

**A PRE-IMPOUNDMENT STUDY OF THE BIOLOGICAL DIVERSITY OF THE
BENTHIC MACRO-INVERTEBRATE FAUNA OF THE SABIE-SAND
RIVER SYSTEM**

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INTRODUCTION

There is an increasing awareness of the value of lotic ecosystems to the environment, and of their importance in maintaining supplies of water for human use in South Africa today. This is due to the growing realisation that South Africa, a semi-arid and hydrologically variable land (Alexander 1985), has major water supply problems created by a rapidly growing human population, which is presently estimated at 31 million people (Walmsley in preparation), and a relatively well-developed economy (e.g. Davies & Day 1986; Ferrar *et al.* 1988; King & O'Keeffe 1989; O'Keeffe *et al.* 1989a). Urbanisation and industrialisation has led to a multitude of water users in South Africa whose national demands, based on 1990 projected estimates include: municipal (12%), industrial (7.6%), mining (2.1%), power generation (2.3%), irrigation (50.9%), stock watering (1.5%), forestry (7.5%) and environmental management (15.5%) (Department of Water Affairs 1986). The major goal of the water resource managers over the last four decades has been to harness utilizable surface water resources in order to make water available to the major sectors, mainly through the impoundment and regulation of rivers. Consequently river systems have become the primary source of water for these sectors and over 50% of South Africa's total river runoff has been impounded, giving a total reservoir capacity of $24.24 \times 10^9 \text{ m}^3$ in 1990 (Walmsley in preparation).

In 1970 it was recognised that water should also be allocated to the environment for conservation purposes (Walmsley & Davies 1991), but the Department of Water Affairs and Forestry (DWAF) has only recently seriously considered the problem of water allocation for the maintenance of ecosystem functioning (Roberts 1983; Department of Water Affairs 1986; Department of Water Affairs and Forestry 1991). However, the amount of water needed to maintain biological diversity and river processes, such as biotic production, energy flow, nutrient cycling, life cycles and the interaction of organisms and their environment, is yet to be adequately quantified.

The Kruger National Park (KNP) in the Eastern Transvaal provides a classic example of the potential conflict of interests between the industrial, agricultural and domestic sectors and conservation. The KNP is situated on the north-eastern border of South Africa and receives the flow of six rivers (Figure 0.1), all of which originate outside the jurisdiction of the Park authorities. Thus, there are demands for water outside the boundaries of the KNP from other sectors of South Africa, as well as several self-governing states that have been set up as political entities within South Africa (see Chunnett, Fourie & Partners 1987, 1990). Due to human development of catchments there has been regulation of these rivers, which are rapidly changing in terms of their flow régimes (O'Keeffe & Davies 1991). For example, the Letaba and the Luvuvhu rivers have both changed from perennial to annual flow régimes (O'Keeffe & Davies 1991), a condition which is detrimental to the maintenance of river ecosystem functioning, while the Crocodile River has been regulated to an almost unvarying flow of *ca* $5\text{m}^3\text{ s}^{-1}$ (O'Keeffe & Davies 1991).

Recognising the need to address the problem of water allocation to the KNP, the Department of Water Affairs (DWA) convened a workshop on minimum flow needs for the environment in 1987 (Bruwer in press). Although tentative values were suggested for minimum flows, the value of the workshop was its recognition of the need for more research into the problem. Such research is currently being undertaken under the auspices of the multi-disciplinary KNP Rivers Research Programme. The goal of the programme is to "...develop the means to predict the impact on the KNP river systems of changing flow régimes and water quality as the basis of a protocol for managing the allocation of water for ecological purposes" (Kruger National Park Rivers Research Programme 1990).

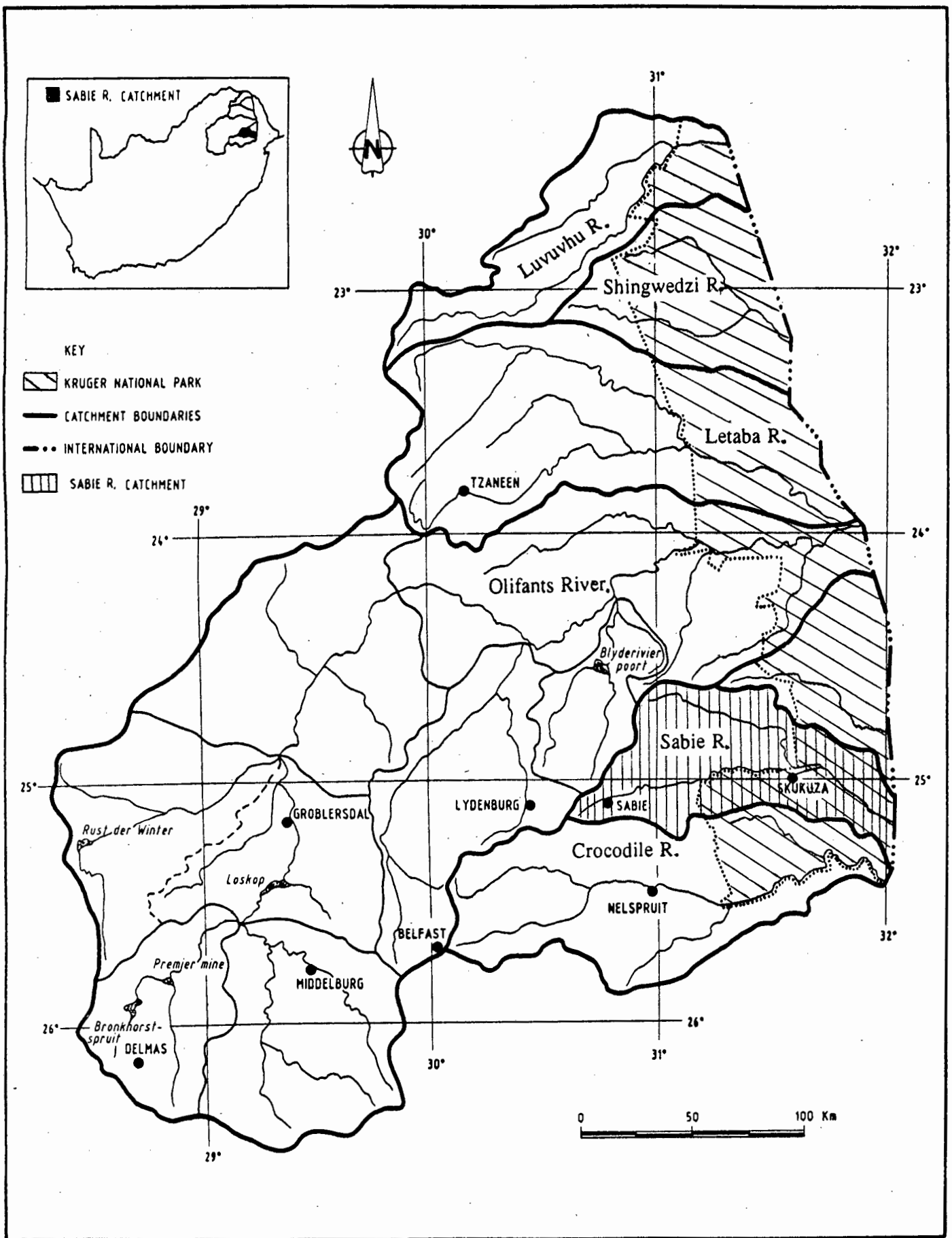


FIGURE 0.1. Map showing the catchments of the six major rivers flowing through the Kruger National Park. The inset shows the placement of the catchments within South Africa. (Adapted from Moore *et al.* 1991).

One of the studies initiated within this programme was a pre-impoundment study of the Sabie River, including its main tributary, the Sand River, which together are referred to as the Sabie-Sand River system (see Figure 0.1). It is the only system in the KNP remaining unregulated and perennial (Davies 1979; Bruwer in press), and the only major river system in South Africa which has not yet been impounded. Due to its pristine character, the Sabie River has also been identified as perhaps the most important river for nature conservation in South Africa (Chutter & De Moor 1983; Moore & Chutter 1988; O'Keeffe *et al.* 1989a; Davies *et al.* in press; O'Keeffe & Davies 1991; Davies & O'Keeffe unpublished). Its biota is apparently undisturbed and, at the moment, its waters are relatively unpolluted (Chunnett, Fourie & Partners 1987, 1990; Davies & O'Keeffe unpublished).

In spite of the conservation value of the Sabie-Sand system, eight dam sites have been identified for future development (Chunnett, Fourie & Partners 1987, 1990) and, although not all eight will necessarily be built, there is a real need for more information on the present condition of the river and on the possible effects of impoundment. The present ecological database for the river system within, and outside, the KNP is sparse (e.g. Hughes 1966a, b; O'Keeffe 1985; Moore & Chutter 1988), and requires expansion in order to be useful as a future management tool.

This thesis deals with one aspect of the Sabie-Sand River system: the biological diversity of the macro-invertebrate riffle/rapid fauna before impoundment. Macro-invertebrates and their diversity have previously been used to assess water quality in rivers (Hynes 1960, 1964) as well as for the biological classification of river sites (Wright *et al.* 1984, 1988, 1989). Gore & Judy (1981) have suggested that benthic macro-invertebrates may also have narrower tolerances to flow changes within a river and, therefore, may be good

indicators, not only of changes in water quality, but also of discharge fluctuations after impoundment (Ward 1984). Chutter *et al.* (in press) have suggested that the riffle habitat is most susceptible to a decrease in flow and, therefore, the riffle/rapid fauna would be particularly sensitive to a change in the flow régime. They are also easily monitored for the purpose of long-term studies and have, therefore, been chosen as the subject of this pre-impoundment study.

Thus, the aims of this thesis are threefold:

- to carry out a preliminary survey of the benthic macro-invertebrate fauna, and to determine the influence of environmental factors on these communities;
- to measure the biological diversity in different reaches over one year, with special reference to the differences in diversity between those reaches and between the Sabie River and its major tributary, the Sand River, as well as below their confluence, and
- to attempt to assess the applicability of accepted measures of biological diversity to river ecosystems.

CHAPTER 1

LITERATURE REVIEW: A SOUTH AFRICAN PERSPECTIVE ON RIVER ECOSYSTEMS AND BIOLOGICAL DIVERSITY

<i>Simulium</i> spp.	201.8	0.0	5.98	29.92
Baetidae sp.A. (juv.)	297.8	1.3	5.95	37.89
Tipulidae sp.B.	61.9	0.6	4.71	44.20

Average dissimilarity between B2 and E, $\delta = 74.70$

Taxon	Mean abundance m ⁻²		δ_i	$\Sigma \delta_i \%$
	Group B2	Group E		
Chironomidae spp.	3792.1	221.2	8.71	12.53
Diptera sp.A.	107.6	0.5	5.20	20.01
<i>Caenis</i> spp.	257.8	18.3	4.36	26.27
Hydracarina spp.	109.5	8.0	4.10	32.17
Elmidae sp.A.	96.5	11.7	3.48	37.17
<i>Bezzia</i> sp.	39.3	5.2	3.18	41.74
<i>Baetis</i> spp.	47.7	0.3	2.96	46.00

INTRODUCTION

The human population of the world passed the 5 billion mark in 1987 and is expected to increase by another 3 billion by the year 2025 (World Resources Institute 1987). Human activities are progressively eroding the earth's capacity to support life, while the increase in population will dramatically increase the pressure on the planet's resources over the next twenty years (World Resources Institute 1990). Phenomena, such as the depletion of the ozone layer, global warming, species extinctions, and starvation of the masses in many third world countries all provide evidence of an imbalance between human activities and the utilization of the earth's resources (e.g. Roberts 1988; IUCN 1989).

