at the site excepting in the form of rainpools).

Results of earlier analyses (Chs 2,3), suggested that two additional factors interacted with hydrological conditions in regulating faunal character were: antecedent hydrological conditions and time of year. On the strength of this, it was decided to subdivide each of the five phases into sub-phases, in order to acknowledge and verify the influence of these additional factors. To restrict the number of sub-phases, the times of year used in these divisions were 'summer' (September to April) and 'winter' (May to August), as results from previous analyses indicated that the major influences were related to these two seasons. The resulting sub-phases are listed in Table 5.1. The second null hypothesis was, accordingly, that there were no significant differences between the fauna of different sub-phases. The development of a simple predictive model based on the use of these sub-phases is considered.

Table 5.1 The phases identified *a priori* in this research, and their division into sub-phases on the basis of time of year (summer/winter) and antecedent hydrological conditions. Sub-phases are coded according to the main phase (upper case), whether it occurs in winter or summer (lower case), and what the antecedent phase was (upper case), e.g. **O**NSET phase in **s**ummer preceded by **D**RY phase would be coded **OsD.**

PHASE	**TIME of YR.**	**ANTECEDENT CONDITIONS** (No. samples)	**CODE**
ONSET	SUMMER	Previous month DRY (9)	OsD
	WINTER	Previous month DRY (0)	OwD
	SUMMER	Previous month POOLS (6)	OsP
	WINTER	Previous month POOLS (6)	OwP
FLOW	SUMMER	Previous month ONSET (17)	FsO
	WINTER	Previous month ONSET (0)	FwO
	SUMMER	Previous month FLOW (22)	FsF
	WINTER	Previous month FLOW (0)	FwF
NO FLOW	SUMMER	(Previous month (7)	Nfs
	WINTER	always FLOW) (1)	Nfw
POOLS	SUMMER	Previous month NO FLOW (5)	PsN
	WINTER	Previous month NO FLOW (4)	PwN
	SUMMER	Previous month POOLS (11)	PsP
	WINTER	Previous month POOLS (6)	PwP
DRY	SUMMER	Previous month DRY (0)	DsD
	WINTER	Previous month DRY (6)	DwD
	SUMMER	Previous month POOLS (0)	DsP
	WINTER	Previous month POOLS (0)	DwP

5.2 SITES

The two sites on the upper Kowie River formed the basis of this study. The sites selected represented two reaches in the upper section of the river, which has a natural flow regime described as 'intermittent aseasonal' (Ch. 2). They are described in detail in Section 3.2.

5.3 DATA SOURCES

One hundred sets of samples (each representing three replicates) were selected at random from the samples collected over the full study period. These were allocated to their respective phases and sub-phases. FLOW and POOLS phases had the greatest overall representation in the study, as NO FLOW and ONSET phases generally only lasted a month, and completely DRY phases only occurred at the beginning of the study. Consequently, of the 100 sample sets, 39 were from the FLOW phase, 26 from POOLS, 21 from ONSET, 8 from NO FLOW, and 6 from DRY (Table 5.1). Not all sub-phases were represented by samples, however, theoretically, all could occur. Because of the discrepancy in numbers of samples per phase and sub-phase, severe data transformation was required to allow for comparisons between them. For analyses using individual samples (grouped replicates), abundance categories similar to those described in Section 3.4.3 were used (**1** = 1-10, **2** = 11-100, **3** = 101-1000). This is in effect a log transformation, which is considered fairly severe, retaining to some extent the quantitative information but down-playing dominant taxa (e.g. chironomids) so that rarer taxa (e.g. tipulids) are of consequence (Clarke and Warwick 1994). For analyses of total (aggregated) samples from sub-phases, only presence/absence data were used. The reduction to presence/absence is considered 'the ultimate transformation' in down-weighting the effects of common species (Clarke and Warwick 1994). Data were standardised for all analyses to account for differences between sampling techniques in the various biotopes.

5.4 METHODS

5.4.1 Biotic information

Sampling of invertebrate fauna involved monthly trips to the Kowie River sites. Invertebrates were sampled following the same procedures described in Section 3.4.1. The five biotopes sampled for aquatic macroinvertebrates were: stones in current (SIC); stones out of current (SOOC); marginal vegetation (MV); sandy substrata (SAND); full pools (POOL), and drying fringes of pools (DRG). Full descriptions of these biotopes are provided in Section 1.3. Three replicate samples were taken in each biotope. Depth and current speed were recorded at each sampling point. Approximate percentage composition of the substratum was assessed visually for the following materials: bedrock, boulders, cobbles, sand (coarse to fine), algae, submerged / aquatic / floating vegetation, detritus, and leaf-fall, as described in Section 3.4.

5.4.2 Abiotic information

Several abiotic variables were measured at the site when surface water was present. Details of equipment used, resolution of measurements, and limits of detection were presented in Sections 3.4 and 4.4. On-site measurements of the following variables were taken: salinity as electrical conductivity ($Ms.m^{-1}$), Ph, water temperature and oxygen concentration (converted to % saturation).

During periods of flow, stream discharge was calculated from a number of flow readings taken at fixed intervals across a flat-bottomed section of the channel, as described in Section 3.4.

5.4.3 Data analysis

STATISTICAL ANALYSES

Non-parametric, multivariate statistics were performed using programs from the PRIMER package, which was designed for community data analysis (Clarke and Warwick 1994). As diversity indices were not appropriate to this study, only resemblance functions between samples were sought. All statistical analyses were thus conducted on the basis of similarity matrices.

Similarity between samples

The non-correlation-based Bray-Curtis coefficient of similarity was used to calculate similarity between samples from different sub-phases and phases, as explained in Section 1.4.2. Three different sets of data were analysed for similarities:

D1 The full matrix of 100 sample sets, representing samples from different biotopes and different sub-phases, in three abundance categories as described;

D2 Total (aggregated) samples from each of the sub-phases represented, in presence/absence categories only;

D3 Total samples from each of the five major phases in presence/absence categories only.

Cluster analysis

Hierarchical agglomerative cluster analysis of data, using group-average linkage, was performed on the basis of Bray-Curtis similarity matrices, in the CLUSTER program. Dendrograms were generated using the program DENPLOT. This procedure is explained in Section 1.4.3.

Ordination

Ordinations were produced using the non-metric multidimensional scaling procedure (MDS) in the MDS and CONPLOT programs. This procedure is outlined in Section 1.4.4.

To check the validity of groupings generated by the clustering procedure, and the compatibility of the clustering and ordination techniques, a line was drawn through an arbitrarily selected similarity value, and clusters to the right of the line(s) were distinguished as separate Groups. These were superimposed on the ordination, to check the coherence of the groups in ordination space, and the distance between them. This procedure also allows for more structured interpretation of the results of both techniques.

Analysis of similarity for testing of null hypothesis

A test of the statistical significance of differences between individual phases and sub-phases was performed using the ANOSIM procedure. The algorithm for the step-wise examination of H_0 using ANOSIM is explained in Section 1.4.6. The procedure generates a value for R which lies within the range (-1,1). $R = 1$ if all replicates within sites are more similar to each other than to any other replicates from different sites. Where R is approximately zero, the null hypothesis is true (i.e. similarities within and between sites will be approximately the same, on average). However, the importance of R is not in its absolute value, but in whether or not it is *significantly* different from zero. Clarke and Warwick (1994) note that it is possible for R to be inconsequentially small, yet significantly different from zero.

Association between biotic and abiotic data

To investigate links between biotic data and univariate environmental variables, values for each abiotic variable were represented as symbols of varying sizes and superimposed on the corresponding biotic ordination, using the CONPLOT program with an environmental data file. Each abiotic variable was plotted separately in this way. This provided a means of checking whether or not there were consistent differences in the particular abiotic variable between biotic clusters (groups), and/or of observing any smooth trends in the abiotic variable which matched the gradients in the biotic ordination (Clarke and Warwick 1994). This procedure is explained in full in Section 1.4.7.

Contributions of individual taxa to similarities between phases

The program SIMPER was used to calculate the contributions of individual taxa to similarities between samples within *a priori* defined groups (hydrological phases) rather than *a posteriori* defined groups (those formed in clustering). This procedure is explained in Section 1.4.5.

5.5 RESULTS

5.5.1 Alteration of biotope character with changes in phase

Approximate changes in the proportional representation of individual biotopes at each site during the five phases are shown in Figure 5.1. The stones-in-current biotope (SIC) was represented during ONSET and FLOW phases only and was the shortest-lived biotope. Following flow cessation (NO FLOW), deeper areas which were previously SIC became stones-out-of-current (SOOC), and vice versa following recommencement of flow (ONSET). There was therefore a physical dynamism between these two biotopes. Marginal vegetation was sparse at the upper site but plentiful at the lower site. MV was inundated during ONSET, FLOW and NO FLOW phases, at both sites, and also during the early POOLS phase at the lower site. SAND, with its variety of overlying organic deposits (from silt to algae, leaves and other organic debris) persisted as an aquatic or semi-aquatic biotope until the channel dried completely. The POOL biotope was inconstant in terms of substratum - pools at the upper site were generally characterised by bedrock or sandy substratum, overlain with matrices of variable character, including stones, leaves, algae and organic debris. The substratum of the single pool at the lower site was mixed coarse and fine sands overlain with scattered leaves. Pools were characterised by variable volume and duration. The DRG 'biotope' was also highly variable in character, extent and duration. Even during low flow periods, 'patches' of the upper-site channel were drying, so that in effect, at the scale of the channel, phases (POOLS, DRY) occurred even within phases (FLOW).

5.5.2 Abiotic variables

There was considerable overlap in the ranges of abiotic variables recorded for the sub-phases (Table 5.2). The influence of season was evident in water temperature and (to some extent) % oxygen saturation values, both of which were notably lower during winter. Maximum discharge measured during the ONSET phase was lower than that recorded during FLOW periods. Conductivity values ranged between 25 and 50mS.m^{-1}, and varied little between phases. Ph was similarly consistent, with the extremes of the range represented by a minimum value of 5.1 in the summer pools phase PsN, and a maximum value of 8.1 in the summer flow phase FsF (Table 5.2).

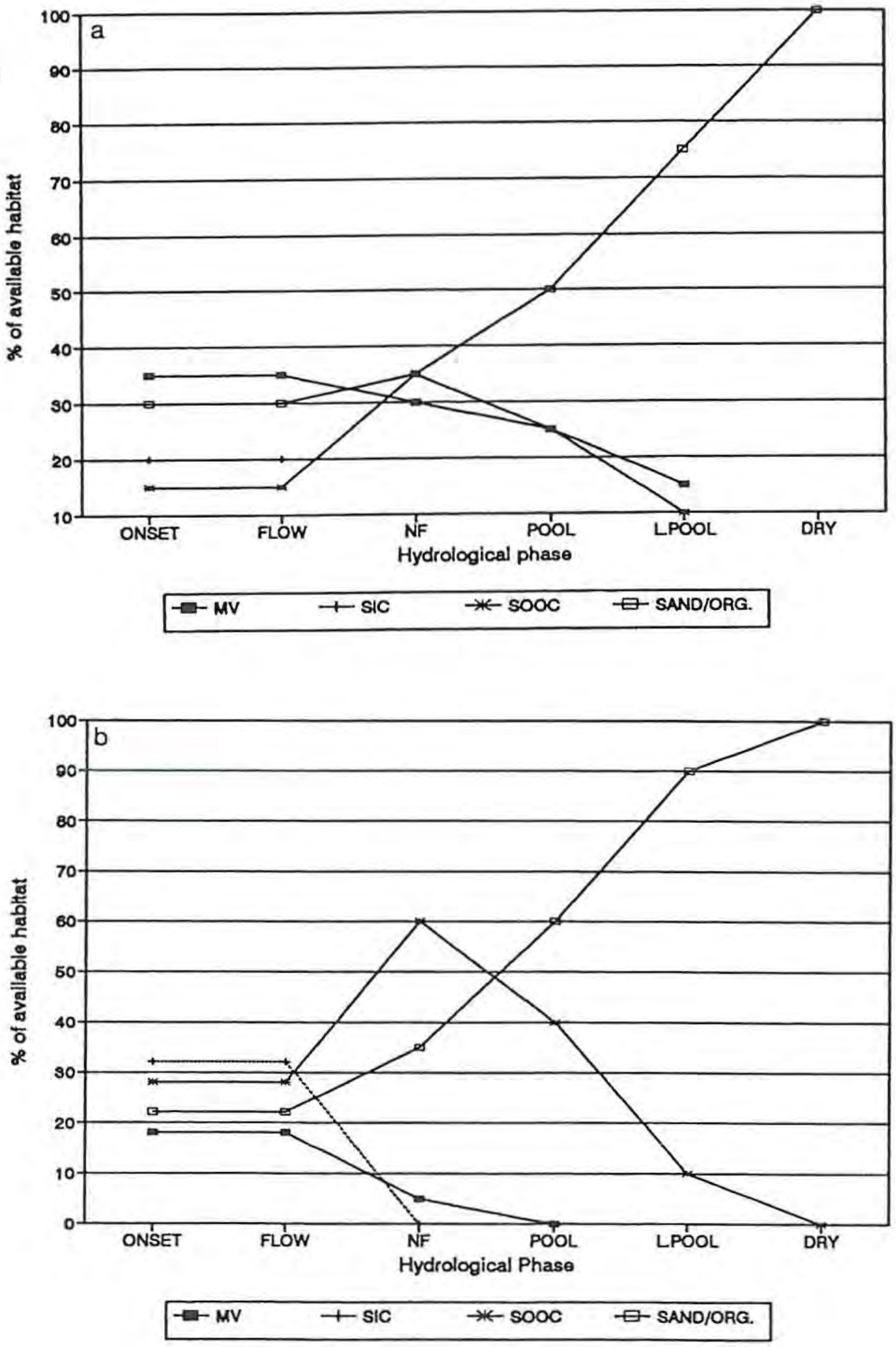


Figure 5.1 Graphs showing the approximate change in extent and availability of each of the five biotopes sampled at the upper Kowie sites a) UK1 and b) UK2, during each of the different hydrological phases.

Table 5.2 Ranges of physical and chemical variables for the phases studied.

PHASE		DISCHARGE (m^3/s)	TEMP (°C)	%OXYGEN SAT. (% sat.)	E.C. (mS/m)	pH
ONSET						
Summer/DRY	**OsD**	0.01-0.05	16.8-21.5	60-106	41-72	6.4-7.5
Summer/POOLS	**OsP**	0.05-0.07	22.3-26	102-124	28-31	7.1
Winter/POOLS	**OwP**	0.01-0.03	13.3-14.4	25-93	37-38	6.8-6.9
FLOW						
Summer/ONSET	**FsO**	0.01-0.17	18-24.5	81-120	28-40	6-7.4
Summer/FLOW	**FsF**	0.01-0.17	17-24.5	52-125	23-36	6-8.1
NO-FLOW						
Summer	**NFs**		15.4-16.0	44-110	46-47	6.9-7.0
Winter	**NFw**		12.0-16.9	51-98	45-51	6.4-6.9
POOLS						
Summer/NO-FLO	**PsN**		16.9-24.3	46-114	36-50	5.5-7.3
Winter/NO-FLOW	**PwN**		9.2-10.3	55-84	30-31	7-7.8
Summer/POOLS	**PsP**		19.1-27.0	37-103	31-40	7-7.9
Winter/POOLS	**PwP**		11.1-16.1	12-18	16-43	6.8-7.1

5.5.3 Cluster analysis and ordination of individual samples

Hierarchical agglomerative clustering based on similarities calculated between individual sample sets per sub-phase (**DsD**) generated a complex dendrogram with major groupings forming at low similarity levels (around 20%). At these levels, samples from individual sub-phases were scattered throughout different clusters and interpretation in the context of this lack of pattern was complex and unwieldy. MDS ordination of this large data-set generated a high-stress (0.3) representation in two dimensions, indicating that the points were close to being arbitrarily placed in the ordination space (see Clarke and Warwick 1994). Attempts to overlay environmental data on this ordination would thus be meaningless. Because of the 'noise' in these results, both the dendrogram and ordination were neglected in favour of analyses of aggregated sample sets. The dendrogram is included for reference in Appendix 5.1.

5.5.4 Cluster analysis and ordination of total samples (sub-phases)

Cluster analysis based on Bray-Curtis similarities between total (aggregated) samples per sub-phase (data-set **D2**) gave clearer results, at greater similarity levels. Two lines were drawn at the arbitrarily selected value of 30% and 50% for the purposes of comparing clustering results with those of the ordination. Clusters to the right of the 50% line were labelled Groups 1 to 3 (Fig. 5.2).

Faunal resemblances were greatest between total samples representing summer flow conditions (Group 1); summer no flow conditions (Group 2); and winter onset and pools conditions (Group 3). Groups 1 and 2 (summer samples) linked at lower similarity levels. The samples from winter (Group 3) joined this clustered at a yet-lower similarity level. The sub-phases ONSET sD and POOLwN,and NO FLOW w and DRYwDpaired off separately at low similarity levels (Fig. 5.2).

MDS ordination based on Bray Curtis similarity data produced a low-stress (0.13) representation of the sample points in 2-dimensional space (Fig. 5.3). Groups 1 to 3, when superimposed on the ordination points, indicated agreement between the clustering and ordination results, and clearly illustrated the relative distances between the different sample groups. The distance between DwD and Nfw on the ordination, however, indicated that the clustering of these two total samples was due to their mutual dissimilarity from other samples rather than on their compositional similarity. Their position on the ordination also suggested that they were significantly different from the remainder of the sub-phases. As Nfw was represented only by single sample set, this was considered unrepresentative of conditions pertaining during that period, and this sample set was scrapped. The distance between DRYwD samples and those from the 'wet' sub-phases was considered significant and further testing of this was not deemed necessary (e.g. Clarke and Warwick 1994).

5.5.5 Cluster analysis and ordination of total samples (phases)

Cluster analysis of Bray-Curtis similarities between total (aggregated) samples from each of the major hydrological phases, using the data set **DsP**, showed the clear split between 'wet' and 'dry' phase samples (Fig. 5.4). Greatest overall resemblance was indicated between fauna from the POOLS and ONSET phases. These, in turn, were more similar to FLOW phase samples than to NO-FLOW phase samples. Lines were drawn at 45% and 55% similarity levels to check the correspondence between groupings generated by cluster analysis and the positioning of sample points in ordination space.

MDS ordination of Bray Curtis similarities between total samples from each phase showed a clear gradient between fauna from the different phases, with the greatest inter-sample distance indicated between the DRY phase and the FLOW phase. The clustering and ordination procedures showed congruence in results.

5.5.6 Analysis of similarity for testing of the null hypotheses

Testing for significance of difference between sub-phases

For this test, two sample sets were omitted: NO FLOW 2 was scrapped for reasons already given, and DRY 2 was omitted as significant difference had already been indicated in clustering and ordination.

The Global *R* value generated by the ANOSIM was 0.19, at a significance level of 0%. At this level (< 5%) the null hypothesis of 'no difference between sub-phases' could be rejected. This indicated that there were significant differences between at least certain of the sub-phases, and this was supported by the results of pairwise tests in ANOSIM. The *R* values and significance levels for each pair of samples are presented in Table 5.3a. Most sub-phases were significantly different to more than 50% of the other sub-phases (inclusive of DwD).

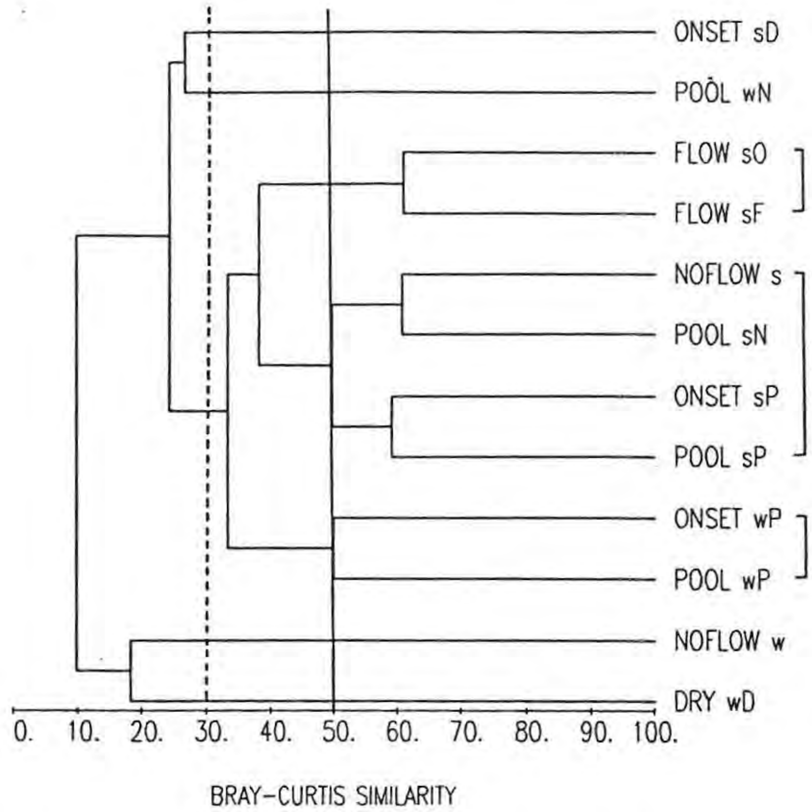


Figure 5.2 Dendrogram representing cluster analysis of total samples per sub-phase. Codes represent the main phase, the time of year (s/w) and the antecedent conditions (e.g D - DRY, F - FLOW, N - NO FLOW). Three groups are discerned.

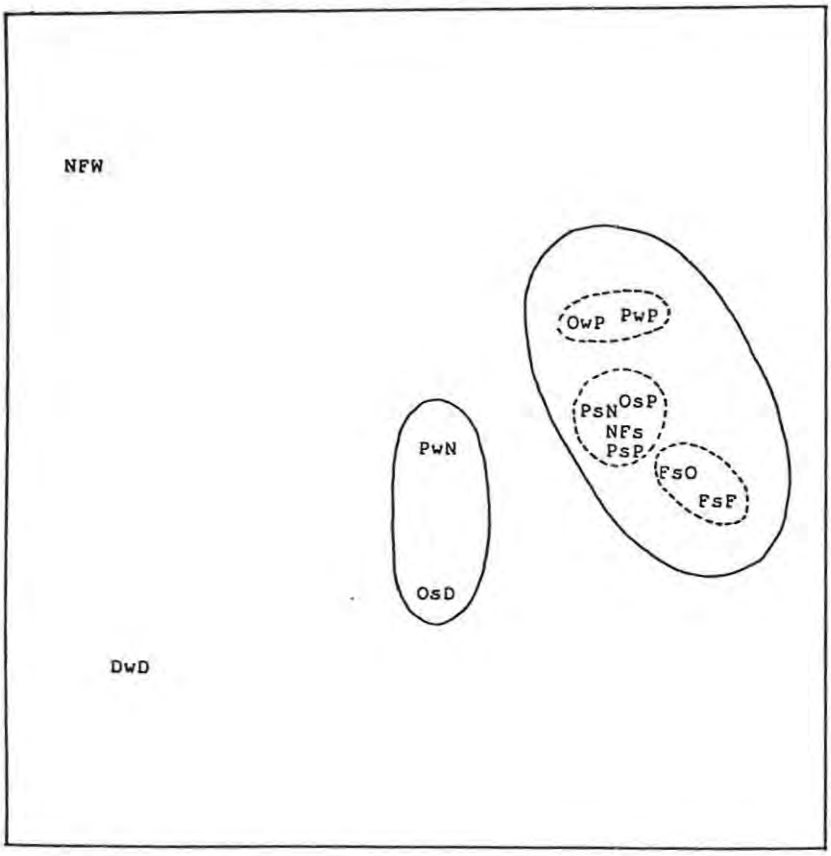


Figure 5.3 MDS ordination based on similarities between total samples from each of the sub-phases. Stress = 0.08. Abbreviations: As given in Table 5.1

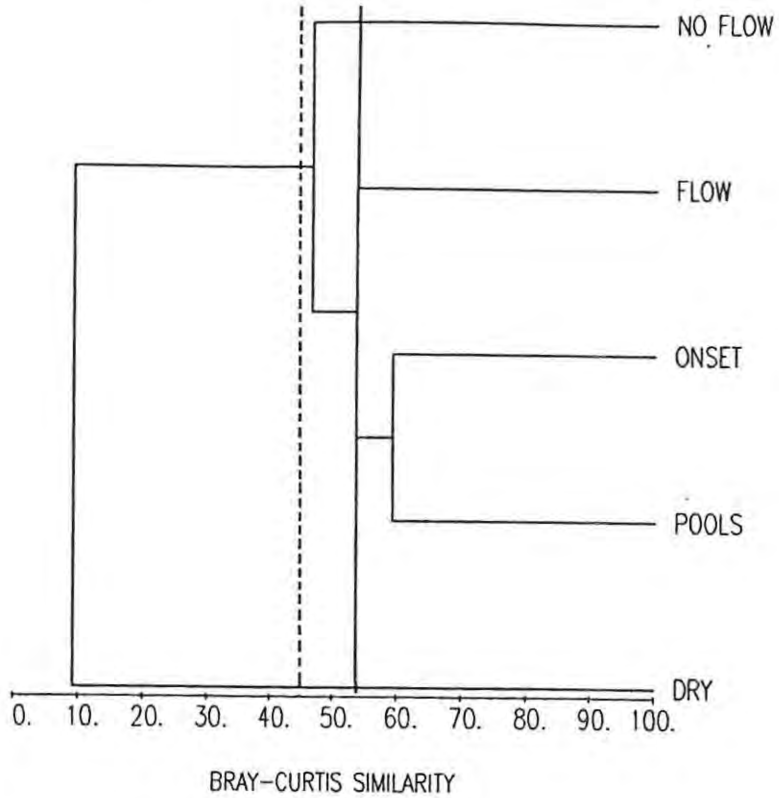


Figure 5.4 Dendrogram representing cluster analysis of total samples from each individual phase.

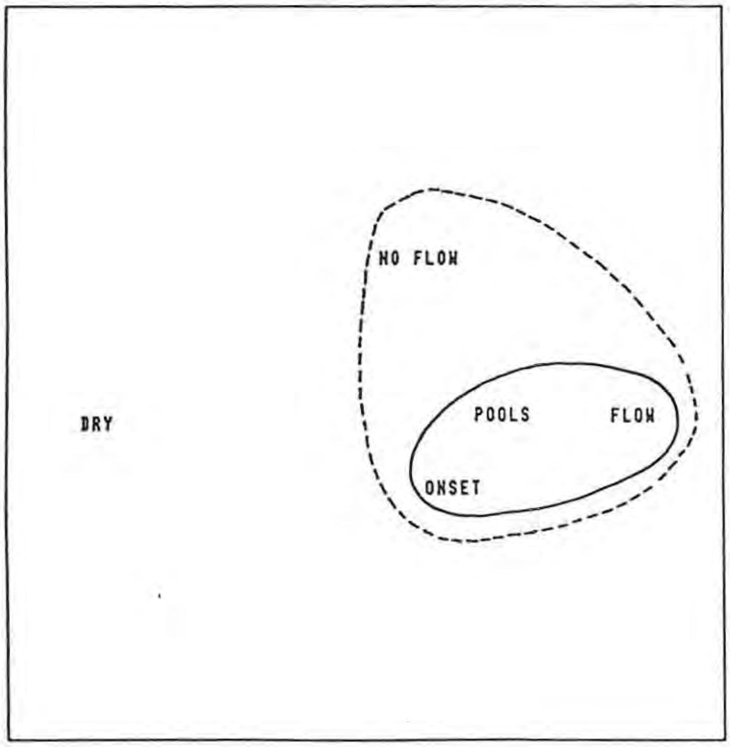


Figure 5.5 MDS ordination based on Bray Curtis similarities for total samples from each phase. Stress = 0.0.

Testing for significance of difference between phases

The ANOSIM test for these groupings produced a Global *R* value of 0.18, at a significance level of 0.0%. Thus the null hypothesis of 'no difference between the fauna of different phases' could be rejected, and significance of differences between individual phases was sought. Pairwise tests indicated that of all the 10 pairs of phases, seven were significantly different (Table 5.3b).

5.5.7 Association between biotic and abiotic variables

The inability to overlay environmental data on the corresponding biotic ordination of all samples has already been discussed (Section 5.5.3, Appendix 5.1). The relative stability (and therefore overlap) in values of most abiotic variables, excluding discharge, over all the sub-phases suggested that there would be poor association between individual variables and biotic data. This could not however be determined statistically.

5.5.8 Characterisation of the fauna of sub-phases and phases

Number of taxa, and representation of different faunal groups in each of the sub-phases and phases is recorded in Table 5.4. It is recognised that total number of taxa collected was affected number of sample-sets representing the sub-phase, and that these values cannot be used comparatively. A full list of taxa collected in each of the sub-phases and phases is presented in Appendix 5.2. Fauna of each of the phases is discussed separately.

Table 5.3 Results of the ANOSIMs between a) sub-phases and b) phases, based on individual (100) sample sets. Where -1 < R < 1, and significance levels (%SIG.) are less than 5%, fauna of the two phases are significantly different.

a)

ONSET		FLOW		NO-FLOW	POOLS				
OsP	OwP	FsO	FsF	NF	PsN	PwN	PsP	PwP	
0.29	**0.41**	**0.59**	**0.34**	**0.27**	**0.47**	0.04	**0.32**	**0.62**	OsD
1.2	**0.4**	**0**	**0**	**2**	**0.1**	36.5	**0.1**	**0.1**	
	0.17	0.04	-0.03	0.11	**0.36**	0.21	0.04	0.22	OsP
	12.3	31.1	59.6	16.9	**2.6**	12.9	33.3	9.3	
		0.26	0.05	0.23	**0.41**	**0.59**	**0.19**	**0.34**	OwP
		3.1	29.3	5.4	**2.2**	**1.4**	**4.1**	**0.9**	
			0.04	**0.23**	**0.43**	**0.58**	**0.22**	**0.28**	FsO
			13.7	**4.1**	**0.2**	**0.1**	**0.3**	**1.7**	
				-0.04	-0.09	**0.2**	**0.12**	0.04	FsF
				61.2	78.1	**4.8**	**4.8**	34.3	
					-0.105	0.006	-0.12	**0.33**	NF
					81.6	46.2	87.7	**1.5**	
						0.56	-0.001	**0.51**	PsN
						0.8	43.5	**0.2**	
							0.05	0.69	PwN
							33.5	**1**	
								0.22	PsP
								3.8	

b)

	FLOW	NO FLO	POOLS	DRY	
R	**0.19**	-0.02	**0.16**	**0.17**	ONSET
%SIG	**0.1**	54.6	**0**	**4.5**	
		0.07	**0.12**	**0.63**	FLOW
		25	**0.1**	**0**	
			-0.11	**0.33**	NO FLOW
			89.2	**1.1**	
				0.4	POOLS
				0	

	SUMMER							WINTER				
Phase:	ONSET		FLOW		NO FLOW	POOLS		ONS	NO FLOW	POOLS		DRY
Sub-phase:	OsD	OsP	FsO	FsF	NFs	PsN	PsP	OwP	NFw	PwN	PwP	PwD
NEMATODA		X	X				X					
OLIGOCHAETA	X	X	X	X	X	X	X	X	X	X	X	
COPEPODA	X	X	X	X		X	X			X	X	X
OSTRACODA	X	X	X	X	X		X			X	X	X
DECAPODA	X	X	X	X			X			X	X	X
HYDRACARINA	X	X	X	X	X		X	X		X	X	
COLLEMBOLA	X		X	X			X		X	X		X
EPHEMEROPTERA (3)		1	2	3	2	2	2					
ANISOPTERA (3)			2	2	2	1	2	2	1	1	3	
ZYGOPTERA (4)		2	4	4	4	3	2	1		1	1	
HEMIPTERA (10)	2	3	7	9	4	2	3	5		4	4	
TRICHOPTERA (5)		2	2	4	1	1	1	2			2	
COLEOPTERA (7)	3	3	6	7	3	3	6	4		4	3	
DIPTERA (11)	7	5	8	8	4	6	5	6	4	3	3	5
MOLLUSCA (5)	3	4	3	5	5	4	3	1		2	1	

Table 5.4 Representation of different taxonomic groups in each of the hydrological sub-phases (as coded in Table 5.1).

ONSET

During the ONSET phases four biotopes were available: SIC, MV, SOOC and SAND (Fig. 5.1). Sixty-one taxa were collected during summer onset periods preceded by pools in the channel (OsP, Appendix 5.2). Many of the commonly-occurring taxa found during this sub-phase were not present in samples collected in the same onset conditions preceded by dry conditions (OsD), or in winter onset periods (OwP, Tables 5.4 and 5.5). Numbers of taxa collected in the latter two phases were 29 and 26 respectively. Taxa found abundantly in each of the onset sub-phases are listed in Table 5.5, and taxa common to all three ONSET sub-phases included hydracarinids, *Amphiops* sp. hydrophilids, *Leptocerus* sp. caddisflies and *Lymnaea columella* gastropods (Appendix 5.2).

Analysis of similarity indicated that there were significant faunal differences between *all* the onset sub-phases (Fig. 5.2a, Table 5.3), despite the fact that in cluster analysis total samples from the OsD and OsP sub-phases clustered together at over 50% similarity levels (Fig. 5.2).

Table 5.5 Taxa found commonly during the various ONSET sub-phases (see Table 5.1 for a description of sub-phases).

COMMON IN OsD	COMMON IN OsP	PRESENT IN OsD AND OsP
Paracypretta sp.	Nematoda	Oligochaeta
Collembola	*Pseudocandona sp.*	Copepoda
	Orthetrum sp.	Ostracoda
	Mesovelia vittigera	*Potamonautes sp.*
COMMON	*Laccophilus sp.*	*Harrisonina petricola*
IN OwP	*Dytiscid larvae*	*Simulium nigritarse*
Laccophilus sp.	*Paramerina sp.*	*Bulinus sp.*
Various Hydrophilids	*Procladius sp.*	
Chironomid pupae	Other Tanypodinae	
Orthocladiinae	*Polypedilum sp.*	PRESENT IN
Polypedilum sp.	Other Chironomini	OsD, OsP AND OwP
Tanytarsini	*Cladotanytarsus sp.*	(Rarely)
Limnophyes sp.	*Rheotanytarsus sp.*	Hydracarina
	Other Tanytarsini	*Leptocerus sp.*

FLOW

During the two summer FLOW phases FsO and FsF, 133 and 147 taxa were collected (Table 5.4). SIC, SOOC, MV and SAND were all sampled during these periods. All the major taxonomic groups recorded during the study were represented during these periods, some by several families. Simuliids, ephemeropterans, hemipterans, coleopterans and zygopterans were especially well-represented (Tables 5.4, 5.5). Total samples from the two sub-phases FsO and FsF showed greatest faunal resemblance, but differed significantly from the majority of other sub-phases (Figs. 5.2, 5.3; Table 5.3). Of all the taxa recorded in the study, many were collected in FsO and FsF, and of these about 30 were found commonly in both, usually in more than one biotope (Table 5.6, Appendix 5.2). The taxa collected only rarely during these phases included *Notogomphus* sp. gomphids, *Orthotrichia* sp. caddisflies, and *Hydaticus* sp. dytiscids.

COMMON IN FsO

Chlorolestes sp.
Laccocoris sp.
Hyphydrus sp. larvae
Tanypodinae

COMMON IN FsF

Paracypretta sp.
Potamonautes sp.
Hydracarina
Aeshna sp.
Sympetrum sp.
Chlorolestes sp
Pseudagrion sp.
Arctocorisa meridionalis
Gerris swakopensis
Microvelia sp.
Cheumatopsyche afra
Dyschimus ensifer
Leptocerus sp.
Copelatus sp.
Colymbetinae larvae
Paramerina sp.
Procladius sp.
Cryptochironomus sp.
Anopheles sp.
Psychodidae
Tipulidae

COMMON IN BOTH
PHASES FsO & FsF

Oligochaeta
Copepoda
Ostracoda
Collembola
Baetis sp.
Cloeon sp.
Orthetrum sp.
Macromia sp.
Micronecta sp.
Hydrometra ambulator
Anisops sp.
Sigara pectoralis
Oxyethira sp.
Laccophilus sp.
Philaccolus lineatoguttatus
Dineutes sp.
Amphiops sp.
Ceratopogonidae
Larsia sp.
Polypedilum sp.
Rheotanytarsus sp.
Chironomini
Tanytarsini
Orthocladinae
Simulium nigritarse
Simulium vorax
Lymnaea columella
Ceratophallus sp.

Table 5.6 Taxa collected commonly during each of the FLOW phases FsO and FsF, and those found frequently in both phases.

NO-FLOW

The three biotopes sampled during NO FLOW were MV, SOOC and SAND (Fig. 5.1). Only the sub-phase Nfs is reviewed here, as the single sample set in Nfw was not considered sufficiently representative of conditions, as discussed. Sixty-one taxa were collected during summer periods of Nfs. Molluscs, mayflies and odonates were well represented (Table 5.4), and families commonly collected included baetids, caenids, dytiscids, hydrophilids, gyrinids, planorbids and sphaeriids (Tables 5.4 and 5.7). Rheophilous taxa (e.g. simuliids, hydropsychids, *Rheotanytarsus* chironomids) were not collected.

Total fauna from the summer Nfs sub-phase showed greatest resemblance to the fauna from the summer PsN sub-phase, which was preceded by no-flow conditions (Figs. 5.2, 5.3). Taxa common to both sub-phases included oligochaetes, ostracods, *Baetis* and *Austrocaenis* mayflies, *Orthetrum* and *Chlorolestes* odonates, *Anisops* and *Sigara* hemipterans, *Laccophilus, Dineutus* and *Amphiops* coleopterans, *Procladius, Polypedilum* and *Tanytarsus* chironomids, and *Ceratophallus* and *Pisidium* molluscs. Fauna from Nfs was significantly different to that from OsD, FsO and PwP (Table 5.3). At the scale of phases, fauna from the NO FLOW phase was the least similar to the fauna of all the other 'wet' phases (Figs. 5.4, 5.5).

Table 5.7 Taxa collected commonly during the NO FLOW phase.

COMMON IN NO-FLOW SAMPLES
Oligochaeta
Copepoda
Ostracoda
Baetis sp.
Austrocaenis sp.
Macromia sp.
Notogomphus sp.
Orthetrum sp.
Chlorolestes sp.
Micronecta citharistia
Sigara pectoralis
Anisops sp.
Hyphydrus sp.
Laccophilus sp.
Dineutus sp.
Amphiops sp.
Ceratopogonidae
Procladius sp.
Polypedilum sp.
Other Chironomini
Ceratophallus sp.
Pisidium sp.