One of the greatest concerns of environmentalists during the last decade has been the impact of human activities on natural habitats and on biological species (IUCN 1980; McNeely *et al.* 1990; IUCN 1991b). Ecologists have introduced the umbrella term, "biological diversity", to encompass the variety of these habitats and the species within them. Indeed, it is a term that is receiving increased usage in biological resource research and management (Magurran 1988; Huntley 1989) as we face the problem of conserving the world's diversity.

In a recent IUCN review, McNeely *et al.* (1990) made statements on issues such as the value of and the approaches to conserving biota and on the strategies, action plans, priorities and information requirements of conserving biological diversity. They stated that "...biological diversity provides the foundation for further progress in enhancing the productivity of our planet, on a sustainable basis" (McNeely *et al.* 1990), and, therefore,

research into and the management of biological diversity should be given top priority by all conservation bodies.

South African nature conservation authorities have subscribed to the IUCN Conservation Strategy (1980; 1991b) and have also issued statements of intent with respect to conserving biological diversity (National Parks Board 1987; Huntley 1989). Despite such statements, however, there is little evidence to show that sufficient attention has been given to developing the required understanding of biological diversity and its management (Huntley 1989). For example, an analysis of South African literature reveals that little attention has been given to the questions of measuring and managing biological diversity of river ecosystems (Noble & Hemens 1978; O'Keeffe 1986a, b; Braune & Rogers 1987; Ferrar *et al.* 1988; O'Keeffe *et al.* 1989a). This paucity is also apparent in the international literature (e.g. Magurran 1988; McNeely *et al.* 1990; Stuart *et al.* 1990).

This review deals with both the complexities of river ecosystems and biological diversity.

It:

1. attempts a broad approach at defining biological diversity, and some common terminologies connected with it;
2. outlines the complexities of river ecosystems, both natural and regulated;
3. discusses macro-invertebrate communities as targets for research in biological diversity;
4. discusses river management objectives in relation to biological diversity;
5. discusses the measurement of biological diversity in general, and
6. outlines possible procedures for the measurement of biological diversity in river ecosystems.

BIOLOGICAL DIVERSITY

Comprehensive reviews on the subject can be found in several seminal publications (e.g. Pielou 1975; Whittaker 1975; Magurran 1988; Huntley 1989; McNeely *et al.* 1990). These, and others, give an array of terminologies that can be confusing. In defining and developing an understanding of what is meant by biological diversity in rivers I wish to emphasize the following points:

- I. The term "biological diversity" (also known as "bio-diversity" or "biotic diversity" encompasses the degree of nature's variety and includes:
 1. *genetic diversity* - the sum of genetic information contained in individuals and in populations;
 2. *species diversity* - the variety and abundance of living organisms;
 3. *ecosystem diversity* - the variety of habitats, biotic communities and ecological processes.

All three categories are interrelated, but for the purpose of this study I shall focus on the last two.

- II. Species diversity encompasses not only species richness (i.e. the number of species present), but also the abundance of species (evenness of distribution).
- III. The definition of the community or habitat with which one is dealing is critical to the measurement of biological diversity (Magurran 1988). Whittaker (1977) proposed a system, known as inventory diversity by which communities or habitats could be

categorised. He introduced four levels, including:

point diversity - sample diversity;

alpha diversity - diversity within a specific habitat;

gamma diversity - diversity within a geographical area;

epsilon diversity - diversity within a region.

Another form of diversity is differentiation diversity (or diversity along a gradient).

This can be split into three categories:

pattern diversity - diversity between samples (Magurran 1988);

beta diversity - diversity between habitats (Pielou 1975);

delta diversity - diversity between geographical areas (Magurran 1988).

IV. Species diversity and ecosystem diversity are integrally associated and are correlated in that a high habitat diversity, which is incorporated in the definition of ecosystem diversity, generally means a high species diversity (Pielou 1975; Whittaker 1977; Stutzner & Higler 1985).

RIVER ECOSYSTEM STRUCTURE - NATURAL AND REGULATED

In his review of stream ecosystem theory, Minshall (1988) states that spatial and temporal dimensions provide the basis of river ecosystem structure. Ward (1989) takes this concept one step further, suggesting that the river ecosystem is four-dimensional, including three spatial dimensions and one temporal dimension. This gives river

ecosystems a high level of spatio-temporal heterogeneity, with changes occurring longitudinally, laterally, vertically and with time (Ward 1989). The problem facing both researcher and resource manager is one of measuring biodiversity within the context of these dimensions.

Spatial dimensions

A river comprises longitudinal, lateral (cross-sectional) and vertical components which create a complex three-dimensional system within which biodiversity requires examination, understanding and management.

The longitudinal component

A river traverses multiple geographical boundaries, all of which introduce numerous factors such as altitude, climate, topography, geochemistry, hydrology and catchment land-use, which in turn influence the distribution of species, communities and habitats (see Minshall *et al.* 1983). One of the key concepts dealing with the longitudinal structure and functioning of river ecosystems is the River Continuum Concept (RCC) of Vannote *et al.* (1980). Due to the importance of the concept in the growth of an understanding of how streams and rivers function (Minshall *et al.* 1985), and the controversy that has built up around it, it is necessary to discuss the concept in greater depth.

The RCC considers the whole fluvial system as a continuous drainage basin gradient (e.g. Cummins 1979; Vannote *et al.* 1980; Cummins *et al.* 1984; Naiman *et al.* 1987; O'Keeffe *et al.* 1989a, b). It states that, from the headwaters to the mouth of *any* river, there is a gradient of physical conditions that elicits a series of responses within the constituent populations, which in turn result in a *continuum* of biotic adjustments and consistent

patterns of loading, transport, utilization and storage of organic matter along the length of the river (Vannote *et al.* 1980). Headwaters tend to be heterotrophic, detrital-based systems, relying on allochthonous inputs of organic material for their energy (Cummins 1979; Ward *et al.* 1984; Davies & Day 1986; Lake *et al.* 1986; Ward & Stanford 1987). The system subsequently becomes more autotrophic downstream, with an increased production of autochthonous organic material (e.g. Cummins 1979; Lake *et al.* 1986; Ward & Stanford 1987; Davies & Day 1989). Thus, the processes in the downstream reaches are directly linked to those of the upstream reaches (e.g. Cummins 1979; Cushing *et al.* 1980; Minshall *et al.* 1983; Cummins *et al.* 1984; Naiman *et al.* 1987; Byren & Davies 1989).

The validity of the concept has generated considerable debate (e.g. Winterbourn *et al.* 1981; Barmuta & Lake 1982; Ward *et al.* 1984; Minshall *et al.* 1985; Statzner & Higler 1985; Lake *et al.* 1986; Naiman *et al.* 1987; Ryder & Scott 1988; Williams 1988; O'Keeffe *et al.* 1989a); the major criticism of the concept being that the RCC may not be as globally applicable as suggested (Winterbourn *et al.* 1981; Williams 1988).

The concept was originally hypothesised for all rivers, although many studies which incorporated the concept were based in the Northern Hemisphere (e.g. Culp & Davies 1982; Bruns & Minshall 1985; Naimann *et al.* 1987; Benke & Meyer in press). It gave an holistic view of stream ecosystem structure and functioning (Minshall *et al.* 1985; Naiman *et al.* 1987). However, Winterbourn *et al.* (1981) suggested that Southern Hemisphere rivers differ from those in the Northern Hemisphere because of the inherent differences between the two Hemispheres (see Davies and Walmsley 1985), and because Southern Hemisphere rivers are more stochastic and are prone to more extremes of drought and

flood. Consequently they tend to exhibit an unstructured biota of hardy opportunists (e.g. Winterbourn *et al.* 1981; O'Keeffe 1986a; O'Keeffe *et al.* 1989a). This viewpoint is supported by other studies relating to Southern Hemisphere stream ecosystems (e.g. Barmuta & Lake 1982; Lake *et al.* 1986; Bunn *et al.* 1986; Boulton & Lake 1988). Statzner & Higler (1985) challenged the RCC, by questioning the five basic tenets, namely:

- the energy equilibrium of the physical system and its biological analogue;
- trophic patterns;
- temporal sequencing of species replacement and utilization of energy inputs;
- time invariance and absence of succession, and
- patterns of biological diversity.

They argued that the tenets are open to interpretation, some need extension, while others cannot be verified with the current state of knowledge. However, the utility of the RCC lies in the identification of a set of general conditions and relationships that can be used to study and compare stream systems (Statzner & Higler 1985; Naiman *et al.* 1987; Ryder & Scott 1988) - it is not intended as a description of biological components of all rivers in an individualistic context (Minshall *et al.* 1985).

The lateral component

The lateral component includes the form and dynamics of the channel itself, and the interactions between it and the catchment (Ward & Stanford 1989). Depending on geomorphological characteristics, a generalised cross-sectional profile through a river reveals numerous habitats that depend on some form of river flow (Figure 1.1). These include, for example, the main channel, the riparian zone adjacent to the channel, the flood terrace, the riparian bank, and the floodplain. Within each of these habitats are

populations and communities which must be considered as part of the ecosystem, and the greater the complexity of the habitats, the higher will be the biological diversity (Whittaker 1975; Magurran 1988).

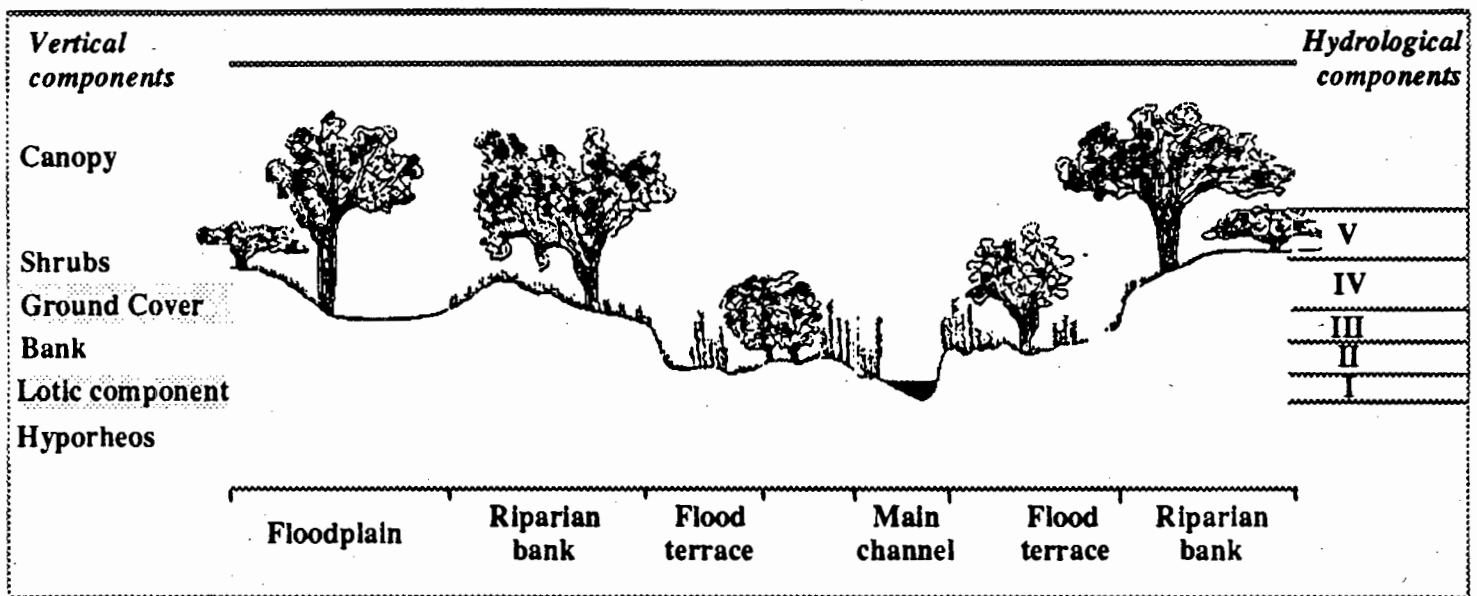


FIGURE 1.1. Generalised cross-sectional profile through a river showing the lateral and vertical spatial components. Habitats within the lateral component are marked across the bottom. The vertical component is split into habitat components (left) and hydrological components (right). (Adapted from Moore *et al.* 1991 and Bruwer in press).