POOLS

During this phase, mainly the POOL and DRG biotopes were sampled, with a few collections made in MV and SOOC in early pools (Fig. 5.1). Comparatively high numbers of taxa were collected in pools sampled in the summer months in sub-phases PsN (47) and PsP (64; Appendix 5.2). Well-represented groups in PsN included zygopterans, dipterans, molluscs, and *Amphiops* sp. hydrophilids. Taxa overlapping between this and other POOLS sub-phases included copepods, ostracods, crabs, notonectids, corixids, beetle larvae and lymnaeids (Table 5.8). The fauna of PsN showed greatest resemblance to that collected during the summer no-flow conditions (Nfs) which represented antecedent conditions to PsN (Table 5.1, Figs. 5.2, 5.3). PsN fauna was significantly different to that collected in all other sub-phases excepting PsP, FsF and NF (Table 5.3). This was to some extent reflected in results of cluster analysis and ordination (Figs. 5.2, 5.3).

Baetis sp. and *Austrocaenis* sp. ephemeroptera, *Orthetrum* sp. and *Chlorolestes* sp. odonates and *Sigara* corixids were common to both summer pools phases (Table 5.8). Winter pools (PwN) yielded 24 taxa, and differed significantly from the other winter pools phase PwP and the summer PsN phase, but not from the summer PsP phase. Shared taxa in PwN and PsP included only ostracods, collembolans and *Procladius* sp. chironomids (Table 5.8). PwN fauna was most similar to that of OsD (PwN conditions may have preceded OsD; Figs. 5.2, 5.3). The only animals occurring regularly in PwN samples were *Ochthebius andronius* hydraenids. Less frequent taxa included copepods, crabs, gomphids, libellulids, gyrinids and helodids.

Mature pools sampled in summer (PsP) had high diversity, and of the total of 64 taxa collected, *Cloeon* baetids, *Ecnomus* sp. trichopterans, *Philaccolus lineatoguttatus* dytiscids and beetle larvae were common (Table 5.8). *Afroptilum* sp. and *Demoulinia* sp. baetids occurred occasionally. Faunal resemblance was greatest between this and the summer phase OsP (Fig. 5.2). Significant differences were found between PsP and most other sub-phases (except those discussed earlier, Table 5.3).

DRY

This phase represented extreme conditions and only 12 taxa were collected in the five sample sets. Only the aquatic and semi-aquatic fauna yielded by DRG samples were identified. These comprised ostracods, copepods, hydracarina, and dipterans including chironomids, stratiomyids, tipulids and tabanids. Although DwD clustered as most similar to NFw, this was not due to 'true similarity' of these samples but rather to mutual dissimilarity from all other samples. In ordination and cluster analysis, the DRY phase was shown to be significantly different from all the wet phases in terms of its fauna (Figs. 5.4, 5.5).

Table 5.8 Taxa collected commonly during the various POOLS phases.

COMMON IN PsN
Amphiops sp.
Clinotanypus sp.
Anopheles sp.

COMMON IN PwN
Ochthebius andronius

COMMON IN PwP
Micronecta sp.
Dineutus sp.
Ablabesmyia sp.
Chironomus sp.
Cryptochironomus sp.

COMMON IN PsP
Nematoda
Potamonautes sp.
Hydracarina
Cloeon sp.
Mesovelia vittigera
Anisops sp.
Ecnomus sp.
Philaccolus lineatoguttatus
Hydroporinae larvae
Helodidae larvae
Haliplidae larvae
Chironomid pupae

COMMON IN PsN, PsP, PwP
Procladius sp.
Larsia sp.
Polypedilum sp.
Other Chironomini
Tanytarsus sp.
Other Tanytarsini

COMMON IN PsN, PwN, PsP
Oligochaeta
Laccophilus sp.
Pisidium sp.

Table 5.9 Taxa collected during the DRY phase

COMMON TO DRY PHASE
Oligochaeta
Ostracoda
Hydracarina
Ceratopogonidae
Tipulidae
Tabanidae
Ephydridae

ONSET		FLOW		NO-FLOW		POOLS		DRY	
Ar	Hydracarina	Ar	Hydracarina	A	Oligochaeta	D	*Polypedilum sp.*	A	Oligochaeta
Cr	Ostracoda	D	Chironomini	D	Chironomini	A	Oligochaeta	Ar	Hydracarina
D	Tanytarsini	D	*Polypedilum sp.*	E	*Austrocaenis sp.*	D	*Procladius sp.*	D	Stratiomyidae
A	Oligochaeta	D	Tanytarsini	Cr	Ostracoda	D	Tanypodinae	D	Ceratopogonidae
C	*Laccophilus lineatus*	C	*Laccophilus lineatus*	D	*Polypedilum sp.*	H	*Anisops sp.*	D	Tabanidae
Co	Collembola	D	*Rheotanytarsus sp.*	M	*Ceratophallus sp.*	N	Nematoda	D	Tipulidae
D	Anopheles sp.	T	*Oxyethira sp.*	E	*Baetis sp.*	E	*Baetis sp.*		
D	Tanypodinae	D	Tanypodinae	O	*Macromia sp.*	D	Chironomini		
D	Chironomini	A	Oligochaeta	H	*Anisops sp.*	H	*Sigara sp.*		
H	Mesoveliidae	E	*Baetis sp.*	D	*Tanytarsus sp.*	E	*Austrocaenis sp.*		
D	Rheotanytarsus sp.	Cr	*Potamonautes sp.*	C	*Hyphydrus sp.*	D	*Tanytarsus sp.*		
C	*Amphiops sp.*	D	Orthocladiinae	O	*Chlorolestes sp.*	Cr	*Potamonautes sp.*		
O	*Orthetrum sp.*	M	*Ceratophallus sp.*	D	*Procladius sp.*	D	*Larsia sp.*		
D	*Krenosmittia sp.*	H	*Anisops sp.*	D	*Tanytarsus sp.*	M	*Pisidium sp.*		
C	*Philaccolus sp.*	D	*Ablabesmyia sp.*	O	*Notogomphus sp.*	D	Ceratopogonidae		
Cr	*Paracypretta sp.*	H	*Hydrometra sp.*	D	*Anopheles sp.*	O	*Chlorolestes sp.*		
D	*Polypedilum sp.*	H	*Micronecta sp.*	M	*Ceratophallus sp.*	Ar	Hydracarina		
C	Dytiscid larva	O	*Orthetrum sp.*	Cr	Ostracoda	O	*Notogomphus sp.*		
D	*Rheotanytarsus sp.*	C	Dytiscid larva	C	*Dineutus sp.*	Cr	Ostracoda		
C	*Hydrochus sp.*	D	*Larsia sp.*	C	*Laccophilus lineatus*	H	*Micronecta sp.*		
O	*Orthetrum sp.*	E	*Cloeon sp.*	M	*Pisidium sp.*	O	*Orthetrum sp.*		
D	*Krenosmittia sp.*	D	Ceratopogonidae	H	*Sigara sp.*	D	Tanytarsini		
C	*Philaccolus sp.*	M	*Lymnaea columella*	O	*Orthetrum sp.*	C	*Laccopilus lineatus*		
Cr	*Paracypretta sp.*	Co	Collembola	H	*Micronecta sp.*	C	*Dineutus sp.*		
D	*Polypedilum sp.*	H	*Mesovelia sp.*	C	*Amphiops sp.*	D	*Chironomus sp.*		
D	*Harrisonina petricola*	O	*Macromia sp.*			C	*Copelatus sp.*		
H	*Hydrometra ambulator*	T	*Ecnomus sp.*						
Cr	*Potamonautes sp.*	D	Tipulidae						
M	*Ceratophallus sp.*	D	*Simulium nigritarse*						
T	*Cheumatopsyche sp.*	Ar	*Cheumatopsyche afra*						

Table 5.10 Contribution of individual taxa to the majority of similarity between samples from a single phase, as determined by SIMPER. Taxa are listed in decreasing order of their contributions. Orders to which each taxon belongs is listed alongside it: A-Annelida, Ar-aquatic Arachnida, C-Coleoptera, Co-Collembola Cr-Crustacea, D-Diptera, E-Ephemeroptera, H-Hemiptera, M-Mollusca, Nematoda, O-Odonata, T-Trichoptera.

5.5.9 Contributions of individual taxa to similarity within a phase

The proportional contributions of individual taxa to average sample similarity within a phase, as determined by SIMPER, are listed (in decreasing order of importance) in Table 5.10. Many of these contributed to similarities in several groups. SIMPER results were interpreted cautiously (see 1.4.6 for discussion on this).

5.6 DISCUSSION

5.6.1 Assessment of the distinctiveness of individual phases

Taking into account the bias in sample numbers, significant differences between fauna from four of the five phases indicated that *on average*, there was less variability in fauna within phases than between phases. This result was not the same as labelling the phases faunally 'distinct'. The variability in fauna within individual phases over time was considerable, according to the results of cluster analysis and ordination of the 100 individual sample sets from each of the sub-phases (Appendix 5.1). Similarities between samples were generally below 50%, and no clusters contained a majority of samples from a single phase or sub-phase, which would have illustrated some stability in faunal composition of a phase over time. It could not therefore be said that the phases were *separable* on the basis of their fauna. However, it was assumed that if each phase could be associated with a faunal core or 'nucleus', and if the phase was hydrologically distinct (which was the basis on which the phases were identified), then it could be considered an ecologically meaningful unit in a river of this nature. In analogy to the model of the atom, this 'nucleus' would represent the stable element of the fauna, with a peripheral, apparently haphazard association of various faunal types - some historically adapted, some facultative and some opportunistic taxa (in analogy to 'electrons') whose proximity to or distance from the nucleus was unpredictable.

Results indicated that it was possible to associate such a 'core nucleus' of animals with each of the phases (except possibly the NO FLOW phase) and its hydrological conditions. This faunal unit may comprise few or many, common or rare taxa, and the taxonomic group to which they belonged would largely depend on the nature of the phase. Taxa would not necessarily be restricted to that phase, but the combination of taxa would be the important factor. The balance of opportunist colonists, facultative taxa, and residents (the three faunal source groups discussed in Section 4.6.4) in the fauna would be determined by the hydrological conditions and the availability of aquatic habitat.

Typically, the following group/s were present during individual phases (dominant groups highlighted):

ONSET: **opportunist colonists**, faculative taxa, residents
FLOW: **opportunist colonists,** facultative taxa, fewer residents
NO-FLOW: fewer opportunist colonists, **facultative taxa**, residents
POOLS: facultative taxa, residents
DRY: residents

The 'peripheral' element of the fauna of each phase would be either taxa collected infrequently during particular conditions, or taxa occurring in a number of phases. In a sense, this could be viewed as another aspect of the continuum between different hydrological states discussed in Chapter 2, as peripheral fauna may overlap or range between contiguous environmental conditions.

The proposed 'core' and 'peripheral' taxa associated with each of the phases were determined on the basis of selected data from SIMPER results (where taxa contributing to group similarity were not common to the majority of other groups, Table 5.9), faunal lists (Appendices 3.2, 4.1., 5.2); data from previous chapters (Chs 3,4), and consideration of original ('raw') data matrices. The core taxa included in these lists are not necessarily absent from other phases, but were collected most frequently in the phase recorded. Some were collected rarely and in small numbers: these often provided greater insight into the river history or condition than did the common taxa: Brown (1993), discussing the tendency to average out variability in science, commented that '(a) *datum far removed from the mean is made to contribute as little as possible to the processed results, or may even be discarded, although in fact the anomalous datum, if real, may represent a finding more interesting than the mean itself*'. Core taxa were not always simple to identify (i.e. not distinguishable without examination of mouthparts, or specialist assistance etc.), which limits their usefulness or practicality somewhat, however it is felt that in many cases it is at the level of genus or species that biotic/abiotic associations are most meaningfully made.

The 'core' and 'peripheral' taxa tentatively proposed for each phase (and subject to revision) are listed.

ONSET PHASE (depending on discharge)

Core	*Simulium nigritarse*, *Harrisonina petricola* diamesids (collected only during ONSET), *Paracypretta syngramma* and other ostracods, copepods, hydracarinids, oligochaetes, culicids, veliids, *Philaccolus lineatoguttatus* dytiscid adults, dytiscid larvae, hydrophilid adults, chironomids (Tanytarsini, *Rheotanytarsus* sp., *Krenosmittia* sp.), lymnaeid snails.
Peripheral	Baetids, zygopterans, anisopterans, trichopterans, physid and planorbid snails.

Harrisonina petricola is particularly interesting, and has been recorded at few other African localities (Harrison, pers. comm.; unpubl.). It belongs to the family Diamesinae, most members of which occur in glacial melt streams. Harrison lists it as an 'aberrant genus' in his chironomid checklist - it was also collected in a stream off a granite dome in Zimbabwe, and in the Olifants River, South Africa. Harrison (1978) noted that it is the one possible candidate for the 'tropical Godwanian group' - this referring to its possible origin as part of the original biota of tropical Godwanaland which broke up during the Cretaceous.

FLOW PHASE

Core Taxa collected only in FLOW phase samples included *Baetis latus*, *Afroptilum excisum* and *Pseudocloeon* sp. baetids, *Aprionyx* complex and *Adenophlebia auriculata* leptophlebiids, *Caenis* sp. caenids, *Cheumatopsyche afra* hydropsychids, *Sympetrum* sp. libellulids, and numerous *Simulium* spp. blackflies. The majority of these were opportunist colonists. Other core taxa included several chironomid taxa, dytiscids, hydrophilid larvae, *Oxyethira* sp. hydroptilids, and *Trithemis* sp. libellulids.

Peripheral A great variety of taxa was associated with the FLOW phase. Many of these are listed in Tables 5.7 and 5.10.

NO FLOW This phase did not differ significantly from the ONSET, FLOW, or POOLS phases. It was thus not considered sufficiently distinctive to have a 'core' fauna. Taxa collected frequently in this phase overlap with those found in the other three phases: *Austrocaenis* sp. caenids, *Baetis* sp. mayflies, *Ceratophallus* sp. planorbids, *Macromia* sp. corduliids, *Notogomphus* sp., *Anisops* sp., *Hyphydrus* sp. and *Laccophilus* sp. dytiscids, *Chlorolestes* sp., a number of chironomids (e.g. *Tanytarsus* sp.), *Ceratophallus* sp. planorbids and *Pisidium* sp. sphaeriids.

POOLS

Core: A range of animals occupied pools, depending on their 'age' and size. There was an increase in relative proportions of predaceous taxa in the samples in more mature pools (PsP and PwP). The 'core' was thus dynamic, but could comprise a Ostracods, *Potamonautes* crabs, *Baetis* sp. (generally *B. harrisoni*) and *Austrocaenis* sp. mayflies, *Orthetrum* sp. libellulids, *Notogomphus* sp. gomphids, *Laccophilus lineatus* dytiscids, *Ecnomus* sp. trichopterans, ceratopogonids, *Dineutus* sp. gyrinids, *Amphiops* sp. hydrophilids, *Chironomus* sp. Chironomini, several Tanypodinae, *Lymnaea columella* lymnaeids, and *Pisidium* sp. sphaeriids.

Peripheral Facultative taxa occurring during these phases included *Afroptilum* sp. and *Austrocaenis* sp. mayflies, *Macromia* sp. corduliids, *Micronecta* sp. and *Sigara pectoralis* corixids, *Ecnomus* sp. caddisflies, *Laccophilus* sp. dytiscids, *Amphiops* sp. hydrophilids, *Paramerina, Procladius, Polypedilum* and *Tanytarsus* chironomids.

DRY PHASE

Core Mostly residents, such as copepods, ostracods, hydracarina, collembolans, hebrids, culicids, ceratopogonids, ephydrids, tipulids, and tabanids. Most of these taxa are described as 'shore-dwellers' or 'semi-aquatic' by McCafferty (1981), and were included in Marchant's (1982) account of taxa predominating during the dry season in an Australian billabong.

Peripheral Facultative taxa collected frequently during damper conditions included *Notogomphus* sp., ecnomids, dytiscid adults, *Lymnaea columella*, and *Ceratophallus* sp. snails.

The facultative and resident taxa included in each group were to some extent semi-aquatic because of their ability to adapt to damp, and in the case of residents, drying conditions. Adaptation is generally of two forms:

- behavioural avoidance as adults, by burrowing into surface layers of damp substratum or mud (e.g. *Orthetrum* sp., gastropods), or sheltering under leaves, stones or algal mats (e.g. *Macromia* sp., tabanid larvae, oligochaetes, gastropods);
- physiological avoidance in the form of hibernation in drying substrata (e.g. some chironomids and gastropoda), resistant or diapausing eggs (e.g. oligochaetes, ephemeropterans, trichopterans, hydracarinids, coleopterans,

culicids), encystment as adults (e.g. copepoda), arrested development of juvenile stages (e.g. ostracods, copepods, collembolans and chironomids), or the secretion of a protective epiphragm of mucous over a shell opening (e.g. *Pisidium* snails) to prevent desiccation (e.g. Harrison 1978, Williams 1987, McCafferty 1981, Brown 1980, Williams and Hynes 1976, Lemkuhl 1973 quoted in Williams 1987, Wiggins 1973, Pennak 1953, Davidson 1932).

Many facultative adults are capable of relocating under adverse conditions (e.g. adult dytiscid, hydrophilid and hemiptera). Dytiscids and hydrophilids particularly are strong fliers capable of relocation during drying (Pennak 1953), and of aerial recolonisation when conditions are favourable (Williams 1987). These taxa also breathe atmospheric air and are thus not constrained by low oxygen (McCafferty 1981), though this was seldom a problem in the upper Kowie River.

The question of whether or not the taxa recorded for each of the phases would represent the fauna found in other temporary rivers in the region or beyond is approached in Chapters 6 and 7.

5.6.2 Assessing the value of hydrological sub-phases

The significant differences shown between the fauna of many of the sub-phases indicated that the sub-division of hydrological phases had some validity. The effect of one or more of the three modifying influences (antecedent conditions, time of year, and character and availability of biotopes) on fauna was noticeable in certain instances.

The differences between fauna of the different ONSET sub-phases illustrated the effect of both antecedent conditions and time of year on fauna. Samples taken during summer ONSET (OsD) periods preceded by dry-channel conditions were significantly different from those taken in onset periods preceded by pools in the channel (OsP and OwP). Samples from OsD also differed significantly from most other 'wet' sub-phases, while those from OsP differed significantly from only two. Many of the taxa collected in the summer months during ONSET preceded by

POOLS (OsP) were not collected in summer months of ONSET preceded by DRY conditions (OsD), e.g. blackflies, baetids, hemipterans, ecnomid caddisflies, beetle larvae. The generally high numbers of taxa collected during OsP were attributed to the presence and resistance or resilience of many of these animals in pools in the channel prior to recommencement of flow. This is supported by the relatively high overall similarities between fauna from the POOLS and ONSET phases, as shown in cluster analyses of total samples per phase.

Along similar lines, the similarity in the fauna of NO FLOW summer phase (NFs), and the POOL summer phase preceded by NO FLOW conditions (PsN) indicated the relationship between previous and present conditions. It is clear from this relationship that during the early POOLS stages, fauna closely resembled that of previous, no-flow conditions. With maturity of pools, however, as in PsP and PwP sub-phases (which were preceded by pools rather than no-flow), greatest similarity was with the OsP and OwP conditions which followed. Despite the lack of surface water continuity in the POOLS phase, and the 'flushing' effect often associated with recommencement of flow, the fauna of PsP and OsP were remarkably similar.

The effects of time of year were illustrated in the comparison between OsP (summer) and OwP (winter) sub-phases, both of which had the same 'present' and antecedent conditions but significantly different faunas. Both sub-phases were represented by the same number of sample sets (6), however 61 taxa were collected in OsP in comparison to 26 in OwP. Developing juveniles typical of summer conditions (e.g. mayflies, caddisflies, some damselflies) were present in OsP but absent from OwP samples.

From these results it was inferred that the division of hydrological phases into sub-phases on the basis of time of year and antecedent conditions; or at least acknowledgement of these auxilliary influences on the fauna of individual phases, was a valid and worthwhile exercise. The twelve sub-phases, while somewhat unwieldy, could form the basis of a simple predictive model for the purposes of establishing an 'expected' fauna in a river of this nature. A possible outline for a model of this nature is shown in Fig. 5.6. A great deal more information on the

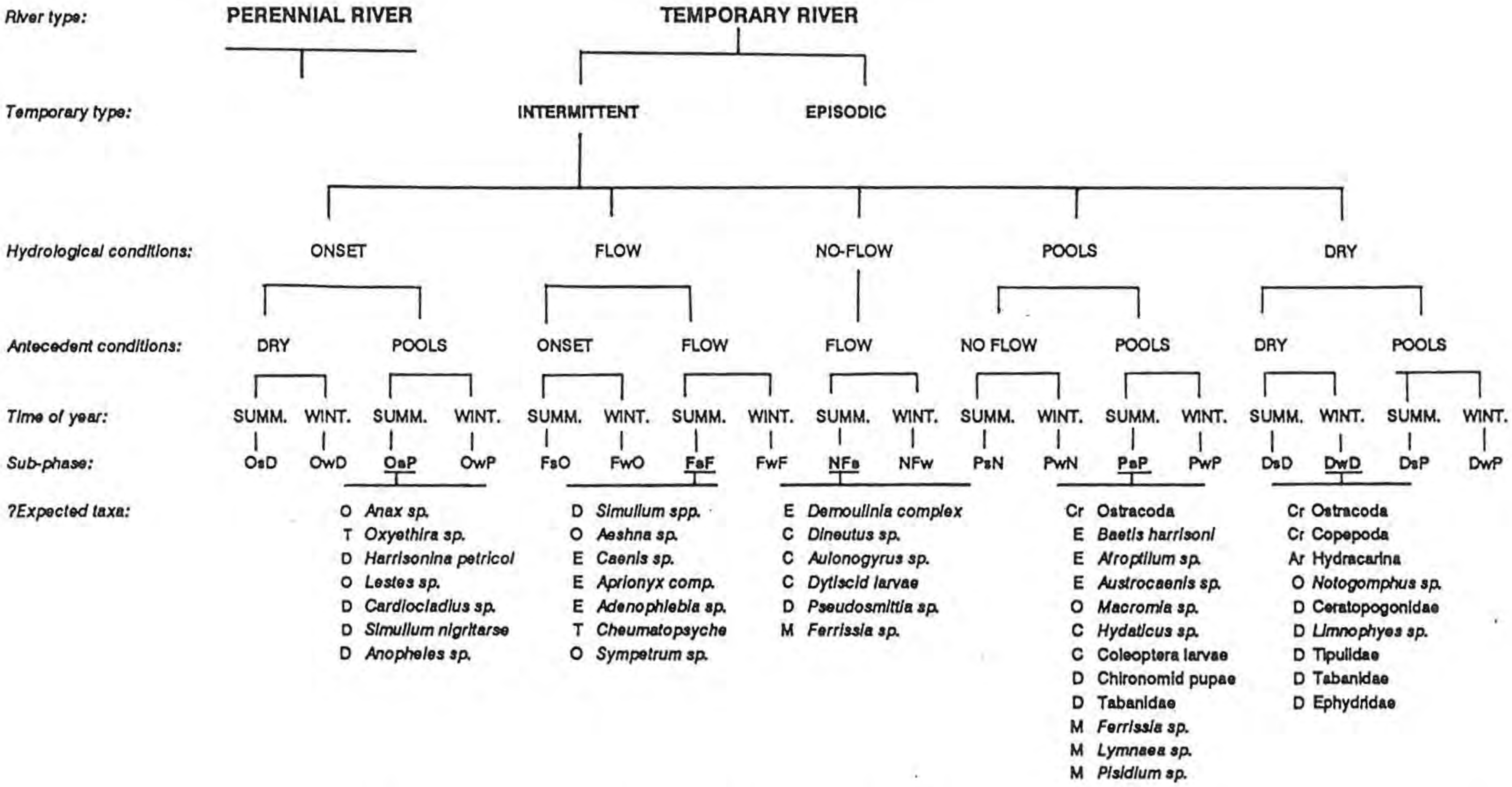


Figure 5.6 A simple basis for a predictive model based on the recognition of hydrological phases and sub-phases in an intermittent river, and their effects on the fauna. Groups of invertebrates associated with four of the sub-phases (which may be the final output of such a model) are tentative and are presented merely to illustrate the sort of refinement attainable through more intensive studies of the fauna of these different phases.

natural fauna of temporary rivers would be necessary before such a model could be applied with any confidence.

5.6.3 Association between abiotic variables and hydrological phases

Unfortunately, no clear statistically-based association between abiotic variables and hydrological phases could be demonstrated for this section of the river, as already discussed. The stability in values of most environmental variables (excluding flow) resulted in significant overlap in values between the different 'wet' phases and sub-phases. Visual inspection of the data, and results presented in previous chapters (Chs 3,4) indicated that the variables most likely to be associated with different phases would be hydraulic (for example, current speed in biotopes as characteristic features of ONSET and FLOW phases) and substratum-related (percentage composition of substrata changed considerably with changes in phase).

5.7 CONCLUDING POINTS

- The five hydrological phases identified at the outset of the study were subdivided into sub-phases on the basis of antecedent conditions in the channel and time of year (summer/winter), to verify the influence of these variables on fauna.

- These sub-divisions were shown to be faunally dissimilar (and therefore valid) for at least some of the phases, with significant differences indicated between 26 pairs of sub-phases out of a possible 45. This was, however, interpreted in the context of different numbers of samples per sub-phase.

- Seven out of 10 possible pairs of hydrological phases were shown to be significantly different, indicating that for the ONSET, FLOW, POOLS and DRY phases, a 'core' of taxa must exist which was dissimilar to that of all other phases. In addition, a peripheral group of more vagile taxa was thought to be associated with each phase.

- A core group and peripheral group of taxa for each of the phases was proposed.

- While no association could be shown between abiotic variables (other than hydrological ones) and biotic elements of the study, the association between hydrological conditions (both present and previous), time of year, and fauna was considered a useful progression in the understanding of the dynamics of intermittent rivers, and the beginnings of a predictive model for the fauna of such systems was presented.

REFERENCES

Abell, D.L. 1984. Benthic invertebrates of some Californian intermittent streams. *In*: S. Jain and P. Moyle (eds). *Vernal pools and intermittent streams.* University of California, Davis Institute of Ecology Publication No. 28. pp.46-60.

Armitage, P.D., Pardo, I. and Brown, A. 1995. Temporal constancy of faunal assemblages in 'mesohabitats' - application to management? *Archiv für Hydrobiologie* **133** (3) 367-387.

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24:** 123-141.

Brown, A.C. 1993. Variability in biological systems. *South African Journal of Science* **89:** 308-309

Brown, D.S. 1980. *Freshwater snails of Africa: and their medical importance.* Taylor and Francis Ltd., London.

Clarke, K.R. and Warwick, R.M. 1994. *Change in marine communities - an approach to statistical analysis and interpretation.* Plymouth Marine Laboratories, Bournemouth.

Clifford, H.T. 1966. The ecology of invertebrates in an intermittent stream. *Investigations of Indiana lakes and streams* **7:** 57-98.

Davidson, J. 1932. Resistance to eggs of Collembola to drought conditions. *Nature* **29:** 867.

Harrison, A.D. (unpublished). Taxonomic information relating to the family Chironomidae in Southern Africa. Available on Website, address http://www.ru.ac.za/departments/zooento/Martin/Aquatics.html.

Harrison, A.D. 1978. Freshwater invertebrates (except molluscs). *in:* M.J.A. Werger and A.C.van Bruggen (eds). Biogeography and ecology of southern Africa. *Monographiae Biologicae* **31:** 1139-1152.

Lemkuhl, D.M. 1973. A new species of *Baetis* from ponds in the Canadian Arctic, with biological notes. *Canadian Entomologist* **10:** 343-346.

Marchant, H.J. 1982. Seasonal variation in the macroinvertebrate fauna of Billabongs near Magella Creek, Northern Territory, Australia. *Australian Journal of Marine and Freshwater Research* **33:** 329-342.

McCafferty, W.P. 1981. *Aquatic Entomology*. Jones and Bartlett Publishers, Boston.

Minshall, G.W. and Minshall, J.N. 1978. Microdistribution of benthic invertebrates in a rocky mountain (USA) stream. *Hydrobiologia* **55** (3): 231-249.

Palmer, C.G., O'Keeffe, J.H. and Palmer, R.W. 1991. Are macroinvertebrate assemblages in the Buffalo River, Southern Africa, associated with particular biotopes? *Journal of the North American Benthological Society* **10:** 349-357.

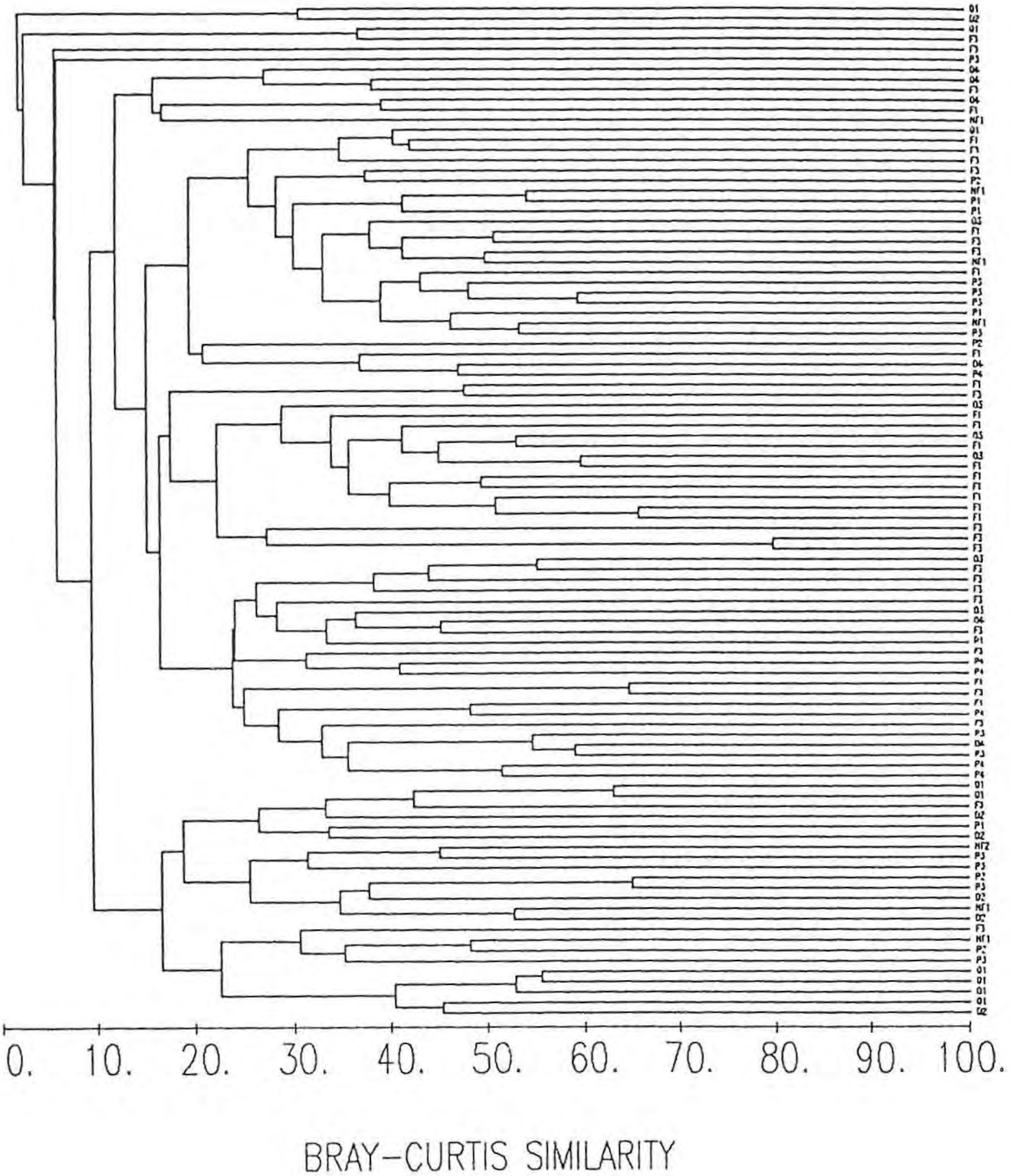
Pennak, R.W. 1953. *Freshwater invertebrates of the United States*. The Ronald Press Company, New York.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. 1997. Ecosystem expansion and contraction in streams. *BioScience* 47 (7): 427-435.

Williams, D.D. 1987. *The ecology of temporary waters*. Croom Helm Ltd., Kent/ Timber Press, USA

Williams, D.D. and Hynes, H.B.N. 1976. The ecology of temporary streams. I. The fauna of two Canadian streams. *Internationale Revue der Gesamten Hydrobiologie* **61:** 761-787.

APPENDIX 5.1 Dendrogram showing hierarchical cluster analysis of the full complement of 100 samples, prior to pooling samples from individual sub-phases. This illustrates the sort of complexity generated when all taxa and samples are included in analyses - these results provide no basis for the detection of pattern, and were one of the reasons for aggregating samples into more manageable groups (e.g all samples per sub-phase), in which all taxa were represented.



APPENDIX 5.2 List of taxa collected in the various phases and sub-phases in the upper Kowie River. Presence is recorded as the first two letters of the 'code' defining the sub-phase. e.g. O-ONSET, s-summer, D-DRY = OsD = ONSET phase, during summer, preceded by dry conditions. Full abbreviations given in Table 5.1.

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	OwP	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
Total no. taxa:		29	61	26	133	147	61	6	47	24	64	36	13
COELENTERATA	*Hydra sp.*					Fs					Ps		
NEMATODA			Os		Fs						Ps		Dw
CLADOCERA					Fs								Dw
COPEPODA	*Ilyocryptus sordidus*												Dw
	Mesocyclops major					Fs							
	Microcyclops crassipes												Dw
	Paradiaptomus natalensis	Os											
	Type A	Os	Os		Fs	Fs	NFs		Ps		Ps		Dw
OSTRACODA	*Paracypretta syngramma*	Os			Fs	Fs			Ps				
	Paracypretta aratra					Fs							
	Candonopsis sp.				Fs				Ps				
	Cypridopsis sp.					Fs							
	Ilyodromus sp.					Fs							
	Physocypria cf capensis		Os			Fs			Ps				
	Pseudocandona gr geratsi		Os										
	Type A				Fs	Fs	NFs				Ps		
	Type B					Fs	NFs				Ps		
	Type C		Os		Fs	Fs	NFs				Ps		
	Type D				Fs	Fs							
	Type E				Fs	Fs					Ps		
	Type F		Os										
	Type X	Os			Fs	Fs	NFs			Pw	Ps	Pw	Dw
DECAPODA	*Potamonautes sp.*	Os	Os		Fs	Fs			Ps	Pw	Ps		
HYDRACARINA	Type A	Os			Fs	Fs	NFs			Pw	Ps		Dw
	Type B				Fs	Fs	NFs				Ps		
	Type D				Fs								
	Type E										Ps		
	Type F		Os										
	Type G		Os										
	Type H		Os										
	Type I		Os										
	Type J			Ow	Fs								
	Type K					Fs							
	Type M				Fs	Fs							
	Type N				Fs								

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	OwP	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
COLLEMBOLA		Os			Fs	Fs		NFw		Pw	Ps		
EPHEMEROPTERA	BAETIDAE												
	Baetis latus				Fs	Fs							
	Baetis harrisoni				Fs	Fs	NFs		Ps	Pw	Ps		
	Baetis sp.		Os		Fs	Fs	NFs				Ps		
	Afroptilum excisum				Fs	Fs							
	Afroptilum pulchrum				Fs						Ps	Pw	
	Afroptilum parvum					Fs							
	Cloeon sp.		Os		Fs	Fs					Ps		
	Demoulinia complex				Fs	Fs	NFs				Ps		
	Pseudocloeon vinosum					Fs							
	Pseudocloeon maculosum					Fs							
	CAENIDAE												
	Austrocaenis sp.				Fs		NFs		Ps		Ps		
	Caenis sp.					Fs							
	LEPTOPHLEBIIDAE												
	Aprionyx complex					Fs							
	Adenophlebia ?auriculata					Fs							
ODONATA	AESHNIDAE												
	Aeshna miniscula					Fs							
	Aeshna subpupillata					Fs							
	Aeshna sp.					Fs							
	Anax sp.			Ow		Fs						Pw	
	CORDULIIDAE												
	Macromia sp.				Fs	Fs	NFs				Ps		
	Syncordulia sp.			Ow	Fs	Fs	NFs					Pw	
	GOMPHIDAE												
	Notogomphus ?pretorius gp.				Fs		NFs		Ps		Ps	Pw	
	LIBELLULIDAE												
	Orthetrum sp		Os		Fs	Fs	NFs		Ps	Pw	Ps		
	Sympetrum ?fonscolombei					Fs							
	Trithemis sp.				Fs	Fs							
	Tetrathemis sp.											Pw	
	COENAGRIONIDAE												
	Enallagma sp.					Fs	NFs		Ps				
	Pseudagrion sp.			Ow	Fs	Fs	NFs		Ps				
	Ischnura sp.					Fs							
	CHLOROLESTIDAE												
	Chlorolestes sp.				Fs	Fs	NFs		Ps		Ps		
	LESTIDAE												
	Lestes plagiatus		Os		Fs	Fs	NFs						

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
COLEOPTERA	DYTISCIDAE												
	Laccophilus lineatus		Os	Ow	Fs	Fs	NFs		Ps	Pw	Ps	Pw	
	Laccophilus sp.				Fs	Fs	NFs			Pw		Pw	
	Copelatus caffer					Fs	NFs			Pw			
	Copelatus sp.			Ow		Fs	NFs		Ps	Pw			
	Coptotomus sp.					Fs							
	Hydaticus caffer	Os											
	Hydaticus capicola ?	Os				Fs					Ps		
	Hydaticus flaveolineatus												
	Hydaticus servillianus				Fs								
	Leiodytes evanescens					Fs							
	Philaccolus lineatoguttatus		Os	Ow	Fs	Fs					Ps		
	Yola sp									Pw			
	Type X		Os	Ow	Fs	Fs				Pw	Ps	Pw	
	Colymbetinae larva	Os			Fs	Fs					Ps		
	Dytiscinae larva	Os			Fs	Fs							
	Hydroporinae larva				Fs	Fs	NFs				Ps		
	Hydaticus sp. larva				Fs	Fs							
	Hydryphus sp				Fs	Fs	NFs		Ps				
	Laccophilus sp		Os		Fs	Fs	NFs				Ps		
	ELMIDAE												
	Stenelmis sp.					Fs							
	Elmid larvae					Fs			Ps				
	GYRINIDAE												
	Aulonogyrus caffer					Fs	NFs						
	Dineutes sp.	Os		Ow	Fs	Fs	NFs			Pw	Ps	Pw	
	Gyrinus sp.									Pw			
	HALIPLIDAE												
	Haliplus sp.					Fs							
	Haliplidae larva										Ps		
	HELODIDAE												
	Adults									Pw			
	Larvae		Os	Ow		Fs					Ps		
	HYDROPHILIDAE												
	Amphiops sp.	Os	Os	Ow	Fs	Fs	NFs		Ps		Ps	Pw	
	Hydrochus sp.			Ow	Fs	Fs						Pw	
	Hydrobius sp.					Fs	NFs		Ps				
	Type A	Os		Ow	Fs	Fs	NFs						
	Hydrophilid larvae		Os		Fs	Fs			Ps		Ps		

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
HEMIPTERA	BELOSTOMATIDAE												
	Diplonychus capensis				Fs	Fs						Pw	
	CORIXIDAE												
	Arctocorisa meridionalis					Fs	NFs		Ps				
	Micronecta citharistia		Os	Ow		Fs	NFs					Pw	
	Micronecta sp.			Ow	Fs	Fs				Pw	Ps	Pw	
	Sigara pectoralis		Os		Fs	Fs	NFs		Ps	Pw	Ps		
	GERRIDAE												
	Gerris swakopensis			Ow		Fs	NFs			Pw			
	Limnogonus capensis				Fs								
	HEBRIDAE												
	Hebrus sp.				Fs								
	HYDROMETRIDAE												
	Hydrometra ambulator	Os		Ow	Fs	Fs	NFs						
	NAUCORIDAE												
	Laccocoris sp.					Fs							
	MESOVELIIDAE												
	Mesovelia vittigera		Os	Ow	Fs	Fs					Ps	Pw	
	Mesovelia sp.					Fs							
	NOTONECTIDAE												
	Anisops gracilis						NFs			Pw			
	Anisops limpida					Fs							
	Anisops sp.		Os	Ow	Fs	Fs	NFs		Ps		Ps	Pw	
	Enithares sobria				Fs	Fs						Pw	
	PLEIDAE												
	Plea pullula	Os				Fs							
	VELIIDAE												
	Microvelia venustissima					Fs				Pw			
	Microvelia sp.					Fs							
TRICHOPTERA	ECNOMIDAE												
	Ecnomus sp.		Os		Fs	Fs			Ps		Ps	Pw	
	HYDROPTILIDAE												
	Oxyethira sp.			Ow	Fs	Fs	NFs						
	Orthotrichia sp.				Fs	Fs							
	HYDROPSYCHIDAE												
	Cheumatopsyche afra					Fs							
COLEOPTERA	DYTISCIDAE												
	Hyphydrus distinctus						NFs		Ps				
	Hyphydrus signatus						NFs					Pw	
	Hydrovatus brownei											Pw	

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
DIPTERA	CERATOPOGONIDAE		Os		Fs	Fs	NFs	NFw	Ps	Pw	Ps	Pw	Dw
	CHAOBORIDAE				Fs		NFs		Ps				
	CHIRONOMIDAE												
	Tanypodinae												
	Ablabesmyia dusoleili					Fs							
	Ablabesmyia sp.				Fs	Fs						Pw	
	Clinotanypus sp.				Fs		NFs		Ps		Ps	Pw	
	Conchapelopia sp.		Os		Fs	Fs							
	Paramerina sp.		Os			Fs	NFs					Pw	
	Procladius sp.		Os		Fs	Fs	NFs		Ps	Pw	Ps	Pw	
	Tanypus sp.												
	Larsia sp.		Os		Fs	Fs	NFs		Ps		Ps	Pw	
	Type A		Os		Fs	Fs					Ps		
	Type B		Os	Ow	Fs	Fs						Pw	
	Type C			Ow	Fs	Fs							
	Type D					Fs							
	Type E					Fs							
	Type F			Ow	Fs	Fs					Ps	Pw	
	Type G				Fs	Fs						Pw	
	Type H												
	Type I		Os										
	Type J			Ow		Fs							
	Type K												
	Type L				Fs								
	Type M												
	Chironomini												
	Polypedilum sp.		Os	Ow	Fs	Fs	NFs		Ps		Ps	Pw	
	Chironomus sp.				Fs	Fs					Ps	Pw	
	Cryptochironomus sp.					Fs						Pw	
	Microchironomus sp.				Fs						Ps		
	Zavreliella sp.		Os								Ps		
	Type A		Os		Fs	Fs	NFs	NFw	Ps		Ps	Pw	
	Type B		Os	Ow	Fs	Fs	NFs		Ps		Ps		
	Type C				Fs	Fs	NFs		Ps				
	Type D				Fs	Fs	NFs		Ps		Ps		
	Type E				Fs	Fs			Ps				
	Type F						NFs		Ps				

	ONSET			FLOW		NO-FLOW		POOLS				DRY
	OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
Chironomini												
Type L		Os		Fs	Fs							
Type P				Fs								
Type S		Os		Fs								
Type T				Fs								
Type W				Fs								
Type X				Fs								
Type Y				Fs								
Type Z				Fs								
Tanytarsini												
Cladotanytarsus sp.		Os						Ps				
Rheotanytarsus sp.		Os		Fs	Fs							
Stempellinella sp.		Os									Pw	
Tanytarsus sp.		Os		Fs	Fs	NFs		Ps		Ps	Pw	
Type A		Os		Fs	Fs	NFs		Ps		Ps	Pw	
Type B		Os		Fs	Fs	NFs		Ps		Ps		
Type C				Fs	Fs	NFs						
Type D		Os	Ow	Fs		NFs					Pw	
Type F				Fs	Fs							
Type N		Os		Fs								
Type R				Fs								
Type T				Fs								
Type V				Fs	Fs					Ps		
Diamesinae												
Harrisonina petricola	Os	Os										
Orthocladiinae												
Cardocladius sp.		Os										
Chaetocladius sp				Fs								
Corynoneura sp.				Fs	Fs							
Cricotopus sp					Fs			Ps				
Krenosmittia sp.	Os		Ow									
Limnophyes sp.	Os			Fs	Fs			Ps				
Limnophyes natalensis			Ow	Fs	Fs						Pw	
Mesocricotopus sp.					Fs							
Nanocladius sp.	Os			Fs	Fs					Ps		
Paratrissocladius sp.	Os											
Parametriocnemus sp.		Os			Fs							

	ONSET			FLOW		NO-FLOW		POOLS				DRY
	OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
Orthocladiinae												
Pseudoorthocladiinae sp.					Fs	NFs						
Pseudosmittia sp.						NFs						
Rheocricotopus sp.		Os		Fs	Fs							
Type A				Fs								
Type B		Os		Fs	Fs							
Type D												
Type C					Fs	NFs						
Type E			Ow	Fs								
Type F				Fs	Fs							
Type G				Fs								
Type I		Os	Ow	Fs								
Type K				Fs								
Type L				Fs								
Type M		Os		Fs	Fs							
Type N												
Type S				Fs								
Type T				Fs								
Type U												
Type V				Fs								
Type W				Fs								
Chironomid pupae												
Pseudoorthocladius pupa				Fs								
Cricotopus pupa			Ow	Fs								
Rheocricotopus pupa				Fs								
Polypedilum pupa		Os		Fs								
Tanytarsus pupa										Ps		
Dicrotendipes pupa										Ps		
Chironomus pupa			Ow									
CULICIDAE												
Anopheles (cellus) squamosu				Fs	Fs					Ps		
Anopheles (an.) crypticus	Os					NFs		Ps		Ps		
Anopheles sp.			Ow	Fs	Fs	NFs		Ps	Pw	Ps		Dw
PSYCHODIDAE	Os		Ow	Fs	Fs							
TIPULIDAE		Os	Ow	Fs	Fs		NFw	Ps			Pw	Dw

		ONSET			FLOW		NO-FLOW		POOLS				DRY
		OsD	OsP	Ow	FsO	FsF	NFs	NFw	PsN	Pw	PsP	PwP	DwD
	SIMULIIDAE												
	Simulium ?alcocki				Fs	Fs							
	Simulium bequaerti					Fs							
	Simulium nigritarse comp.	Os	Os		Fs	Fs							
	Simulium ruficorne				Fs								
	Simulium vorax					Fs							
	Simulium adersi				Fs	Fs							
	*Simulium harg./med.**				Fs	Fs							
	Simulium impukane					Fs							
	STRATIOMYIDAE	Os							Ps				Dw
	TABANIDAE		Os	Ow				NFw	Ps		Ps		Dw
	THAUMALIDAE	Os				Fs							
	EPHYDRIDAE	Os			Fs	Fs		NFw		Pw			Dw
MOLLUSCA	ANCYLIDAE												
	Burnupia sp.												
	Ferissia farquhari					Fs							
	Ferissia sp.		Os			Fs	NFs		Ps		Ps		
	LYMNAEIDAE												
	Lymnaea columella	Os	Os	Ow	Fs	Fs	NFs			Pw	Ps	Pw	
	PHYSIDAE												
	Bulinus sp.					Fs							
	Bulinus forskalii	Os	Os		Fs	Fs	NFs						
	PLANORBIDAE												
	Ceratophallus sp.	Os	Os		Fs	Fs	NFs		Ps				
	SPHAERIIDAE												
	Pisidium sp.					Fs	NFs		Ps	Pw	Ps		

**Simulium hargreavsi/medusaeforme*

CHAPTER 6

THE INVERTEBRATE BIOTA OF TEMPORARY RIVERS WITH DIFFERING FLOW REGIMES IN THE EASTERN CAPE REGION OF SOUTH AFRICA

*This chapter has been prepared as a paper for submission to the journal **Freshwater Biology**, under the authorship of M.C. Uys and J.H. O'Keeffe.*

ABSTRACT

A range of different temporary river types occur in South Africa. It is not known to what extent different degrees of intermittency affect invertebrate fauna, and whether or not a characteristic fauna could be associated with temporary rivers in general. The invertebrate biota of three temporary rivers in a semi-arid area of the Eastern Cape known as the 'drought corridor', were sampled at four-monthly intervals over a 20-month period to investigate the range and variability in biotic and abiotic elements of the systems. Family-level and more detailed taxonomic data were collected. At the family level, no significant differences were indicated between sites, suggesting that at this coarse scale, there may be a recognisable fauna for most of the rivers studied. At more detailed taxonomic levels, however, significant differences were indicated between all rivers and most sites, indicating that at these finer scales, generalisations about temporary river fauna may be hazardous. At these detailed taxonomic levels, diversities were highest at two sites: one an unstable, intermittent aseasonal river with highly variable flow and low-conductivity, and the other a stable, high-conductivity site at which no flow was recorded during the period. The fauna of both was more diverse than that of the site where flow was almost continuous. The lowest number of taxa were collected at a small, episodic site which exhibited the longest dry period. Of all the abiotic variables measured in the study (excluding flow), only conductivity showed any trends in common with the biota, however there was only a weak (if any) correlation between conductivity and diversity.

6.1 INTRODUCTION

> *'Most of the Eastern Province rivers, such as the Bushman's .. are usually placid pools of muddy water, linked by long stretches of dry, bushy river beds. But when the rains come they thunder down in roaring torrents, a potent menace to the man or beast foolhardy enough to pit his puny strength against them.' (F.C. Metrovich, 1968).*

The gradient of climatic change and the nature of the geological change from east to west in South Africa results in a heterogeneity in river types that has led specialists to separate the country's rivers into 18 different 'bioregions', based on both on the historical distribution patterns of fish, macroinvertebrates and riparian vegetation, and on known physical and geomorphological characteristics (Eekhout *et al.* 1996).

The area distinguished in this system as 'Bioregion 14', the 'arid corridor', encompasses the Great Fish, Sundays, Kowie and Bushmans Rivers in the Eastern Cape (Fig. 6.1). This is part of a southern African belt first described by Balinsky (1962) as the 'drought corridor'and later by Allanson *et al.* (1990) as the 'arid west' zone, stretching from Port Elizabeth inwards and westwards into Namibia and southern Botswana. Rivers in this area are characterised by intermittent year-round rainfall and temporary surface waters with high TDS (total dissolved solids) and alkaline pH (Dallas and Day 1993, Davies *et al.* 1993).

Intermittent rainfall generally corresponds to intermittency in flow, as in the case of many rivers in this arid corridor. A variety of non-perennial river types, from intermittent to episodic, occur along the continuum between perennial and episodic rivers conceptualised in Chapter 2. The purpose of this chapter is to investigate the invertebrate biota occurring in a number of temporary river types within this corridor of the Eastern Cape, and to establish to what degree the faunas of these different systems overlap - i.e. is there a characteristic fauna for these rivers?

Selected physico-chemical and biological attributes of six sites (both natural and modified) on three rivers exhibiting varying degrees of intermittency were monitored at four-monthly intervals over a period of 20 months. This was a low-intensity study, designed to provide a broader context within which to interpret the findings of a more thorough investigation of the ecology and invertebrate fauna of the upper Kowie River (Chs 3 to 5). Because of the nature of the study, invertebrates were collected following a field technique developed for the monitoring of South African rivers, and identifications were to the taxonomic level of family. For two of the six sampling events, this technique was used alongside more intensive collection of invertebrates, which were identified to detailed taxonomic levels to enable finer resolution examination of the differences between fauna of different sites. It was hypothesized that invertebrates of at least

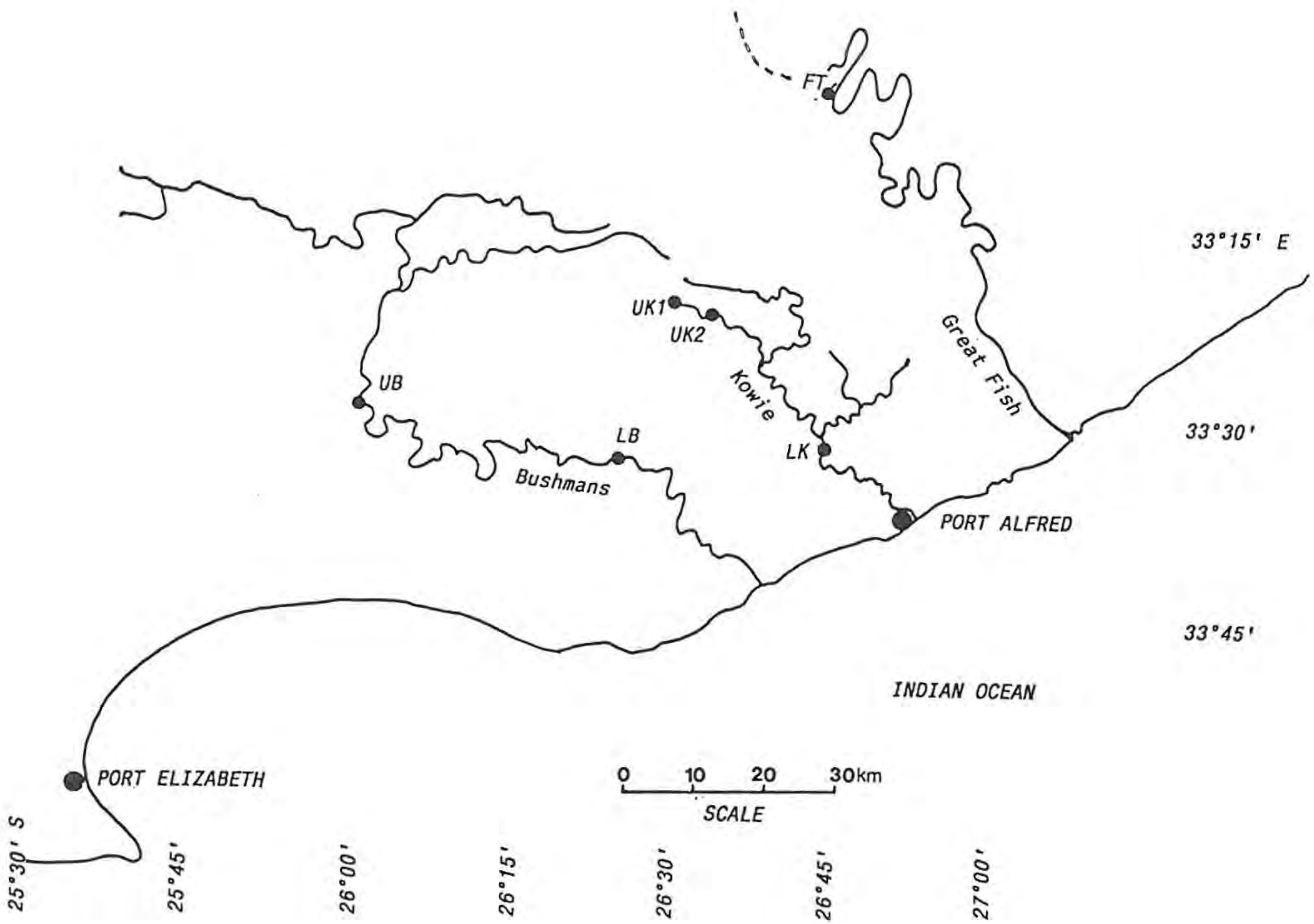


Figure 6.1 Map of southern Africa showing the position of the 'arid corridor' which encompasses the Great Fish, Kowie and Bushmans Rivers included in this study.

some of the different temporary river types (represented by diferent sites) would differ to a significant extent, and that variability within a site over time would be lower than that between sites. Two null hypotheses were framed on the basis of these premises:

H_0: there are no differences between the fauna of the different temporary river sites at the taxonomic level of family

H_0: there are no differences between the fauna of the different temporary rivers sites, at detailed taxonomic levels.

Further areas of interest were, the extent of hydrological variability within systems (as a criterion for the assessment of disturbance, see 1.3.6), the nature of ecosystem expansion and contraction (opening up and loss of habitable space, *sensu* Stanley *et al.* 1997), the extent of habitat (or biotope) duration, and the range in values of individual physico-chemical variables. Distance of the sites from the nearest colonising sources was not considered an issue in terms of their repopulation, as all sites were located within a kilometer of permanent water.

This work also provided an opportunity to assess the value and appropriateness of using of a river biomonitoring technique, the South African Scoring System version 4 (SASS4, Chutter 1994), in temporary waters in general. The SASS4 method was devised for the broad assessment of river water quality (Chutter 1994), and has been recommended for use in the South African National Biomonitoring Programme for aquatic ecosystems (Uys *et al.* 1996). SASS4 indices of river condition are based on a scoring system which allocates a score to each invertebrate family on the basis of its sensitivity to deteriorating water quality conditions. Scores range between 1 and 15, with lower scores representing tolerance to degraded conditions (e.g. pollution), and progressively higher scores indicating increasing sensitivity to pollution. The indices generated are total score (sum of the scores of all families present) and Average Score per Taxon (ASPT, the total score divided by the number of families present). The SASS4 technique is non-destructive and involves the sampling of several subjectively (and visually) discernible biotopes for aquatic invertebrates. Personnel trained in the identification of live aquatic invertebrates record all families present in three abundance classes (1=1-10, 2=11-100, 3=101-1000).

One of the limitations of the SASS4 system is that it was designed with the bioassessment of flowing rivers in mind. Practitioners and reviewers of the method have expressed concern that the design and scoring system of the technique cannot be expected to provide a measure of river condition in non-flowing waters - be they naturally temporary rivers or sections of rivers in which flow has been altered to intermittent (e.g. downstream of an impoundments or in an area of heavy abstraction). This poses a problem in a country in which temporary rivers are ubiquitous, and intermittent conditions are becoming more and more common due to modifications to rivers (Davies *et al.* 1993, 1995). Results of the study on the upper Kowie River invertebrate fauna (Chs 3 to 5), and personal observations suggest that the majority of taxa occupying intermittent waters are adapted to those conditions, and as a result are often the more tolerant animals, capable of withstanding low-oxygen conditions and often a lack of surface water. These are generally the lower-scoring families in the SASS4 system. Boulton *et al.* (in press) made the point that water quality deterioration in intermittent rivers was natural at during certain phases of the flow regime, and that during these periods, the diversity of intolerant taxa was likely to decrease. They continued that .. *'(u)nless this is understood, uncritical application to intermittent rivers of water quality criteria and biological indicator species used for assessing the health of permanent rivers will prove misleading'.*

The concerns are, firstly, that low scores which are indicative of natural conditions may be wrongly interpreted as representative of deteriorating water quality due only to anthropogenic influences (e.g. pollution, poor land-use practises in catchments), and secondly, that the little knowledge that we have of the invertebrates of temporary waters disallows us to build an 'expected' or 'reference' condition for the range of types encountered. The establishment of such a reference condition was recommended as an adjunct to site selection in the SANBP (Eekhout *et al.* 1996)

The total SASS4 scores and ASPT values of the six temporary river sites are examined over all sampling events.

6.2 SITES

The Eastern Cape is largely a transition zone of climate types, and seasonality of rainfall is far less pronounced than in other parts of the country. Great variation occurs in temperature, rainfall and windiness over short distances in the region (Stone 1988). The chief influences on the prevailing atmospheric conditions are altitude, mountain orientation, and distance from the Indian Ocean (Stone 1988). Spatial variation in temperature and rainfall for some towns in the Eastern Cape are superimposed on the map of the river sites studied (Fig. 6.1).

Sites on three naturally temporary rivers with varying flow regimes were selected for this study:

The Kowie River

Though the upper sections of this river have been described in previous chapters, all site descriptions for Kowie River are repeated here briefly for convenience and completeness.

The Kowie rises close to Grahamstown in the Eastern Cape, and flows approximately 60km to its mouth at Port Alfred (Fig. 6.1). It is naturally temporary, and has a mean annual discharge of $23x10^6m^2$ (Stone 1988). Yearly rainfall for the catchment is of the order of 650mm (South African Weather Bureau *SAWB* data). The $652km^2$ catchment occurs within a vegetation biome described by Lubke and Van Wijk (1988) as *subtropical thicket* (dense woody vegetation comprising small trees with a closed canopy up to three metres high). Inland plant formations are described as *valley bushveld* (succulent thicket which extends into the coastal grassland zone). The Kowie is underlain by rocks of the Bokkeveld Group, characterised by dark shales and sandstones.

Two sections of the Kowie River were studied. In the upper section, close to the source, the two sites selected for the intensive study over a period of years, UK1 and UK2, were used. In the lower section of the river, a single site (LK) was selected for the study reported here.

Upper Kowie:

(Plates 3.1 - 3.8)

Upper site (UK1) (26°33'11"E, 33°20'50"S)

This site is approximately 5km downstream of the spring-fed source (Fig. 6.1), at an altitude of about 550m. It is about 50m in length and 1 to 10m wide, with a gradient of 40m.km^{-1}. The chief substratum is bedrock, overlain in places with boulders and a mosaic of rocks, cobbles and coarse sand. The stream is dimly-lit due to heavy canopy cover provided by riparian trees. Upstream of the site is a derelict concrete roadbridge which was built over a decade ago but still has the effect of damming a small proportion of the flow. This does not seem to significantly affect discharge volumes.

Lower site (UK2) (26°33'50"E, 33°21'00"S)

This site is situated less 1 to 2km downstream of UK1. There is virtually no gradient over its 30 to 40m length, and it is 3 to 10m wide. No bedrock is visible in the channel. The chief substratum is mixed coarse and fine sands, with rocks, cobbles and stones occurring at the upper end of the site. The right bank of the river is overhung by a steep, vegetated bedrock bank, which shades the stream for most of the day throughout the year. The left bank is heavily vegetated with indigenous and exotic grasses, trees and shrubs. The single pool formed at this site during no-flow periods appears to be the most persistent water in this section of the river. Approximately 1km upstream, the left bank of the river is heavily eroded owing to the construction of a dirt farm-road adjacent to the river several years ago (but no longer in use). This modification may account for much of the sand deposition at the lower site.

In terms of the proposed terminology for temporary rivers (Section 2.6), the upper Kowie would be termed '*intermittent aseasonal*'.

Lower Kowie River site (LK) (32°30'05"S, 26°44'08"E)
(Plate 6.1)

This site was approximately 30m long and 4 to 10m wide. It occurred approximately 25km upstream of the mouth of the river (Fig. 6.1), at an altitude of about 300m. It was located about 15km below the confluence with the Bloukrans River, which carries water from Grahamstown (including treated sewage), and immediately below the confluence with the Lushington River which runs through agricultural land and is known to carry high-conductivity water (Cambray, pers. comm). Although there was flow at the site at all sampling events for this study, several months of zero flow have been recorded for this site during drier years (DWAF data), and in its natural state the river was temporary. Because flow is augmented by water from Grahamstown, the lower Kowie in in its present state could be termed *'modified intermittent aseasonal, tending towards perennial aseasonal'*. Rivers of the latter type are described as occurring in *'climatic transition areas in which rainfall occurs throughout the year, and discharge is unpredictable year-round, as are discharge peaks'* (Section 2.6). The site was bedrock-dominated. A riffle-run sequence in its upper portion ended in a large sandy-bedded pool strewn with boulders. There was marginal vegetation (*Cyperus* sp. sedges) along most of the length of the site. A roadbridge was situated upstream of the site.

The Bushmans River

The Bushmans River catchment occurs to the west of the Kowie River and is 2 688km^2 in size, with a mean discharge of 38x10^{6}m^3
(Stone 1988). Mean annual rainfall for the region is 600mm. The naturally-temporary river occurs in Valley Bushveld vegetation (Lubke and van Wijk 1988). It runs through steeply-incised valleys and is underlain variously by the Uitenhage Group (sandstone and marl conglemerate), Coastal Limestone (sand and sandy limestone), Karoo Supergroup (tillites of the Dwyka Formation) and, closer to the coast, Cape Supergroup geology (dark shales and sandstones of the Bokkeveld Group).

6.1

6.2

6.5

Plates 6.1 - 6.5

6.1 Lower Kowie R., 6.2 Upper Bushmans River
6.3 & 6.4 Lower Bushmans (with and without water)
6.5 Fish River tributary site.

6.3

6.4

The Bushmans River has been extensively dammed (in-channel) along its length, chiefly by farmers. The observed flow regime is thus not a natural one. For the majority of the time, pools occur along the length of the channel. The hydrological regime of the river has been described according to the terminology (Section 2.6) as 'modified intermittent aseasonal, tending towards ephemeral'. The latter term is defined thus: *'Rivers which flow for less time than they are dry. Flow or flood for short periods of most years in a five year period in response to unpredictable high rainfall events. Support a series of pools in parts of the channel'* (Section 2.6). Two sites were studied on this river:

Upper Bushmans River (UB, 33°28'03"S, 26°04'02"E).
(Plate 6.2)

This site occurs below the confluence of the Bushmans and New Year's River (Fig. 6.1), at an altitude of about 400m. It runs through agricultural land. The river channel in this section is up to 20m wide, has a zero gradient and is sandy-bottomed. Dense riparian vegetation occurs on either side of the channel (*Acacia sp.,* indigenous grasses etc.). The site is characterised by a long stretch of non-flowing water, which dries towards the lower end of the site. The substrate of this 'pool' is fine sands, anoxic below 5cm. Depth ranges from 0.2m to 1.2m. The pool is fringed with (reeds) and supports dense growth of submerged aquatic vegetation.

Lower Bushmans River (LB, 33°32'08"S, 26°24'00"E)
(Plates 6.3, 6.4)

This site occurs about 70km downstream of UB, at an altitude of approximately 300 to 350m, in unused and uncultivated farmland. An instream weir has been constructed upstream of the site by the land-owner, however substantial leakage (and sometimes overflow) from the weir allows movement of water downstream even during no-flow periods. The site comprises a single, shallow pool up to 10m wide and 20m long. The pool is fringed with *Cyperus* sp. sedges and indigenous grasses. The substratum is coarse sand with scattered rocks, most of which are covered by silt. Depth varies from 0.3 to 0.7m.

The Fish River tributary (FT, 33°05'08"S, 26°45'30"E)
(Plate 6.5)

This site is a tributary of the Great Fish River (Fig. 6.1). The main channel of the Great Fish River was naturally temporary but now flows permanently due to the import of water from the Orange River (described in Ch. 8). This site occurs in an arid area with a mean annual rainfall of approximately 400mm (SAWB data), and at an altitude of about 450m. The geology of the area is Ecca Group shales and sandstones (in the Karroo Supergroup). The entire tributary is located in nature reserve and is considered unimpacted. It is located within a kilometre of the Great Fish River. The channel, which is normally dry but for pools, consists of bedrock overlain in places with coarse sand. Small, persistent pools in the channel are fed by low quantities of water emerging from the sediments (probably in bedrock faults), which re-enter the sediments a short way downstream. This 'seepage' of hyporheic water ensures the continuance of scattered pools in the channel. The hydrological regime of this site was considered to fit the description of '*ephemeral*' which is described as - 'rivers which flow for less time than they are dry .. flow or flood for short periods of most years in response to high rainfall events' (Section 2.6). Two to three pools, varying from 1 to 4m in width, and 0.2 to 0.6m in depth, were generally present in the channel at sampling.

6.3 METHODS

This study involved two levels of sampling. Six site visits were made at approximately four-monthly intervals between May 1994 and January 1996. At each of these sampling trips, family-level data was collected, using the field-based SASS4 technique (Chutter 1994). During January and May 1995, both SASS4 and more intensive, replicated sampling were done. The intention behind this was to gather abundance data and identify taxa to more detailed taxonomic levels which would provide insight into the three river systems at a finer level of resolution, and also allow the calculation of various diversity indices for comparative purposes.

6.3.1 SASS4 sampling

Biotopes sampled for aquatic macroinvertebrates were identified on the basis of those recommended by Chutter (1994) for the SASS4 technique, and further by observation of biotopes available, as described in Section 1.3.3. All biotopes in the SASS4 technique were the same as those identified for normal replicated sampling in the upper Kowie River (Chs 3 to 5): stones-in-current (SIC), marginal vegetation (MV), stones-out-of-current (SOOC), and sandy substrata (SAND). Where the small volume of individual pools prevented the sampling of SIC, SOOC or SAND as separate biotopes, the full pool was sampled as a single biotope (POOL). In these circumstances, and when surface water was absent altogether, drying substrata were also sampled as a separate biotope (DRG).

When collecting SASS4 samples, all biotopes except DRG were sampled using standard SASS4 500μm mesh nets. Fauna from MV were collected by sweeping the net once forwards and once backwards through 1 to 2m of marginal vegetation (when inundated with water). SIC and SOOC were kick-sampled for a period of 30 seconds to 1 minute. SAND was sampled by stirring an area of the substratum with the feet, and then sweeping the net over the disturbed area for half a minute. POOLS were sampled in a similar manner, and when submerged algae or vegetation were present in the water column these were shaken underwater by hand, and the net was then swept backwards and forwards through the water column.

6.3.2 Intensive sampling over two months

During January and May 1995, sampling involved both SASS4 and the collection of three replicate samples in each of the available biotopes, as described in Section 3.4.1, using nets with a mesh size of 100μm. Samples thus collected were preserved in 70% ethanol and returned to the laboratory for sorting and identification to the lowest possible taxonomic level. Identification of animals from all 6 sites was standardised to the same taxonomic level, in order to allow for comparison of data across sites. The final list of invertebrates included a number of taxonomic levels, and individuals were termed 'equivalent taxa' following King and Tharme 1993 (see Section 1.3.2).

6.3.3 Measurement of abiotic variables

Several physical and chemical variables were measured. As the procedures for measurment, and the details of instruments used, has been detailed elsewhere (Section 3.4.2), this information is presented in summarised form. Water temperature, pH, oxygen saturation and salinity (as electrical conductivity, $mS.m^{-1}$) were measured at each site on each sampling occasion. Where flow was present an estimate of discharge was obtained by taking cross-channel flow measurements as described in Section 3.4.2. Depth and current speed (where applicable) were recorded in each biotope.

6.3.4 Statistical analyses

Family-level data and that at more detailed taxonomic levels were analysed using both univariate statistical methods, and non-parametric, multivariate statistical programs from the PRIMER package, designed for the analysis of community data (Clarke and Warwick 1994), as described fully in Section 1.4.

Diversity indices

For SASS4 family-level data in abundance categories, only 'total number of taxa' was computed, as indices for richness and diversity can only be computed on the basis of abundances (see Section 1.4.1). It was possible to compute two additional indices for the data collected during intensive sampling in January and May 1995: taxonomic diversity and taxonomic evenness (because many of the identifications of taxa collected during these months were incomplete or tentative, and mixed taxonomic levels have been used, the word 'species' has been replaced by 'taxon' for these measures).

Taxonomic diversity: using the Shannon Weiner diversity index (H'), the formula for which is given in Equation 1.1 (Section 1.4.1).

Taxonomic evenness: Pielou's evenness index (J') was used to express how evenly the individuals present are distributed among the different taxa. The index scores between 0 and 1, with 1 representing even distribution. Lower values represent dominance of individual taxa. This index was computed with Equation 1.3 (Section 1.4.1).

Similarity analyses

Faunal similarities between samples (at the level of family or lower taxonomic levels) were calculated using the non-correlation-based Bray-Curtis coefficient of similarity (Bray and Curtis 1957), as described in Section 1.4.2.

For family-level analyses, similarity measures were calculated based on total number of families collected at each site and sampling event, recorded in abundance categories. Data were standardised but not transformed, as the use of abundance categories effectively represented a log-transformation of data.

For analysis of more detailed taxonomic-level abundance data from January and May 1995, double-root transformations were used to downweight the importance of common taxa and emphasise the importance of rarer taxa in the measure of sample similarity (Clarke and Warwick 1994). This transformation is considered severe, but was necessary as different numbers and types of biotopes were sampled at each of the sites over these two months, with concommitant effects on absolute abundances (see Section 6.5.2).

Cluster analysis

Groupings of most similar samples were computed in the CLUSTER program, using hierarchical agglomerative clustering with group-average linking, on standardised (and where necessary, transformed) data. This procedure is described and discussed in Section 1.4.3.

Ordination

The ordination procedure, which summarises a high-dimensional data set in to low-dimensional space was performed on similarity matrices using the technique of non-metric multidimensional scaling (MDS), as described in Section 1.4.4.

Contribution of individual taxa to group similarities

The program SIMPER was used to examine the contribution of individual taxa to the Bray-Curtis similarity measures within a group or cluster of samples. As this programme generates lengthy lists of all taxa responsible for group similarities, only taxa contributing to up to 75% of the average similarity between samples in a group were recorded.

Analysis of similarity for examination of null hypotheses

This study possessed *a priori* defined structure between the different groups (river sites). Analysis of similarity, using the ANOSIM procedure in PRIMER, was used to examine the null hypothesis of no difference between river sites. This procedure is explained in Section 1.4.6.

Association between abiotic and biotic data

Where it was possible to investigate links between biotic data and univariate environmental variables, values for each abiotic variable were represented as scaled symbols of varying sizes, and superimposed on the corresponding biotic ordination, using the MDS program with an environmental data file, as described in Section 1.4.7. Each abiotic variable was plotted separately in this way. This provided a means of checking whether or not there were consistent differences in abiotic variables between sample groups (labelled 'Groups'), and of observing any trends in the abiotic variable which may match the gradients in the biotic ordination (Clarke and Warwick 1994).

6.4 RESULTS

6.4.1 Abiotic variables

The variable which showed the greatest variance over time and between sites was conductivity (table 6.2). At the upper Bushmans River site, values ranged from 170 to 306mS.m^{-1}. At the lower site, conductivities from 330 to 832 mS.m^{-1} were recorded. In the Fish River tributary, fluctuations between 273 and 785mS.m^{-1} were recorded, with substantial variance between individual pools both within and between sampling occasions (Table 6.3). At the upper Kowie River, values of between 25 and 41mS.m^{-1} were recorded over the period, and in the lower Kowie between 176 and 236mS.m^{-1} (Table 6.2). Oxygen saturation fluctuated both within and between sites. Values as low as 25% and up to 350% were recorded over the period (Table 6.2).

Table 6.1 Hydrological information for the sites on the Kowie and Bushmans Rivers over the study period. These are given only as an approximation of conditions in the river, as the gauging weirs were, in most cases, many kilometres from the site in question. Upper Kowie flow data was measured at the site during sampling. The Fish River tributary was not gauged for flow and hence no data are available for that site.

HYDROLOGICAL PHASES		May 94	Sep.94	Jan.95	May 95	Sep.95	Jan.96
Upper Kowie R.	UK1	NO FLOW	LOW FLOW	ONSET	FLOW	POOLS	POOLS
Upper Kowie R.	UK2	NO FLOW	LOW FLOW	ONSET	FLOW	POOLS	POOLS
Lower Kowie R.	LK	FLOW	FLOW	FLOW	FLOW	FLOW	LOW FLOW
Upper Bushmans R.	UB	POOL	POOL	POOL	POOL	POOL	POOL
Lower Bushmans R.	LB	POOL	POOL	POOL	POOL	POOL	DRY
Fish R. tributary	FT	POOLS	POOLS	POOLS	POOLS	POOLS	POOLS
DISCHARGE (m3/s)							
Upper Kowie		0.00	0.01	0.07	0.03	0.00	0.00
MAX.DAILY AVERAGE FLOW RATE (m3/s)	Station no.						
Kowie River weir *(near lower site)*	P4H001	0.015	0.137	23	0.477	0.014	0.107
Bushmans River weir *(upstream of upper site)*	P1H003	0.009	0.006	21.2	0.013	0.013	0.013
MIN. DAILY AVERAGE FLOW RATE (m3/s)							
Kowie River weir	P4H001	0.003	0.029	0.721	0.141	0.006	0.003
Bushmans River weir	P1H003	0.005	0.004	0.004	0.004	0.004	0.004
Fish River weir	Q9H012-A01	2.69	3.26	4.12	3.14	2.78	2.39

Changes in water temperature reflected seasonal changes (Table 6.2). pH values were relatively consistent both at individual sites over time and between different sites, and indicated that in general, water was near-neutral to alkaline, with highest pH occurring in the upper Bushmans River during September 1994, and January and May 1995. Large variation in pH values of individual pools was recorded in the Fish River tributary, with a range of 6 to 8.2 over the period (Table 6.3). Total suspended solids (TSS) varied little between sites and over time, ranging from 0.015 to $0.062g.l^{-1}$. Upper limits may have been higher had flood waters been tested. Particulate organic matter (POM) was in the region of 0.01-$0.03g.l^{-1}$ for the six sites.