The interactions between these habitats include active and passive movements of organisms between the channel and the adjacent riparian or floodplain system, as well as exchanges of nutrients and organic matter (Ward 1989). Lateral interactions are highly developed in "flood rivers" where there are extensive floodplains and predictable annual flooding.

The vertical component

Similar to the cross-sectional approach, a vertical profile of the river ecosystem (Figure 1.1) reveals several habitat types which require consideration. They range from the hyporheic and phreatic habitats (see Ward & Stanford 1987, 1989; Stanford & Ward 1987, 1988), to the river channel itself (e.g. see Cummins 1979; Godbout & Hynes 1982; Culp *et al.* 1983; Minshall *et al.* 1983; Cummins *et al.* 1984; Bescha & Platts 1986; Townsend 1989), the canopy of vegetation within the riparian zone and the floodplain (Townsend 1989; Cummins *et al.* 1984).

Bruwer (in press) separates this vertical profile into five distinct hydrological components, within each of which different species are found (Figure 1.1). The components are as follows:

- I. the depth of water needed to maintain natural pools, to replenish groundwater resources, and to sustain refugia throughout the year;
- II. the depth of water required to maintain seasonal migratory species;
- III. the depth of water required for inundation of secondary channels which are important nursery sites for fish and for other organisms. This component also replenishes the soil moisture for the riparian vegetation;
- IV. the depth of water periodically needed to maintain flushing flows and bankfull flows of the system (e.g. see Reiser *et al.* 1987), and
- V. the depth of water needed to inundate flood plains during the flood season.

Boundaries

A key aspect of the overall spatial environment is the importance of boundaries, which can be defined as "zones of transition between adjacent habitats" (Naiman *et al.* 1988).

Good examples of boundaries may include the riparian zone or the point at which a tributary enters a system. The major attribute of boundaries is that they act like "semi-permeable membranes" (Naiman *et al.* 1988) between ecological systems by modifying information and material exchange between them. As transitional zones they are extremely important in that they often display a high diversity, due to the "edge-effect" (Naiman *et al.* 1988). Communities at the boundary between terrestrial and freshwater systems (e.g. riparian forests, marginal wetlands, littoral lake zones, floodplain lakes and forests and areas with significant groundwater-surface water exchange) appear to be particularly sensitive to change and usually have a high biological diversity. It is postulated by Naiman *et al.* (1988) that these boundaries may show early responses to change and that they are therefore important areas in which to examine biological diversity.

Temporal dimensions

Minshall (1988) proposed three broad temporal components that may influence river ecosystems, viz.: short-term, medium-term and geological (see Table 1.1. and below). These components describe the time-spans through which changes to both habitats and species occur.

Short term

This scale covers a time span between seconds and several years, and includes phenomena such as circadian intervals, seasonality and life cycles. Many studies have dealt with the seasonal variation of macro-invertebrate communities in river ecosystems (e.g. Hawkins 1981; Furse *et al.* 1984; Pearson 1984; Hart 1985; Dolédec 1989; McElravy *et al.* 1989). It incorporates life history stages of organisms and is important in the

structure and functioning of river ecosystems.

Temporal variation in the short term is likely to permit even greater biological diversity if ecologically similar species operate during different seasons (temporal niche separation; Bader & Ward 1987; Townsend 1989).

TABLE 1.1. Temporal scale in stream ecosystems (Adapted from Frissel *et al.* 1986, and Minshall 1988)

MAGNITUDE (years)	TIME SPAN	DYNAMICS (Examples)	SCALE
10^{-7}	1 sec	Metabolic interaction	SHORT-TERM
10^{-6}	10 sec	Insect moves 1mm	
10^{-5}	1 - 15 min	Taking a benthos sample	
10^{-4}	15 min - 45 days	Community metabolism	
10^{-3}	45 days - 364 days	r-adapted macro-invertebrate life cycles	
10^{-2}		Leaf pack decay	
10^{-1}		Annual budgets	
10^0	1 year	Seasonal cycle	MEDIUM-TERM
10^1	10 years	Regional climatic change	
10^2	100 years	Global climatic change	GEOLOGICAL
10^3	1000 years	Development of new first order channels	
10^4	10 000 years	Channel floor downwearing	
10^5	100 000 years	Drainage network development	
10^6	1 mill. years	Tectonic and Geomorphological events	
10^7	10 mill. years		
10^8	100 mill. years		

Medium term

Medium-term phenomena cover a scale of several years to several decades. This time-span includes phenomena such as regional climatic and vegetation changes (Elliott 1990; Macdonald & Crawford 1988), and may affect the relationship between the stream and the watershed, and changes in the riparian vegetation and aquatic habitats.

Geological

Geological events can be defined as those that take place over a time-span greater than 100 years. They include global climatic shifts, continental drift, glaciation and geomorphological events. Within this definition are included two other time scales: *cyclic* time and *graded* time. Cyclic time is in the order of 1 million to 10 million years and may involve, for example, such a cyclic phenomenon as an erosion cycle (Minshall 1988), while graded time comprises scales up to 10 million years, and involves fluctuations within the system that allow it to approach a steady state equilibrium (Minshall 1988).

Space and time

Space and time function together to shape lotic communities (Minshall 1988). The key areas which influence habitats, communities and species both in time and space are discussed below.

Longitudinal movement

This incorporates both the flow of water (Minshall & Petersen 1985; LeRoy Poff & Ward 1989) and the movement of organisms (Minshall & Petersen 1985; Pearson & Jones 1987; Bergey & Ward 1989; Williams 1989; Wilzback & Cummins 1989).

The flow of water in a downstream direction imposes a spatial vector on temporal change through

the transport of biota and their by-products. It plays a large role in determining habitat diversity due to its effect on habitat parameters such as the substrata, marginal vegetation and physico-chemistry (e.g. Ward & Stanford 1983b), and therefore, it also determines the nature and diversity of the organisms in the system. A reduction in flow, relative to the natural flow régime, can result in the reduction of habitat diversity, the appearance of pest species, the desynchronisation of life cycles and, ultimately, in the elimination of part of the natural biota of the system (e.g. Ward & Stanford 1983b; O'Keeffe *et al.* 1989b).

A concept closely linked to the longitudinal movement of water in a river is the Nutrient Spiralling Hypothesis (NSH) of Webster (1975) (see also Newbold *et al.* 1982; Newbold 1987). The NSH highlights the differences between lake and river ecosystems (Ward *et al.* 1984; Ferrar *et al.* 1988). In a river, nutrients are envisaged as moving downstream in a "helical" fashion (e.g. Newbold *et al.* 1982), as they alternate between the organic and the inorganic phases (e.g. being fixed in invertebrate tissues and later released by decomposition after their death), rather than remaining in a closed cycle (e.g. Cummins 1979; Ward *et al.* 1984; Byren & Davies 1989; Davies & Day 1989). The spiralling length of an element or compound is an index of the efficiency of utilization of nutrients supplied from the watershed, since it reflects the number of times the nutrient molecule or compound is recycled within a stream reach (e.g. Ward & Stanford 1987). This concept also has applications in situations where nutrient transfer in streams is interrupted by impoundment (e.g. Armitage 1984; Ward *et al.* 1984; Newbold 1987; Ward & Stanford 1987; Byren & Davies 1989; Palmer & O'Keeffe 1990a).

Climate

Climate may be considered as "weather with a temporal axis" (Minshall 1988) and it is spatially defined on a long-term basis (e.g. global warming), but it is temporally defined on a short-term

basis (e.g. diurnal variations of light and temperature).

Scale

Scale affects both temporal (see Table 1.1) and spatial considerations and, in both cases, stretches over sixteen orders of magnitude (Minshall 1988). A change in scale may change the perception of the main controlling factors in the river ecosystem, due to different variables becoming dominant at different levels of resolution (Frissell *et al.* 1986). In many cases the scale at which stream ecologists work appears to be outside the dimensions of a given ecological interaction (Minshall 1988). Examples of this given by Minshall (1988) are the use of a single sample to characterise a habitat or a single segment to characterise a river. Therefore, in order to measure biodiversity one needs to define the scale at which one is working. Frissell *et al.* (1986) have suggested the use of a nested hierarchical model in which any particular system is partly determined by the larger scale system. For example a river may be separated hierarchically into streams, zones, segments, reaches, habitats and micro-habitats, each of which are determined by the system directly above on the hierarchy. This is useful for defining both temporal and spatial scales (see Chapter 4).

Disturbance

Disturbance is a concept which has long been recognised in ecology, but which has only recently gained prominence as a central theme in community organisation (Reice 1987). Its theory and application in determining stream community structure is discussed in detail by Resh *et al.* (1988). Disturbance may be defined as any change in the environment which exceeds the normal range of conditions experienced by a substantial number of organisms (Minshall 1988), and which may affect the "dynamic equilibrium" of the system (Huston 1979; see also Minshall & Petersen 1985). The degree of disturbance is affected by the size of the disturbed area (spatial), the magnitude

of the disturbance (spatial), the length of time for which it was disturbed (temporal) and its frequency (temporal) (Reice 1984). It may lead to an increase or to a decrease in biotic diversity depending on the severity of the disturbance. The Intermediate Disturbance Hypothesis (e.g. Connell 1978; Ward & Stanford 1983b - see also Ward *et al.* 1984; Reice 1985; Ferrar *et al.* 1988) predicts that biotic diversity will be greatest in communities subjected to moderate levels of disturbance. In this thesis disturbance refers to the extent of change, and it may be either natural or anthropogenic.

Episodic events, such as floods (Resh *et al.* 1988) and droughts (Kownacki 1985), are natural disturbances and may severely influence stream ecosystem dynamics, especially if they take place on a time scale greater than a year.

However, one of the major disturbances experienced by the river ecosystem (next to pollution, which is considered as the greatest single disturbance) is anthropogenic; it is the regulation of rivers by impoundment. Due to the lasting effect that impoundments have on rivers and the fact that the Sabie River is soon to be impounded, I have set aside a section of this review to briefly discuss the consequences of impoundment.