Table 6.2 Abiotic variables for the Kowie River, Bushmans River and Fish River Tributary over the period of the study. Note that values from single pools in the Fish River Tributary are given in Table 6.3.

		May 94	*Sep.94*	*Jan.95*	*May 95*	*Sep.95*	*Jan.96*
% OXYGEN SATURATION							
Upper Kowie R.	UK1	40	25	118	109	52	44
Upper Kowie R.	UK2	51	93	122	117	104	103
Lower Kowie R.	LK	99	70	123	108	139	93
Upper Bushmans R.	UB		93	128	60	114	155
Lower Bushmans R.	LB	83	99	94	115	128	DRY
Fish River trib.	FT	79	61	130	137	167	92
WATER TEMP. (C)							
Upper Kowie R.	UK1	18	24	22	16	17	21
Upper Kowie R.	UK2	16	24	23	17	17	23
Lower Kowie R.	LK	17	25	24	16	19	23
Upper Bushmans R.	UB		25	34	12	18	30
Lower Bushmans R.	LB	20	31	33	15	20	DRY
Fish R. trib.	FT	18	30	27	17	25	25
CONDUCTIVITY (mS/m)							
Upper Kowie R.	UK1	38	37	25	24	33	37
Upper Kowie R.	UK2	41	38	26	25	28	40
Lower Kowie R.	LK	199	236	182	200	176	197
Upper Bushmans R.	UB		183	222	170	213	306
Lower Bushmans R.	LB	556	832	378	330	609	DRY
Fish R. trib.	FT	560	685	326	390	505	578
pH							
Upper Kowie R. 1	UK1	7.2	7.3	6.9	7.8	7.4	7.2
Upper Kowie R. 2	UK2	7.0	7.3	7.7	8.2	7.6	7.6
Lower Kowie R.	LK	7.3	7.4	7.5	7.4	7.5	7.5
Upper Bushmans R.	UB		8.5	8.9	8.2	7.2	7.2
Lower Bushmans R.	LB	7.2	7.6	7.2	9.6	7.1	DRY
Fish R. trib.	FT	7.2	8.2	7.5	7.2	7.3	6.0

*** Note: values for Fish River tributary are averaged over all pools sampled. See Table 6.3.**

Table 6.3 Values of abiotic variables for individual pools sampled in the Fish River tributary.

	May 94	*Sep.94*	*Jan.95*	*Sep.95*	*Jan.96*
% OXYGEN SATURATION					
Pool 1	77	30	129	182	105
Pool 2	62	54	225	320	172
Pool 3	99	99	37		
WATER TEMP. (C)					
Pool 1	18	30	26	25	24
Pool 2	19	31	30	26	26
Pool 3	19	30	25		
CONDUCTIVITY (mS/m)					
Pool 1	725	785	325	483	603
Pool 2	513	703	381	527	552
Pool 3	443	570	273		
pH					
Pool 1	7.2	8.2	7.5	7.1	6.0
Pool 2	7.2	8.1	7.3	7.3	6.0
Pool 3	7.3	8.2	7.8		

6.4.2 Relationship between no. of biotopes and no. of taxa

As one of the purposes of this investigation was to establish the range of aquatic invertebrate families occupying different temporary rivers in the region, sampling was designed to give as broad as possible a picture fauna at each site by sampling available biotopes. Variability in the number and type of biotopes available both within sites over time and between sites was substantial, and there was considerable difference in the percentage of time that various biotopes were sampled (Table 6.4a).

The ratio of families collected in a single biotope to total number of families collected at site indicated the influence of certain biotopes on numbers of taxa. To test for the effect of biotope diversity on taxonomic diversity (as number of taxa), a regression was performed on the number of biotopes sampled at a site against the total number of families collected at that site. The value for the correlation coefficient r was 0.7 (where $r = 1$ implies an exact linear relationship), suggesting a relatively strong positive relationship between the two

(Table 6.4b). While this relationship was not applicable to all sample sets, it was evident in many, and had to be taken account of in interpretation, particularly where comparisons were concerned.

Table 6.4 a) The proportion of 34 sampling events (all sites, all months) in which individual biotopes were sampled, and their average contribution to total numbers of families collected. b) Result of regression analysis of biotopes sampled against number of families collected.

	MV	SIC	SOOC	SAND	POOL	2ND POOL	3RD POOL
a) *% of 34 sampling events during which individual biotopes were sampled*	71	29	50	15	47	27	9
Average ratio of 'No. of families collected in a single biotope' to 'Total no. of families collected at a site (expressed as a % with standard deviation in brackets).	76 (20)	53 (14)	45 (19)	44 (17)	65 (25)	51 (22)	47 (11)
b) *Regression of number of biotopes sampled against number of families collected*		Constant = 4.55 Std error of y = 4.61 $r^2 = 0.49$ ($r = 0.7$) X coefficient = 5.2 Std error of coefficient = 0.93					

6.4.3 Family-level analyses:
Invertebrates present at the various sites over the study

Altogether 62 families (or higher taxa) were collected across all sites during the study (Table 6.5). Of these, 18 were common to all sites: oligochaetes, decapod crabs, baetid and caenid mayflies, coenagrionid damselflies, aeshnid and libellulid dragonflies, notonectid, naucorid, corixid, gerrid and veliid bugs, dytiscid and hydrophilid beetles, and tipulid, culicid, chironomid, and ceratopogonid fly larvae.

Groups found at four or more sites (under varying conditions) included ostracods, water mites, hydrometrid bugs, hydropsychid and leptocerid caddisflies, gyrinid beetles, simuliid blackflies, and planorbid, physid and ancylid molluscs (Appendix 6.2).

Information regarding physico-chemical changes and fauna collected is reviewed on a sample-to-sample basis. Sampling months are highlighted at first mention in the text. (*Note the common names of orders to which taxa belong are noted at first mention, and then usually omitted in favour of brevity*).

During **May 1994** (autumn), 16.7mm rainfall was recorded in the Grahamstown region, in comparison to May's mean monthly precipation (MMP) figure of 45.2mm. During sampling, flow was only present at the lower Kowie River. At the upper Kowie sites, flow had ceased but surface water was still continuous (no pools). The lower Bushmans River site consisted of a single long-lived pool with high conductivity (556ms.m^{-1}; Table 6.2). At the Fish River tributary site, surface water was restricted to three pools with conductivities ranging from 443 to 725mS.m^{-1} (Table 6.3).

At the lower Kowie River site (LK), 30 families and higher taxa (hereinafter referred to only as *families*) were collected. High numbers (> 100) of cladocerans and relatively high numbers (11-100) of simuliid blackflies, hydropsychid caddisflies, baetid mayflies, coenagrionid damselflies, aeshnid dragonflies and gyrinid beetles were present. Taxa collected only at LK included heptageniid, leptophlebiid and tricorythid mayflies, and chlorolestid damselflies (Appendix 6.2). At the upper Kowie sites, UK1 and UK2 samples yielded 11 and 15 families respectively. Baetids, dytiscid beetles, chironomid flies, coenagrionid damselflies and philopotamid caddisflies were found at both sites and were numerically abundant at either one or both (Appendix 6.2). At the lower Bushmans River, 20 families were collected, of which three (ostracods, coenagrionid damselflies and pleid bugs) occurred in high numbers (>100). Other abundant taxa included baetid and caenid mayflies, aeshnid dragonflies, libellulid damselflies, gerrid bugs, and chironomids (Table 6.4). Overall, the fewest families (12) were collected at the ephemeral Fish River tributary site. Chironomids dominated samples, and relatively high numbers of culicids and libellulid dragonflies were collected.

Table 6.5 Number of families recorded in individual biotopes and in total at the 6 temporary river sites over the sampling period. Abbreviations: MV - marginal vegetation, SIC - stones in current, SOOC - stones out of current, POOL - shallow pools.

Upper Kowie UK1	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
MAY 94	8		7					**11**
SEP.94	6		2					**20**
JAN.95	15	6	8					**16**
MAY 95	11	12	9					**21**
SEP.95					2			**2**
JAN.96					6	2	5	**10**

Upper Kowie UK2	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
MAY 94	13		7					**15**
SEP.94	23		20	8				**30**
JAN.95	22	20	5					**28**
MAY 95	10	7	9					**19**
SEP.95					5	12		**16**
JAN.96			20		17	4		**24**

Lower Kowie LK	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
MAY 94	13	18	9	7				**30**
SEP.94	11	7	7					**19**
JAN.95	13	12						**16**
MAY 95	17	14	7					**21**
SEP.95	11	8	8					**15**
JAN.96	20	9	8					**24**

Upper Bushmans UB	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
SEP.94					9			**9**
JAN.95					11			**11**
MAY 95	23			15				**23**
SEP.95	14				8			**16**
JAN.96	12							**12**

Lower Bushmans LB	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
MAY 94	16		12		6			**20**
SEP.94	14		3					**14**
JAN.95	23			13				**22**
MAY 95	24		20		8			**29**
SEP.95	20				8			**19**

Fish R. Trib. FT	MV	SIC	SOOC	SAND	POOL	POOL	POOL	**TOTAL**
MAY 94					7	7	7	**12**
SEP.94					11	10	5	**16**
JAN.95	11				15	12		**20**
MAY 95					10	9		**13**
SEP.95					13	3		**13**
JAN.96	10			10	10	15		**21**

In August 1994, approximately 120mm rain (MMP = 42.8mm, SAWB) over a few days in the Grahamstown region caused the onset of flow in the upper Kowie River. By **September 1994**, rainfall was of a lower order (29.3 mm, MMP = 60.7) and there was little flow in the upper Kowie. The lower Kowie was flowing (Table 6.1), but conductivity at this site was elevated to $236mS.m^{-1}$ (Table 6.2). As customary, only pools were present at the upper and lower Bushmans River and Fish River tributary sites. Conductivities recorded at the upper and lower Bushmans sites were $183mS.m^{-1}$, and $832mS.m^{-1}$ respectively (Table 6.2), and elevated values of 570 to $785mS.m^{-1}$ were recorded in pools in the Fish River tributary (Table 6.3).

There was an increase in number of families collected during this period of flow onset at the upper Kowie River sites. At UK1 chironomids were particularly abundant, and corixid and notonectid bugs, dytiscid and gyrinid beetles, libellulids, corduliid dragonflies and ceragopogonids were present in high numbers (11-100 individuals; Table 6.4). At the lower Kowie River site, numbers of taxa were substantially reduced relative to the previous sampling (Table 6.5), however simuliid densities had increased by an order of magnitude and hydropsychids, coenagrionids and dytiscids were still common. Heptageniid and tricorythid mayflies were now absent (Table 6.5). At the upper Bushmans River, which was sampled for the first time, conditions were alkaline (pH 8.9) and only 12 families were collected. All but chironomids occurred in low abundances (< 10 individuals per sample; Table 6.5). At the lower site, abundances of individual taxa remained high, with large numbers of ostracods, coenagrionids and pleids (> 100 individuals per sample), and plentiful water mites, baetids, aeshnids, libellulids, gerrid bugs and chironomids. In the Fish River tributary, water temperature in pools was close to 30°C, conductivities were raised, and in one pool, oxygen saturation was as low as 30% (Table 6.3). Within the 16 families collected, bugs were well-represented by different genera, and were abundant (Appendix 6.2).

During January and May 1995, fauna was identified to more detailed taxonomic levels, as discussed at some length in a later section. Only brief details are given here.

Sampling in **January 1995** followed heavy rainfall in late December (271mm in contrast to MMP of 62.4mm, SAWB) which affected all three catchments. High flows were recorded at the lower Kowie and upper Bushmans River gauging stations (Table 6.1). Flow had resumed into an almost-dry channel in the upper Kowie. At both sites on the Bushmans River, recommencement of flow had been inhibited by the many farm dams in the channel and by water atraction, but pool volumes were substantially increased. An oxygen saturation of 350% and elevated conductivity was recorded at the upper site. At the lower site, the conductivity value had decreased by over 50% to 378mS.m^{-1} (Table 6.2). A flash flood had occurred in the Fish River tributary during December (East Cape Nature Conservation officials; details of discharge volume and duration not recorded), however only small pools remained in the channel by the time of sampling, and these were presumed to be fed by hyporheic water. Conductivity was reduced to less than half its values at the previous sampling (Table 6.3). During January, samples from the upper and lower Kowie sites yielded slightly lower numbers of families than Septembers' samples had. Increased numbers were recorded at the upper and lower Bushmans and Fish River tributary sites (Table 6.4).

By **May 1995**, rainfall was sparse (19.1mm, MMP= 45.2mm, SAWB), and flow was substantially reduced at all three sites on the Kowie River (Table 6.1). Pools were still present at all other sites. High oxygen saturation was recorded for all but the upper Bushmans River, where 60% saturation and a substantially reduced conductivity of 70mS.m^{-1} were measured (Table 6.2). Conductivity at the lower Bushmans River and Fish River tributary sites remained almost equivalent to that measured in January. Largest numbers of families within-site for the study were collected at the upper Kowie River (site UK1) and upper and lower Bushmans sites (Table 6.4).

The spring month of **September 1995** followed several low rainfall or dry months, and 42.9mm precipitation was recorded (MMP = 60.7, SAWB). Low flows had been recorded since June at the gauging weirs on both the Kowie and Bushmans Rivers (Table 6.1). At the upper Kowie River sites there were a number of pools in the channel, and oxygen saturation was reduced at UK1 (Table 6.2). Low discharge values were recorded for the lower Kowie River (Table 6.1). Pools were present at the Bushmans River and Fish River tributary sites, and conductivities at these three sites were elevated relative to those recorded a few months previously, measuring 213mS.m^{-1} at the upper Bushmans, 609mS.m^{-1} at the lower Bushmans, and 483 and 527mS.m^{-1} at the Fish River tributary (Table 6.2, 6.3).

Low numbers of families were collected at all sites. Only two, dytiscid beetles and culicid flies, were recorded from the single pool remaining at the upper Kowie site UK1. At UK2, the 16 families collected in POOL samples were predominantly resilient or air-breathing, mobile taxa (e.g. dytiscids, various bugs, baetids, chironomids, planorbid molluscs). At the lower Kowie River, only 15 families were collected, amongst them corduliid dragonflies, helodid beetles and sphaeriid bivalves (for the first time). Simuliids and hydropsychids were still abundant, and tipulids and ceratopogonids were common in samples.

At the upper and lower Bushmans River and Fish River tributary sites, families collected were generally those which had been abundant in previous samples at each of the sites: baetid and caenid mayflies, coenagrionid nymphs, pleid bugs, dytiscids, chironomids and ceratopogonids. Samples from pools at the Fish River tributary yielded aeshnid dragonfly nymphs for the first time, and increased numbers of caenids.

During November and December 1995, rainfall figures were above-average (91 and 90mm, MMP = 76 and 62mm respectively), but rain was scattered. During **January 1996**, 59mm rainfall was recorded (MMP = 60), and elevated flow figures were recorded for the lower Kowie River (Table 6.1). There had been no flow in the upper Kowie for several months, and pool volumes were small relative to those of September 1995. Reduced flow was recorded in the upper Bushmans River catchment (Table 6.1). The pool at the upper Bushmans River site was shallow and had diminished in volume, and conductivity was the highest it had been through the study (306mS.m^{-1}). The lower Bushmans River site had dried completely such that the surface was cracked (Plate 6.4), and sampling of these hard sediments was not possible with the equipment available. At the Fish River tributary, two small pools were present in the channel.

At the lower Kowie, simuliids were absent from samples for the first time. Chlorolestids, libellulids, notonectids, and corixids, which had last been collected in 1994, were present, and hydrophilid beetles and culicids were collected for the first time. Relatively high numbers of families were found at the pool at UK2, the lower Kowie River, and the Fish River pools. At UK2, 21 families were found in damp substrata fringing the single pool remaining at the site. At the lower Bushmans, families collected (excepting veliid bugs and culicids) were those common to the majority of the samples during the study. The highest number of families for the Fish River tributary were collected during this month (Table 6.4), with additional taxa including lestid damselflies, corduliid dragonflies, veliid bugs and tabanid flies.

6.4.4 Family-level analyses: Resemblances between samples

Cluster analysis of total samples per site per month

In cluster analysis based on similarity measures between the samples from different sites, major clusters were formed at below 50% similarity (Fig. 6.2). A line was drawn through the 30% similarity point and clusters to the right of that were marked Groups 1 to 7 (both for convenience of interpretation, and to check for agreement with the results of ordination, see Section 1.4.3). The majority of Groups represented samples collected in the same or consecutive sampling events, rather than samples from a single site over time:

Group 1: Upper Kowie River samples from January and May 1996.

Group 2: Kowie River samples from May and September 1994, January 1995.

Group 3: Samples collected at various sites during May and September 1994.

Group 4: Samples collected at from four of the six sites during the high rainfall month of January 1995. UK1 and UK2 samples absent.

Group 5: Samples from Kowie River and lower Bushmans River, During May and September 1994 and May 1995.

Group 6: Samples from September 1995 and January 1996 samples from LK, UB, LB and FT.

Group 7: Samples from UK2, LB and FT from in the low-rainfall month of January 1996.

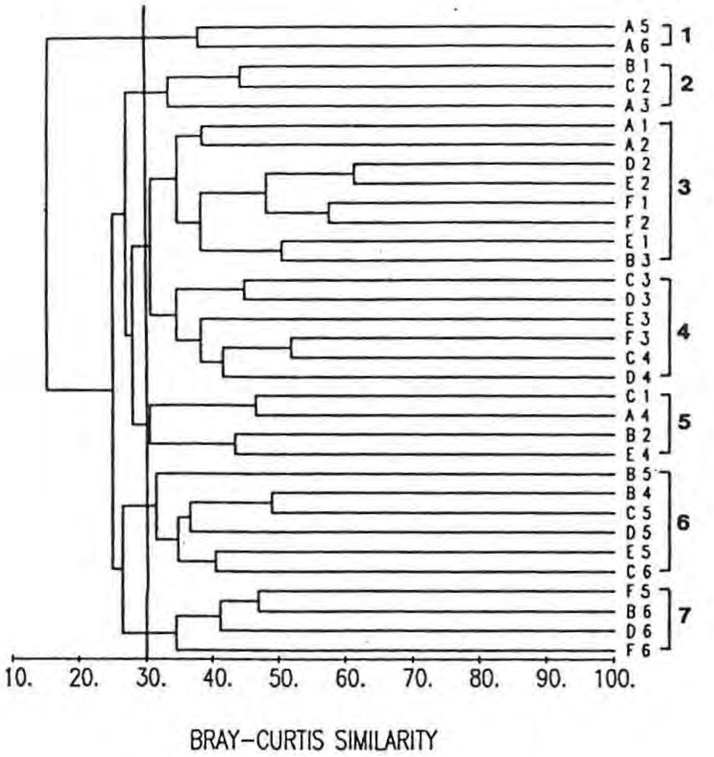


Figure 6.2 Dendrogram of hierarchical cluster analysis of total samples (Family level only) from all six sites over the full sampling period. Abbreviations: A-Upper Kowie UK1, B-Upper Kowie UK2, C-Lower Kowie, D-Upper Bushmans, E-Lower Bushmans, F-Fish River tributary. 1-May 1994, 2-September 1994, 3-January 1995, 4-May 1995, 5-September 1995, 6-January 1996.

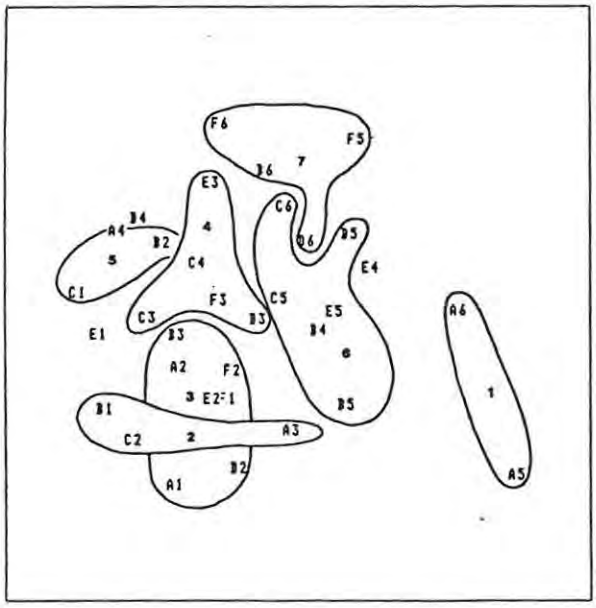


Figure 6.3 MDS ordination based on Bray Curtis similarities between total samples collected at all sites and during each sample month. Stress = 0.26 indicates that while this is a useful, but not entirely reliable representation of samples in two-dimensional space (Clarke and Warwick 1994). Abbreviations as for Figure 6.2.

Ordination of total samples per site per month

MDS ordination based on Bray Curtis similarity data generated a 2-d picture with a relatively high stress of 0.26. A cursory examination of this ordination (Fig. 6.3a) suggested a relatively high degree of scatter in individual sites. There was a greater degree of coherence within sampling times (1 to 6) than within sampling sites, with a discernible left-right gradient between samples taken at the first four sampling dates (May 1994 - May 1995), during which there was relatively high rainfall, and those taken in the drier months of September 1995 and January 1996.

Analysis of similarity for examination of the null hypothesis

The test for significant differences between sites using analysis of similarity (ANOSIM) on the ranked similarity matrices for total families yielded a Global *R* value of 0.102, at a significance level of 5.2%, indicating that there was over 5% chance of the Global *R*-value occurring under the null hypothesis of 'no differences between sites (at a family level)', and that the null hypothesis could thus not be rejected (see Section 1.4.6). Pairwise tests indicated that there were significant differences between only two pairs of sites (Table 6.6).

Table 6.6 Results of the pairwise tests conducted in ANOSIM to check for significance of difference between different sites. Where $R < 1$ and significance levels (%sig.) are less than 5%, sites in a pair can be considered significantly different (i.e. greater variability between sites than within a site over time). Significantly different pairs of sites are highlighted.

	UK1	UK2	LK	UB	LB
UK2	0.09 22.7%	R %SIG.			
LK	**0.3** **1.7%**	-0.09 72.1%			
UB	0.09 25.3%	0.13 21.6%	0.115 19.0%		
LB	**0.28** **4.1%**	-0.03 53.9%	0.195 10.8%	0.012 44.4%	
FT	0.16 11.9%	0.09 24.5%	0.112 21.2%	0.04 34.9%	-0.05 57.9%

6.4.5 Family-level analyses:
Association between biotic and abiotic variables

Four abiotic variables representing conditions at the site at a whole (rather than within a biotope) were superimposed over the biotic ordination to establish whether any showed an increase or a decrease in a similar direction to the gradient shown by the biotic ordination. No clear association was evident for any of the variables tested: dissolved oxygen, temperature, conductivity or pH, and as this was probably also associated with the high stress levels of the ordination, these diagrams are omitted here but included in Appendix 6.1 for reference. Because of the extent of variability in salinities over time and space, this variable was analysed further. Regression between conductivity values and the total number of taxa found per site gave an r^2 value of 0.01 ($r = 0.1$) indicating a weak relationship if any between the two variables.

6.4.6 Family-level analyses:
Occurrence of invertebrates over a range of conditions

Sample sites were divided into three 'hydrological' categories:

Tnf	Temporary with no flow (upper Kowie River during no-flow periods, upper and lower Bushmans River, and Fish River tributary)
Tf	Temporary with flow present (upper Kowie during flow),
Tmf	Temporary with modified (almost continual) flow (lower Kowie).

A further two categories were distinguished for high-conductivity waters:

C4	where conductivity over 400mS.m^{-1} was measured; and
C8	where conductivity over 800mS.m^{-1} was measured.

Occurrence of families was recorded in each of these categories, together with the biotopes in which each of the families were collected (Table 6.7).

Table 6.7 Occurrence of various families in the different 'categories' of temporary rivers. Tnf - temporary during no-flow conditions (presence recorded simply as 'T', Tf - temporary during flow conditions, Tmf - modified temporary with almost continual flow; C4 - conductivities over 400mS.m^{-1}, C8 - conductivities over 800mS.m^{-1}. Biotopes in which each family was collected are listed alongside. mv - marginal vegetation, sic - stones in current, sooc - stones out of current, pool - shallow pools.

Category:		Tnf					Tf		Tmf	C4	C8	BIOTOPES
Site:		1	2	4	5	6	1	2	3			
NEMATODA		T	T		T		Tf	Tf				sooc,pool
OLIGOCHAETA			T	T	T	T	Tf	Tf	Tmf			all
CRUSTACEA	DECAPODA	T	T	T	T	T	Tf	Tf	Tmf			mv,sic,sooc,pool
	CLADOCERA		T	T	T				Tmf	+		mv,sooc,pool
	COPEPODA		T	T				Tf				mv,sooc,pool
	OSTRACODA	T	T	T	T		Tf	Tf	Tmf	+		mv,sic,sooc,pool
HYDRACARINA		T	T		T	T	Tf	Tf	Tmf	+	+	all
PLECOPTERA	NEMOURIDAE	T										mv,sic
COLLEMBOLA		T										pool
EPHEMEROPTERA	BAETIDAE	T	T	T	T	T		Tf	Tmf	+		all
	HEPTAGENIIDAE								Tmf			mv,sic,sooc
	LEPTOPHLEBIIDAE	T							Tmf			mv,sic,sooc
	TRICORYTHIDAE								Tmf			sic
	CAENIDAE	T	T	T	T	T	Tf		Tmf	+	+	all
ODONATA	CHLOROLESTIDAE		T	T	T				Tmf			mv,sic,sooc,pool
	LESTIDAE		T		T	T		Tf		+		mv,sooc,sand
	PROTONEURIDAE			T	T					+		mv,sand
	COENAGRIONIDAE		T	T	T	T		Tf	Tmf	+	+	mv,sooc,sand,pool
	GOMPHIDAE		T	T		T				+		sooc,sand,pool
	AESHNIDAE	T	T	T	T	T			Tmf	+	+	all
	CORDULIIDAE		T		T	T			Tmf	+		mv,sic,sand
	LIBELLULIDAE	T	T	T	T	T	Tf	Tf	Tmf	+		all
HEMIPTERA	NOTONECTIDAE	T	T	T	T	T	Tf	Tf	Tmf	+		all
	PLEIDAE			T	T	T	Tf			+	+	mv,sooc,sand,pool
	NAUCORIDAE		T	T	T	T	Tf	Tf	Tmf	+	+	all
	NEPIDAE								Tmf			mv
	BELOSTOMATIDAE					T			Tmf			mv
	CORIXIDAE	T	T	T	T	T	Tf	Tf	Tmf	+		all

Category:		Tnf					Tf		Tmf	C4	C8	BIOTOPES
Site:		1	2	4	5	6	1	2	3			
	GERRIDAE	T	T	T	T	T		Tf	Tmf	+	+	mv,pool
	HYDROMETRIDAE	T		T	T	T			Tmf	+	+	mv
	VELIIDAE	T	T	T	T	T		Tf	Tmf	+		mv,sooc,pool
	MESOVELIIDAE		T				Tf	Tf				mv,sooc
TRICHOPTERA	HYDROPSYCHIDAE	T			T				Tmf			mv,sic,sooc
	ECNOMIDAE		T				Tf					mv,pool
	PHILOPOTAMIDAE	T	T									sooc
	HYDROPTILIDAE		T		T				Tmf			mv
	PISULLIDAE	T										sic
	LEPTOCERIDAE	T			T			Tf	Tmf	+	+	all
COLEOPTERA	DYTISCIDAE	T	T	T	T	T	Tf	Tf	Tmf	+	+	all
	DYTISCID L.		T	T			Tf	Tf	Tmf			all
	GYRINIDAE	T	T				Tf	Tf	Tmf	+		mv,sic,sooc,pool
	GYRINID L.							Tf	Tmf			mv,sic
	HALIPLIDAE			T								mv
	HALIPLID L.		T									pool
	HELODIDAE								Tmf			sooc
	HELODIDAE L.			T								pool
	HYDRAENIDAE	T		T								mv,sic,sooc,pool
	HYDROPHILIDAE	T	T	T	T	T	Tf	Tf	Tmf	+		mv,sooc
	HYDROPHILID L		T					Tf				mv,sooc,sand,pool
DIPTERA	TIPULIDAE			T	T	T	Tf	Tf	Tmf	+		all
	CULICIDAE	T	T	T	T	T	Tf	Tf	Tmf	+		all
	SIMULIIDAE	T			T	T	Tf	Tf	Tmf	+		mv,sic,sooc,pool
	CHIRONOMIDAE	T	T	T	T	T	Tf	Tf	Tmf	+	+	all
	CHIRONOMID P.		T		T		Tf	Tf				mv,sic,sooc
	CERATOPOGONIDAE	T	T	T	T	T		Tf	Tmf	+	+	all
	TABANIDAE	T				T		Tf	Tmf	+		mv,sic,pool
	ATHERICIDAE							Tf				sic
GASTROPODA	LYMNAEIDAE		T	T	T			Tf		+		mv
	PLANORBIDAE		T	T	T		Tf	Tf	Tmf	+		mv,sic,sooc,pool
	PHYSIDAE		T	T	T	T		Tf		+		mv,sooc,sand,pool
	ANCYLIDAE				T			Tf	Tmf	+	+	mv,sic
PELECYPODA	SPHAERIIDAE		T					Tf	Tmf			mv

Of the 62 families (or higher taxa) listed, 56 (90%) were collected at temporary sites during no-flow conditions (Tnf), 39 (63%) at temporary sites during flow conditions (Tf), and 43 (69%) at temporary sites with modified, almost continual flow (Tmf). There was considerable overlap of families in the three categories: 61% of taxa were collected in both Tnf and Tf, 58% in both Tnf and Tmf, and 45% in Tf and Tmf.

Animals collected only in the Tnf category included gomphid dragonflies, protoneurid damselflies, hydraenid beetles, and philopotamid caddisflies. Rheophilous athericids were collected only in the Tf class. Leptophlebiid mayflies and pisullid caddisflies were collected only in the overlapping Tf and Tmf categories, both representing flow conditions. Taxa found in Tmf (modified, almost continual flow) only included heptageniid and trichorythid mayflies and nemourid stoneflies.

Taxa capable of withstanding high salinities (> 400mS.m^{-1}) were in the majority, and the only taxa not collected under these conditions were copepods, stoneflies, tricorythid, leptophlebid and heptagenid mayflies, all caddisflies listed except leptocerids, all beetles listed except dytiscids and hydrophilids, chlorolestid damselflies, belostomatid bugs, athericid flies and sphaeriid molluscs. In the over 800mS.m^{-1} category, leptocerid caddisflies, water mites, caenid mayflies, coenagrionid damselflies, aeshnid dragonflies, pleid bugs, dytiscid beetles, ancylid molluscs, and chironomids were collected.

Generally, families were widely distributed within a stie over time, with few restricted to single biotopes. Only tricorythid mayflies, pisullid caddisflies and athericid flies were restricted to the SIC biotope. The greatest numbers of families were generally collected in the MV and POOL biotopes (Table 6.5). Most of the taxa were found in MV at some or other time, and lymnaeid and sphaeriid molluscs, haliplid beetles, hydroptilid caddisflies and several hemipterans were collected only in this biotope.

6.4.7 Detailed taxonomic-level analyses: Invertebrates collected during January and May 1995

During January and May 1995, invertebrates collected in replicate samples were identified to the lowest possible taxonomic level, and abundances recorded. Altogether 139 taxa were identified for this study (note, chironomid 'types' were listed as 'Other Chironomini' etc.; Table 6.8). The total number of taxa collected at each site over the sampling period reported were: 92 at the upper Kowie, with 54 from UK1, and 59 from UK2; 47 from the lower Kowie; 23 from the upper Bushmans; 54 from the lower Bushmans; and 29 from the Fish River tributary (Table 6.8).

Although it was thought that highest number of equivalent taxa collected at the upper Kowie site may be attributable to intensity of longer-term sampling, a greater number of taxa collected at the Bushmans River largely dispelled this notion.

During the high rainfall month of January 1995, the upper Kowie site UK2 yielded 40, and the lower Bushmans River 35 taxa. At the former site, abundances of individual taxa were low (<20 individuals per sample), and taxonomic evenness high (Table 6.8), indicating a relatively even spread of individuals across the groups and a lack of dominance by particular taxa. At the lower Bushmans River site, far greater abundances were recorded, and taxonomic richness and taxonomic evenness were comparatively low (Table 6.8). Large numbers of *Demoulinia* complex baetids, caenid mayflies, *Ennallagma* sp. damselflies and *Pseudagrion* sp. coenagrionids, pleid bugs, *Tanypus* sp. chironomids, culicid flies and microcrustaceans were collected during this month (Appendix 6.3).

At the lower Kowie River, upper Bushmans River and Fish River tributary sites, less than 25 taxa were collected per site. Taxonomic richness and diversity indices were low relative to those of the upper Kowie. At the lower Kowie River, where flow was present during all sampling events (but does cease for periods, according to flow records from DWAF), low taxonomic evenness was reflected by the high numbers of *Simulium adersi* blackflies, *Cheumatopsyche* sp. caddisflies, *Afroptilum* spp. and *Baetis harrisoni* baetids, *Caenis* sp. caenids, and

Rheotanytarsus sp. chironomids. Similarly, at the Fish River tributary site, low evenness was recorded due to the high numbers of *Demoulinia* complex baetids, *Chironomus* sp. chironomids, dytiscid larvae and anopheline culicids.

During May 1995, there was an increase in total numbers of taxa at all sites excepting UK2 on the upper Kowie River. Greatest numbers of taxa were found in the lower Kowie (43) and lower Bushmans Rivers (42). At the former site, taxonomic richness had increased, however evenness was relatively low, with a dominance of *Simulium damnosum* blackflies and high numbers of taxa already listed for January. At the lower Bushmans River site, evenness was elevated as only nematodes were collected in large numbers (> 100 per sample) in the SAND biotope. At the upper Kowie River site UK1, taxonomic richness increased, but diversity and evenness decreased, with the occurrence of large numbers of *Simulium nigritarse* and *S. vorax* blackflies in the samples. Taxonomic evenness was high at the upper Bushmans River, and several hemipteran families not present in January were collected (Table 6.8).

During the two months, certain taxa were collected at individual sites only - although this was not necessarily an indication that they were absent from other sites at other times. *Aprionix* complex leptophlebids, *Neurocaenis* tricorythids, *Cheumatopsyche maculata* hydropsychids, *Orthotrichia barnardi* hydroptilids, *Xenochironomus* sp. chironomids (found only in sponges) and *Cardiocladius* sp. chironomids were collected only in the lower Kowie river, under almost continual flow conditions. Taxa collected only at the upper Kowie River sites included *Micronecta* sp., *Arctocorisa* sp. and *Sigara* sp. corixids, *Microvelia* sp. veliids, haliplid, hydraenid and hydrophilid beetles, and *Zavrelliela* sp., *Limnophyes* sp. and *Conchapelopia* sp. chironomids. *Anax* sp. aeshnids, *Anisops sardea* notonectids, and *Microchironomus* chironomids were collected only in the Bushmans River, and *Microtendipes* sp. chironomids only in the Fish River tributary (Appendix 6.3).

Of the 139 taxa identified during January and May 1995, a total of 108 taxa were collected in MV, 55 in SIC, 12 in SOOC, 34 in SAND and 39 in POOL samples. The majority of taxa were found in two or more biotopes (Appendix 6.3).

Table 6.8 Diversity indices for samples taken at the six sites during January 1995 and May 1995. MV - marginal vegetation; SIC -stones in current, SOOC - stones out of current, SAND - sandy substrata, POOL - shallow pools.

		TOTAL TAXA		*SHANNON DIVERSITY*		*TAXONOMIC EVENNESS*	
SITE	*BIOTOPE*	*Jan.*	*May*	*Jan.*	*May*	*Jan.*	*May*
Upper Kowie	MV	24	25	2.9	2.9	0.93	0.91
UK1	SIC	6	16	1.7	2.0	0.93	0.71
	SOOC	7		1.9		0.96	
	TOTAL	**30**	**35**	**3.1**	**2.9**	**0.91**	**0.82**
Upper Kowie	MV	27	25	3.0	3.0	0.91	0.94
UK2	SIC	19	11	2.8	2.3	0.96	0.96
	SOOC	6		1.8		0.99	
	TOTAL	**40**	**32**	**3.4**	**3.2**	**0.93**	**0.93**
Lower Kowie	MV	17	26	1.7	2.0	0.61	0.62
	SIC	16	26	1.9	2.0	0.67	0.60
	SOOC		15		1.8		0.65
	TOTAL	**23**	**43**	**1.9**	**2.5**	**0.59**	**0.66**
Upper Bushmans	POOL	21		2.8		0.92	
	MV		20		2.5		0.84
	SAND		17		2.1		0.75
	TOTAL	**21**	**31**	**2.8**	**2.9**	**0.92**	**0.84**
Lower Bushmans	MV	32	32	2.1	2.7	0.59	0.77
	SAND	11	23	1.8	1.9	0.76	0.60
	TOTAL	**35**	**42**	**2.2**	**2.7**	**0.63**	**0.72**
Fish R. Trib.	POOL	19	15	1.7	2.2	0.56	0.80
	POOL	9	16	0.7	2.4	0.31	0.87
	TOTAL	**21**	**22**	**1.4**	**2.6**	**0.47**	**0.84**

6.4.8 Detailed taxonomic analyses:
Similarity analyses on total samples

Cluster analysis

Bray Curtis similarities between total (aggregated) sample-sets from January and May were computed on standardised, double-root transformed data (see Statistical Methods). Cluster analysis based on these similarities produced three clear groupings at low similarities (Figure 6.4). Lines were drawn through the 30% and 50% similarity points to discern Groups and to check congruence between clustering and ordination results. Clusters to the right of the 30% line were marked as Groups 1 to 3.

In the majority of cases, January and May samples from individual sites paired off, and clustered at lower similarities with samples from other sites. Groups comprised the following samples:

Group 1:	Upper Kowie River samples from January and May.
Group 2:	Lower Kowie River samples from January and May.
Group 3:	Upper and lower Bushmans River and Fish River tributary samples from January and May.