Effects of impoundments on rivers

Impoundment has become a cause for concern for river biologists, and the literature on stream regulation is expanding rapidly (e.g. Ward & Stanford 1979a; Lillehamer & Saltveit 1984a; Petts 1984; Craig & Kemper 1987; Gore & Petts 1989; Petts *et al.* 1989). Until recently, the ecological consequences of impoundments have played a negligible role in the decision making of the siting, design, construction and management of dams (Hellowell 1988); economic, political and social considerations have been of prime importance (Palmer & O'Keeffe, in preparation).

The regulation of running waters by impoundment has diverse manifestations (e.g. Ward *et al.* 1984; Davies *et al.* 1989), many of which are due to a discontinuity in the system. The Serial Discontinuity Concept (SDC) (Ward & Stanford 1983a) states that few stream ecosystems are uninterrupted continua but are more often regulated by dams, which are interruptions to the longitudinal gradients predicted by the RCC. These discontinuities disrupt a wide variety of biotic and abiotic processes, which require a "recovery distance" (*sensu* O'Keeffe *et al.* 1989a) to "reset" to their original state (Ward & Stanford 1983a; Stanford *et al.* 1988; Byren & Davies 1989; Davies & Day 1989; O'Keeffe *et al.* 1989a). Two parameters are used to evaluate the relative impact of impoundments on riverine structure and functioning. They are the longitudinal shift of a given variable in a stream, and the intensity of the perturbation (Ward & Stanford 1989; Stanford *et al.* 1988).

There are four types of modifications which take place due to impoundments (Palmer & O'Keeffe, in preparation). They are:

- Hydrological modifications
- Thermal modifications
- Chemical modifications
- Biotic modifications

Hydrological modifications

Hydrologically, impoundments affect rivers both upstream and downstream of the wall (e.g. Simons 1979; Armitage 1984; Walker 1985; Hadley *et al.* 1987). Upstream, an impoundment reduces the velocity of flow, increases the depth of flow and causes deposition of sediment and aggradation, which increases river-bed elevation, increasing the propensity for flooding (Buma & Day 1977; Simons 1979; Armitage 1984). Downstream, the water is clearer, due to sediment

trapping within the impoundment. This means that the water is more "silt-hungry" and tends to erode the channel more readily causing degradation (Simons 1979; Armitage 1984). This may lead to an increased gradient and a lowering of the water table (Simons 1979) as well as lowering of river-bed elevation, and to substratum hardening or armouring.

An important effect of impoundment is the dampening of seasonal flow fluctuations (Hellawell 1988). In particular, the flood régime is affected (Ward *et al.* 1984; Higgs & Petts 1988; Palmer & O'Keeffe in preparation). Flooding flushes rivers of sediment and opens the mouth to the sea. Many biological processes (e.g. fish migration and spawning) also coincide with the flooding cycle of a river (Ward *et al.* 1984) and, if mismanaged, dam releases in the wrong period may cause an imbalance in the life cycles of the biota.

In South Africa the effect of flow regulation by reservoirs has been to dampen the frequencies of medium flows and to reverse the flow seasonality of rivers (Chutter 1973; Byren & Davies 1989). However, Higgs and Petts (1988) suggest that the effect of flow regulation has usually been to increase low flows. The preferred approach when dealing with flows where releases are varied, is to maintain flow at a particular threshold to a downstream point (i.e. compensation flows; Gustard & Cole 1987; Gustard 1989).

Thermal modifications

Water temperature influences distribution, growth, maturity and emergence of stream invertebrates (e.g. Ward & Stanford 1982; Armitage 1984; Ward 1985). The temperature régime in regulated streams may be altered in five ways:

- increased diel constancy (e.g. Armitage 1984; Crisp 1987; Hellawell 1988; Byren & Davies 1989; Palmer & O'Keeffe in preparation);

- increased seasonal constancy (e.g. Crisp 1987; Puig *et al.* 1987; Hellowell 1988; Byren & Davies 1989; Palmer & O'Keeffe in preparation);
- summer cooling (e.g. Armitage 1984; Crisp 1987; Byren & Davies 1989; Palmer & O'Keeffe 1989; Palmer & O'Keeffe in preparation);
- winter warming (e.g. Armitage 1984; Crisp 1987; Byren & Davies 1989; Palmer & O'Keeffe in preparation), and
- thermal pattern changes (e.g. Armitage 1984; Gregoire & Champeau 1984; Walker 1985; Crisp 1987; Byren & Davies 1989).

Large modifications such as these may have significant impacts on seasonal timing of major biotic processes (e.g. Ward, 1982). However, the extent to which impoundment modifies downstream thermal conditions depends on operational variables (release depth and discharge patterns), limnological variables (retention times, stratification and thermal gradients) and the position of the dam along the longitudinal profile (Ward & Stanford 1983a; Ward 1985; Palmer & O'Keeffe 1989; O'Keeffe *et al.* 1990).

Chemical modifications

The most dramatic chemical changes occur in deep, stratified reservoirs. These are many and varied, and the most common are discussed below.

Nutrients: Reservoirs may act as nutrient sinks (e.g. Armitage 1984; Newbold 1987; Ward & Stanford 1987; Byren & Davies 1989; Palmer & O'Keeffe 1990a; O'Keeffe *et al.* 1990).

The effluent of many reservoirs is often lower in nitrogen and phosphorus than the influent (Soltero *et al.* 1973, Palmer & O'Keeffe 1990a), and the quality of reservoir releases depends on their timing and depth characteristics (Ward 1982; Armitage 1984; Davies *et al.* 1989). Byren & Davies (1989) found, on the Palmiet River, western Cape,

that the nutrient loads *increased* downstream of the dams, but that recovery was rapid.

Ionic concentrations: Ward (1982) observed that the influent and effluent of dams was similar in respect of ionic concentrations. However, this is not always the case, and considerable differences in the quality of influent and effluent waters may occur depending on the reservoir morphometry and retention time. The change observed by Byren & Davies (1989) was that both total dissolved solids and conductivity decreased below dam sites.

Salinity: Impoundments act as sinks for dissolved solids (e.g. Soltero *et al.* 1973; Armitage 1984). This, compounded with increased evaporation, leads to an increase in salinity in many man-made lakes (Armitage 1984). The salinity/dissolved solids cycle may also undergo a complete reversal or a delay in seasonal maxima and minima (Byren & Davies 1989; Palmer & O'Keeffe in preparation).

Oxygen: Deoxygenation is expected in hypolimnetic-release dams, due to stratification (Krenkel *et al.* 1979) but oxygen is rapidly restored in turbulent release conditions (Armitage 1984; Hellawell 1988). It is often linked to an increase in hydrogen sulphide concentrations, which may be lethal to fish. This is often a very localised effect, with rapid recovery downstream (Armitage 1984; Davies & Day 1986).

Biotic modifications

Many recent papers have dealt with the changes experienced by macro-invertebrates (Gore 1977; Armitage 1977, 1984; Davies 1979; Lillehammer & Saltveit 1984b; Armitage *et al.* 1987; Chessman *et al.* 1987; Doeg *et al.* 1987; Saltveit *et al.* 1987; Ward 1987; Ward & Stanford 1989; Bader & Ward 1988; Boon 1988; Carling 1988; Marchant 1989; Voelz & Ward 1989), plant matter (Ward 1976; Krenkel *et al.* 1979; Dufford *et al.* 1987; Ward & Stanford 1987) and fish communities (Edwards 1978; Ranta & Sevola 1984; Fraley & Decker-Hess 1987; Bain *et al.* 1988;

Russel & Rogers 1989) in regulated rivers. The most pronounced biological modification which occurs after dam closure is an increase in the density of the fauna downstream from the dam (Butorin & Monakow 1984; Palmer & O'Keeffe in preparation). The reasons for this vary from dam to dam. Deep release dams release organically-enriched water which increases productivity (e.g. Palmer & O'Keeffe in preparation), while surface-release water introduces large quantities of zooplankton (see Ward & Stanford 1979b; Palmer & O'Keeffe in preparation).

A review of the responses of benthic macro-invertebrates to stream regulation (Armitage 1984) shows that biological diversity decreases below dams. However, Palmer & O'Keeffe (1990b) found that in the Great Fish River in South Africa the relative abundance of invertebrate taxa increased. There are also alterations in community composition and feeding guilds, and pest species are often favoured (Chutter 1969; Davies 1979; Ward *et al.* 1984; O'Keeffe & De Moor 1988); and there may be an increase or decrease in the abundance of organisms, depending on the flow régime (Palmer & O'Keeffe 1990b).

Fish are also adversely affected by impoundment (Stanford & Ward 1984; Walker 1985). Their population density, growth, biomass, fecundity, production, species composition and movements change after dam closure (e.g. Edwards 1978; Ward *et al.* 1984; Fraley & Decker-Hess 1987; Bain *et al.* 1988). The fish that are most affected are diadromous and semi-diadromous species; they can no longer reach their spawning grounds (e.g. Butorin & Monakow 1984). The reduction in flow after impoundment also leads to the closure of estuary mouths, leading to loss of nursery areas for marine fish species (Ward *et al.* 1984; Whitfield & Bruton 1989).

Some typical responses of aquatic vegetation to river regulation include an increase in standing crop and total streambed cover, and invasion by angiosperms and bryophytes (Davies 1979; Ward

& Stanford 1989). Butorin & Monakow (1984) also noted that there is a considerable increase in the number of phytoplankton species and their biomass below impoundments (Talling & Rzóska 1967; Rzóska 1976).

Flow requirements of rivers

In recent years, some freshwater research has begun to examine the flow requirements of rivers (e.g. Gustard 1984; Greer 1987; Gore 1987; Orth 1987; Reiser *et al.* 1987; Scott & Shirvell 1987; Wesche *et al.* 1987; Gore & Nestler 1988; Courot 1989; Gore & King 1989; Gustard 1989; O'Keeffe *et al.* 1989b; Wolff *et al.* 1989; Wright *et al.* 1989; Gore & King unpublished a,b) and hydraulic as well as the hydrological parameters associated with riverine biota (Chutter 1969; Canton *et al.* 1984; Ranta & Sevola 1984; Statzner & Higler 1986; Gaschignard & Berly 1987; Irvine 1987; Williams & Winget 1987; Boulton & Lake 1988; Hooper & Ottey 1988; Power *et al.* 1988; Statzner *et al.* 1988; Hall *et al.* 1989; Vásquez 1989; Smith *et al.* 1990). I shall discuss this in detail, as the greatest single impact on the Sabie-Sand River system will be the future regulation and extraction of water from the system.

In the United States, the U.S. Fish and Wildlife Service has developed a documentation and computer programme system known as the Instream Flow Incremental Methodology (IFIM) (Bovee 1982). This is considered to be one of the most advanced and sophisticated of all available methodologies for instream flow assessments (Shirvell 1986; O'Keeffe *et al.* 1989b) and is used as a basis for legislated flow allocation in the United States (Gore & King unpublished a). In recent years researchers in South Africa have begun to assess the flow requirements of rivers (Ferrar 1989; King & O'Keeffe 1989). Accordingly the application of IFIM is escalating (Gore & King 1989; Gore & King unpublished a) and, if used effectively, may give information on the minimum flow requirements for a number of South African rivers. Preliminary studies have been

completed on the Eerste and Olifants rivers (western Cape) (Gore & King 1989), and on the rivers of the KNP (Bruwer in press; Gore *et al.* 1987). Future research will include more detailed research of these rivers, including the Sabie River (Dr J. King, FRU, Zoology Department, UCT, pers. comm.).

IFIM combines hydraulic and hydrological information on the flow within selected river reaches using the physical-habitat requirements of riverine organisms as indicators of ecosystem integrity (Gore & King 1989). Physical Habitat Simulation (PHABSIM2) (Milhous *et al.* 1984, 1989) is the computer model that implements IFIM, and which quantifies changes in physical habitat, with increments of flow change (Gore & Nestler 1988).

The underlying principles of PHABSIM2 are that each species is assumed to exhibit specific habitat preferences, and the range of habitat conditions it is able to tolerate can be defined for each species as "suitability-of-use curves" (Bovee & Cochnauer 1977; Gore & Nestler 1988; Belaud *et al.* 1989). For the application of PHABSIM2, both macro-habitat variables such as channel structure, water quality, temperature and sediment yield, and micro-habitat variables, including water velocity and discharge, depth and substratum composition are measured (Bovee 1982). This leads to the development of "species-suitability-criteria" for both macro- and micro-habitats. Overlaying usable macro- and micro-habitat then provides a "Weighted Usable Area" (WUA) estimate for the target species, as a function of the series of discharges under assessment.

Biological Indicators and Target Species

Organisms are adapted to live within certain environmental limits and have a wide range of tolerances to a large number of environmental parameters. These limits indicate a community's resilience, and if environmental changes exceed these limits at any point along a river, the

community structure may collapse and a new altered community structure may develop (King *et al.* 1989). This may have distinct consequences for the biological diversity within the system. Biological indicators or target species are those communities or species which are most sensitive to change within the system and it is crucial to the successful assessment of minimum flow requirements of rivers to make a prior identification of target species.

Despite the major ecological roles played by insects in aquatic habitats, their environmental requirements have only been given cursory consideration; only rarely are they considered as an integral part of habitat management (Ward 1984). Initially, IFIM was used to quantify the water requirements of fish only (King *et al.* 1989; Gore & King unpublished b), but the methodology has since been modified for invertebrate studies (Gore & Judy 1981; Gore 1987). More recent research has indicated that some riverine invertebrates may have narrower tolerances to flow changes than do many fish species, *particularly during different life stages* (Gore & Judy 1981), and a "small loss" in fish habitat may cause a "large loss" for benthic macro-invertebrates (King *et al.* 1989). Also, any imbalances in benthic community structure could lead to further decreases in invertebrate numbers, with ramifications for the complex assemblage of biota associated with a river (Gore 1987). Ward (1984) has identified possible modifications to insect communities which may occur due to a change in the flow régime. Thus, it might be important to look towards the macro-invertebrate assemblages to identify a target species.

The use of macro-invertebrate target or indicator species, and of biotic indices, have long been tools utilised in the assessment of water quality (e.g. Hynes 1960, 1964; Chutter 1972; Wright *et al.* 1988). Chutter (1972) and Washington (1984) discussed the different indices and systems that have been used to determine water quality, of which some may be useful for application in PHABSIM2. Two types of biological indicator exist: those that rely on a single indicator species

which is sensitive to change, as used in the SAPROBIENSYSTEM (Kolkwitz & Marsson 1908, 1909, cited by Chutter 1972), and diversity measures (Chutter 1972; Washington 1984), which assess a whole community. Even Beak's index (Beak 1965, cited by Chutter 1972), which looks at a whole macro-invertebrate community, like the SAPROBIENSYSTEM, relies on a subjective decision as to the sensitivity of organisms to water quality (Chutter 1972). Biological measures based on diversity, however, are less subjective and, because they do not require the organisms to be identified taxonomically, they may be used by investigators who have a limited taxonomic background (Chutter 1972).

A single sensitive species may be used to identify the threshold at which a river becomes degraded, in terms of flow and water quality. However, a diversity measure shows the extent of change, as more species are lost or gained. Chutter (1972) has stated that a diversity measure used to monitor change is based on three assumptions:

- that faunal communities of pristine streams and rivers are definable;
- that such communities change in a predictable manner, with a change in water quality,
and
- the greater the disturbance, the greater the change in the fauna.

RIVER MANAGEMENT OBJECTIVES AND BIOLOGICAL DIVERSITY

Nature conservation organisations in South Africa have all adopted the IUCN credo of preserving biological diversity (e.g. National Parks Board 1987). Because of the increased pressure being placed on water allocation and the intensive way in which water is utilized in South Africa, river ecosystems are beginning to receive more attention in this respect. For example, Venter &

Deacon (1990) state that river ecosystems are vital components of the Kruger National Park and that one of the objectives of river management is to ensure that the full spectrum of aquatic biota is conserved in the KNP rivers.

The questions arise as to the realism of this objective and the role of water resource managers and scientific researchers in achieving it.

The decision-maker requires expertise (manpower) and information from which policies, strategies and action plans can be formulated. Therefore, certain prerequisites need to be addressed. Based on McNeely *et al.* (1990) it is possible to state the following pre-requisites for the management of biological diversity in river ecosystems and possible methods by which they can be fulfilled:

- The species present in river ecosystem need to be documented. This would require the participation of researchers and the development of the taxonomic skills necessary to identify species in key communities.
- Ecological field work needs to be undertaken in order to understand the functioning of communities within specific habitats of the river ecosystem. This may include experimental studies, as well as *in situ* comparative studies, such as the assessment of the differences between disturbed and undisturbed systems.
- Once basic inventorization and an understanding of the system has been achieved, any changes in the ecosystem diversity and functioning must be monitored. This means that appropriate methodologies to quantify diversity and to monitor changes require development and utilization.
- Factors causing these changes can then be identified, and a predictive capability developed.
- Research also needs to be carried out in the social sciences to determine how biological diversity in the river ecosystem contributes to human needs. Thus, the research approach

required, before the system can be properly managed as a sustainable resource, is a multi-disciplinary one.

MEASUREMENT OF BIOLOGICAL DIVERSITY IN RIVERS

Resource managers require fast and effective methods to monitor, to measure and to assess changes in biological diversity. In a recent document by the IUCN (1991a) they state that a "...great deal of work remains to be done refining scientific understanding of biodiversity and tools for measuring its magnitude and loss".

Diversity measures

Magurran (1988) has reviewed methods of measuring biological diversity, not all of which are simple and comparable, or even applicable to river ecosystems; Tables 1.2 and 1.3 list some of the more common measures.

The tools available to measure biological diversity are essentially numerical, statistical and empirical models and indices (Magurran 1988). These include:

- species richness indices;
- species abundance models;
- species abundance indices;
- indices based both on species richness and abundance, and
- comparative measures.

TABLE 1.2. Summary of the equations and characteristics of a range of diversity statistics (adapted from Magurran 1988). See Table 1.3 for the definition of symbols

STATISTIC	EQUATION	WIDELY USED?
SPECIES ABUNDANCE MODELS		
α (log series)	$\alpha x, \alpha x^2 / 2, \alpha x^3 / 3 \dots \alpha x^n / n$	Yes
λ (log normal)	$S(R) = S_0 \exp(-a^2 R^2)$	No
Q statistic	$Q = S / 2 \log (R_2 / R_1)$	No
SPECIES RICHNESS INDICES		
S (species richness)	S = no. of species per unit area	Yes
Margalef index	$D_{mg} = (S - 1) / \ln N$	No
INDICES BASED ON BOTH SPECIES RICHNESS AND ABUNDANCE		
Shannon index	$H' = \sum p_i \ln p_i$	Yes
Brillouin index	$HB = (\ln N! - \sum \ln n_i!) / N$	No
SPECIES ABUNDANCE INDICES		
McIntosh U index	$U = \sqrt{(\sum n_i^2)}$	No
Simpson index	$D = \sum [(n_i(n_i-1) / N(N-1))]$	Yes
Berger-Parker index	$D = N_{max} / N$	No
Shannon evenness	$E = H' / \ln S$	No
Brillouin evenness	$E = HB / HB_{max}$	No
McIntosh D index	$D = (N - U) / (N - \sqrt{N})$	No
COMPARATIVE MEASURES		
Whittaker's measure	$\beta_w = S / \alpha - 1$	Yes
Wilson & Shmida's measure	$\beta_T = [g(H) + l(H)] / 2\alpha$	No
Jacard's similarity	$C_J = j / (a + b - j)$	Yes
Sorenson's similarity	$C_N = 2jN / (aN + bN)$	Yes

TABLE 1.3. Definition of symbols for the diversity equations found in Table 1.2.

αx = number of species having one individual

$\alpha x^2/2$ = number of species having 2 individuals

$S(R)$ = number of species in the Rth octave (class) to the right and to the left of the symmetrical curve

S_o = the number of species in the modal octave

σ = standard deviation

a = the inverse width of distribution ($\sqrt{2\sigma^2}$)

S = number of species

R_1 = number of individuals in the lower quartile (25%)

R_2 = number of individuals in the upper quartile (75%)

N = total number of individuals in a sample

p_i = proportion of individuals found in the i th species

n_i = number of individuals found in the i th species

N_{\max} = number of individuals in the most abundant species

$$HB_{\max} = \frac{1}{N} \ln \frac{N!}{[(N/S)!]^{S-r} \cdot [(N/S+1)!]^r}$$

$$U = \sqrt{\sum n_i}$$

α = average sample diversity where each sample is a standard size and diversity is measured as species richness

$g(H)$ = the number of species gained along the habitat transect

$l(H)$ = the number of species lost along the habitat transect

j = the number of species found at both sites

a = the number of species at site A

b = the number of species at site B

aN = total number of individuals at site A

bN = total number of individuals at site B

jN = sum of the lower of the two abundances

Species richness indices

This involves the sampling of specific habitats and the enumeration of the number of species present (inventorization). It may be expressed as:

$$S_d = \text{number of species per unit area} \quad (1.1)$$

or $S_n = \text{number of species per specified number of individuals.} \quad (1.2)$

Margalef's index, D_{mg} , combines these two by the formula:

$$D_{mg} = \frac{(S - 1)}{\ln N} \quad (1.3)$$

where S = number of species recorded,

N = number of individuals.

Species abundance models

Species abundance models contain information on the number of species and on their relative abundances, which may be described mathematically or visually. They utilize all the information and produce the most complete mathematical description of the data (Magurran 1988). They may be summarised as rank abundance plots (Figure 1.2), and their curves can follow 4 distribution types:

- the broken stick distribution;
- the log normal distribution;
- the log series distribution, and
- the geometric series distribution.