Taxa responsible for the clustering of Group 1, as discerned by SIMPER, were (in decreasing order of importance) *Tanytarsus* chironomids, *Laccophilus lineatus* dytiscids, 'Other' Tanytarsini and Tanypodinae, *Potamonautes* sp. crabs, *Orthetrum* sp. libellulids, *Rheotanytarsus* sp. tanytarsines, ostracods, and *Microvelia* sp. veliids, and *Anisops* sp. notonectids. Those accountable for the majority of similarity in Group 3 samples were (in decreasing order of importance) oligochaetes, dytsicid larvae, *Tanytarsus* sp., *Psectrocladius* sp. and 'Other' Tanytarsini chironomids, ceratopogonids, *Demoulinia* complex baetids, *Chironomus* sp. and *Larsia* sp. chironomids, *Austrocaenis* sp. caenids, *Bulinus* sp. physids and *Ennallagma* sp. coenagrionids.

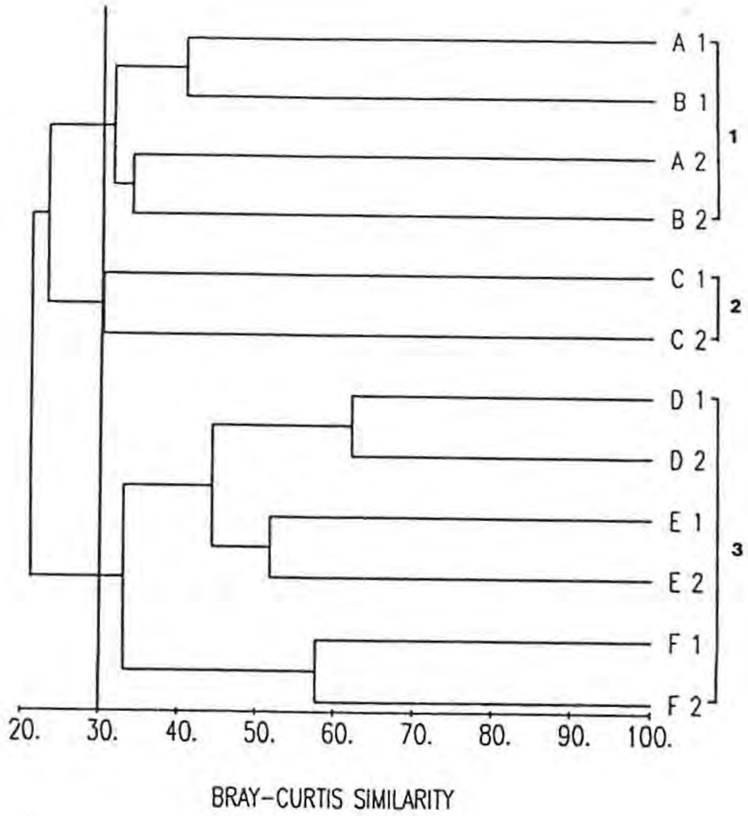
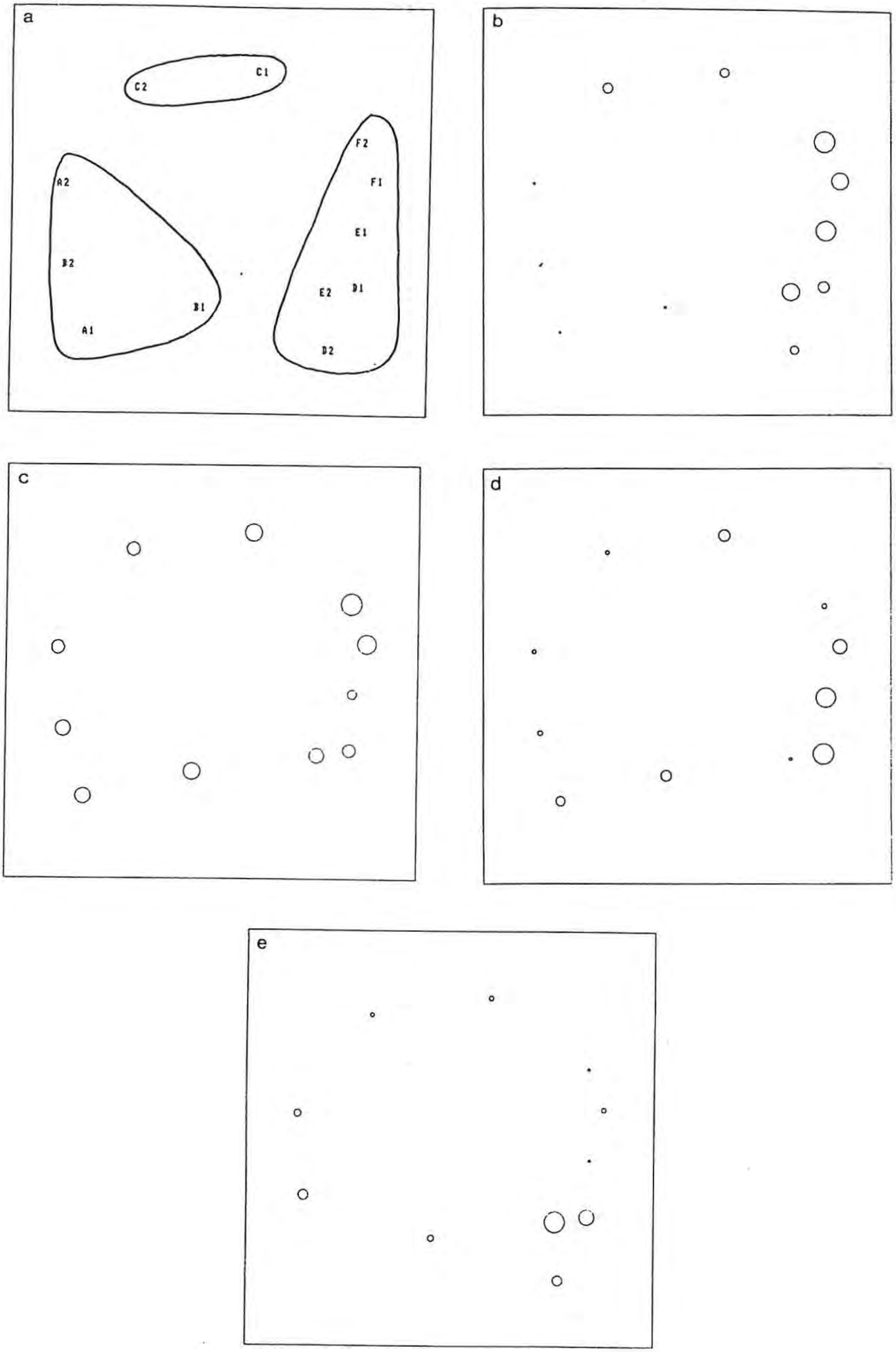


Figure 6.4 Dendrogram showing cluster analysis of faunal similarities using detailed taxonomic-level identifications, and total (aggregated) sample sets from January and May 1995 at all six sites. Similarities calculated using standardised, double-root transformed abundance data.

Ordination

MDS ordination based on similarity matrices produced a low-stress 2-dimensional picture showing the clear separation of the three groups, as clarified by superimposing the three Groups over ordination points (Fig. 6.5a). Groupings indicated agreement between the clustering and ordination procedures.

Figure 6.5 a-e (overleaf). a) MDS ordination based on faunal similarities between aggregated samples from all sites, during January and May 1995. Stress = 0.16. Clusters formed at over 30% similarity (solid line) and 50% similarity (dashed line) are superimposed. b) - e) Scaled symbols representing values of individual abiotic variables superimposed on the corresponding biotic ordination to check for trends in common. b) Conductivity, c) % Oxygen saturation, d) Water temperature, e) pH.


a
C1
C2
F2
A2
F1
E1
B2
E2
D1
B1
A1
D2
b
c
d
e

Analysis of similarity for examination of null hypothesis

The ANOSIM test on single sample sets samples from the individual sites (*a priori* groups) from January and May generated a global *R* value of 0.64, at a significance level of 0%, at which level the null hypothesis of 'no differences between sites (at detailed taxonomic levels)' could be rejected. There were thus significant differences between at least some of the sites at these taxonomic levels. Pairwise comparisons indicated that the majority of sites differed significantly at these taxonomic levels (Table 6.9). The only sites which did not show significant differences were UK1 and UK2, and the upper and lower Bushmans sites.

Table 6.9 Results of the pairwise tests conducted in ANOSIM to check for significance of difference between different sites, using detailed taxonomic-level data from January and May 1995. Where $-1 < R < 1$ and significance levels (%sig.) are less than 5%, sites in a pair can be considered significantly different (i.e. greater variability between sites than within a site over time). Significantly different pairs of sites are highlighted.

	UK1	**UK2**	**LK**	**UB**	**LB**
UK2	0.21 13.5%	**R** **% SIG.**			
LK	**0.74** **0.8%**	**0.61** **0.8%**			
UB	**0.88** **0.8%**	**0.56** **3.2%**	**0.82** **0.8%**		
LB	**0.93** **0.8%**	**0.66** **0.8%**	**0.66** **1.6%**	0.3 5.7%	
FT	**0.96** **0.8%**	**0.72** **1.6%**	**0.72** **1.6%**	**0.87** **2.9%**	**0.63** **2.9%**

6.4.9 Detailed taxonomic analyses:

Association of biotic and abiotic variables

Four environmental variables were individually superimposed on the corresponding MDS ordination of total faunal samples from January and May

1995 (Fig. 6.5a) in order to check for trends in common between abiotic and biotic variables. Conductivity, dissolved oxygen, temperature, and pH were tested (Figs. 6.5 b-e). Of these, only conductivity showed a clear gradient which matched the groupings in the biotic ordination (Fig. 6.5b).

6.4.10 SASS4 scores for the period

Although SASS4 is also family-based, many of the groups included in the earlier section regarding family-level information are not allocated scores in this method (e.g. microcrustaceans, hydrometrid bugs, beetle larvae) and SASS4 results for 'numbers of families' thus differ somewhat from results presented in the previous section.

Total SASS4 scores at a site (summed scores for each of the listed taxa, in all biotopes) ranged between 6 and 149 (Table 6.10), and the median score for all sites and samples was 76. Average score per taxon (ASPT), which represents the SASS4 score divided by the number of families present, ranged from 3 to 6 (Table 6.10).

Variation in scores within biotopes and sites was high over time, as was that between sites (Table 6.10). But for the lower Kowie River site, SASS4 scores at the sites sampled during the autumn month of May 1994 were comparable, with most showing an increase in September 1994 (early spring). In January 1995, following heavy rains in the region and flow in all of the catchments see Section 6.4.3) a decrease in scores was recorded for the upper Kowie River and Fish River tributary sites, while scores at all other sites increased. After January, scores showed similar trends for all sites. The elevated scores in May 1995 were followed by reduced scores in September 1995, when rainfall was low and drying had commenced; and by another increase in January 1996 after relatively substantial rains. During the final month, disparity between scores from different sites was greatest.

Table 6.10 SASS4 scores for the Kowie and Bushmans River sites and Fish River tributary over the full period of the study.

		NO. OF FAMILIES	TOTAL SCORE	ASP
May 94	UK1	10	58	5.8
	UK2	13	60	4.6
	LK	25	149	6
	LB	15	76	5.1
	FT	12	55	4.6
Sept. 94	UK1	17	86	5.1
	UK2	22	108	4.9
	LK	18	86	4.8
	UB	8	35	4.4
	LB	16	83	5.2
	FT	12	69	5.8
Jan. 95	UK1	9	37	4.1
	UK2	15	66	4.4
	LK	13	76	5.8
	UB	11	47	4.3
	LB	20	103	5.2
	FT	17	76	4.5
May 95	UK1	21	120	5.7
	UK2	18	79	4.4
	LK	20	115	5.8
	UB	24	115	4.8
	LB	25	126	5.0
	FT			
Sept. 95	UK1	2	6	3.0
	UK2	13	57	4.4
	LK	15	76	5.1
	UB	12	54	4.5
	LB	18	93	5.2
	FT	13	59	4.5
Jan. 96	UK1	6	34	5.7
	UK2	15	72	4.8
	LK	24	127	5.3
	UB	12	58	4.8
	LB	18	89	4.9
	FT	20	101	5.1

6.5 DISCUSSION

6.5.1 Differences in faunal composition between sites

While the null hypothesis of 'no differences between sites' was rejected for detailed taxonomic-level information, it could not be rejected for family-level data. While, on the face of it, this discrepancy would seem to point to an inadequacy in coarser-level taxonomic comparisons, other factors were also contributary.

At the family level, pairwise tests between sites indicated that only the upper Kowie site UK1 was significantly different to other sites (lower Kowie and lower Bushmans). The effect of sapling time was also clear in cluster analysis of family-level data (Fig. 6.2): individual Groups generally comprised samples from a number of sites at individual or consecutive sampling times, rather than samples from a single site over time. Each sampling period represented particular rainfall conditions and the effects thereof on the hydrology and physico-chemistry of the river sites. This indicated that the character of the fauna at individual sites, and the resemblances between sites were at least partly related to extent and duration of rainfall in the region, subsequent hydrology, and the effects of both on the physico-chemistry of the surface waters.

At more detailed taxonomic levels and over a shorter period, however, results indicated that the majority of sites were significantly different. This finding was again borne out in cluster analysis and ordination, where greatest similarities were recorded between samples from single sites over time (Groups 1 to 3, Fig. 6.4). In contrast to the family-level analyses, these suggested that the character of the site itself was as important an influence on faunal make-up as were prevailing environmental conditions. It is acknowledged that these two months happened to be high-rainfall periods, and that environmental conditions were relatively stable at individual sites, so that in contrast to the longer-term study, the ratio of variability within a site to variability between sites would have been low.

The clear difference in results of family-level and lower taxonomic-level analyses cannot thus be related *only* to scale of resolution, but also to the extent of rainfall and hydrological variability over the time period represented by the individual analyses (high variability over the full period, lower variability between January and May 1995), and its effects on faunal make-up. Detailed taxonomic studies were only conducted over two sampling periods, and greater temporal replication would be required to establish true levels of variability over time at these taxonomic scales.

Despite the effects of other variables, the outcome of this section of the discussion remains that at a family level, fauna of different sites could not be said to differ significantly, whereas at finer taxonomic levels, significant differences between faunas were indicated. It is proposed that at the level of family, a fauna characteristic of the various temporary rivers in the study could be discerned based on commonality of presence (or absence) at the various sites (this is attempted in Section 6.5.2). This principal could also be extended to the level of subfamily, genus and species, but *only* where commonality of occurrence applied broadly. In general, the fact that sites were clearly faunally distinct at these finer taxonomic levels suggests that the *range* of subfamilies, genera and species representing the common families is broad, and that generalities regarding presence or absence of genera or species should be avoided.

Alongside the concept of a characteristic fauna, there should be recognition of the gradients in diversity and composition along the temporary - episodic river continuum (see Chapter 2). With increasing duration of the dry phase, as in ephemeral and episodic rivers, taxonomic diversity is likely to decline (e.g Williams 1996, Boulton and Suter 1986). This was evident at the ephemeral Fish River tributary site, where numbers of families or other taxa were consistently low. Along the perennial-episodic continuum (Ch. 2), it is possible that faunal character may differ more between intermittent and episodic rivers than between intermittent and perennial rivers. It would be worth examining this postulate further. Along these lines, Williams (1996) commented that there was a need for *'more extensive surveying of habitats to confirm the global nature of temporary waters, and to extend/confirm the known ranges of taxa along the permanent-temporary water habitat gradient'.*

6.5.2 Factors influencing faunal composition and diversity

Altogether 62 families were collected over the less intensive study, and 139 taxa were identified to lower taxonomic levels over the two months of the more intensive study. Of these 139, up to 59 were collected at individual sites over the period. While these total numbers are low in comparison to the 200-plus taxa reported for the upper Kowie River over longer periods (Chs. 3,4) and the 250-plus reported by Boulton and Lake (1992a) and Abell (1984) in their long-term studies of intermittent streams, temporal replication for the detailed taxonomic level study was low, and numbers cannot be considered a true reflection of the 'complete' faunas. This exercise was aimed rather at investigating the ranges in composition and diversity at the various temporary river sites.

During the intensive study, the majority of taxa were collected at the upper Kowie sites UK2 (59) and UK1 (54), and at the lower Bushmans site LB (54). While numbers at the upper Kowie sites may have been somewhat biased by the fact that these sites were sampled intensively over a long period (greater familiarity with layout and sampling of site, faunal identifications etc.), this was not considered to have played a major role, as - for the purposes of this study - an equivalent sampling effort was applied at all sites, and the lower Bushmans yielded numbers as high as those of the upper Kowie.

Assuming that results are an adequate reflection of reality, a greater number of taxa were recorded at these three temporary sites than at the lower Kowie River LK (47 taxa) where flow was almost continual. This was an unexpected finding. While it was anticipated that species composition at the lower Kowie (where flow was almost continuous) would have indicated the presence of a fauna susceptible to environmental change, only trichorythid mayflies, *Orthotrichia barnardi* hydroptilids, and *Cheumatopsyche maculata* hydropsychids were 'restricted' to LK samples, and the remainder of taxa collected there were present at one at one or more of the more temporary river sites. Despite the heterogeneity in biotopes at LK, many of the animals present at the more temporary sites were absent e.g. pisullid and ecnomid caddisflies, pleid, hebrid and mesoveliid bugs, lestid and protoneurid damselflies, gomphid dragonflies, hydraenid beetles, and lymnaeid and physid snails. Their absence in an environment exposed to almost continual flow may be explained by the preference of most of these taxa for more lentic conditions (e.g. McCafferty 1981, Pennak 1953), which are common in intermittent rivers.

These findings sustain the suggestion that diversity in intermittent rivers is partly attributable to the environmental heterogeneity of these environments (Boulton and Lake 1992a).

It is speculated that the high diversities at the upper Kowie and the lower Bushmans were attributable to almost opposite influences. At the upper Kowie, flow in the river affected diversity positively, and the general maintenance of diversity was, considered in part due to environmental heterogeneity (e.g. Boulton and Lake 1992a). High rates of change in hydrological state or phase (one of the criteria for disturbance, as defined in Section 1.3.6) resulted in regular expansion and contraction of aquatic habitat (*sensu* Stanley *et al.* 1997). Expansion of the aquatic habitat and increase in biotope diversity opened up space for immigration of colonist and facultative taxa (e.g. mayflies, dragonfly and damselfly adults, hemipterans, dytiscids). Contraction (loss of surface water and drying) resulted in losses of colonist taxa, but favoured the persistence of resident and facultative taxa and their juvenile stages. Taxonomic evenness was consistently high (i.e. dominance was low). Stanford and Ward (1983) maintained that intermediate levels of disturbance introduced optimal environmental variability into stream systems, disallowing the attainment of competitive equilibria and thus allowing coexistence of a greater total number of species and few dominant species. Along similar lines, the intermediate disturbance hypothesis (IDH) of Connell (1978) predicted that biotic diversity would be highest in communities sujected to moderate levels of disturbance. While the identification of 'intermediate' levels of disturbance in an environment such as the upper Kowie is difficult, these concepts may be applicable.

At the lower Bushmans River (LB), in contrast, the comparatively high numbers and abundances of taxa were attributed both to the durational stability of the habitat (Schneider and Frost 1996), and to the reduction in conductivity values at the site over the high rainfall period of January to May 1995. Relative to the upper Kowie sites, the lower Bushmans showed low hydrological variability over the study period: prior to drying, the pool had a duration of over 18 months. (This longevity was due in some part to an inhibition of flow from upstream sources because of farm dams in the channel - under natural conditions, pools in the channel would probably have been disrupted by irregular and unpredictable flow). The resultant stability in the aquatic environment at this site favoured both the persistence of individual taxa over time (sensu Townsend *et al.* 1987), and increases in relative abundances of typical pools taxa such as baetid and caenid mayflies, pleid bugs, leptocerid caddis, and chironomids. High abundances of animals in the pool suggested that physical constraints on the fauna were relaxed (Stehr and Branson 1938). Taxa which persisted in the evironment were presumably adapted to withstand both the fluctuations and extremes in conductivities. While there is little information available about tolerances of freshwater macroinvertebrates to increased (or absolute) conductivities, Dallas and Day (1993) reported that it was generally the rate of change rather than the absolute change that was important. The authors maintained that many animals are capable of adjusting to slow change by a process of physiological acclimation which could not be accomplished if environmental change was rapid. At the lower Bushmans, increases in conductivity (due to evaporation and leeching) and decreases (due to dilution) were gradual processes, which may also have favoured high abundances. During the months when conductivity was low (though still > 300mS.m^{-1}), taxa collected included chlorolestid and protoneurid damselflies, hydroptilid caddisflies, hydrophilid beetles, tipulid dipterans, simuliids and planorbid molluscs. Many of these taxa are associated with flow conditions (e.g. simuliids, protoneurids) and may have originated from upstream sources (in seepage or overflow). The importance of such 'drifting' as a source of colonists was emphasized by Minshall and Petersen Jr. (1985).

The extreme conductivity values recorded at the lower Bushmans were matched by those recorded in the unimpacted Fish River tributary, where water in the pools was chiefly subterranean in origin and high conductivities could only be explained in terms of the underlying geology and high evaporation rates. Fish River tributary pools differed in that they were small and isolated and occurred in a channel where the dry period was extensive and there was seldom flow. The majority of the taxa collected at this site were considered 'facultative' or 'resident' taxa, with the exception of aeshnids and simuliids (opportunist colonists).

6.5.3 A 'characteristic fauna' for temporary rivers?

Williams (1987) posed the question of whether or not a group of organisms could be discerned as being universally characteristic of temporary waters. Earlier discussion has indicated that it may be possible to distinguish a range of taxa - at the family level at least - which are characteristic of the 'arid corridor' temporary rivers included in this study. These invertebrates are allocated to three groups, on the basis of those suggested by Williams and Hynes (1977), and discussed in Chapter 4: 'residents', 'facultative taxa' and 'opportunist colonists'.

The group of specialist temporary river fauna, or 'residents' for this range of temporary rivers included oligochaetes, cladocern, copepod and ostracod microcrustaceans, water mites, certain chironomid and tipulid fly larvae, ?decapod crabs, ?hydraenid beetles, and lymnaeid, physid, planorbid, ancylid and ?sphaeriid molluscs.

'Facultative taxa' included those taxa naturally occurring in both lentic and lotic environments. These included representatives of gomphid, libellulid and corduliid dragonflies; corixid, notonectid, pleid, naucorid, hydrometrid and veliid bugs; and dytiscid and hydrophilid beetles. The bugs and beetles listed were capable of surviving the majority of the surface water conditions encountered in the temporary river environment, but due to their powers of flight, could relocate to more favourable environment if necessary (e.g. during drying periods). Other facultative taxa were behaviourally equipped to avoid desiccation (e.g. certain libellulid and gomphid nymphs burrow into damp sand, and corduliid nymphs have developed the habit of hiding amongst damp leafpacks which allows them to survive at least the early stages of drying; Wilmot unpubl.).

Opportunist colonists were those taxa generally associated with perennial waters, and not particularly adapted to intermittent flow conditions, but able to survive in streams with short-dry periods (Williams and Hynes 1977), or - where environments were less predictable - at least to opportunistically breed there. None of the juvenile stages of these animals would be expected to survive drying conditions, but may follow cues (e.g. diminishing water) to leave the environment (either actively or passively in drift) under threat of adverse conditions. Although no organism is entirely r-, k- or A- (adversity) selected (Pianka 1970), these taxa would be best served by r-selected characteristics such as high intrinsic rate of natural increase, large numbers of eggs, rapid development, small body size, early reproduction in life cycle, short life span (MacArthur and Wilson 1967, Williams 1987). Opportunist colonists in the 'arid corridor' temporary rivers included baetid and caenid mayflies, chlorolestid, lestid and coenagrionid damselflies, aeshnid dragonflies, leptocerid, pisullid, hydroptilid and (scarce) hydropsychid caddisfly larvae, and simuliid blackflies.

Taxa absent in - or scarce from the more temporary of habitats but present in reasonable numbers at the lower Kowie, where flow was present throughout the study (and surface water is consistently present) were tricorythid and heptageniid mayflies, stoneflies, and hydropsychid caddisflies, most of which show a preference for flow conditions (McCafferty 1981). The absence of stoneflies in many temporary streams has been remarked on by Williams (1996), who mentioned that it seemed this family was less capable of dealing with lentic conditions than with drought, and that stoneflies survived drough only in running water conditions. Harrison (1978) commented on the 'conspicuous absence' of tricorythid mayflies and hydropsychids in an intermittent Western Cape stream. Flow preference does not prevent certain groups from occupying temporary river environments, and if rheophilous species such as simuliids are transported to a site in drift or seepage from upstream, they may to be capable of surviving in pools in temporary rivers (probably only for short periods). Certain simuliids were also collected in the high-conductivity pools at the lower Bushmans River and Fish River tributary sites, a testimnony to their tolerance levels.

6.5.4 The value of a biotic index for temporary rivers

The variation in SASS4 and ASPT scores at all sites (both unimpacted and modified) was high, and reflected a combination of seasonal influences, changes in water chemistry, and unpredictable fluctuations in rainfall and hydrology over time and space. No temporal or seasonal trends were discerned in the scores within or across sites (for example, scores in May 1994 differed substantially from those in May 1995).

One of the key requirements in using SASS4 to determine river condition is to establish the degree of variability in SASS4 scores in a catchment or at a site over time. The degree of variability encountered in this study, and more importantly the lack of pattern in scores from a single site over time, would compromise the ability to establish a meaningful reference condition, which is strongly advised for the South African National Biomonitoring Program (Eekhout *et al.* 1996). The reference condition tells the practitioner what the expected score or range of scores should be for a site under natural conditions. It is derived either from the average SASS scores of a number of unimpacted ('natural') sites within the relevant river type, or - where necessary - is constructed from historical flow and faunal information (Eekhout et *al.* 1996). The value of the biomonitoring concept lies in its ability to reflect deviation of observed scores from expected or reference scores. Even if a reference 'range' were to be calculated for some of the temporary rivers in this study, based on scores from unimpacted sites, deviation from this reference due to genuine water quality deterioration could not be properly discerned because of the high *natural* variation at a site over time.

Chutter's (1995) categories of water condition, which assign a description to a site on the basis of its SASS4 and ASPT scores, are listed in Table 6.13. How valid are these categories in the case of Eastern Cape temporary rivers?

Table 6.13. Guideline values for rating biological condition on the basis of the combined SASS4 and ASPT scores as proposed by Chutter (1995):

SASS4	ASPT	WATER CONDITION
>100	>6	Water quality natural, habitat diversity high.
<100	>6	Water quality natural, habitat diversity reduced.
>100	<6	Borderline case between water quality natural and some deterioration in water quality, interpretation should be based on the extent to which SASS4 exceeds 100 and ASPT is less than 6.
50-100	<6	Some deterioration in water quality.
<50	ASPT variable	Major deterioration in water quality.

An ASPT of > 6 was not recorded during the study, so the description of 'water quality natural, habitat diversity high' would not apply to any sites, despite the 'naturalness' of certain of them. Neither could sites be described as having 'natural water quality with habitat diversity reduced' according to these categories. SASS scores of >100 with ASPTs of <6 occurred once at the upper Kowie site UK1, twice at the lower Kowie River, and once at the lower Bushmans River and the Fish River tributary. During those months, these sites could thus have been described as 'borderline case between water quality natural and some deterioration in water quality..'. This then represented the best-possible description for temporary river sites in the region, whether they were close-to-natural or relatively modified.

At the present state of development of the SASS4 method, interpretation of scores for temporary rivers is too complex. Some development is required to address the issues of high variability (with low pattern) in scores from a single site, the inability to discern a reference condition, and the condition categories. Nevertheless, the technique, if used conservatively, yields useful information, and provides an excellent field method for low-intensity invertebrate 'surveys' of this type.

6.6 CONCLUDING POINTS

- Unpredictable rainfall and hydrology in the Eastern Cape region resulted in substantial variability in faunal character of temporary and perennial sites over space and time.

- At the family level, there was substantial overlap in the fauna inhabiting the temporary rivers studied, and faunal differences between sites were generally not significant.

- At more detailed taxonomic levels, overlap between sites was far lower, and significant differences were indicated between the majority of sites.

- High diversities in fauna were considered to be related to seemingly contradictory factors, depending on the river in question. At least two influences could apply - either
  - temporal heterogeneity in habitat caused by variable and unpredictable hydrology; or
  - durational stability of the aquatic habitat, and low rates of change in environmental conditions.

- A characteristic family-level fauna was tentatively proposed for the 'arid corridor' rivers studied. The importance of recognising the gradient in faunal diversity and composition between intermittent and episodic rivers was discussed.

- Interpretation of SASS4 scores recorded for the temporary rivers in the study was complex, and further development of the method may be required if it is to be used in these systems. However, the field technique and sampling methods of SASS4 are considered excellent for use in low-intensity studies of this nature.

REFERENCES

Abell, D.L. 1984. Benthic invertebrates of some Californian intermittent streams. *In*: S. Jain and P. Moyle (eds). *Vernal pools and intermittent streams.* University of California, Davis Institute of Ecology Publication No. 28. pp46-60.

Allanson, B.R., Hart, R.C., O'Keeffe, J.H. and Robarts, R.D. 1990. Inland Waters of Southern Africa: an Ecological Perspective. *Monographiae Biologicae* **64**. Kluwer Academic Publishers, Dordrecht, 458pp.

Balinsky, B.I. 1962. Patterns of animal distribution on the African continent. *Annals of the Cape Provincial Museum* **2:** 299-310.

Boulton, A.J. and Lake, P.S. 1992. The macroinvertebrate assemblages in pools and riffles in two intermittent streams (Werribee and Lerdeberg Rivers, southern central Victoria). *Occasional Paper of the Museum of Victoria* **5:** 55-67.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective *In:* P. De Deckker and W.D. Williams (eds.). *Limnology in Australia.* CSIRO/Junk Publications, Melbourne.

Boulton, A.J., Sheldon, F., Thoms, M.C. and Stanley, E.H. (in press). Problems and constraints in managing rivers with contrasting flow regimes. *In:* P.J. Boon, B.R. Davies, and G.E. Petts. *Global Perspectives on River Conservation: Science, Policy and Practice.*

Bray, J.R. and Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconisin. *Ecological Monographs* **27:** 325-349.

Cambray, Dr J. Personal communication. Albany Museum, Grahamstown, South Africa.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199:** 1302 - 1310.

Eekhout, S., Brown, C.A. and King, J.M. 1996. *National Biomonitoring Programme for Riverine Ecosystems: Technical considerations and protocol for the selection of reference and monitoring sites.* NBP Report Series No.3. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Chutter, F.M. 1995. *Research on the rapid biological assessment of water quality impacts in streams and rivers.* Report to the Water Research Commission. WRC reference no. K5/422/0/1.

Chutter, F.M. 1994. The rapid biological assessment of stream and river water quality by means of the macroinvertebrate community in South Africa. *In:* M.C. Uys (ed). *Classification of rivers and environmental health indicators.* Proceedings of a joint South African/Australian workshop, Cape Town. Water Research Commission Report No. TT 63/94.

Clarke, K.R and Warwick, R.M. 1994. *Change in Marine Communities: An approach to Statistical analysis and interpretation.* Natural Environment Research Council, U.K. 144pp.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199:** 1302-1310.

Dallas, H.F. and Day, J.A. 1993. *The effect of water quality variables on riverine ecosystems: A review.* Water Research Commission Report No. TT 61/93.

Davies, B.R., O'Keeffe, J.H and Snaddon, C.D. 1995. River and stream ecosystems in southern Africa: predictably unpredictable. *in:* C.E.Cushing, K.W. Cummins and G.W. Minshall (eds). *Ecosystems of the World 22: River and Stream Ecosystems.* Elsevier publishers.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* WRC Report no. TT 62/93.

Harrison, A.D. 1978. Freshwater invertebrates (except molluscs). *in:* M.J.A. Werger and A.C.van Bruggen (eds). Biogeography and ecology of southern Africa. *Monographiae Biologicae* **31:** 1139-1152.

King, J.M. and Tharme, R.E. 1993. *Assessment of the instream flow incremental methodology and initial development of alternative instream flow methodologies for South Africa.* Water Research Commission Report No. 295/1/94.

Lubke, R.A. and van Wijk, Y. 1988. Terrestrial plants and coastal vegetation. *In:* Lubke, R.A., Gess, F.W. and Bruton, M.N. (eds.). *A field guide to the Eastern Cape Coast.* The Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown, South Africa.

MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton.

McCafferty, W.P. 1981. *Aquatic entomology. The fishermen's and ecologists illustrated guide to insects and their relatives.* Jones and Bartlett Publishers inc., Boston.

Metrovich, F.C. 1968. Fronteir flames. Books of Africa.

Minshall, G.W. and Petersen, R.C. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv für Hydrobiologie* **104:** 49-76.

Pianka, E.R. 1970. On *r*- and *K*- selection. *American Naturalist.* 592-597

Pennak, R.W. 1953. *Fresh-water invertebrates of the United States.* The Ronald Press Company, New York.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. 1997. Ecosystem expansion and contraction in streams. *BioScience* 47 (7): 427-435.

Townsend, C.R., Hildrew, A.G. and Schofield, K. 1987. Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* **56**: 597-613.

Uys, M.C., Goetsch, P-A, and O'Keeffe, J.H. 1996. *National Biomonitoring Programme for Riverine Ecosystems: Ecological indicators, a review and* *recommendations.* NBP Report Series No. 4. Institute for Water Quality Studies, Department of Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa,.

Williams, D.D. 1987. *The ecology of temporary waters.* Croom Helm (London and Sydney) and Timber Press (Portland, Oregon).

Williams, D.D. 1996. Environmental constraints in temporary fresh waters, and their consequences for the insect fauna. *Journal of the North American Benthological Society* **15**(4): 634-650.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue de gesamten Hydrobiologie* **62:** 53-61.

Schneider, D.W. and Frost, T.M. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* **15:**(1) 64-86.

Stanford, J.A. and Ward, J.V. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. *in:* J.R.Barnes and G.W. Minshall (eds). *Stream Ecology: Application and testing of general ecological theory*. pp265-278. Plenum Press, New York.

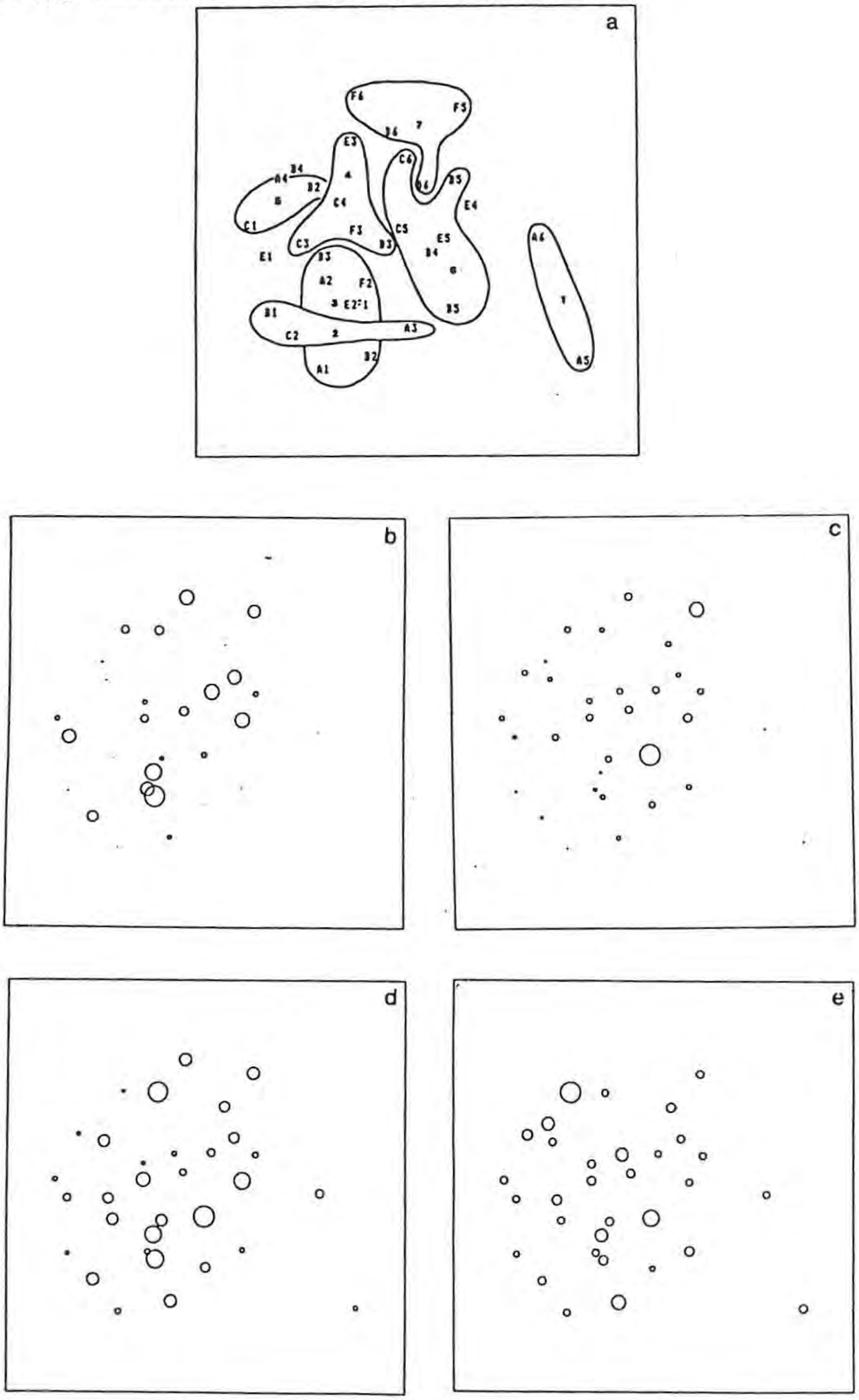
Stehr, W.C. and Branson, J.W. 1938. An ecological study of an intermittent stream. *Ecology* **19:** 294-310.

Stone, A.W. 1988. Climate and weather. in: R.A. Lubke, F.W.Gess and M.N.Bruton 1988. *A field guide to the Eastern Cape Coast.* The Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown, South Africa.

Wilmot, B. Unpublished. Odonata - A Key to the Southern African Species. Albany Museum, Grahamstown.