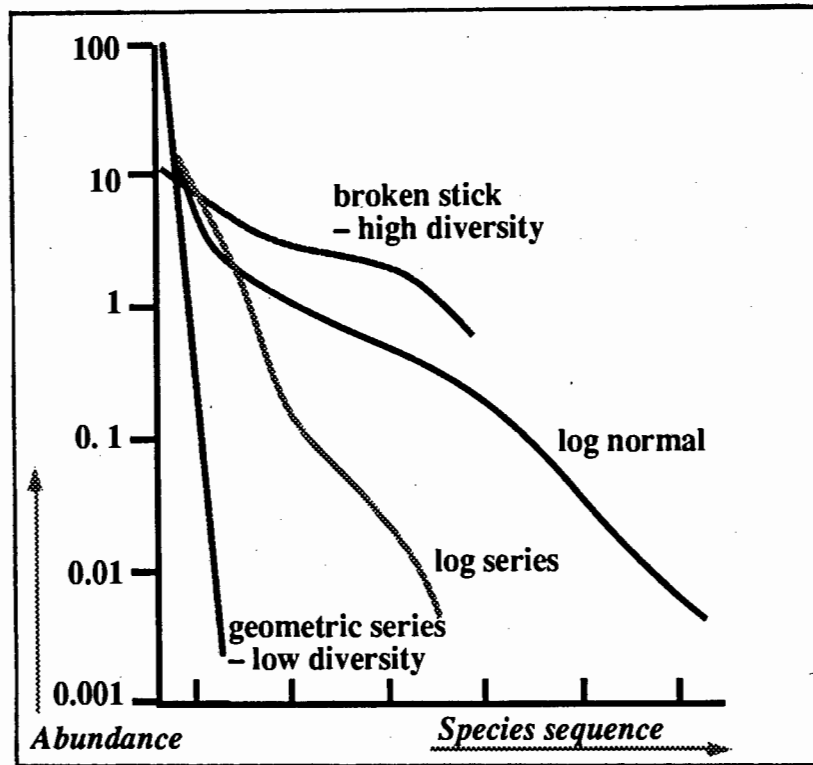


FIGURE 1.2. Hypothetical rank abundance plots illustrating the typical shape of four species abundance models: geometric series, log series, log normal and broken stick. The abundance of species is plotted on a logarithmic scale against the species' rank, in order from most abundant to least abundant. Species abundances may be expressed as a percentage for a comparison between communities (Adapted from Magurran 1988).

The models have been used to demonstrate changes in species, habitat and ecosystem diversity for a wide range of cases, for example, birds of deciduous forests, agricultural fields following abandonment, and plants of sub-alpine forests (Kempton & Taylor 1976; Magurran 1988).

numerical term which fits in with this approach is the 'Q' statistic where:

$$Q = \frac{S}{2\log(R_2/R_1)} \quad (1.4)$$

where S = number of species,

R_1 = lower quartile of species abundance,

R_2 = upper quartile of species abundance.

However, according to Magurran (1988) the preferred mathematical description of the abundance curves is Fisher's logarithmic series model (Fisher *et al.* 1943). This series closely approximates the geometric series (May 1975). The log series takes the form:

$$\frac{\alpha x}{1}, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3} \dots \frac{\alpha x^n}{n} \quad (1.5)$$

where αx = number of species having one individual,

$\alpha x^2/2$ = number of species having 2 individuals etc.

Species abundance indices

Both Samways (1984) and Magurran (1988) recommend the use of the Berger-Parker index because of its relative simplicity:

$$D = \frac{N_{\max}}{N} \quad (1.6)$$

where N_{\max} = number of individuals within the most abundant species,

N = sum of number of individuals in all species.

This measure is a direct measure of the dominance (inverse of evenness) within the community, and must be used in conjunction with richness indices.

Indices based on species abundance and richness

These indices combine species abundance and richness into a simple statistic (see Table 1.2 for examples). Such indices are widely used but their comparability is limited (Samways 1984), and a controversy has arisen over the best diversity measure to utilize, due to the wide array of indices and their different qualities (Goodman 1975; May 1975; Pielou 1975; Kempton & Taylor 1976; Southwood 1978; Routledge 1979). Even though the Shannon index comes under much criticism (Peet 1974; Alatalo & Alatalo 1977; Routledge 1979) it is still widely used, and for comparative studies it may be best to calculate this index. It takes the form:

$$H' = \sum p_i \ell np_i \quad (1.7)$$

where p_i = proportion of individuals found in the i th species.

Comparative measures

Differentiation diversity is essentially a comparative measure of how different (or similar) a range of samples, habitats or areas are in terms of variety. There are various comparative methods associated with its measurement.

The most common is the use of an index to measure the turnover or differences in species between areas. Wilson & Shmida (1984) have reviewed the indices available, assessing them against four criteria: the number of community changes, additivity, independence from alpha diversity and independence from excessive sampling. They concluded that the one index which

fulfills all these criteria is Whittaker's measure (β_w) which takes the form:

$$\beta_w = \frac{S}{\alpha} - 1 \quad (1.8)$$

where S = total number of species recorded in the system,

α = average sample diversity where each sample is a standard size and diversity is measured as species richness.

Another method of measuring differentiation diversity is indirectly through the use of similarity coefficients, which highlight the difference between species in different samples rather than turnover between samples. One such coefficient is Sorenson's quantitative similarity coefficient, which has the advantage of simplicity with no loss of information. It takes the form:

$$C_N = \frac{2jN}{aN + bN} \quad (1.9)$$

where aN = total number of individuals at site A,

bN = total number of individuals at site B,

jN = sum of the lower of the two abundances.

This similarity can be graphically represented in the form of a dendrogram (Magurran 1988).

Another graphic method is to plot the frequency distribution of differentiation diversity values

calculated from similarity coefficients for different samples (Figure 1.3). In this case differentiation diversity is measured using the equation:

$$\beta = (a + b)(1-S) \quad (1.10)$$

where S = similarity coefficient,

a = number of species in quadrat A,

b = number of species in quadrat B.

Guidelines for the analysis of biological diversity

Before biological diversity in river ecosystems is measured, the temporal and spatial scales require definition, and the boundaries of the study must be determined. A method of doing this uses Whittaker's (1977) diversity categories. Wells & Walmsley (in preparation) provide a framework to the spatial scale, which may be applicable to river ecosystems (Figure 1.4). They apply the same type of framework to a temporal scale (Figure 1.5), (Wells & Walmsley in preparation). This provides a 2-dimensional vector system, a spatial vector in one direction and a temporal vector in the other. The diversity of both vectors may be measured concurrently, but for simplicity the one vector may be defined absolutely. If the spatial scale is defined absolutely then the change in diversity over time may easily be measured. If, however, the temporal scale is absolutely defined, and if change is to be monitored, a magnitude needs to be chosen that includes cyclic variability in the system (Wells & Walmsley in preparation). Once the boundaries have been defined then one can proceed to the measurement and analysis of diversity.

The measurement and analysis of biological diversity may be split into two sections. The first

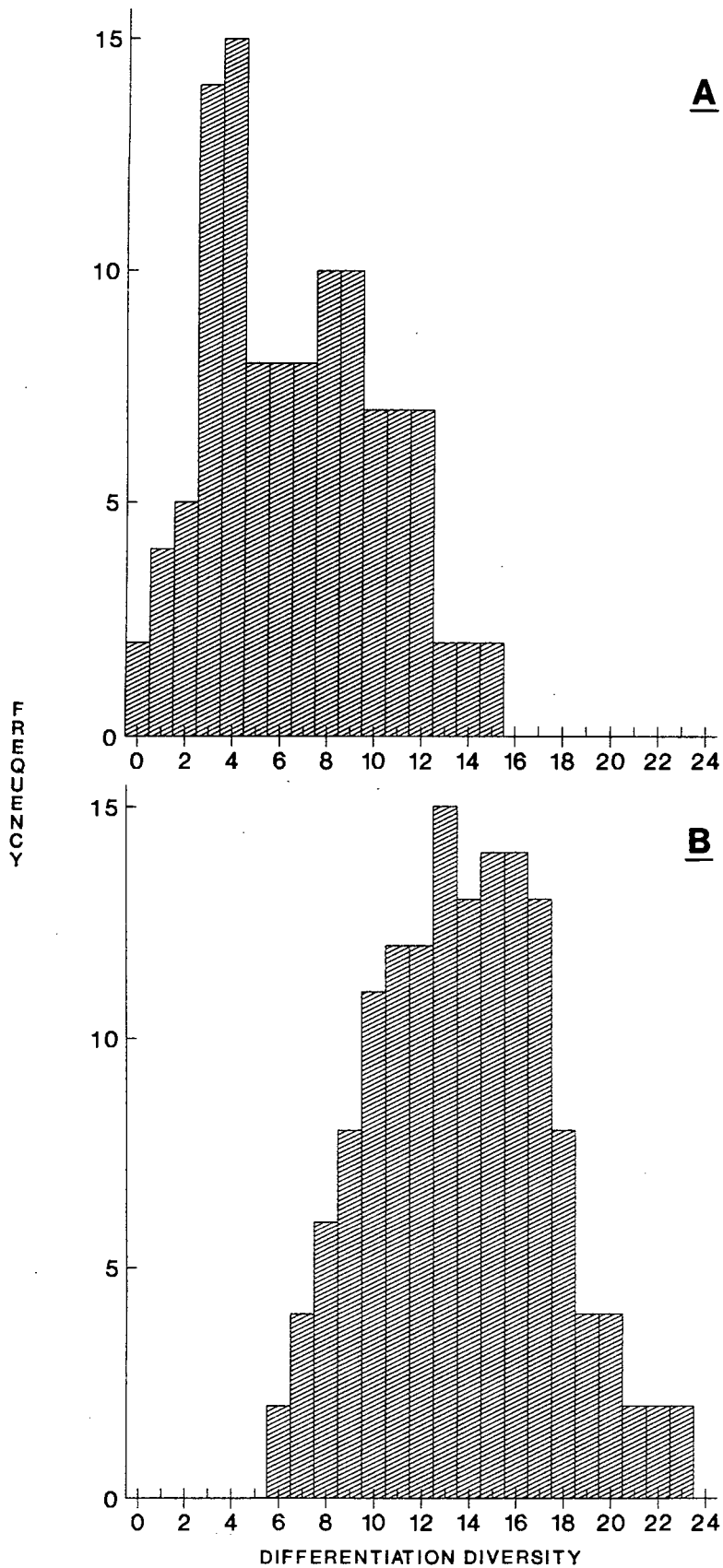


FIGURE 1.3. Hypothetical frequency distributions of differentiation diversity values calculated from similarity coefficients for different samples (frequency is plotted as the number of samples). Histogram B shows a higher diversity than histogram A.

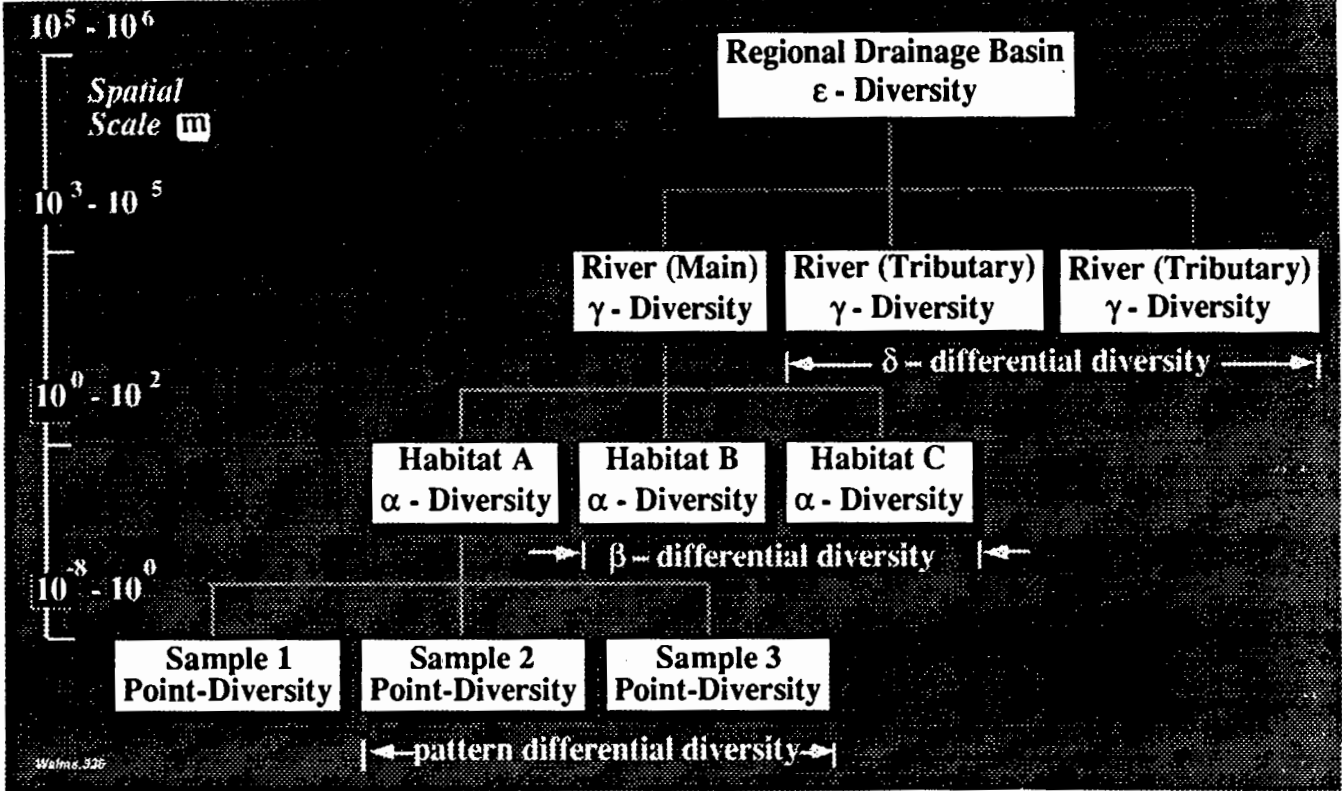


FIGURE 1.4. A framework for determining diversity on a spatial scale (units in meters) using inventory and differentiation diversity (after Wells & Walmsley in preparation).

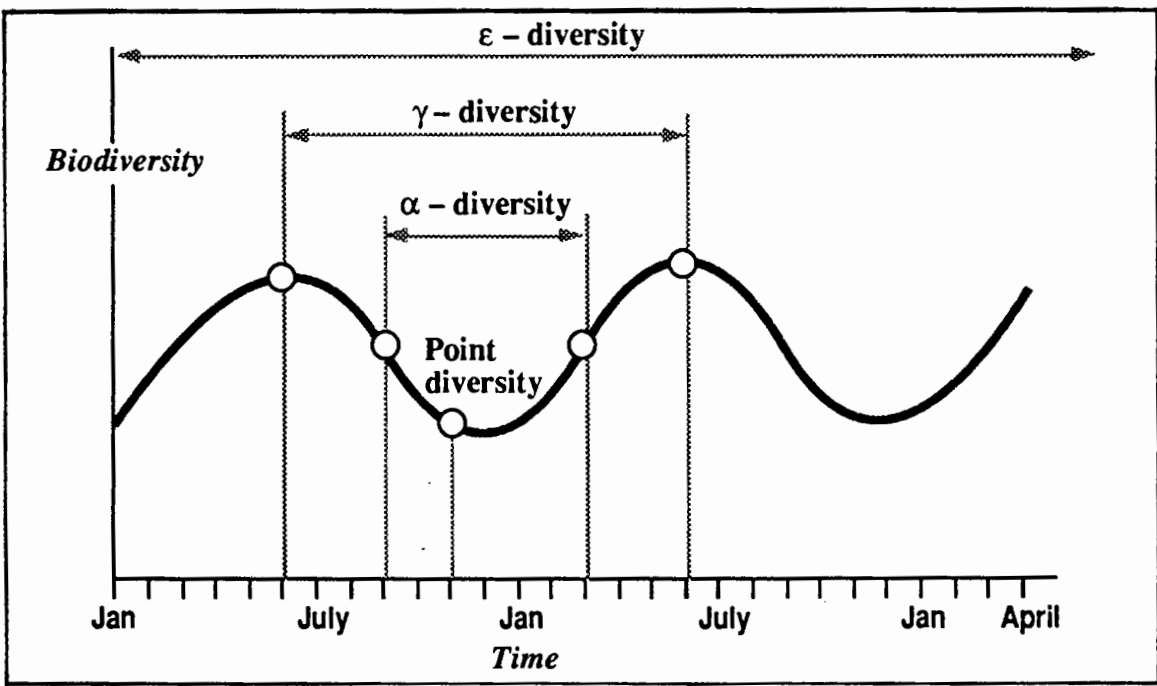


FIGURE 1.5. A framework for determining diversity on a temporal scale using inventory and differentiation diversity (after Wells & Walmsley in preparation).

deals with the inventory diversity (Whittaker 1977) of the system, in particular the measurement of point, alpha, gamma and epsilon diversity. This gives a good characterization of the community structure on different spatial scales (Kempton 1979) and displays fundamental ecological patterns (Kempton 1979). Species richness indices, species abundance models, species abundance indices and indices based on both species richness and abundance are all used in the measuring of inventory diversity. The second covers the differentiation diversity of the system: the patch, beta and delta diversity. This shows the change in species between areas of diversity which may or may not retain the same community structure, and may be measured using comparative measures (Magurran 1988). It may also be used to determine the change in species over time where the spatial dimensions have been defined absolutely.

Guidelines for the analysis of inventory diversity are given in Magurran (1988). They are expanded upon here to give a fuller understanding of their application:

1. Ensure that sample sizes are equal and are large enough to be representative. Magurran (1988) points this out as one of the problems associated with the measurement of diversity. However, in most cases, common methodologies, which are generally used, suffice.
2. Draw a rank abundance graph, and determine the distribution of the data. This gives an indication of which distribution the data follow, and gives a graphic representation of the diversity (both evenness and richness).
3. Determine the log series α . This measure can be used to describe both the log normal and the log series distributions, both of which are commonly found in ecological communities. If the data do not follow either of these distributions then the Q statistic may be used as a suitable alternative. Both these measures are used as suitable diversity indices.
4. Test the goodness of fit of the species abundance models (see also Clarke in preparation).

This is important when fitting the log series to a log normal distribution.

5. Calculate the Margalef and Berger-Parker Indices. These give a quick measure of the species abundance and the dominance components of diversity respectively.
6. Use statistical tests such as analysis of variance (ANOVA) and Student-Newman-Keuls tests (SNK) to test for significant differences between communities once normality of the data has been ascertained (Zar 1984; Clarke 1988). Statistical differences are differences in community structure and are not related to differentiation diversity which deals with the differences in species composition.

Similar guidelines can be set up for the measurement of differentiation diversity. They are:

1. As for inventory diversity, ensure that sample sizes are equal and are large enough to be representative.
2. Calculate β_w . This gives a good measure of the species turnover between samples, while fulfilling the criteria set out by Wilson and Shmida (1984).
3. Calculate Sorenson's similarity coefficient and plot a dendrogram. This gives a good graphic description of how close two areas are in terms of species present.
4. Draw frequency plots of the differential diversity values calculated from the similarity coefficient. This gives an indication of the patchiness of the system and complements inventory diversity measures.

CONCLUDING REMARKS AND PROPOSED PROCEDURES

The above review indicates that both the river ecosystem structure and concepts pertaining to biological diversity are highly complex. A better understanding of the measurement of biological

diversity in river ecosystems is also complicated by the array of techniques, of which only those applicable to river communities were discussed. In conclusion, I would like to outline a possible procedure for studying biological diversity in river ecosystems. I shall be using this procedure in this thesis and commenting on its applicability at the end.

1. Before data collection takes place the scientist must determine the best methodologies to use and ensure a statistically valid sample size. Magurran (1988) stresses the importance of sample size when dealing with the measurement of diversity. In practice most people take a pragmatic approach and sample until time or money run out or until they feel that they have adequately described the community. In terms of river ecosystems, the approach often taken is to use an accepted methodology (e.g. a Surber Sample) and to take a statistically valid number of replicates (see Chapter 3).
2. Because of the four-dimensional character of river ecosystems (Minshall 1988; Ward 1989), the communities under study need to be defined both temporally and spatially (see Chapter 4). Temporal definition must take into account natural variability in the system such as seasonal changes, and the scale on which one is working must be defined. The definition of spatial boundaries is best done using the concepts of inventory and differentiation diversity (Pielou 1975; Whittaker 1977; Magurran 1988). Each level of inventory and differentiation diversity must be defined on a different spatial scale.
3. It is also important to define the taxonomic boundaries (see Chapter 4). In the case of mammals, birds and fish it may be possible to identify all specimens to Species level, in which case diversity can be measured at Species level. With aquatic insects and macro-

invertebrates, however, it may only be possible to identify them to Genus or Family level. It is not possible to determine diversity using different taxonomic levels, therefore the level of identification must be determined at the beginning of the study.

4. Because of the complexity of river ecosystems, and their individual characteristics, a preliminary study, which will give an insight into the general characteristics of the river, should be initiated. This may include a catchment study (see Chapter 2) and a study of the river itself. In particular, the physico-chemical properties of the river, and the associated faunal groups need to be examined (see Chapter 5). A method of doing this would be ordination and classification analyses (Field *et al.* 1982).
5. Finally, the biological diversity of the communities in question can be examined, using the concepts and measurements of inventory (see Chapter 6) and differentiation diversity (see Chapter 7). *Both* these diversity types should be measured as they complement each other; one gives the diversity as it stands, the other gives the turnover in diversity between samples, or on a temporal scale. Detailed guidelines to the measurement of the two types of diversity are given above. These measurements are simple and give the most complete picture of diversity (Magurran 1988).

CHAPTER 2

SABIE-SAND CATCHMENT DESCRIPTION

INTRODUCTION

In order to place the study of the benthic macro-invertebrate riffle fauna of the Sabie-Sand River in perspective, it is necessary to have an understanding of the characteristics of the catchment. Table 2.1 lists the comparative statistics for different areas within the Sabie-Sand catchment. It also gives the outline of some catchment characteristics which, amongst others, will be dealt with in greater detail in this chapter.

LOCALITY AND GEOGRAPHICAL SUB-DIVISION

The Sabie-Sand River catchment (see Figure 0.1 in introduction) falls within the Incomati River Basin, an international drainage basin that falls within the boundaries of the Republic of South Africa, the Kingdom of Swaziland and the People's Republic of Moçambique (Chunnett, Fourie & Partners 1990). It comprises a total area of 709 600ha (see Table 2.1) and stretches from the Drakensberg in the west, across the Lebombo Mountains in the east, to the confluence with the Incomati River in Moçambique (Chunnett, Fourie & Partners 1987, 1990).

The Sand River and the Marite River are major tributaries of the Sabie River (Figure 2.1). While the catchment area of the Sand River is considered a sub-catchment, the catchment areas of the Mac-Mac and Marite rivers are treated as tertiary catchments (Chunnett, Fourie & Partners 1990).