APPENDIX 6.1

a) Summary of MDS ordination based on similarities of total families collected at all six temporary river sites and during each sample month. Stress = 0.26 indicates that while this is a useful, but not entirely reliable representation of samples in two-dimensional space (Clarke and Warwick 1994). b) - e) Scaled symbols representing values of individual abiotic variables superimposed on the corresponding biotic ordination to check for common trends. b) Conductivity, c) % Oxygen saturation, d) Water temperature, e) pH.



APPENDIX 6.2 Families (and higher taxa) collected at each of the 6 temporary river sites over the six samping periods. Abundances are recorded as 1 (1-10), 2 (11-100) and 3(101-1000). Sampling dates indicated as 1 - May 1994, 2 - September 1994, 3 - January 1995, 4 - May 1995, 5 - September 1995, 6 - January 1996.

Site:	U.KOWIE UK1						U.KOWIE UK2						L.KOWIE LK						U.BUSHMANS					L.BUSHMANS					FISH R. TRIB				
Sampling event:	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	2	3	4	5	6	1	2	3	4	5	1	2	3	5	6
NEMATODA			1			1			1		1																1						
OLIGOCHAETA			1					1	1	1		1	1		1	1	1	2			2	2		1		1	1	1			1		
DECAPODA			1	1		1			1	1		1	1		1	1	2	1			1						1				1		
CLADOCERA								1				1	3									1		1			1						
COPEPODA		1					1	1	1		1										1	1											
OSTRACODA		1	1			1		1	1		1	1	1	2					1					3									
HYDRACARINA		1				1	2	1	1			1	1	1										2	2	2	2	2	1		1		
PLECOPTERA																																	
NEMOURIDAE													1																				
COLLEMBOLA						1																											
EPHEMEROPTERA																																	
BAETIDAE	1	1		2			2	1	1	2	2	1	2	2	2	3	2	2	1	1	1	1	2	2		3	2	2		1	3	1	2
HEPTAGENIIDAE													1			1																	
LEPTOPHLEBIIDAE				1									1	1	1	1	1	1															
TRICORYTHIDAE													1																				
CAENIDAE				1			1	1				1	1	1	2	3	1	1			1	1		2	1	2	2	2	1	1	1	2	1
ODONATA																																	
CHLOROLESTIDAE								1			1	1	1					1			1		1				1						
LESTIDAE								1	1																			1					1
PROTONEURIDAE																					1					2							
COENAGRIONIDAE		1					2	1		1	2		2	1	1	1	1	1	1	1	2	2		3	2	3	2	2		1	1	1	1
GOMPHIDAE								1				1							1	1										1			2
AESHNIDAE	1			1			1			1			2			1	1	1	1		1		1	2	1	1	1	1				1	1
CORDULIIDAE								2									1	1									1	1					2
LIBELLULIDAE	1	2	1	2			1	1	1	1		1	1	1				1		2				2			1	1	2	1	1	1	2

Site:	U.KOWIE UK1						U.KOWIE UK2						L.KOWIE LK						U.BUSHMANS					L.BUSHMANS					FISH R. TRIB				
Sampling event:	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	2	3	4	5	6	1	2	3	4	5	1	2	3	5	6
HELODIDAE																	1																
LARVA																						1											
HYDRAENIDAE				1		1																1											
HYDROPHILIDAE		1	1	1		1	1	1			1							2			1	1	1			1			1	1	2	1	1
LARVA									1			1																					
DIPTERA																																	
TIPULIDAE		1							1				1			1	2	1			1					1			1		1		1
CULICIDAE			1		2			1	1		2	1						1					1	1		2	1	2	2	1	2	2	2
SIMULIIDAE			1	2					1	3			2	3	3	3	2									1					1		
CHIRONOMIDAE	2	3	2	2		1	1	2	1	1	2	2	1	1	1	2	1	2	2	2	2	1	2	2	1	3	2	2	3	1	3	1	2
PUPAE			1					1	1			1															1						
CERATOPOGONIDAE		2		1		1		1	1		1	1	1		1		2	2		2	3		1	1	1	1	1	1		2	1	1	1
TABANIDAE				1					1	1			1		1	1															1		1
ATHERICIDAE				1																													
GASTROPODA																																	
LYMNAEIDAE								1	1	1		1									2	2					1	2					
PLANORBIDAE			1					1	1		1		1			1						1				2	1						
PHYSIDAE								1	1										1		2		1	1	2		1			1			
ANCYLIDAE		1							1	1			1	1	2	2		2							1		1						
PELECYPODA																																	
SPHAERIIDAE								1	1			1				1																	

Site:	U.KOWIE UK1						U.KOWIE UK2						L.KOWIE LK						U.BUSHMANS					L.BUSHMANS					FISH R. TRIB				
Sampling event:	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	2	3	4	5	6	1	2	3	4	5	1	2	3	5	6
HEMIPTERA																																	
NOTONECTIDAE	1	2						1	1	1	1	1	1	1				2	1	2	3	1	1			1	1	1	1	2	2	2	2
PLEIDAE										2										2	2	3		3	2	2	3	2	1	2	1		
NAUCORIDAE		1					1				1		1		2	2		1					1	1	2	1	1	1	1	1	2	1	1
NEPIDAE										1								1															
BELOSTOMATIDAE															1																1		
CORIXIDAE	1	2	1	2			2	1	1	2	2	1		1				2	1	2	2							1		2	2	1	2
GERRIDAE		1		1			2	1		3			1	1				2		1	2	1	2	2	1	2	1	1		2			1
HYDROMETRIDAE	1												1								1			1	1	1							1
HEBRIDAE																																	
VELIIDAE	1	1		1							2		1	1									2	1		2	1						1
MESOVELIIDAE			1						1			1																					
TRICHOPTERA																																	
HYDROPSYCHIDAE				1						2			2	2		3	2										1						
ECNOMIDAE			1									1																					
PHILOPOTAMIDAE	2						1																										
HYDROPTILIDAE								1								1											1						
PISULLIDAE				1																													
LEPTOCERIDAE		1		1					1						1	1		1						1	1	1	2	3					
COLEOPTERA																																	
DYTISCIDAE	2	2	1	1	1	1	3	1	1	3	2	1	1	2		2		1		1		1			1	1	1		1	1	2	1	2
LARVA			1					1	1			1		1							1												
GYRINIDAE		2		1			1	1		1			2	1	1	1		1											1				
LARVA		2													1																		
HALIPLIDAE																					1												
LARVA												1																					

Appendix 6.3 Taxonomic list compiled for detailed taxonomic-level identifications conducted during January and May 1995 at sites on the Kowie River, Bushmans River and Fish River tributary. M- marginal vegetation, I - stones-in-currnt, O - stones-out-of-current, A - sand, P - pool. Abundances are indicated by size of letters, thus: m= 1-10, M = 11-100, M* = 101-1000. Total number of taxa collected at each site is recorded in brackets.

Site:		UK1	UK2	LK	UB	LB	FT
No. of taxa:		(54)	(59)	(47)	(23)	(54)	(29)
NEMATODA			o			A	
ANNELIDA	Oligochaeta		i	m i	A P	A	p
CLADOCERA						a	
COPEPODA			m	M			
OSTRACODA	*Physocypria cf capensis*		m				
	Pseudocandona gr geratsi	m	m				
	Other ostracoda	i	M i o				
DECAPODA	*Potamonautes sp.*	m i	m	i			
HYDRACARINA			M i				p
COLLEMBOLA		m					
EPHEMEROPTERA							
Baetidae	*Afroptilum excisum*			M I		m	
	Afroptilum parvum		i	m I			
	Afroptilum pulchrum						
	Baetis latus			m i			p
	Baetis harrisoni	m		m I		m	
	Baetis sp.		m i			m	p
	Cloeon sp.	m	m		a p	a	
	Pseudocloeon sp.	m i					
	Demoulinia complex	i		m		M A	P*
Caenidae	*Austrocaenis sp.*			m	a P	M A	P
	Caenis sp.			m I	p	M A	p
Leptophlebiidae	*Adenophlebia ?auriculata*	m		i			
	Aprionyx complex	i					
Trichorythidae	*Neurocaenis sp.*			i			
ANISOPTERA							
Aeshnidae	*Aeshna sp.*	m	m	i		M	
	Anax sp.					m	
Corduliidae	*Macromia sp.*		m			m	
	?Syncordulia sp.						
Gomphidae	*Notogomphus sp.*	m	m				
Libellulidae	*Orthetrum sp.*	m	m i				
	Trithemis sp.	i				a	
	Other Libellulids	m					
ZYGOPTERA							
Coenagrionidae	*Enallagma sp.*				a p	M a	
	Pseudagrion sp.		m	m		M* A	
Protoneuridae						M a	
Chlorolestidae	*Chlorolestes sp.*						
Lestidae	*Lestes sp.*		m				

Site:		UK1	UK2	LK	UB	LB	FT
HEMIPTERA							
Belostomatidae	*Diplonychus capensis*		m	m			p
Corixidae	*Arctocorisa meridionalis*		m				
	Micronecta citharistia	m					
	Micronecta sp.		m		a		
	Sigara sp.		i				
Gerridae	*Gerris swakopensis*	m					
Hydrometridae	*Hydrometra ambulator*	m				m	
Naucoridae	*Laccocoris limigenus*	o				m	
Mesovelidae	*Mesovelia vittigera*	m					
Notonectidae	*Anisops gracilis*						
	Anisops limpida		m				
	Anisops sardea					m	
	Anisops letitia				M		
	Anisops sp.	m	m				
	Enithares sp.	o	m i			m	
Pleidae	*Plea pullula*					M	
Veliidae	*Microvelia venustissima*	m					
	Microvelia sp.	m	m o				
TRICHOPTERA							
Ecnomidae	*Ecnomus sp.*	m				m	
Hydroptilidae	*Oxyethira sp.*					m	
	Orthotrichia barnardi			m			
Hydropsychidae	*Cheumatopsyche afra*	i	i	m i			
	Cheumatopsyche maculata			i			
Leptoceridae	*Leptocerus sp.*		m			m A	
Pisullidae	*Dyschimus ensifer*	i				m	
COLEOPTERA							
Dytiscidae	*Hydaticus sp.*	m					
	Laccophilus lineatus	m	m				
	Philaccolus lineatoguttatus	m					
	Other dytiscids	m o	m			m a	p
	Larvae		m		a p	M a	P
Elmidae	*Stenelmis sp.*		m				
Gyrinidae	*Dineutus grossus*		i	m i			
	Aulonogyrus caffer	m					
	Aulonogyrus sp.			i			
	Other Gyrinidae			m i			
Haliplidae	*Haliplus sp.*		m				
Helodidae	Larvae	m i	m				
Hydraenidae	*Ochthebius andronius*		m				
Hydrophilidae	*Hydrobius sp.*	m					
	Other hydrophilids	m					
	Larvae		m			a	
DIPTERA							
Ceratopogonidae	*near Bezzia*		i		a p	a	p
Chironomidae							
Chironominae	*Polypedilum sp.*	m	m i o	m i	a p	m a	
	Chironomus sp.				p	m	P
	Cryptochironomus sp.					a	
	Dicrotendipes pilosimanus				a p	m	
	Dicrotendipes sp.				a p	m	
	Microchironomus sp.					M	
	Microtendipes sp.						p

Site:		UK1	UK2	LK	UB	LB	FT
Chironominae	*Parachironomus sp.*						
	Zavreliella sp.		m				
	Xenochironomus sp.			m			
	Other chironomini	m o		i	p		
	Cladotanytarsus sp.	m	m	m i	m p	m a	
	Rheotanytarsus sp.	m i o	i o	M i		m a	
	Stempellinella sp.	m					
	Tanytarsus sp.	m i	m i o	m i	p	m a	p
	Other Tanytarsini	m i	m i	i	m p	m A	p
Diamesinae	*Harrisonina petricola*	m	i				p
Orthocladiinae	*Cardiocladius sp.*			m i			
	Limnophyes sp.	i					
	Nanocladius sp.			i			
	Parametriocnemus sp.		m				
	Paratrichlocladius sp.						p
	Psectrocladius sp.			m	a p	m A	P
	Pseudosmittia sp.						p
	Rheocricotopus sp.		i	m i			
	Other orthocladiinae	m i o					
Tanypodinae	*Clinotanypus sp.*				p	m a	
	Conchapelopia sp.	m					
	Paramerina sp.		m i				
	Procladius sp.	m	i	m	a p	m	
	Tanypus sp.					M	
	Larsia sp.	m			a p	a	p
	Other Tanypodinae	m i o	m i	m			p
Chironomid	Pupae	m	i	m		m a	
Psychodidae							p
Culicidae	*Anopheles sp.*		m	m		M a	P
Simuliidae	*Simulium alcocki*		i				
	Simulium damnosum			m l			
	Simulium nigritarse	l	i	i			
	Simulium ruficorne		m	m			
	Simulium adersi	i		M l		m	p
	*Simulium hargr/medusae**			m i			p
	Simulium letabum			m i			
	Simulium vorax	l		m			
Tabanidae			i	m i			p
Thaumalidae		m					p
Tipulidae		i	m i			m a	p
GASTROPODA							
Ancylidae	*Burnupia sp.*			m i		m	P
Ancylidae	*Ferissia sp.*		m	m i			
Lymnaeidae	*Lymnaea columella*		m	m			
Physidae	*Bulinus forskalii*		m			m	
Physidae	*Bulinus sp.*				a p	m a	
Planorbidae	*Ceratophallus sp.*		M i			m	

* Simulium hargreavsi/medusaeforme

CHAPTER 7

INVERTEBRATES IN NATURAL AND MODIFIED TEMPORARY AND PERENNIAL RIVERS IN DIFFERENT REGIONS OF SOUTH AFRICA

This chapter is based on a paper entitled 'Invertebrate responses to natural and modified perennial and temporary flow regimes' by J.H. O'Keeffe and M.C Uys. The paper was presented by Professor J. O'Keeffe at an INTERCOL Conference in Perth, Australia, in September 1996. It is presently in press in the proceedings of the conference.

Certain modifications have been made to the original paper. More work was done on the Kowie River between writing the paper and writing this chapter, and this has altered the original database to some extent. Discussions between the two authors and colleagues resulted in a decision to include data on the Buffalo River in the Eastern Cape, which was intensively studied in the early 1990s. The species list appearing in the original paper has been modified in favour of greater conservatism in approach to this study.

ABSTRACT

As scarce water resources are developed for human use in South Africa, many of the flow regimes in naturally perennial rivers are being modified to temporary or intermittent flows. In other rivers, temporary flows are being converted to permanent by inter-basin transfers of water, and in some others, irrigation demands have resulted in unseasonal water releases downstream of dams and IBTs. This paper presents a coarse-level comparison of existing invertebrate databases for South African rivers in the following categories: naturally perennial (the Sabie and Mutale Rivers), naturally temporary (the upper Kowie River), modified perennial to temporary (Luvuvhu and Letaba rivers), and modified temporary to perennial (the Great Fish River). At coarse levels of taxonomic resolution and presence/absence information, taxonomic diversity was related to the geographical position of the rivers, but did not appear to be related to the perenniality of the flow regime. Temporary rivers were found to be as taxonomically rich as those with permanent flow, if not somewhat more so. It is suggested that the natural variability of the flow regime may be more important than flow constancy in maintaining a natural community balance in semi-arid zone rivers.

7.1 INTRODUCTION

South Africa is largely a semi-arid country, with an average rainfall of about 500mm and a conversion to runoff of 8.6% (Braune 1985). Both rainfall and runoff are highly variable in time and space, with a wetter east coast and arid north-western areas (Davies *et al.* 1993). It has been estimated that more than 11 million people (one quarter of South Africa's present population) still have no direct access to potable water (Yeld 1997), and over 20 million lack basic sanitation (Department of Water Affairs 1997). In order to provide for domestic supply, agriculture, industry, and mining, and the development in each of these spheres, the rivers in South Africa have been, and continue to be, exploited by means of direct water abstraction and impoundment. To provide water to areas of high population and economic activity, but with scarce water resources, such as Gauteng (Transvaal region), inter-basin transfers are increasingly being implemented. As a result of these developments, coupled with catchment land-use changes such as commercial forestry and the removal of natural vegetation, the flow regimes of South Africa's rivers are becoming progressively modified.

Under natural conditions, it has been estimated that over 40% of the length of South Africa's rivers have a temporary flow regime (Davies *et al.* 1993). At present, a number of rivers (such as the Luvuvhu and Letaba in the north-east of the country, Mpumalanga region) which used to flow constantly, now flow for months at a time during most years. Others, such as the Great Fish River in the Eastern Cape, were naturally temporary rivers, but now flow continuously as a result of augmented base-flows from inter-basin transfers (IBTs). These hydrological changes are bound to have ecological consequences, caused by the changes in hydraulic habitat conditions, in water quality, in erosional and depositional process, and in natural disturbance regimes. For instance, the importation of water into the Great Fish River from the Orange River resulted in striking changes in the dominant species of Ephemeroptera, Chironomidae, Simuliidae and Trichoptera. Prior to the opening of the Orange/Fish tunnel, predominantly *Simulium adersi* and *S. nigritarse* had been collected in the Fish River. Following the IBT, the invertebrates of the regulated sections were dominated by the blackfly *Simulium chutteri,* which had previously been found in low numbers in the river. This cattle-biting simulid reached pest-proportions during summer, causing severe problems to farmers in the area (O'Keeffe and de Moor 1988). This high-profile economic problem has received much attention, but there remain important general questions about the effects of these flow modifications which have not yet been addressed. These include fundamental questions such as: Which invertebrates inhabit temporary rivers in South Africa, and how do they differ from those of permanent rivers? What are the consequences to the biota of changing a permanent flow to an intermittent one, or of changing a temporary flow to a permanent one?

Very little work has so far been attempted on temporary rivers in South Africa - possibly because of their unpredictable nature, and because development and research funding is directed towards water supply and water quality, and thus to the higher-yielding perennial rivers (see Williams 1988 for a discussion on the paucity of research on temporary waters). With increasing water demands and development directives, temporary rivers and their catchments will come under greater pressure. In addition, many perennial rivers will be subject to intermittent flow in sections (e.g. below impoundments).

The South African Department of Water Affairs and Forestry (DWAF) has instituted a policy of integrated environmental management which requires that impact assessments be carried out for all water developments. The new Water Act, currently in the final stages of preparation, will require the assessment of environmental water requirements for rivers under development (Department of Water Affairs 1997). Consequently, there is an urgent need for research on temporary rivers. This has been initiated in the north-east of the country, where considerable research has focussed on the rivers which flow through the Kruger National Park (Mpumalanga region); in the Western Cape region, where experimental reductions in flow are being analysed (Tharme in prep.), and in the Eastern Cape, where the invertebrates of a few temporary streams have been studied, as reported here (Chs 3 to 5).

In this chapter, some of the existing data on invertebrate communities are synthesized and presented in a preliminary examination of the 'biotic distance' between naturally perennial and naturally temporary rivers, and between these and rivers which have been modified from temporary to perennial and vice versa. Two null hypotheses are tested: H_0: that there are no differences between the invertebrate biota temporary and perennial rivers, and H_0: that there are no differences between the invertebrate biota reported from rivers in the two regions in the study.

Based on the proposed terminology presented in Chapter 2, data from four river 'types' have been used. *Naturally perennial* rivers are represented by the Sabie and Mutale Rivers (Mpumalanga region) and by the Buffalo River below its headwater reaches (Eastern Cape). *Naturally temporary* rivers are represented by the upper reaches of the Kowie River, and the headwater reaches of the Buffalo River (Eastern Cape). *Naturally perennial, modified to temporary* rivers are the Luvuvhu and Letaba Rivers (Mpumalanga), and *naturally temporary, modified to perennial* rivers are represented by the Great Fish River (Eastern Cape). The relative positions of each of the rivers is shown in Figure 7.1.

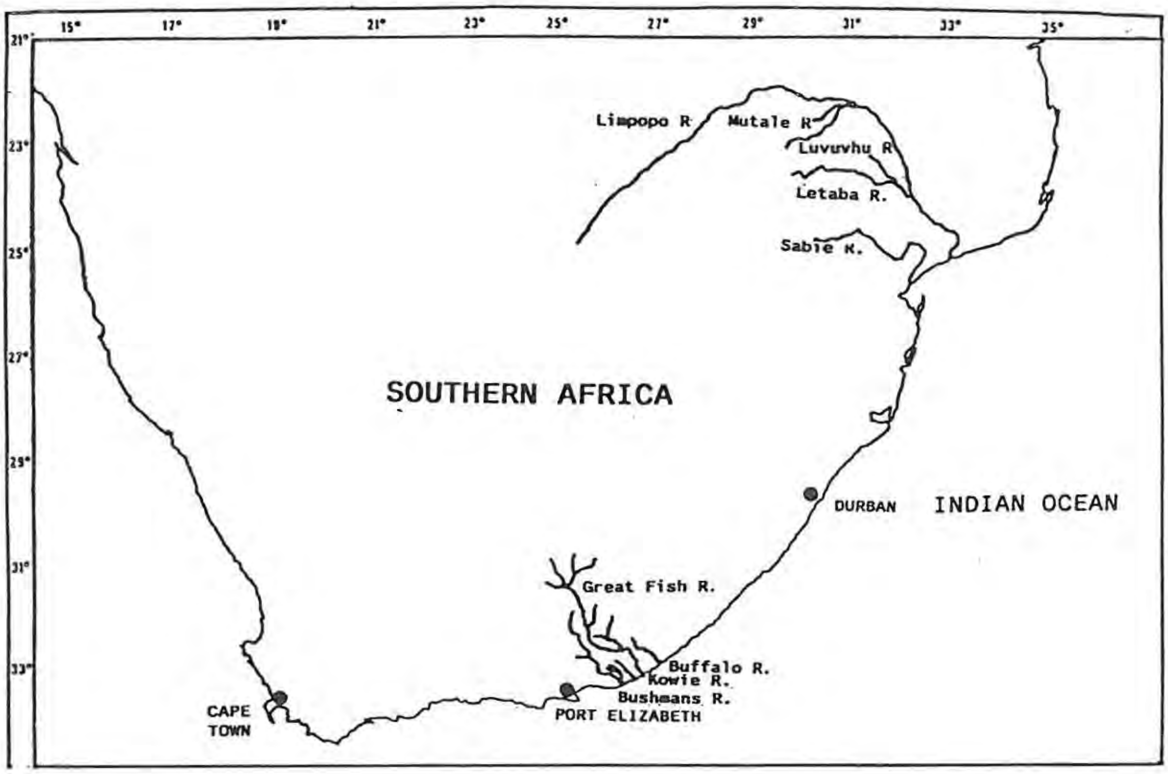


Figure 7.1 Map of South Africa showing the positions of each of the rivers included in this study

The problems in making comparisons between different river systems are severalfold:

- While rivers in the same region may be subject to similar climatic and geological influences, across regions the natural biogeographic variability may be great - as attested to by the 18 different river bioregions recently identified for South Africa on the basis of historical biological distributions (Eekhout *et al.* 1996). Variability between, for example, perennial and intermittent rivers within a region may also be high.

- The individual data-bases used in this comparative analysis have been produced over time and during different years (when broad climatic influences may have varied extensively). The invertebrates have been collected by several researchers, often using different methods and investigating separate problems. In certain of the studies only a few of the available habitats were sampled, while in others all available habitats were sampled.

- Invertebrates have been identified to different taxonomic levels in the various studies. The systematics of South African aquatic invertebrates is still poorly known, and many of the groups are in the process of - or urgent need of - taxonomic revision. The autecology of taxa has, as a result, not been developed to any major extent.

These difficulties have been compensated for as far as possible in this analysis, and conclusions are conservative. It is felt that if the limitations of this comparative analysis are understood, it provides a useful and instructive perspective on temporary river fauna in parts of South Africa.

7.2 INFORMATION SOURCES

The information used in this paper is drawn from a number of different studies (Table 7.1). Moore and Chutter (1988) sampled all the main rivers of the Kruger National Park. Their data are used in this paper for the **Sabie, Letaba, Mutale** and **Luvuvhu Rivers**. Their report described the results of seven sampling trips during 1985/6 to two sites in the Sabie River, two in the Letaba, five in the Luvuvhu and two in the Mutale tributary of the Luvuvhu. All biotopes were sampled. Chutter and Heath (1993) did a further study on the Letaba River to investigate the effect of the gradient of flow permanency from west to east in the river. Their focus was on the benthic macroinvertebrates which were obligate rheophiles (i.e. in areas of hard substrata in strong current were sampled). These data supplemented the Letaba River database. For the Sabie River data, information from a more recent source (Weeks *et al.* 1996) was also added.

The **Great Fish River** has been studied over a long period. Data contributing to this study were drawn from two sources. O'Keeffe and de Moor (1988) conducted a resurvey of six sites on four occasions during 1984/5, following the opening of the Orange/Fish tunnel, and compared their biotic data (collected in riffles only) to those collected at the same sites prior to the IBT. These data were supplemented by Grahamstown's Albany Museum database on the Great Fish River, which comprises a record of samples taken between 1964 and 1994 in few biotopes (principally marginal vegetation and riffles) by a number of scientists. For the purposes of this chapter, data from these two sources were divided into two categories - 'Great Fish Temporary' (**GFt**; invertebrates collected prior to the IBT), and 'Great Fish permanent' (**GFp**; invertebrates collected subsequent to the IBT).

Information on the **Buffalo River** was derived from research conducted on the river by C.Palmer (1991) between 1987 and 1988. Several papers have been published on the basis of this research (Palmer and O'Keeffe 1992, Palmer *et al.* 1991, 1994). Only data referring to the least-modified sites (Sites 0, 1, 5) are considered here. The headwater site (Site 0), 1km from the source, and with a gradient of 200m.km^{-1} was temporary in nature and had 'unique species composition' (Palmer *et al.* 1994). This site has been labelled 'Buffalo Temporary' (**Bt**), and the remainder of sites along the river, which experience virtually continuous flow, are referred to as 'Buffalo Permanent' (**Bp**).

The upper **Kowie River** was studied between 1993 and 1996, as reported in this thesis (Chs 3 to 5). Data from the upper section of the river (sites UK1 and UK2) were used in this study. This river is labelled 'Kowie Temporary' (**Kt**).

7.3 HYDROLOGICAL REGIMES OF THE SEVEN RIVERS

In order to assess faunal diversity in relation to the perenniality or intermittency of flow, this section summarises what is known of the flow regimes for each of the rivers. The known or estimated extent of periods of no-flow under natural and present-day conditions are listed in Table 7.2. As mentioned, flow regimes (in brackets) are distinguished according to the terminology proposed in Chapter 2.

RIVER	REGION	YEARS	BIOTOP SAMPLED	REFERENCES
Buffalo (perenn. & temp)	E. CAPE	'86-'88	riffle	Palmer 1991, Palmer & O'Keeffe 1992, Palmer et al. 1991, 1994.
Great Fish (temp.)	E. CAPE	pre-'84	all	Various scientists Albany Museum database, Grahamstown
Great Fish (perennial)	E. CAPE	post-'84	all	O'Keeffe & de Moor 1988
Upper Kowie (temporary)	E. CAPE	'93-'96	all	Uys, this thesis
Letaba (perenn. & temp.)	Mpumalanga	'90-'91	rapids	Moore & Chutter 1988, Chutter & Heath 1993
Luvuvhu (temporary)	Mpumalanga	'80, '85,86 '91-'92	all	Moore & Chutter 1988
Mutale (perennial)	Mpumalanga	'85-'86	all	Moore & Chutter 1988
Sable (perennial)	Mpumalanga	'85-'86 '90-'93	all	Moore & Chutter 1988 Weeks et al. 1996

Table 7.1 Information sources for the data used in the analysis of fauna from different temporary and perennial rivers in South Africa.

The Sabie River

(Perennial seasonal)

The Sabie River is perennial and has never ceased flowing during the period of record. During recent years, and particularly during the drought of 1991/2, flows in the middle reaches were reduced to below $0.5m^3.s^{-1}$, but generally, flows are above $1m^3.s^{-1}$ even during the dry season.

The Letaba River

(Naturally perennial seasonal, modified to intermittent seasonal)

The Letaba was a perennial river under natural conditions. The majority of the river lies outside of the Kruger National Park in Mpumalanga (formerly Eastern Transvaal), however the lower section runs through both Letaba Ranch and the Park itself. Perennial flow in the lower 100km has not been experienced since the 1960s, due to major exploitation of its water resources, including impoundments and abstraction (Chutter and Heath 1993). In 1977, the Fanie Botha Dam was built in the upper part of the river, resulting in regulation of flow in the river. This resulted in enhanced dry-season flow immediately downstream of the dam, but major abstraction of water for irrigation purposes caused considerable flow reductions in the lower river in spring and early summer (rainy season). Following the major drought of the early 1980s (when flow cessation in the lower section was lasting for up to five months at a time) it was decided in 1988 that a minimum flow of $0.5m^3.s^{-1}$ should be ensured in the section of the river adjacent to the Kruger National Park. During the wet months, the present flow is approximately half the natural volume (December to March), and during the wet months, less than one-tenth (June to September). The Letaba is considered to be the most degraded of the rivers flowing through the Kruger National Park.

The Luvuvhu River

(Naturally perennial seasonal, modified to intermittent seasonal)

The Luvuvhu River was perennial under natural conditions. It was first observed to stop flowing in 1969, and has become progressively drier over time. During the 1991/2 drought, there was no flow in the middle and lower reaches to the Limpopo confluence for 14 months, and no surface water in the lower reaches.

The Mutale River

(Perennial seasonal, tending towards intermittent)

The Mutale is a major tributary of the Luvuvhu River, rising to the north of the main river and joining it at the western boundary of the Kruger National Park. Flow records from the upper catchment (1932-1989, DWAF data) indicated perenniality in flow, with no zero flows recorded. However, gauging weirs recently installed in the lower reaches of the river indicate that flow cessation has occurred in the late 1980s and early 1990s in this section of the river.

The Great Fish River

(Naturally intermittent aseasonal, modified to perennial aseasonal)

In 1977 an inter-basin transfer (IBT) from the Orange River to the Great Fish River was initiated, and the base-flow in the Fish River has since been maintained at 3 to $5m^3.s^{-1}$ to provide irrigation water to farmers in the middle catchment. Prior to the IBT, flow in the middle reaches stopped for at least one complete month a year during 50% of the years on record.

The upper Kowie River

(Intermittent aseasonal)

The upper and middle reaches of the Kowie River are not gauged, and therefore the historical flow regime of the upper part of the river is not precisely known. During the study of the upper Kowie River, however, monthly discharge measurements were taken and a record was kept of the hydrology of the river over time. The flow was intermittent and unpredictable. Prolonged spells of no flow resulted in discontinuities of surface water (pools in the channel), and if of sufficient duration, complete drying. The hydrology of this section of the river has been explained in more detail in Chapters 3 to 5.

The Buffalo River

Upper site (Intermittent seasonal)

Lower sites (Perennial)

Flow at the headwater site of the Buffalo River (Site 0, 1120m above sea level, 1km from source) was aseasonal, however flow at the foothill site (Site 1, 530m a.s.l, 7km from source) and the two sites downstream of that (Sites 5 and 6, 450m a.s.l, 18km from source) were perennial (Palmer *et al.* 1994).

Table 7.2 Assessments of the degree of perennial or temporary flow in the rivers discussed in the text, under natural and present conditions. Percentage no-flows are derived from actual gauged flow records of different durations for all rivers except for the present day conditions for the Luvuvhu and Letaba Rivers (marked '?'), which are estimates from monthly simulated flows. [*Sources: Smakhtin (in prep.), Department of Water Affairs and Forestry*].

	% Time of no-flows	
RIVER	NATURAL	PRESENT
Sabie	0	0
Mutale	0	?
Luvuvhu	0	?20
Letaba	0	?30
Kowie	40+	40
Great Fish	50	0
Buffalo	0	0

7.4 A DATABASE FOR INVERTEBRATES COLLECTED IN THE SEVEN RIVERS

There was considerable variance in the levels to which different taxa were identified in each of the studies (Table 7.3). The first database incorporated the full list of taxa recorded in each of the rivers, and only presence or absence from a river was recorded. The task of summarising this database in such a way as to allow for comparative analyses was done as follows:

1) For each taxon, the most detailed level of identification common to all the studies was sought. For example, in the Kowie and Great Fish River studies, attempts were made to distinguish between the different species of chironomid larvae, even if only by designating 'Types' (A,B,C etc). In the Kruger Park and Buffalo River studies, however, chironomids were generally identified to the level of sub-family (e.g. Chironominae) or tribe (e.g. Chironomini). For comparative purposes, all chironomid data had to be summarised to the level of sub-family or tribe.

2) Where identification of a particular taxonomic group was detailed in all the rivers, as in the family Baetidae where genera or species were commonly recorded, it was assumed that genera or species not listed were absent. If a particular species of baetid (for example) occurred in three or more separate rivers, it was included in the database. Thus a double 'filtering' system was used.

Diversity is recorded as 'number of taxa' - and should not be interpreted as true 'biodiversity' which includes a measure of abundance (Clarke and Warwick 1994). Numbers of taxa, while based on common taxonomic levels between the 7 rivers, cannot be compared with any other studies, as individual groups are listed at a variety of taxonomic levels (Table 7.3)

The considerably reduced database which was used in analyses is presented in Appendix 7.1.

Table 7.3 Taxonomic levels to which the major groups were identified in each of the individual studies. O - Order only; C - Class; F - family; Sf - Subfamily, T - Tribe, G - Genus, S - Species. Where more than one letter is indicated, mixed taxonomic levels were listed. * indicates that the group did not appear in taxonomic lists.

	BUFF.	FISH	KOWIE	LETABA	LUVUVHU	MUTALE	SABIE
Coelenterata	G	G	G	G	G	G	G
Turbellaria	O	C	*	*	*	*	O
Platyhelminthes	O	G	*	F	G	G	C
Nemertea	*	*	*	*	G	*	O
Nematoda	O	O	O	F	O	O	O
Annelida	C	C	C	C/G/S	S	S	C/F
Cladocera	*	G	O	O	G/S	G/S	O
Copepoda	*	G	G/S/t	O	C	C	O
Ostracoda	*	G	G/S/t	O	G	G	O
Decapoda	G	S	S	G/S	G	G	S
Hydracarina	O	t	t	O	t	t	O
Collembola	O	F	O	*	O	O	F
Plecoptera	F	*	*	*	S	S	O
Ephemeroptera	S/t	S	G/S	S	G/S	G/S	S
Odonata	O	G	G/S	O/F/G	F/G	F/G	F
Hemiptera	O	G/S	F/G/S	F	F/G	F/G	F
Megaloptera	O	*	*	*	*	*	*
Neuroptera	*	F	*	F	F	F	*
Trichoptera	S	S	G/S	G/S	G/S	G/S	S
Coleoptera	F/G	G	F/G/S	F/G	F/G	F/G	F
Diptera	F	F/G	F/G/S	F/G	F/G	F/G	F
Chironomidae	SF/T	G/S/t	Sf/T/G/S/t	Sf/T/G	Sf/T/G	Sf/T/G	T
Simuliidae	S	S	S	S	F	F	F
Gastropoda	F	G/S	G/S	G	F/G/S	F/G/S	S
Pelecypoda	*	G/S	G/S	G	O	O	S

7.5 STATISTICAL ANALYSES

Computation of similarity

Faunal similarities between river sites (at the taxonomic levels of analysis) were calculated using the non-correlation-based Bray-Curtis coefficient of similarity described in Section 1.4.2, on presence/absence data only.

Cluster analysis

Hierarchical agglomerative cluster analysis was performed on the basis of Bray-Curtis similarity matrices, as described in Section 1.4.3.

Ordination

The MDS ordination procedure was performed on similarity matrices, as described in Section 1.4.4.

Analysis of similarity for examination of the null hypothesis

This study possessed *a priori* defined structure between different river sites, different flow types (temporary and perennial sites) and different regions (Eastern Cape and Mpumalanga). Analysis of similarity was used to test for significance of difference between different flow types and different regions, using the ANOSIM procedure explained in Section 1.4.6.

Significance of difference could not be tested between river sites, as each was represented by only one set of data ('replicate') and two or more replicates are required for the computation of the test statistic (which is based on the relationship between variability within a site over time and variability between sites).

The two ANOSIMs computed for the testing of the null hypotheses were:

ANOSIM 1 Where *a priori* groups were the two regions, and rivers in each region provided the 'samples' for the two groups

ANOSIM 2 Where *a priori* groups were temporary and perennial rivers, and the two groups were represented by the respective rivers or sections thereof.

7.6 RESULTS

7.6.1 Numbers of taxa

Analysis of the highly-summarised taxonomic information indicated clear regional differences in numbers of taxa, with greatest numbers recorded in the Mpumalanga rivers. Of the 140 taxa in the database, 75 were recorded in the Luvuvhu River, 71 in the Sabie, 69 in the Mutale, 63 in the Letaba in its perennial sections and 48 in the Letaba in its temporary sections. Smaller proportions of the total number were recorded for the Eastern Cape rivers, with 47 in the upper Kowie River, 45 in the Great Fish River in its perennial state, 39 in the Buffalo in its perennial sections, 35 in the Great Fish River in its temporary state, and 34 in the temporary headwater section of the Buffalo (Appendix 7.1).

7.6.2 Faunal similarities between different rivers

Cluster analysis

Hierarchical agglomerative clustering based on Bray Curtis similarities between sites indicated a clear splitting of Mpumalanga rivers from Eastern Cape rivers (Fig. 7.2). Within the Mpumalanga group, the Luvuvhu, Mutale and Sabie Rivers showed the greatest faunal resemblance, and clustered at progressively lower similarity levels with the Letaba permanent and temporary sites. In the Eastern Cape group, fauna from the Buffalo temporary and perennial sites clustered as most similar. The Great Fish River (perennial state) clustered with the upper Kowie River, and at a lower similarity with the Great Fish River (temporary). Lines were drawn through the arbitrary similarity points of 50 and 70% to check for congruence between the results of clustering and ordination.

Ordination

MDS ordination based on Bray-Curtis similarities produced a low-stress (0.03) 2-dimensional representation of the data which clearly supported the groupings indicated by the dendrogram (Fig. 7.3).

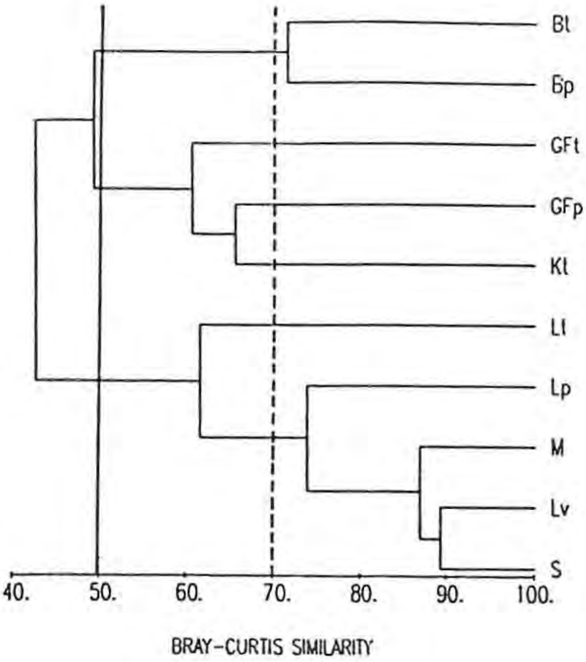


Figure 7.2 Dendrogram showing hierarchical cluster analysis of Bray Curtis similarities, based on presence/absence data from all sites. Abbreviations: Bt and Bp - Buffalo River (temporary and perennial sections), Gft and Gfp - Great Fish River (temporary and perennial conditions), Kt - Upper Kowie River (temporary), Lp and Lt - Letaba River (perennial and temporary sections), LV - Luvuvhu River (temporary), M - Mutale River (perennial), S - Sabie River (perennial).

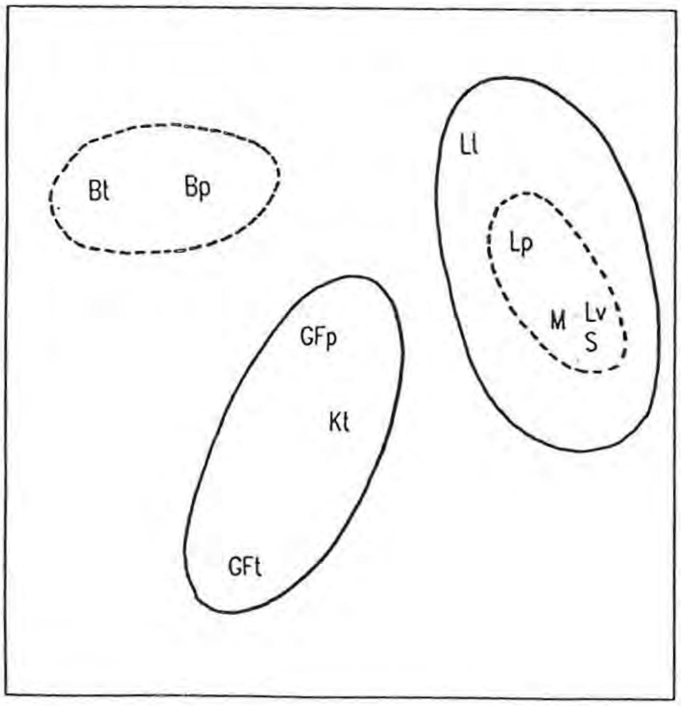


Figure 7.3 MDS ordination of the 10 sites, based on presence/absence data at coarse taxonomic levels, and Bray Curtis similarities. Stress = 0.03. The groupings from the cluster analysis are indicated (Solid line - 50% similarity, broken line - 70% similarity). Abbreviations as for Fig. 7.2

Analysis of similarity for examination of null hypothesis

ANOSIM 1: Global analysis of similarity yielded an *R* value of 0.718 at a significance level of 0.0%, at which the null hypothesis of 'no difference between rivers of different regions' could be rejected. This indicated that, at the taxonomic levels under consideration, the rivers of the two regions were significantly different in terms of their fauna.

ANOSIM 2: Global analysis of similarity yielded an *R* value of - 0.128 at a significance level of 78.6%, at which the null hypothesis of 'no difference between faunas of temporary and perennial rivers' could not be rejected. It could not therefore be said that (at the taxonomic levels of the investigation) the faunas of temporary and perennial rivers differed significantly.

7.6.3 Fauna occurring in the different river types

Representatives of all the families occurring in perennial conditions were collected at the temporary sites. Not one of the 94 taxa listed was absent from the full range of temporary rivers. Animals common to all 10 sites were *Baetis* sp. and *Afroptilum* sp. baetids, *Cheumatopsyche afra* hydropsychids, and Tanytarsini and Orthocladiinae chironomids. Taxa recorded under temporary but not perennial conditions included stratiomyid beetles, thaumalid dipterans, and *Physa* sp. and *Physopsis* sp. physids. None of the taxa included in the comparison were confined to perennial river sites *per se*. Individual orders or families were, however, best-represented in terms of genera in Mpumalanga rivers (Appendix 7.1), and there was a great deal more consistency in fauna between rivers of this region than there was betweem semi-arid Eastern Cape rivers.

Genera or species recorded only in the Mpumalanga rivers included oligoneurid mayflies, *Adenophlebiodes* sp. leptophlebiids, *Dicermyzon* sp. trichorythids, *Ellatoneura* sp. protoneurids, platycnemidids, *Zygonyx* sp. and *Olpogastra* sp. libellulids, *Methles* sp. dytiscids, staphylinid and chrysomelid beetles, *Aethaloptera* sp. and *Amphipsyche* sp. hydropsychids, *Oecetis* sp. and *Trichosetodes* sp. leptocerids, *Catoxyethira* sp. hydroptilids, *Eupera* sp. pelecypods, *Biomphalaria* sp. planorbids, and *Melanoides* lymnaeids (their absence from the Eastern Cape river collections does not necessarily infer their absence from these or other rivers in the region).

Notonemourid stoneflies were collected only in the Buffalo River, and *Adenophlebia* sp. leptophlebiids, *Neurocaenis* sp. trichorythids, *Caenis* sp. caenids, *Macrostemum* sp. hydropsychids, *Aulonogyrus* and *Gyrinus* sp., athericids and thaumalid dipterans were absent from the Mpumalanga river, but were recorded in Eastern Cape rivers.

7.7 DISCUSSION

7.7.1 Numbers of taxa

Factors influencing faunal character were detected at several scales in this study. At the largest spatial scale, geographical position of rivers was indicated as a major influence on faunal diversity, with all rivers in the tropical Mpumalanga region having higher numbers of taxa (at these taxonomic levels) than all those of the Eastern Cape region, despite the fact that some of them were intermittent. The Great Fish River in its present perennial state, and the perennial sites on the Buffalo River in the Eastern Cape, yielded only 50% - 60% the number of taxa listed for the Mpumalanga Rivers.

This geographical influence provides further support for the recent division of the country into river bioregions and sub-regions, and classification of river types and sub-types on this basis (Eekhout *et al.* 1996). While the data presented here is not considered representative of the absolute diversities of each of the rivers, at *comparable* taxonomic levels, the tropical rivers showed somewhat greater taxonomic richness than the semi-arid zone rivers. Williams (1988) noted that it had become almost axiomatic that tropical faunas had high diversities, and questioned whether such environments actually had *higher* diversities. Total numbers of fauna reported in the Mutale, Luvuvhu, Sabie and Letaba studies were below 170 (Moore and Chutter 1988), in comparison to the over 200 taxa reported for the temporary upper Kowie study. The variability in taxonomic levels between studies was large and precludes any inferences being made on the basis of these figures, however (hence the extensive summarisation of data). The question of which rivers have highest diversities would be best served by a rigorous sampling programme in which methodologies, biotopes to be sampled, and levels of taxonomic identification were prescribed.

Within regions, results provided no evidence that the highest diversities were associated with perennial flow, nor that reduced flows or flow cessation necessarily led to lower numbers of taxa. In each of the regions, biota representing temporary flow conditions were equivalent to or greater in number than those representing perennial flow conditions. At these taxonomic levels, more taxa were recorded in the now-temporary Luvhuvhu River than in the perennial Sabie River and the perennial sections of the Letaba River. In the Eastern Cape, similarly, diversity in the temporary section of the Kowie River was greater than that in both the perennial sections of the Buffalo River and in the now-perennial Great Fish River.

That the taxonomic diversity of temporary rivers was virtually equivalent to (or exceeded) that of perennial rivers of a region, at coarse taxonomic levels, may be met with distrust. Indeed, these findings should be interpreted cautiously, even in the context of a conservative approach, as ecological and methodological factors could have influenced results. The Kowie and Luvuvhu were both sampled more intensively than most other sites, and several biotopes were sampled at each.

However, it is a misconception that temporary rivers are faunally impoverished. While on average, temporary waters may not support quite as diverse a number of families and orders as permanent waters (Williams 1996), diversity of certain groups (e.g chironomids, dytiscids) may exceed that of perennial rivers.
Boulton and Lake (1992b) reported high species richness (> 250 taxa) in the intermittent rivers they studied in Victoria, Australia, but noted that only four other studies they knew of had found comparably high numbers of taxa, while most studies had reported lower diversities.

Findings in this chapter correlate with Williams' (1987) registered that most of the major groups inhabiting permanent fresh waters were represented in intermittent lotic environments, and noted that a large majority of temporary water species were insects or mites, both of which evolved on land. He suggested that adaptation to water loss may not be as difficult as thought, and that perhaps the factors controlling both temporary and permanent river fauna were equally rigorous.

A further point of interest in this regard is the influence of the duration of flow and surface water, and the importance of recognising the distinction between intermittency and ephemerality. While rivers exposed to short periods of no-flow or drying provide both physical and hydraulic heterogeneity which may account for high numbers of taxa, those towards the 'episodic' end of the permanent-temporary continuum (Ch. 2) are exposed to long periods of drying ('press' disturbances) and sometimes dramatic disturbances such as flash floods ('pulse' disturbances). The inverse relationship shown between flow duration and diversity of fauna for some streams in Australia (Boulton and Suter 1986) seems to apply to similar environments in South Africa (e.g. Fish River tributary, see Ch. 6). There may in fact be more difference between the fauna of intermittent and ephemeral/episodic streams than between perennial and intermittent systems! Establishing where along the continuum a temporary river is situated may assist in establishing what sort of faunal composition and diversity could be anticipated.

7.7.2 The effects of flow modifications

To look at diversity only in terms of the presence/absence of a species, and lumped together over the different seasons, is to take a one-dimensional look at a complex situation. Given the differences in sampling methods between different habitats, the synthesized nature of the data from Moore and Chutter (1988), and the preliminary nature of the data from the Kowie River, it has not been possible to compare differences in abundance, or seasonal changes in communities in this chapter. However, it is possible to document major changes within particular rivers. Although the numbers of taxa remained fairly constant in the Great Fish River before and after the IBT, O'Keeffe and de Moor (1988) found that only 33%

of the taxa were common to both phases, and there had been a considerable change from typical standing water species to those preferring running water: they concluded that 60% of the pre-transfer species were true inhabitants of stones-in-current, compared to 80% of post-transfer species. The post-transfer community, while consisting of 47 different taxa, was dominated to an extreme degree by the pest blackfly *Simulium chutteri,* which often constituted more than 99% of the community by numbers. In this case, the imposition of a stable base-flow had created ideal conditions for a single species, and the loss of the natural disturbance regime had led to the exclusion of many of the species occurring naturally from the river.

A more recent study of the Sabie-Sand River system by Weeks *et al.* (1996) also provided valuable insights into the effects of reduced flows during severe drought. The study fortuitously spanned a three-year period, comprising a year of good flows (1990), followed by the worst drought on record (1991/2), and a few months of recovery following heavy rains in November 1992. They concluded that invertebrate communities living in riffles in the Sabie Sand are extremely sensitive to flow conditions. A similarity analysis indicated that different communities were far more closely related to the progression of the rivers into, through and out of the drought than they were to other factors such as altitude, river order, tributary, or season. The diversity of the communities was drastically reduced with the reduction in discharge in the river, both in terms of the number of taxa (reduced by half), and the density (reduced by almost an order of magnitude). When high flows did recommence, in November 1992, there was some evidence of recovery, in the form of the reapperance of the reophilous mayfly *Trichorythus* and the appearance of large numbers of small net-spinning caddis larvae (Hydropsychidae). However, the recovery was by no means complete by the time the fieldwork ended in May 1993, and Weeks *et al.* (1996) concluded that communities may take much longer than expected to recover from major droughts, if indeed they ever do so completely.

Both the studies of the Sabie and the Kowie Rivers, have also highlighted the importance of the dipteran family Chironomidae in studies of temporary rivers. Despite difficulties in identifying this group, over 30 genera and at least 30 further 'types' of chironomids have been recognised, out of a total of over 200 taxa listed from the Kowie River (this total would be far greater if all taxa were identified to genus or species level). Chironomids thus represent approximately a third of the known fauna of this section of the river. The group also often comprises a large proportion of the animals collected on any one occasion. In the Sabie, chironomids constituted 48% by numbers of the animals collected in pre-drought samples, 52% during the drought, and 33% during the post-drought recovery. The paucity of systematic expertise in this group is a major stumbling block to the understanding of the effects of different flow regimes on different invertebrate communities. Williams (1996) remarked that it would be useful to examine why the Plecoptera, Odonata and brachyceran Diptera (e.g. stratiomyids, athericids, empidids, ephydrids etc.) were poorly represented in temporary streams, yet the Tipulidae and Chironomidae (nematoceran dipterans) were so successful. While Odonates clearly were well-represented in the temporary streams studied in South Africa, the issue of chironomid diversity would be of particularly interest.

From these results reported here, it is obvious that the consequences of reducing flows are not straightforward. It cannot be said that changing a perennial river into a temporary one will necessarily reduce the taxonomic diversity of the river, and it seems possible that it might even increase it. However, it is likely that the faunal composition of such a modified system will gradually alter to include a greater proportion of taxa more tolerant of lentic conditions, low oxygen concentrations (e.g. *Chironomus* sp., dytiscids, hemipterans, planorbids), or even gradual loss of surface water (e.g. microcrustaceans, gomphids, certain chironomids).

This indicates that future studies will have to concentrate more on the effects of flow reduction on faunal character, rather than relying on the disappearance of species as an indication of environmental degradation. This interpretation is in agreement with the conclusions of Weeks *et al.* (1996) on the fish communities of the Sabie-Sand River. During periods of low-flow, different fish families such as the cichlids (tilapia) became dominant in the river - this occurred naturally during the low-flow season. The prediction of Weeks *et al.* (1996), which could as well apply to invertebrates, was that prolonged low-flows, or no-flows, would result in the community balance tilting permanently towards the dry-period assemblages, with possible dominance by one or a few hardy species, adapted to the new conditions. In regulated permanent flow, the same thing could happen, as events in the Great Fish River have shown.

The lesson, particularly for river management in arid areas, is that the maintenance of natural flow variability (both for high and low flows) is of crucial importance in sustaining the natural assemblages of temporary rivers (e.g. Boulton *et al.* in press).

CONCLUDING POINTS

- Rivers within the same geographical regions showed greatest faunal resemblances at the coarse taxonomic levels used for this comparative exercise.
- Equivalently high diversities were indicated for certain of the temporary and perennial rivers of each of the regions.
- Faunal overlap between temporary and perennial stream fauna was high at the taxonomic levels of comparison used in this exercise. This is merely an indication that many of the major groups occurring in perennial rivers are present in temporary rivers both within the same region and beyond it.

REFERENCES

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective. *In:* P. De Deckker and W.D. Williams. (eds.) *Limnology in Australia.* CSIRO/Junk Publishers, Melbourne and the Netherlands.

Boulton, A.J., Sheldon, F., Thoms, M.C. and Stanley, E.H. (in press). Problems and constraints in managing rivers with contrasting flow regimes. *In:* P.J. Boon, B.R. Davies, and G.E. Petts. *Global perspectives on river conservation: science, policy and practice.*

Braune, E. 1985. Aridity and hydrological characteristics: Chairman's summary. *Hydrobiologia* **125:** 131-136.

Brown, C.A., Eekhout, S. and King, J.M. 1996. The National Biomonitoring Programme for Riverine Ecosystems. Proceedings of a spatial framework workshop. National Biomonitoring Programme (NBP) Report Series No. 2. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria.

Chutter, F.M and Heath, R.G.M. 1993. *Relationships between low flows and the river fauna in the Letaba River.* Water Research Commission Report WRC 293/1/93.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* Water Research Commission Report No. TT 62/93. 232pp.

Department of Water Affairs and Forestry, 1997. *White Paper on a National Water Policy for South Africa.*

Eekhout, S., Brown, C.A. and King, J.M. 1996. *National Biomonitoring Programme for Riverine Ecosystems: Technical considerations and protocol for the selection of reference and monitoring sites.* NBP Report Series No.3. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Moore, C.A. and Chutter, F.M. 1988. *A survey of the conservation status and benthic biota of the major rivers of the Kruger National Park.* Report to the National Institute for Water Research, Council for Scientific and Industrial Research, Pretoria. 102pp.

O'Keeffe, J.H. and De Moor, F.C. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research and Management* **2:** 39-55.

Palmer, C.G. 1991. *Benthic assemblage structure, and the feeding biology of sixteen macroinvertebrate taxa from the Buffalo River, eastern Cape, southern Africa.* PhD Thesis, Rhodes University, Grahamstown, South Africa.

Palmer, C.G. and O'Keeffe, J.H. 1992. Feeding patterns of four macroinvertebrate taxa from the headwaters of the Buffalo River, Eastern Cape. *Hydrobiologia* **228:** 157-173.

Palmer, C.G., Palmer, A., O'Keeffe J.H. and Palmer, R. 1994. Macroinvertebrate community structure and altitudinal changes in the upper reaches of a warm temperate southern African river. *Freshwater Biology* **32:** 337-347.

Palmer, C.G., O'Keeffe, J.H. and Palmer, A.R. 1991. Are macroinvertebrate assemblages in the Buffalo River, Eastern Cape, associated with particular biotopes? *Journal of the North American Benthological Society* **10:** 349-357.

Reavell, Mr P.E. University of Zululand, P.O. Box 1535, Empangeni, Zululand, 3880, South Africa.

Smakhtin, V. (in prep.). *Low flow estimation and analysis in South Africa.* Report to the Water Research Commission, Pretoria.

Weeks, D.C., O'Keeffe, J.H., Fourie, A. and Davies, B.R. 1996. *A pre-impoundment study of the Sabie-Sand system, Eastern Transvaal, with special reference to predicted impacts on the Kruger National Park. Volume 1: The ecological status of the Sabie-Sand River system.* Water Research Commission Report WRC 294/1/96.

Williams, D.D. 1987. *The ecology of temporary waters.* Croom Helm (London and Sydney) and Timber Press (Portland, Oregon).

Williams, D.D. 1996. Environmental constraints in temporary fresh waters, and their consequences for the insect fauna. *Journal of the North American Benthological Society* **15**(4): 634-650.

Williams, W.D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshwater Biology* **20:** 407-420.

Williams, P.H. and Gaston, K.J. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* **67:** 211-217.

Yeld, J. 1997. *Water - Some for all, forever.* Supplement to the Cape Argus Group newspapers.

APPENDIX 7.1 Summarised list of taxa for the seven rivers, for the purposes of comparison. Only taxa identified to common levels in all studies are included in the list, as discussed in the text. Abbreviations: Bt and Bp - Buffalo River (temporary and perennial sections), Gft and Gfp - Great Fish River (temporary and perennial conditions), Kt - Upper Kowie River (temporary), Lp and Lt - Letaba River (perennial and temporary sections), LV - Luvuvhu River (temporary), M - Mutale River (perennial), S - Sabie River (perennial).

Site:		Bt	Bp	GFt	GF	Kt	Lt	Lp	Lv	M	S
No. of taxa:		34	39	35	45	47	48	63	75	69	71
COELENTERATA	*Hydra sp.*	0	1	0	1	1	1	0	1	1	1
PLATYHELMINTHES		1	1	0	1	1	1	1	1	1	1
NEMATODA		1	1	1	1	1	1	1	1	1	1
ANNELIDA	Oligochaeta	1	1	1	1	1	1	1	1	1	1
	Hirudinea	0	0	0	0	0	1	1	1	1	1
DECAPODA	*Caridina spp.*	0	0	0	0	0	1	1	1	1	1
	Potamonautes spp.	1	1	0	1	1	0	1	0	0	0
HYDRACARINA		1	0	0	1	0	1	1	1	1	1
COLLEMBOLA		1	1	0	1	1	1	1	1	1	1
PLECOPTERA		1	1	0	0	0	0	1	1	0	1
EPHEMEROPTERA											
Polymitarcyidae		0	0	0	0	0	1	1	1	0	0
Baetidae	*Afroptilum spp.*	1	1	1	1	1	1	1	1	1	1
	Centroptiloides sp.	0	1	0	0	0	0	0	1	1	1
	Cloeon spp.	0	0	1	1	1	1	1	1	1	1
	Pseudocloeon spp.	0	1	0	1	1	1	0	1	1	0
	Baetis spp.	1	1	1	1	1	1	1	1	1	1
	Other baetids	0	0	0	0	0	1	1	1	1	1
Oligoneuriidae		0	0	0	0	0	0	0	1	1	1
Heptageniidae	*Afronurus sp.*	0	1	0	0	0	1	1	1	1	1
Leptophlebiidae	*Adenophlebiodes sp.*	0	0	0	0	0	0	0	1	1	1
	Adenophlebia spp.	1	1	0	1	1	0	0	0	0	0
	Castanophlebia spp.	1	1	0	0	0	0	1	0	0	1
	Choroterpes spp.	1	1	0	1	0	1	1	1	1	1
Tricorythidae	*Trichorythus spp.*	0	0	0	1	0	1	1	1	1	1
	Dicercomyzon sp.	0	0	0	0	0	0	0	1	1	1
	Neurocaenis sp.	1	1	0	1	0	0	0	0	0	0
Caenidae	*Austrocaenis sp.*	0	0	1	1	1	0	1	1	1	1
	Caenis sp.	0	0	1	0	1	0	0	0	0	0
	Other caenids	1	1	0	0	0	1	1	0	0	0
ODONATA		1	1	1	1	1	0	1	1	1	1

Site:		Bt	Bp	GFt	GF	Kt	Lt	Lp	Lv	M	S
TRICHOPTERA											
Hydropsychidae	*Aetholoptera sp.*	0	0	0	0	0	1	1	1	0	1
	Amphipsyche sp.	0	0	0	0	0	1	1	1	1	1
	Cheumatopsyche 'afra'	1	1	1	1	1	0	1	1	1	1
	Macrostemum sp.	1	1	0	1	0	1	1	0	0	0
Philoptamidae	*Chimarra sp.*	1	1	0	0	0	0	1	1	1	1
Ecnomidae	*Ecnomus sp.*	0	1	1	1	1	1	1	1	1	1
Leptoceridae	*Athripsodes sp.*	0	0	1	0	0	0	0	1	0	1
	Leptocerus spp.	0	0	1	0	1	0	0	1	1	1
	Oecetis sp.	0	0	0	0	0	1	1	1	1	1
	Trichosetodes sp.	0	0	0	0	0	1	1	1	1	1
Lepidostomatidae	*Dyschimus sp.*	1	0	0	0	1	0	0	0	0	1
Hydroptilidae	*Hydroptilia sp.*	0	0	1	0	0	1	1	1	1	1
	Catoxyethira sp.	0	0	0	0	0	1	1	1	1	1
	Orthotrichia spp.	0	0	0	1	0	1	1	1	1	1
	Other hydroptilids	1	0	0	0	1	1	0	1	1	1
Dytiscidae		0	0	1	1	1	1	1	1	1	0
Haliplidae		0	0	1	1	1	0	0	0	1	0
Hydrophilidae		0	1	1	1	1	0	1	1	1	1
Gyrinidae	*Aulonogyrus sp.*	1	0	1	1	1	0	0	0	0	0
	Gyrinus spp.	1	1	0	0	1	0	0	0	0	0
	Other gyrinids	0	1	1	1	1	1	1	1	1	1
Hydrophilidae		0	0	1	1	1	1	1	1	1	1
Hydraenidae	*Ochthebius sp.*	0	0	0	0	1	1	1	1	1	0
	Other hydraenids	0	0	1	1	1	0	0	1	1	1
Psephenidae		0	1	0	0	0	0	0	1	1	0
Dryopidae		0	0	0	0	0	0	0	1	1	1
Elmidae	*Leptelmis sp.*	0	0	0	0	0	1	1	1	0	1
	Stenelmis sp.	0	0	0	1	0	1	1	1	1	1
	other Elmidae	1	1	0	1	0	1	1	1	1	1
Helodidae		0	0	0	0	1	0	0	1	0	1
	Other Coleopterans	0	0	0	0	1	0	0	1	1	1

Site:		Bt	Bp	GFt	GF	Kt	Lt	Lp	Lv	M	S
DIPTERA											
Tipulidae		1	1	1	1	1	0	1	1	1	1
Psychodidae		0	0	0	0	1	0	0	0	1	1
Chaoboridae		1	0	0	0	1	0	1	0	0	0
Culicidae	*Anopheles sp.*	0	0	1	0	1	0	0	0	0	0
	Other culicidae	0	0	1	1	1	0	1	1	1	1
Simuliidae	*Simulium spp.*	1	1	1	1	0	1	1	1	1	0
Chironomidae	Chironomini	1	0	1	1	1	1	1	1	1	1
	Tanytarsini	1	1	1	1	1	1	1	1	1	1
	Tanypodinae	1	1	1	1	1	1	0	1	1	1
	Orthocladiinae	1	1	1	1	1	1	1	1	1	1
Ceratopogonidae	*Bezzia sp.*	0	0	1	0	1	0	1	1	1	1
	Dasyhelea sp.	0	0	1	1	0	0	1	1	1	1
	Forcipomyia sp.	0	0	0	0	0	0	1	1	1	1
	Atrichopogon sp.	0	0	1	0	0	0	0	0	0	0
	Other ceratopogonids	1	1	1	1	1	1	1	1	1	1
Tabanidae		0	1	0	0	1	1	1	1	1	1
Rhagionidae		0	0	0	0	0	1	1	1	1	1
Ephydridae		0	0	1	1	0	0	1	0	1	0
Empididae		0	1	1	1	0	0	0	0	0	1
Muscidae		0	0	0	0	0	0	0	1	1	1
Anthomyidae		0	0	0	0	0	0	0	1	1	1
Athericidae		1	1	0	1	0	0	0	0	0	0
MOLLUSCA											
Gastropoda	*Biomphalaria sp.*	0	0	0	0	0	0	1	1	1	1
	Bulinus sp.	0	0	0	1	1	0	1	1	0	1
	Lymnaea sp.	0	0	0	0	1	0	1	1	1	0
	Melanoides sp.	0	0	0	0	0	1	1	1	1	1
	Ferrissia sp.	0	0	0	0	1	0	0	1	0	0
	Burnupia sp.	0	1	1	1	1	1	1	0	0	0
	Other Ancylidae	1	1	0	0	0	0	0	1	1	1
	Other Gastropoda	0	0	0	0	0	1	1	1	1	1
Pelecypoda	*Corbicula spp.*	1	1	0	1	0	1	1	1	1	1
	?Eupera sp.	0	0	0	0	0	1	1	1	1	1
	Other Pelecypoda	0	0	0	0	1	0	1	1	0	1

CHAPTER EIGHT

SYNTHESIS AND GENERAL DISCUSSION

What you're up against is the great unknown, the void of all Western thought. You need some ideas, some hypotheses. Traditional scientific method, unfortunately, has never quite gotten around to saying where to pick up more of these hypotheses. Traditional scientific method has always been at best 20-20 hindsight. It's good for seeing where you've been. It's good for testing the truth of what you think you know, but it can't tell you where you ought to go, unless where you ought to go is a continuation of where you were going in the past. Creativity, originality, inventiveness, intuition, imagination - 'unstuckness' in other words - are completely outside its domain.

Robert Pirsig
Zen and the Art of Motorcycle Maintenance

8.1 INTRODUCTION

The invertebrate biota of with a number of temporary rivers in the Eastern Cape region of South Africa has been investigated at varying intensities and at a number of temporal and spatial scales. A general synthesis of the research is presented here, following which the major aims and questions posed at the outset of the research are examined in light of the research findings.

8.2 A BRIEF REVIEW OF THE STUDY

8.2.1 A framework and terminology for the research

While all rivers are affected by the semi-arid character of the southern African subcontinent (Davies *et al.* 1993), there is clearly a gradient in the seasonality and permanency of flow of both natural and modified rivers. The conceptual framework proposed in Chapter 2 recognises this in the form of a continuum of different hydrological regimes existing between perennial and the most temporary of river states. Two 'changes of state' occur along this continuum: one where surface flow ceases but surface water remains, and another where surface water disappears from the channel completely. Directional trends along the continuum include flow variability, disturbance frequency and intensity, and the influence of abiotic versus biotic controls on faunal character.

The supporting terminology for the conceptual framework aims to provide a simple and systematic means of identifying and describing any natural or modified river (or section thereof) on the basis of the timing, extent and duration of flow and/or surface water conditions. These descriptions were used through the thesis to identify different river types. In the interim, a number of South African river specialists have assisted in the process of classifying South African rivers into a hierarchy of 'bioregions', 'sub-regions' and 'types' on the basis of their biological attributes and to some extent geo-physical and hydrological features (Eekhout *et al.* 1996). This classification has been widely adopted, and proves useful alongside the terminology, allowing for the association between river flow types and geophysical characteristics of the system (providing the bioregion or subregion is known).

8.2.2 Studies of the invertebrates of the upper Kowie River

The first stage of the investigation focussed on a geographical area of South Africa in which temporary rivers are common - the Eastern Cape 'arid corridor.' The invertebrate fauna of an intermittent aseasonal river was studied across various temporal and spatial scales, and factors influencing faunal character were sought. Each of the scales of consideration were dealt with separately. The biota of individual biotopes and reaches (sites) of the upper Kowie River was studied over the spatial scales of months (Ch. 3) and years (Ch. 4), concentrating on the effects of environmental variability on faunal composition and distribution.
Results of these studies suggested that the biota was largely unstructured and regulated primarily by interacting physical factors, of which the most important were thought to be: 1) present and antecedent hydrological conditions in the channel; 2) time of year (either winter or summer); 3) character, availability and duration of available biotopes.

This was followed by an examination of the invertebrate biota in relation to hydrological conditions, which had been 'categorised' into five distinct phases at the beginning of the study (as discussed in Chs 1 and 4). By this stage, it was clear that the effect of hydrology (and its variability) on the fauna was modified to some extent by antecedent conditions and the time of year in which the conditions occurred. The concept of hydrological phases was expanded to incorporate these auxilliary factors, and 12 sub-phases were distinguished (Ch. 4). Results indicated that each of the major phases could be associated with 'core' and 'peripheral' fauna - the former adapted to the prevailing conditions, and the latter utilising the environment opportunistically. The differences between fauna of sub-phases within a single phase indicated that the inclusion of time of year and antecedent hydrological conditions enhanced the ecological relevance of the phases.

8.2.3 Studies in a range of Eastern Cape temporary rivers

Moving to a regional scale, the invertebrates of a number of temporary rivers in the 'arid corridor' of the Eastern Cape were surveyed at a less intensive level, to establish the extent of faunal variability within and between rivers, both at the family level and at more detailed taxonomic levels (Ch. 6). Three different rivers were selected, and six sites exhibiting various degrees of intermittency were identified for the study.

While at a family level, no significant differences were indicated between the fauna of the different temporary river sites, at more detailed taxonomic levels, the majority of sites were faunally distinct. Biotic diversity at some of the more temporary sites was greater than that at the site exhibiting almost continual flow. Highest numbers of taxa were recorded at two different localities displaying quite different hydrological characteristics. At one, the high diversities were attributed to the considerable environmental variability and the resultant heterogeneity at the site, while at the other, high diversities were related to habitat duration/stability and low rates of change in hydrological and physico-chemical variables (Ch. 6).

8.2.3 Studies in temporary and perennial rivers of two regions

At the largest spatial scale of investigation, invertebrate databases from a range of rivers in the Eastern Cape and Mpumalanga (formerly Eastern Transvaal) were examined. This provided an opportunity to contrast fauna occurring in natural and modified temporary and perennial rivers, and to consider the effects of flow regulation on biota. Data from a number of studies were used, and a highly summarised (but comparable) invertebrate list was compiled for analyses.

At these coarse taxonomic levels, rivers within each region showed greatest similarity to one another, and highest numbers of taxa were recorded in the tropical Mpumalanga Rivers. There was no indication that within a region, the fauna of intermittently-flowing rivers was less taxa-rich than of perennial rivers. On the contrary, the rivers with the greatest numbers of taxa in each of the regions were intermittent. From these findings, together with results of pre- and post- modification studies on river fauna (e.g. O'Keeffe and de Moor 1988), it was inferred that the long-term effect of the loss of hydrological variability (through IBTs, flow regulation, etc.) may not necessarily be a reduction in diversity, but a change in the taxonomic balance of the fauna, and the possibility of species dominance becoming a feature of the fauna..

8.3 AN EXAMINATION OF RESEARCH AIMS AND QUESTIONS IN THE LIGHT OF THE RESULTS PRESENTED

The principal aims of this research were: to investigate the aquatic macroinvertebrates in an Eastern Cape River at several spatial and temporal scales within a period of two to three years; to establish the extent to which findings with could be generalised in terms of other temporary systems within the region; and to contrast the invertebrate biota of natural and modified temporary and perennial streams in two regions of the country.

The research required to fulfil these aims addressed a series of questions posed at the outset of the study. Each of these will be examined in turn. Where specific results are referred to, these are cross-referenced.

8.3.1 Which invertebrates live in temporary rivers in the Eastern Cape?

Over 200 invertebrate taxa were identified (some as 'types' only) in the upper Kowie River over the total period of the study. Because the fauna of the five other temporary river sites in the Eastern Cape were only examined at detailed taxonomic levels over a period of two months, far fewer taxa were recorded (< 60 per site, Ch. 6), and considerably more would be expected over longer time periods.

Following descriptions of Williams and Hynes (1977), the animals collected in these rivers were assigned to three groups:

- 'Residents'- those taxa either behaviourally or physiologically adapted to the range of conditions in a temporary river, and often restricted to it by their low mobility;
- 'Facultative taxa' - those animals which occurred in both lentic and lotic waters, and were capable of relocating under drying conditions; and
- 'Opportunist colonists' - those taxa generally associated with perennial rivers, not particularly well adapted to temporary conditions, but able to survive in (or relocate from) rivers in which the dry period was short.

INSECTS

Of the taxa collected in temporary rivers, by far the greatest proportion were insects. This group was well represented by baetid and caenid mayflies; gomphid and corduliid dragonflies; libellulid and coenagrionid damselflies; corixid and notonectid hemipterans, hydroptilid trichopterans, dytiscid and hydrophilid beetles, and chironomid, tabanid, ceratopogonid and tipulid dipterans. These were identified either as residents or facultative taxa.

Chironomids

Of all the insects, chironomids were the most prolific, and the family was collectively identified as resident. Williams (1996) remarked that it would be useful to examine why this group and the tipulids were so successful in temporary streams. In the upper Kowie River, 30 chironomid genera and over 30 'types' of chironomids were collected over the study period, often in large numbers. The family was also well-represented in the other temporary rivers in the region (Ch. 6).

Many chironomids are adapted to damp or 'trickle' conditions (e.g. the ubiquitous *Limnophyes natalensis*) and may be capable of dormancy in the egg phase (although this is uncertain according to Harrison, pers. comm.). Williams and Hynes (1976) suggested that certain orthoclad eggs may require exposure to drying shortly after being laid, in order to prevent hatching before recommencement of flow. Some species are also capable of breeding in damp soil (e.g. the orthoclads *Pseudosmittia* and *Chaetocladius*; Harrison, pers. comm.).

Chironomus sp., which are capable of tolerating low-oxygen conditions, were collected in mature pools in the Kowie River, and were prolific in the small, long-lived pools in the Fish River tributary.

The most unusual chironomid collected was *Harrisonina petricola*, a rare diamesid which is 'usually collected in clean water flowing over bedrock near the source of intermittent streams' (Harrison pers. comm.). This description matched the collecting locality (upper Kowie River site UK2) and this chironomid could be considered an indicator species of these conditions. As it was only collected during flow onset (and may thus have originated in drift from an area slightly closer to the source), it was also associated with these conditions. This diamesid is of further interest from an evolutionary perspective, as it is the only chironomid thought which may have originated from tropical Godwanaland (while the majority of chironomids are postulated to be Pan-Ethiopian in origin; Harrison 1978).

The larvae of *Mesocricotopus* collected in the upper Kowie River was the first record of this genus in Africa south of the Sahara (Harrison, pers. comm.), which raised the possibility that many more unrecorded (possibly relictual) taxa may be found in unstudied intermittent streams or small tributaries similar to the upper Kowie.

Odonates

Although the absence of odonates from temporary streams was commented on by Williams (1996), the group was represented in Boulton and Lake's (1992a) temporary river taxa, and representatives of this group were collected frequently (though not in large numbers) in the upper Kowie and the other temporary rivers in the Eastern Cape. Of those recorded, *Notogomphus* sp. gomphids, *Orthetrum* sp. libellulids, and *Macromia* sp. corduliids were the only taxa collected in damp or dry conditions, and were described as facultative. Burrowing or hiding mechanisms evidently equip nymphs for survival during the early stages of drying. Wilmot (unpubl.) described *Orthetrum* as a 'mud-dweller', *Notogomphus* sp. as a common inhabitant of 'leaf trash', and *Macromia* sp. as having adopted the 'hiding habit' most widely. Coenagrionids, aeshnids and lestids (opportunist colonists) were usually collected in marginal vegetation, during periods of sufficient surface water or flow (although *Pseudagrion* and *Ennallagma* coenagrionids were collected once in a damp fringe habitat on the edge of a drying pool).

Hemipterans

Hemipterans are common inhabitants of lotic and lentic waters, and because of their high mobility and ability to use atmospheric oxygen, were seldom absent from the sites studied. Where marginal vegetation was plentiful, hemipterans occurred in their greatest number and variety. Generally this group showed a preference for the quieter waters, out of flow (e.g McCafferty 1981). Corixids and notonectids were particularly well represented.

At least 19 hemipteran taxa were collected during the study. A South African heteropterist (Reavell, pers. comm.) termed the collection an 'unremarkable hemipteran fauna which is fairly typical of streams south of the subtropical areas .. may indicate an extremely variable flow regime as certain expected stream species are missing (*Laccocoris spurcus*, *Rhagovelia infernalis* veliids)'. Hemipterans were collected at all times of the study, and were present in all the temporary rivers. They occurred in their greatest numbers where there was plentiful marginal vegetation, and in pools. In particular, corixids and notonectids were well represented at the upper Kowie River, and pleids were collected in large numbers at the lower Bushmans River site (Ch. 6). Macan (1939, quoted in Williams 1987) recorded up to six species of corixids commonly on the wing in Cambridgeshire, and reported frequent colonisation, with a succession of different corixids depending on the proportion of organic matter in the enviroment. Pleids are common only in lentic habitats (such as the lower Bushmans), and were capable of withstanding conductivities of over 800mS.m^{-1} (Table 6.7).

Coleopterans

Dytiscids, hydrophilids and gyrinids were the most common beetles in the temporary rivers studied. Gyrinids were only present when adequate surface water was present, and were not collected often during high flow conditions. All three families generally occurred in quieter areas out of flow, which are there preferred environment (McCafferty 1981). *Laccophilus lineatus* dytiscids were the most common beetle occurring throughout the study, in all phases, to the extent that they could be considered residents (except that their response to long dry periods was not known). If any animal 'characterised' the upper Kowie fauna it was this species. McCafferty (1981) noted that species of *Laccophilus* were often the first insects to inhabit newly-formed pools and other environments. Dytiscid larvae were diverse and common in the upper Kowie River within the first month of flow (Ch. 4). Hydrophilid adults and larvae were collected less frequently than, in marginal vegetation, pools, and the quieter waters of rivers. Hydraenid beetles were collected seldom and then along wet margins of rivers or pools.

Ephemeropterans

Mayflies were seldom found in great numbers in the upper Kowie, however in the lower Kowie where flow was continuous during the sampling period, baetids and caenids were common and persistent, and leptophlebiids were present in lesser numbers. Tricorythid and heptageniid mayflies were only collected in the lower Kowie River, which exhibited continual flow during the study. Harrison (1978) remarked on the lack of Tricorythids in temporary streams in the Western Cape.

Generally, resilient taxa such as *Baetis harrisoni* and *Austrocaenis* sp. occurred in the temporary rivers, and these occurred in all conditions except drying. Early baetid instars were particularly fond of algal mats, which may have afforded them protection. Harrison (1958) noted that baetids were among the early colonists of a temporary Western Cape stream, and that with stability in conditions, increases in baetids occurred. Shortly before the stream dried, *Baetis harrisoni* was replaced by another *Baetis* sp. mayfly.

Plecopterans

Stoneflies were virtually absent from all sites except the lower Kowie River (nymphs were collected on one occasion at the upper Kowie). Both Williams (1996) and Harrison (1978) have remarked on the conspicuous absence of this order from temporary rivers, although Boulton and Lake (1992b) recorded several plecopterans species in intermittent Australian rivers. According to Williams (1996), stoneflies seem less able to deal with standing water conditions than with drought, and survive drought only in running water habitats. This is borne out by the presence of nemourid stoneflies in the lower Kowie river, which is naturally temporary but flows for lengthy periods due to augmented water supply.

ARACHNIDS

Certain water mite genera are characteristic of temporary ponds and are capable of surviving buried in wet mud and debris of the substrate (Pennak 1953). Although this group was not identified to the level of genus, 15 recognisably different types were recorded. (Because of the low frequencies of individual types, this group was recorded only as 'Hydracarina' to accord it adequate representation in the database).

CRUSTACEANS

Williams (1987) reported that microcrustaceans may be scarce in temporary streams due to the dominance of the running water phase. In the Kowie River, however, cladocerans, copepods and ostracods were collected in the quieter areas of the rivers (e.g. in marginal vegetation or pools), during no-flow periods, and in the damp substrate during the DRY phase in the upper Kowie River (Ch.4). Certain copepods are able to arrest their development in the egg or near adult stage - this is thought to be an adaptation to high summer temperatures and low oxygen levels (Williams and Hynes 1977). Ostracods were particularly abundant at times. Six species and a further six types were identified in the upper Kowie.

Freshwater crabs (*Potamonautes* sp.) were collected in all but the dry conditions in the upper Kowie.

MOLLUSCS

Of the freshwater molluscs collected in the river, *Lymnaea columella* lymnaeids and *Ceratophallus* sp. planorbid gastropods were most frequently present, and ancylids, physids and sphaeriids were common under certain conditions. *Ferrissia* ancylids are characteristic of stagnant waters and are capable of modifiying their shells (by production of a septum) in anticipation of drying conditions (Brown 1981). *Ferrissia* sp. ancylids, planorbids and sphaeriids were listed for two intermittent streams in Australia (Boulton and Lake 1992b), and lymnaeids were recorded in temporary streams in Ontario (Williams and Hynes 1976). Certain species of *Lymnaea* and *Ceratophallus,* and *Bulinus forskalii* physids (uncommon) are distinguished as 'good aestivators' by Brown (1981). All of these groups excepting sphaeriids were collected in waters with conductivities over $400mS.m^{-1}$, and in the case of ancylids (*Ferrissia* sp.), over $800mS.m^{-1}$ (Table 6.7). All of the molluscs collected were (conservatively) grouped as facultative taxa, although being good aestivators, they may even qualify as residents.

8.3.2 What is the extent of variability in the invertebrate fauna of the upper Kowie at various scales

The majority of null hypotheses relating to the intensive study on the upper Kowie River were formulated on the basis of this question (see Section 1.4). The answer to the question provides the basis for the majority of this chapter. Each of the null hypotheses examined is listed here. Whether or not it was rejected is noted, and cross-referenced to the relevant chapter. Subsequent sections deal with the variability itself, and the conditions resulting from it.

H_0: There is no difference between the invertebrate biota of different biotopes within the upper Kowie River
Rejected (Ch. 3, Section 3.5.7).

At the upper site (UK1), approximately half the biotope sample pairs tested differed significantly. At the lower site (UK2), only fauna of marginal vegetation was shown to be significantly different to that of other biotopes.

H_0: There is no difference between the invertebrate biota of different reaches (sites) on the upper Kowie River
Rejected (Ch. 3, Section 3.5.7)

Significant differences were indicated between the fauna of the upper site (UK1) and the lower site (UK2). Faunal variability was thus greater between sites than within a site over time.

H_0: There is no difference between the invertebrates occurring in individual months within a year in the upper Kowie River
Rejected (Ch. 3, Section 3.5.7)

The majority of pairs of months tested showed significant differences in terms of their faunas. Thus variability in fauna within a year was considered high.

H_0: There is no difference between the invertebrates occurring in consecutive midsummer periods in the upper Kowie River
Rejected (Ch. 4, Section 4.5.6)

All midsummer phases differed significantly in terms of their fauna. Thus year-to-year changes in the fauna (within the same period) were considerable. No cyclical or seasonal pattern was thus detectable in the biota of the upper Kowie over this period.

8.3.3 How do abiotic variables (other than flow) fluctuate over time and with different environmental conditions, and which of these factors influence faunal character?

Over the period of the study on the upper Kowie River, the variability in timing, extent and duration of rainfall was reflected in the erratic hydrology of the river (Figs. 4.1, 4.2). The hydrological phases in the river showed only broad seasonal or periodic trends and did not necessarily occur in a repetitive (or predictable) sequence. In the study of the fauna over eight consecutive months, the sequence of phases was: POOLS, ONSET, FLOW, NO FLOW, POOLS, ONSET, FLOW (Ch.3). Similar hydrological variability was detected between years of the study, as illustrated with the comparison of three consecutive midsummer periods (Ch. 4). These findings contrasted with the cyclical and sequential nature of the flow phases described by Boulton and Lake (1990).

Although amplitudes in abiotic variables are often greater in temporary than in perennial rivers (Williams 1987, Boulton and Lake 1990), most physico-chemical variables, other than discharge and current speed, varied relatively little in the upper Kowie River over the period of investigation (Chs 3 to 5). Of the variables measured, only current speed in individual biotopes and the percentage proportion of stones and cobbles in the substratum showed trends which matched up with the grouping of invertebrate samples in MDS ordinations, suggesting that they may in some way be associated with these groupings (3.6.1; 4.5.1). The influence of current speed simply reflected the difference in the faunas of flow and non-flow conditions. The fauna occurring in areas with high percentage proportions of stones and cobbles were generally stones-in-current dwellers (typically lotic taxa such as simuliids and hydropsychids).

In the study of temporary rivers elsewhere in the region, the amplitudes in physico-chemical variables were more noticeable. At those sites where small or shallow pools were found, and flow was rare or non-existent (e.g. lower Bushmans River, Fish River tributary), conductivity values ranged between 300mS.m^{-1} and over 800mS.m^{-1} (Table 6.2). These high values were attributed in part to the geology of the area, but also to high evaporation and low dilution from rainfall.

Highest conductivities were recorded during dry periods, and these conditions were generally associated with lower numbers of taxa (Tables 6.2, 6.11). However, following heavy rain falls, conductivity values were significantly reduced at the lower Bushmans River pool (which had not flowed), where the highest number of taxa of all the sites surveyed was collected. Reduced conductivity may not have been causal: in the overall study of the different temporary rivers (Ch. 6), no significant correlation was found between conductivity and numbers of taxa collected. Day (1990), in her review of the fauna of surface waters of Namibia, also reported no significant correlation between these two variables. Day commented that if anything, there was a tendency towards an increase in diversity at least at intermediate salinities, and this scenario may also be true in the case of the lower Bushmans River. Notwithstanding the lack of a clear relationship between conductivity and numbers of taxa, an association *could be* shown between conductivity and faunal character at the various different temporary river sites (Section 6.4.8, Figure 6.5). In general, particular causes cannot be inferred from apparent correlations, and it would require experimental procedures to confirm these here.

8.3.4 Which factors could be considered the *most important* in regulating faunal character?

Biota occurring in the temporary rivers are subject to enormous variability and unpredictability in surface water volume, extent and state. Variability and unpredictability cannot themselves be considered *influences* in themselves, but rather supply the *context* within which physical and biological influences on the fauna operate.

Biota of highly variable environments are considered to be primarily regulated by physical factors (e.g. Power *et al.* 1988), and this was considered true of the temporary rivers in the Eastern Cape. Influences on fauna were considered syncronous and to some extent hierarchical in their action (e.g. Minshall and Minshall 1978), with the order of the hierarchy varying according to the locality, the environmental conditions pertaining, and the scale of investigation.

The major influences were identified as:

- Present and antecedent hydrological conditions, and their duration (wet phase, dry phase etc.).
- Rate of change of conditions (this was one of the criteria for recognising disturbance in this study; see Section 1.3.6).
- Time of year (chiefly the influence of air and water temperatures rather than seasonally-mediated changes in the physical environment, as seasonality in hydrology was lacking).
- Character and availability of substratum (or biotopes).

'Present' hydrological conditions were generally recognised in terms of the surface water conditions which disinguished the five hydrological phases identified, e.g. surface flow conditions (FLOW), diminishing surface water (POOLS).

The variables acting to modify the effect of hydrological conditions on fauna were recognised early in the thesis (Ch. 3). The incorporation of two of these (antecedent conditions, time of year) into the concept of hydrological phases, by the creation of sub-phases (Ch. 5), provided satisfactory evidence of their supplementary influence.

Time of year strongly influenced faunal composition and diversity, however, this was generally a modifying influence rather than a governing influence, as seasonality in rainfall and flow was lacking in the region of study (Figs. 4.1 and 4.2). The significant differences between the invertebrate fauna of three consecutive midsummer periods (Ch. 4) indicated that the variability in hydrological conditions in the river prevented cyclical patterns from developing in the biota. This contrasted with findings in intermittent seasonal rivers, where consistent cycles of seasonal change in assemblage composition were shown by Boulton *et al.* (1992b). The authors reported high faunal variation within seasons, but a clear association of faunal assemblages with different seasons. In the upper Kowie River, it could only be said that the fauna collected within any of the hydrological phases in the river were substantially influenced by seasonal factors such as air and water temperature and their correlates (e.g. algal growth).

Duration of conditions is generally associated with stability (or instability) in lotic systems, and displays a reciprocal relationship with disturbance frequency (Schneider and Frost 1996). Decreases in numbers of taxa were reported with increasing length of the dry period in temporary waters in Ontario (Williams 1996), and a similar relationship between faunal diversity and flow duration was shown for the intermittent Australian streams studied by Boulton and Suter (1986). In this study of Eastern Cape temporary rivers, the lowest numbers of taxa overall were recorded for the Fish River tributary site, which was described as ephemeral due to the length of the dry period, and infrequent flash flooding (Ch. 6). In addition to the low numbers of taxa collected, the fauna present were generally hardy, ubiquitous taxa associated with temporary or stagnant water conditions, and dominated by *Austrocaenis* caenids and *Chironomus* chironomids (Table 6.9).

Persistence of flow conditions over a period of three months in the upper Kowie resulted in a gradual increase in faunal diversity at the lower site, UK1 (Section

3.6.7). The conditions and the time of year (early summer) were favourable for colonisation of the environment by hemipterans and coleopterans, and the development of juvenile forms. Following flow cessation, the marginal vegetation biotope at this site remained inundated with water, and during the month of no-flow conditions, numbers of taxa continued to increase. During the following month, surface water loss accelerated so that marginal vegetation was exposed and diversity decreased substantially. As many animals were collected on the fringes of the pool as in the pool itself. Hildrew and Giller (1992) relate the example of patches of vegetation persisting on the floodplains of the upper Amazon for several generations of the organisms concerned, allowing time for succession. Although this example represents far larger spatial and temporal scales, the principal is similar to that in the upper Kowie. Persistence of flow, of surface water, or of a small area of aquatic habitat, engenders stability - even if this only applies to one 'patch' in an otherwise unstable environment and fauna. If faunal persistence, or the tendency for faunal composition to persist unchanged, is a satisfactory index of stability (Townsend *et al.* 1987), then - under these sort of circumsances, at least a small portion of the fauna could be considered stable.

Schneider and Frost (1996) suggested that pond assemblages were structured by random processes, life-history characteristics and biotic interactions, but that the relative importance of these processes depended on duration of habitat. In the lower Bushmans River, surface water persisted uninterrupted in the form of a single pool over a period of approximately 18 months (when it dried over a period of months; Ch. 7). Despite salinities of over $400mS.m^{-1}$ in high rainfall periods and up to $800mS.m^{-1}$ in low rainfall periods (Table 6.2), more taxa were collected at this site than at the lower Kowie River site, where flow was virtually continuous over the same period. The high diversities at the site were attributed to the duration of hydrological conditions, and the gradual rate of change in both surface water volume (through seepage and overflow) and conductivity (through dilution). High abundances reflected the low intensity of disturbance (low rate of change of phase) and the relaxation of physical constraints on the fauna (*sensu* Stehr and Branson 1938).

The influence of habitat (as substratum or biotope) on faunal assemblage structure is a vast and multi-dimensional topic in lotic ecology (see Minshall 1984, 1988).

In this study, the aspects of habitat focussed on in relation to fauna were character (biotope types), availability (extent), and heterogeneity (number of biotopes). Only the upper Kowie River is considered, in this context.

The habitat templet concept of Southwood (1977) suggested that community organisation should progressively decrease in areas where physical characteristics of the habitat show increased temporal variability. In the upper Kowie river, the frequency of hydrological change resulted in a continual expansion and contraction of aquatic habitat (*sensu* Stanley *et al.* 1997). This was, as suggested by Southwood's model, reflected in a paucity of structure and pattern in the fauna at all spatial and temporal scales (Chs 3 to 5). Biotope availability and heterogeneity was greatest during periods of flow, and declined progressively following cessation of flow (see Fig. 5.1).

It was the loss of specific biotopes rather than the loss of biotopes in general which had the greatest effect on the fauna. In particular, the exposure of marginal vegetation had a marked effect on faunal diversity (see Table 3.3), and especially at the lower site where MV provided a stable, extensive habitat for a variety of taxa. At the upper site, UK1, the configuration of the site was thought to have prevented the movement of animals from drying areas of stones-in-current to pool refugia, as a 1m vertical drop separated the SIC areas from the POOL biotope and may have presented a barrier to movement. Faunal overlap between the POOL fauna and elements of the MV, SAND, and (some) SOOC biota suggested that when the latter biotopes were exposed, at least a portion of the animals occupying them relocated to nearby pools and used them as refugia. Boulton and Lake (1992a) reported similar relocation of fauna between riffle and pool areas following the drying of riffles.

8.3.5 Do the five hydrological phases identified *a priori* represent ecologically meaningful 'units'? Could a characteristic fauna be associated with any of the phases?

The absence of strong seasonal or cyclical trends in both biotic and abiotic elements of this study further emphasized the need for some other 'unit' in this study which would incorporate both spatial and temporal scales simultaneously. This was important for the consideration of both disturbance-related features of the ecosystem, and the factors which shape the fauna (Minshall 1988). Working on intermittent Australian streams, Boulton and Lake (1990) objectively distinguished five flow phases (preflow, early flow, main flow, diminishing flow, and post-flow) *a posteriori* by ordination and classification of the complex interactions among a number of abiotic variables. These phases represented fairly discrete, clear cut entities which followed a predictable and cyclical sequence. No phase was characterised by a single variable, but rather by a complex suite of interacting variables, and different faunal assemblages were associated with each of the groups. Williams and Hynes (1976) allocated taxa into three groups: a 'Fall - Winter' stream assemblage that usually appeared after flow began, a 'Spring Pool' assemblage consisting of species which reproduced after flow ceased, and a 'Summer Terrestrial' assemblage comprising taxa which invaded the drying bed. Each of these faunal units was predictable in terms of some variable, in this case season and flow. The faunal groupings distinguished on the basis of research by Clifford (1966) were, likewise, associated with particular seasons and conditions in the channel.

The five hydrological phases identified at the outset of this study (Chs 1 and 5) were initially based only on surface water conditions, and were not linked to any seasonal variables or other external influences. The absence of seasonal or cyclical trends in flow and in faunal character was illustrated by the variability of the fauna over three consecutive midsummer periods (Ch. 4). However, certain environmental variables such as air temperature, day length etc. followed consistent and predictable seasonal patterns. The resemblance in fauna collected in similar hydrological conditions *and* time of the year (and the dissimilarity between fauna from same hydrological conditions but different times of year) suggested that time of year was an additional factor shaping fauna. Further, it was acknowledged that there was only a partial association between *present* surface water conditions and the biota, and that an understanding of the full effect of hydrology on biota required the acknowledgement of immediately previous (antecedent) hydrological conditions in the river, and their duration. Finally, invertebrates collected in certain of the biotopes included in the study (particularly marginal vegetation and pools) showed reasonable consistency, even sometimes across a range of different hydrological conditions. The character, heterogeneity and availability of habitat (in the form of biotopes) was accordingly added to the list of faunal modulators (Chs 3 to 5). Twelve sub-phases were identified on the basis of two of these three auxilliary influences - time of year (winter/summer) and antecedent conditions.

Physical changes wrought by each of the five hydrological phases clearly affected biota (to varying extents), and there were significant differences between phases. However, high faunal variability *within* phases and the presence of many taxa in more than one phase meant that the fauna of each phase could not be considered distinct. They were nonetheless considered to be ecologically meaningful units, in the sense that each represented a distinct hydrological state and was identifiable to some extent with 'core' (nucleus) and 'peripheral' groups of taxa (Ch. 4).

The effects of time of year and antecedent hydrological conditions were also clear from analyses of sub-phases, many of which were also shown to differ significantly in terms of their fauna. Summer and winter samples from the same phase (e.g. POOLS) may have been similar compositionally, but summer samples generally showed higher diverisities, reflecting an abundance of developing larvae. Further, invertebrates present during ONSET periods preceded by POOLS period differed from that found in ONSET phases preceded by DRY conditions.

The most distinctive faunas were collected during the DRY phase and the FLOW phase, both of which were significantly different to the majority of the other phases. The hydrological changes occurring in the other three phases did not affect fauna to as great an extent. During the NO FLOW phases, the SIC biotope disappeared, and generally only rheophilic taxa (e.g. simuliids, hydropsychids) were lost from the fauna - this did not represent a substantial decrease in diversity (to the contrary, faunal diversity sometimes increased during this phase). With continued drying, connectivity between surface water habitats was lost (POOLS phase) and areas of SOOC were generally exposed. In the early POOLS phase, diversity of fauna remained initially high, however this declined rapidly with evaporative water loss and decreasing pool volume (e.g. during December 1994, see Chs 3,4).

The ONSET phase had variable effects on the fauna, depending on the conditions under which flow commencement occurred (i.e. into a dry or semi-wet channel). Diversity measures were generally affected positively following recommencement of flow, and within a month faunal diversity was high, with representatives of all the major aquatic invertebrate groups present in the river (Chs 3 to 5). Where initial flows were into a channel filled by pools, the fauna collected during the ONSET period showed some similarity to that of the late POOLS phase (Chs 3 to 5). The similarity between samples from the two phases demonstrated a measure of resistance to the disturbance caused by flow commencement (sensu Grimm and Fisher 1989). Early POOLS phase samples most closely resembled NO FLOW samples (these also represented consecutive phases).

The faunas of FLOW and DRY periods were most distinctive in terms of their fauna - the former because of the high numbers of taxa collected and the rheophilous species restricted to these conditions (e.g. hydropsychids, simuliids, certain baetids); the latter because of the extremely low number of taxa, rather than their preference for the conditions (all these taxa were residents and thus common to most phases).

8.3.6 What is the range and variability of invertebrates in different temporary rivers with different hydrological regimes within the Eastern Cape ?

A faunal comparison can be considered at different scales, for example between streams with different flow regimes in the same catchment (e.g. Delucchi 1988, Dance and Hynes 1979), between temporary river systems in the same region (e.g. Boulton and Suter 1986), and between different temporary rivers and temporary/permanent rivers in different parts of the same country.

Delucchi (1988) attributed differences in community structure between sites with different flow regimes to a number of factors, including differences in current speed, substratum, stream size, and length of the dry period. She commented that some of the common adaptations of stream organisms (e.g. timing of developmental stages, desiccation-resistant eggs, colonisation abilities etc.) may reduce the expected differences in community structure between the fauna of temporary and permanent stream sites.

Results of quarterly surveys of six temporary-river sites with various hydrological regimes indicated high overlap and similarity at a family-level, but significant differences between most sites at lower taxonomic levels (though upper and lower sections of one river showed high similarities). Thus, the null hypothesis of 'no differences between sites' was rejected for detailed taxonomic-level information, but could not be rejected for family-level data. This indicated that, at coarse taxonomic resolution, there was an identifiable fauna for the temporary rivers in the Eastern Cape. However, at finer scales (e.g. genus and species), the biota of the different rivers and/or sites was *relatively* distinct, with - again - a small core of taxa common to the majority of them.

The five sites differed chiefly in terms of their flow regimes and salinities. At the lower Bushmans and Fish River tributary sites, salinity (measured as electrical conductivity) reached over $800 mS.m^{-1}$ during low-rainfall months. When conductivity values for all sites over the full study were overlaid on the corresponding biotic ordination, they showed similar trends to those shown by the biota, suggesting that salinity was a factor in biotic organisation. This was further emphasized at high-conductivity sites when faunal diversity increased during high rainfall months when salinities were substantially reduced (but still $> 300 mS.m^{-1}$). During these periods, diversities and abundances of fauna in the lower Bushmans River pool were greater than or equivalent to those of the lower Kowie River site where flow was present (Ch. 6).

Samples from sites were divided into three hydrological 'categories': temporary under no-flow conditions, temporary under flow conditions, temporary under almost continual flow. At the family level, there was considerable overlap of families in the three hydrological categories, with 61% overlap between temporary conditions with and without flow, 58% overlap between temporary conditions with almost continuous flow and without flow, and 45% similarity between temporary conditions with flow and those with almost continuous flow.

No families were specific only to temporary conditions, and only tricorythid and heptageniid mayflies were restricted to almost-continuous flow conditions. The unexpected presence of simuliids at all sites, even those in which flow was rare (e.g. Fish River tributary, lower Bushmans River) was attributed to their transport in seepage or drift.

Faunal studies of this nature indicate that both geo-physical and hydrological context plays a major role in shaping faunal character, and that diversity (especially when recorded as 'number of taxa') provides relatively little information about the nature of influences on an ecosystem. For example, while high diversities at the lower Bushmans River were attributed at least in part to habitat duration and hydrological stability, similarly high diversities at the upper Kowie sites were attributed to habitat heterogeneity and hydrological instability (6.5). Thus, while disturbance frequency may be high at one site and low at another, effects on diversity may, paradoxically, be similar.

The different results obtained in analyses at the different taxonomic levels may be rather obvious, however they indicate that the use of coarse taxonomic levels alone is insufficient in studies of this nature (biological monitoring has far less rigorous requirements and serves only to 'blow the whistle' when conditions are deteriorating). Findings raise a significant question to the biomonitoring fraternity - are too many inferences being made about the state, character, or faunal comparability of rivers on the bases of infrequent, family-level analyses?

8.3.7 How do the faunas of different temporary and perennial rivers (natural and modified) in different geographical regions of South Africa compare ?

While certain authors have found the fauna of temporary waters more allied to that of lentic systems than to that of running waters (Williams & Feltmate 1992), others have recorded the similarity between the temporary and permanent river fauna in nearby rivers. Boulton and Suter (1986), in their study of two intermittent rivers in Victoria, Australia, commented on the similarity of fauna found in these systems to that 'typical' to nearby permanent systems. They warned that their findings contrasted to studies elsewhere in Australia (e.g. Towns 1985). Williams and Hynes (1977), working in Ontario, found only 11.3% faunal overlap between a permanent stream and one of its temporary tributaries; and 13.3% faunal similarity between a temporary stream and a permanent stream only 200m apart. In another study in Ontario (Dance and Hynes 1979), high numbers of chironomid midges were found in two tributaries of the same river - one temporary and the other permanent. Differences between the two faunas were only clear, however, at the level of sub-family: only certain Chironominae and Tanypodinae occurred in the temporary tributary, while Diamesinae and Orthocladiinae were found in the permanent stream.

In this study, various natural and modified temporary and permanent river fauna were compared at coarse taxonomic levels (Ch. 7). At this resolution, overlap in fauna was higher between certain temporary and perennial rivers in the same region, than between temporary rivers of different regions (see Figs. 7.2, 7.3). Within the same region, temporary and perennial rivers were shown to have similar numbers of taxa and faunal composition at these coarse taxonomic levels. In the tropical Mpumalanga (formerly Eastern Transvaal) region, certain of the temporary rivers - all of which were perennial in their natural state - were close to 90% similar to perennial rivers in terms of their fauna, and in fact showed marginally higher numbers of taxa (at these coarse taxonomic levels). In the semi-arid Eastern Cape region, greatest similarity (> 60%) was recorded between the biota of an intermittent river with highly variable hydrology, and a formerly-intermittent river presently in a state of continual flow due to import of water. The small intermittent river, again, had higher numbers of taxa.

While none of these findings can be considered definitive (due to different methods of investigation and levels of identification in the varous rivers), they point to a number of issues, many of which would benefit from further research.

- **The influence of geographic location**

Where perennial and temporary rivers were subject to similar latitudinal, climatic, and geo-physical influences, fauna were similarly diverse, and indeed compositionally similar with respect to *certain* families, genera and species.

Hildrew and Giller (1992) noted that *'species richness in any one stream is dependent, proximally, on density-independent processes that control extinction and recolonization rates, and ultimately, on biogeographic processes determining the regional species pool'.* The natural diversity and species richness in an area may itself, over the *short term,* be resistant or resilient, as a result of the adaptation of species to the environment over geological time. But, as Hildrew and Giller (1992) again pointed out, *'clearly, stream communities track average environmental conditions over time, and are fragile in the face of such sustained perturbations'.* Investigations of the responses of biota to modifications, along the lines of that conducted by O'Keeffe and de Moor (1988) on the Great Fish River, are critical to our understanding of the effects of flow transformation.

- **Diversity versus composition**

Some of the families or orders collected in perennial rivers were absent from, or scarce in, temporary rivers (e.g. plecopterans, tricorythid mayflies, heptageniid mayflies, hydropsychid trichopterans). Diversity at these taxonomic levels may thus have been marginally lower in the temporary rivers, as suggested by Williams (1996). However, the majority of groups were present, and in temporary rivers, certain families were better represented in terms of genera (e.g. chironomids, dytiscids, hydrophilids). The use of 'diversity' in comparison of systems is a double-sided coin, on the one hand providing a useful index of the condition of a system, but on the other hand generating the somewhat misleading notion that equivalent diversity implies equivalence in community composition and dynamics. The focus on taxonomic composition is a far more meaningful one, and - although rapid, coarse taxonomic-level investigations are becoming more common (Clarke and Warwick 1994) and possibly more acceptable than previously - at the scale of the individual organism, *only the species-level is of ecological relevance* (particularly in terms of resistance/resilience in the face of anthropogenic disturbance). A great deal of work is required on the life-history, ecology and taxonomy of southern African river invertebrates. While this thesis was aimed at broad-level investigations of temporary rivers, and was thus constrained to coarser-resolution analyses, this type of research would be substantially enhanced by autecological investigations into the groups of taxa particularly characteristic of temporary rivers (e.g. chironomids).

- **The worst scenario**

The modification of perennial rivers to temporary (in part) may not (depending on the extent of modification) result in negative effects on faunal diversity, but would, over time, be likely to shift the species balance in the direction of a more resilient taxa, with a possible loss of more stenotypic species. Where a suitable source of colonisers remains (e.g. a nearby perennial river), chances are that many of the taxa 'lost' from the modified river would opportunistically colonise it during periods of flow, from these sources. A different scenario may play out in rivers in semi-arid areas, where sources of colonists may be few and distant.

However, river alterations do not just affect flow, and the numerous 'ripple effects' of modifications (e.g. sedimentation, loss of habitat, alteration of channel form, introduction of species etc. etc.) could have major consequences for biota. For the rivers of semi-arid zones, in particular temporary rivers, it seems the greatest danger facing biota is the loss of flow variability. Unfortunately, there are few data to support the probability that persistence of many species in these rivers relies on the maintenance of intermittency (Boulton *et al.* in press).

Taxonomic composition of the fauna is often more instructive than the diversity of the system. In the upper Kowie, the greatest diversity and abundance was recorded in the chironomid fauna, and the majority of other taxa were collected in low numbers (< 10 individuals per sample), although simuliid density was sometimes high during raised flow. As discussed, other groups represented by several taxa included predaceous dytiscids and odonates, other dipterans, and gastropods. In contrast, in the perennial sections of the Buffalo, most abundant taxa recorded were the larvae of typically rheophilous species: *Afronemoura* spp. stoneflies, *Adenophlebia auriculata* mayflies, *Goerodes caffrariae* caddisflies, and *Simulium dentulosum* blackflies (Palmer and O'Keeffe 1991). Williams (1996) suggested that useful future research on temporary streams may investigate the success of groups such as Chironomidae and Tipulidae, and the relatively poor representation of Plecoptera, brachyceran Diptera and Odonata (although this group was relatively well-represented in the upper Kowie River, as discussed).

The difference in the components of the fauna of the temporary and permanent rivers seems to point to a hardy fauna comprising both opportunists and taxa well adapted to flow variability in the temporary river (e.g. Winterbourn *et al.* 1981); and a more sensitive fauna showing biotope preferences (Palmer *et al.* 1991) and less adaptability to flow variability in the permanent river. Davies *et al.* (1995), however, suggest that 'many' southern African systems (temporary rivers are not specified) comprise hardy opportunists, able to exploit suitable habitats between catastrophic floods and droughts, and with sufficient life-history adaptations to survive adversity. This statement may indeed apply to many perennial as well as temporary rivers, and this illustrates the importance of viewing temporary and perennial rivers along a continuum, particularly when considering fauna at a large temporal scale. As Williams (1996) points out, it is possible that the fauna of temporary rivers is not as species-poor and distinct from permanent river fauna as previously thought.

REFERENCES

Boulton, A.J. and Lake, P.S. 1990. The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology* **24:** 123-141.

Boulton, A.J. and Lake, P.S. 1992a. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology* **27**: 99-121.

Boulton, A.J. and Lake, P.S. 1992b. The macroinvertebrate assemblages in pools and riffles in two intermittent streams (Werribee and Lerderberg Rivers, southern central Victoria.) *Occasional Papers from the Museum of Victoria* **5:** 55-67.

Boulton, A.J. and Suter, P.J. 1986. Ecology of temporary streams - an Australian perspective. In: De Deckker P, Williams W.D. (eds). *Limnology in Australia*. Council for Scientifiic and Industrial Research, Dr WW. Junk, Melbourne. pp. 486-96.

Boulton, A.J., Sheldon, F., Thoms, M.C. and Stanley, E.H. (in press). Problems and constraints in managing rivers with contrasting flow regimes. ..

Brown, D.S. 1980. *Freshwater snails of Africa: and their medical importance.* Taylor and Francis Ltd., London.

Clarke,K.R. and Warwick, R.M. 1994a. *Change in marine communities - an approach to statistical analysis and interpretation.* Plymouth Marine Laboratories, Bournemouth.

Clifford, H.T. 1966. The ecology of invertebrates in an intermittent stream. *Investigations of Indiana lakes and streams* **7:** 57-98.

Dance, K.W. and Hynes, H.B.N. 1979. A continuous study of the drift in adjacent intermittent and permanent streams. *Archiv für Hydrobiologie* 20: 349-406.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* Water Research Commission Report No. TT62/93.

Davies, B.R., O'Keeffe, J.H. and Snaddon, C.D. 1995. River and stream ecosystems in southern Africa: Predictably unpredictable. In: C.E. Cushing, K.W. Cummins, G.W. Minshall. *Ecosystems of the World 22. River and Stream Ecosystems.* Elsevier Publishers, Amsterdam. PP. 537-599.

Day, J.A. 1990. Environmental correlates of aquatic faunal distribution in the Namib Desert. *In:* M.K. Seely (ed.). *Namib ecology: 25 years of Namibian research.* Transvaal Museum Monograph No 7. Transvaal Museum Pretoria. pp. 99-107

Delucchi, C.M. 1988. comparison of community structure among streams with different temporal flow regimes. *Canadian Journal of Zoology* **66:** 579-586.

de Moor, Dr F. Personal Communication. Albany Museum, Aquatic Invertebrates. Grahamstown, South Africa.

Eekhout, S., Brown, C.A. and King, J.M. 1996. National Biomonitoring Programme for Riverine Ecosystems: Technical considerations and protocol for the selection of reference and monitoring sites. NBP Report Series No.3, Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Grimm, N.B. and Fisher, S.G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of North American Benthological Society* **8** (4): 293-307.

Harrison, Dr A.D. Personal Communication. 111a Berg Road, Fish Hoek 7975, South Africa.

Harrison, A.D. (unpublished). Taxonomic information relating to the family Chironomidae in Southern Africa. Available on Website, address: http://www.ru.ac.za/departments/zooento/Martin/ Aquatics.html.

Harrison, A.D. 1978. Freshwater invertebrates (except molluscs). *in:* M.J.A. Werger and A.C.van Bruggen (eds). Biogeography and ecology of southern Africa. *Monographiae Biologicae* **31:** 1139-1152.

Harrison, A.D. and Elsworth, J.F. 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part 1. General description, chemical studies and main fatures of the flora and fauna. *Transactions of the Royal Society of South Africa* **35:** 125-226.

Hildrew, A.G. and Giller, P.S. 1992. Patchiness, species interactions and disturbance in the stream benthos. *In:* P.S. Giller, A.G. Hildrew, and D.G. Raffaelli (eds). *Aquatic ecology scale, pattern and process.* Blackwell Science.

McCafferty, W.P. 1981. *Aquatic Entomology.* Jones and Bartlett Publishers, Boston.

Minshall, G.W. and Minshall, J.N. 1978. Microdistribution of benthic invertebrates in a rock mountain (USA) stream. *Hydrobiologia* **55** (3): 231-249.

Minshall, G.W. 1988. Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* **7** (4): 263-288.

Minshall, G.W. 1984. Insect substratum relationships. *In:* V.H. Resh and D.M. Rosenberg (eds). The ecology of aquatic insects. Praeger Scientific, New York.

O'Keeffe, J.H. and De Moor, F.C. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research and Management* **2:** 39-55.

Palmer, C.G. and O'Keeffe, J.H. and Palmer, A.R. 1991. Are macroinvertebrate assemblages in the Buffalo River, southern Africa, associated with particular biotopes? Journal of the North American Benthological Society **10**(4): 349-357.

Pennak, R.W. 1953. *Freshwater invertebrates of the United States.* The Ronald Press Company, New York.

Power, M.E., Jean Stout, R., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Statzner, B., and Wais de Bagen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *Journal of North American Benthological Society* 7 (4): 456-479.

Reavell, Dr P. Personal Communication. Department of Zoology, University of Zululand. c/o P.O. Box 1535, Empangeni, Zululand.

Schneider, D.W. and Frost, T.M. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* **15** (1): 64-86

Southwood, R.T.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46:** 337-365.

Stehr, W.C. and Branson, J.W. 1938. An ecological study of an intermittent stream. *Ecology* **19**: 294-310.

Stanford, J.A. and Ward, J.V. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. *In:* J.R. Barnes and G.W. Minshall (eds). Stream ecology: Application and testing of general ecological theory. Plenum Press, New York.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. 1997. Ecosystem expansion and contraction in streams. *BioScience* 47 (7): 427-435.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society **8**: 36-50.

Townsend, C.R., Hildrew, A.G. and Schofield, K. 1987. Persistence of stream invertebrate communities in relation to environmental variability. Journal of Animal Ecology **56:** 597-613. 1987

Williams, D.D. 1987. *The ecology of temporary waters.* Croom Helm Ltd., Kent/ Timber Press, USA

Williams, D.D. and Feltmate, B.W. 1992. *Aquatic insects.* CAB International, UK.

Williams, D.D. and Hynes, H.B.N. 1977. The ecology of temporary streams. II. General remarks on temporary streams. *Internationale Revue der Gesamten Hydrobiologie* **62:** 53-61.

Williams, D.D. and Hynes, H.B.N. 1976. The ecology of temporary streams. I. The fauna of two Canadian streams. *Internationale Revue der Gesamten Hydrobiologie* **61:** 761-787.

Winterbourn, M.J., Rounick, J.S. and Cowie, B. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* **15:** 321-328.

RHODES
UNIVERSITY
LIBRARY