TABLE 2.1. Some comparative statistics for the Sabie-Sand catchment in the Republic of South Africa and the Self-Governing

Territories (after Chunnnett, Fourie & Partners 1990)

DESCRIPTION	SABIE RIVER SUB-CATCHMENT				SAND RIVER SUB-CATCHMENT				TOTAL SABIE RIVER CATCHMENT						
	TOTAL	PERCENTAGE DISTRIBUTION			TOTAL	PERCENTAGE DISTRIBUTION			TOTAL	PERCENTAGE DISTRIBUTION					
		GAZAN-KULU	KA-NGWANE	LEBOWA		RSA	GAZAN-KULU	KA-NGWANE		LEBOWA	RSA	GAZAN-KULU	KA-NGWANE	LEBOWA	RSA
Area (km ²)	4 472	10,7	2,5	7,4	79,4	1 965	39,2	0,0	26,2	34,6	6 437	19,4	1,8	13,1	65,7
MAP (million m ³)	3 800	9,3	2,3	8,4	80,0	1 510	36,7	0,0	36,4	26,9	5 310	17,1	1,7	16,3	64,9
Natural MAR (million m ³)	606	7,3	1,5	5,9	85,3	158	21,5	0,0	77,8	0,6	764	10,2	1,2	20,8	67,8
Gross Area of Irrigable Soils (ha)	104 233	17,1	5,5	13,5	63,9	66 025	61,6	0,0	33,4	5,1	170 258	34,4	3,4	21,2	41,1
Irrigable Soils within Tentative Primary Irrigation Zone :															
Gross Area (ha)	20 083	19,3	11,3	29,6	39,8	28 856	57,7	0,0	42,3	0,0	48 939	41,9	4,7	37,1	16,3
Net Area (ha)	13 810	16,9	9,9	25,8	47,4	17 310	57,7	0,0	42,3	0,0	31 120	39,6	4,4	35,0	21,0
Population Dependent on Water from the Sabie River Catchment :															
1985 : Inside Catchment (No.)	168 099	33,0	18,8	29,9	18,3	169 472	43,2	0,0	56,4	0,4	337 571	38,1	9,4	43,2	9,3
Outside Catchment (No.)	44 122	0,0	100,0	0,0	0,0	35 705	63,1	0,0	36,9	0,0	79 827	28,2	55,3	16,5	0,0
2010 : Inside Catchment (No.)	337 000	34,4	19,6	31,2	14,8	354 000	43,2	0,0	56,5	0,3	691 000	38,9	9,6	44,1	7,4
Outside Catchment (no.)	92 000	0,0	100,0	0,0	0,0	74 000	63,5	0,0	36,5	0,0	166 000	28,3	55,4	16,3	0,0
Livestock (No. ELSU)	36 950	46,3	14,7	32,6	6,4	47 632	60,2	0,0	39,8	0,0	84 582	54,1	6,4	36,7	2,8
Game (No. ELSU)	18 463	0,0	0,0	0,0	100,0	5 840	0,0	0,0	0,0	100,0	24 303	0,0	0,0	0,0	100,0
Existing Irrigation (ha)	8 445	13,8	0,0	8,6	77,6	2 875	39,8	0,0	60,2	0,0	11 320	20,4	0,0	21,7	57,9
Existing Dry Land Cultivation (ha)	6 770	43,9	36,9	19,2	0,0	4 800	79,2	0,0	20,8	0,0	11 570	58,5	21,6	19,9	0,0
Afforestation :															
Existing (ha)	64 500	0,0	0,0	3,3	96,7	7 600	0,0	0,0	100,0	0,0	72 100	0,0	0,0	13,5	86,5
Currently Permitted (ha)	66 621	0,0	0,0	3,7	96,3	7 600	0,0	0,0	100,0	0,0	74 221	0,0	0,0	13,6	86,4
Potential (ha)	116 000	9,5	2,6	24,1	63,8	26 000	30,8	0,0	69,2	0,0	142 000	13,4	2,1	32,4	52,1
Maximum Expected Mean Sediment Yield (t/a)	1 431 000	15,7	3,6	9,3	71,4	780 000	47,1	0,0	26,8	26,2	2 211 000	26,8	2,3	15,5	55,5

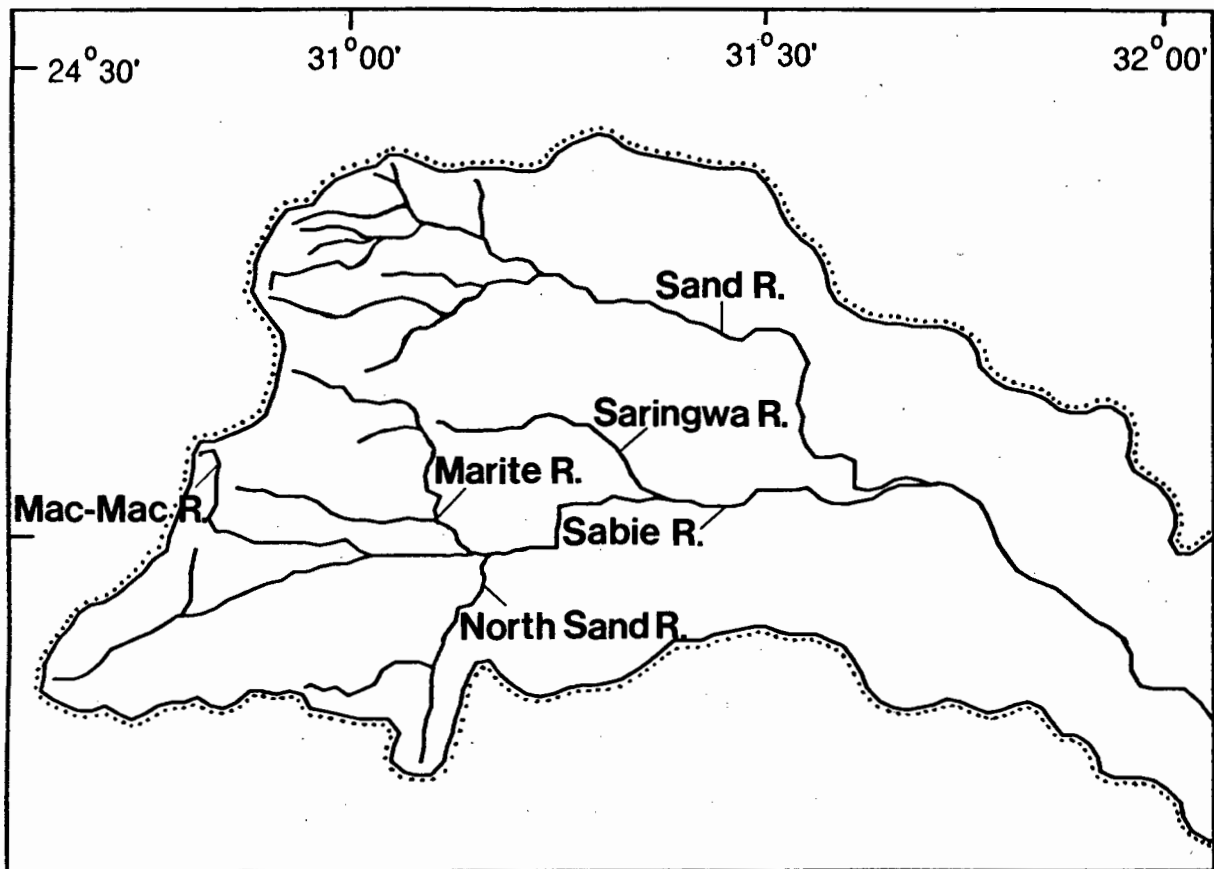
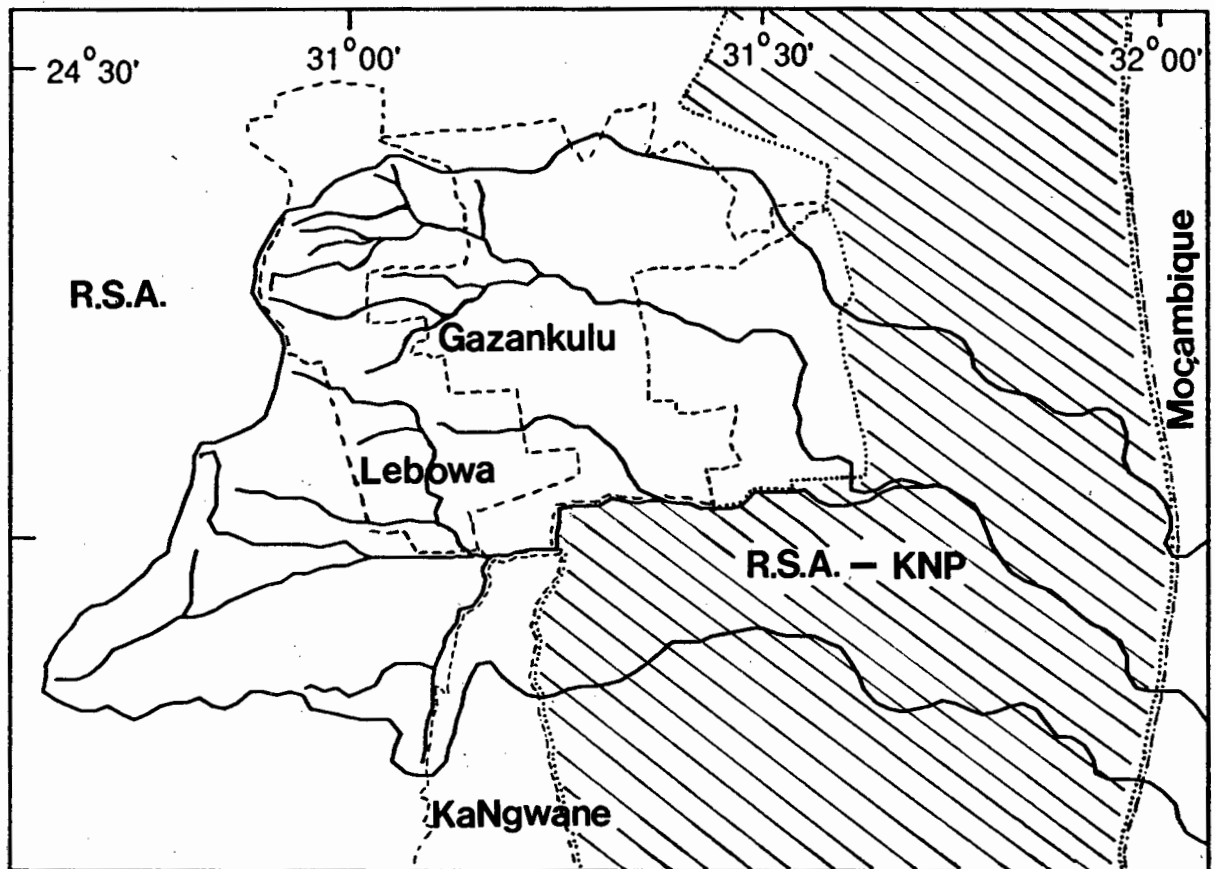


FIGURE 2.1. Map of the Sabie-Sand catchment showing the Sabie river and its tributaries.

The catchment comprises five main political regions (Figure 2.2):

- the Republic of South Africa;
- Lebowa (Mapulaneng District);
- Gazankulu (Mhala District);
- KaNgwane (Nsikasi Region), and
- the People's Republic of Moçambique.



----- INTERNATIONAL BOUNDARIES

..... NATIONAL BOUNDARIES

▨ KRUGER NATIONAL PARK

FIGURE 2.2. Map of the Sabie-Sand catchment showing political regions within the catchment, and the area covered by the Kruger National Park.

TOPOGRAPHY

The Sabie River rises in the Mauchsberg (part of the Drakensberg chain) at an altitude of 2 130mAMSL (O’Keeffe 1985) and flows for 175km before reaching the Moçambique border at 120mAMSL (Figure 2.3), and 230km before the confluence with the Incomati River at an altitude of 40mAMSL. The Sand River also rises in the Drakensberg, about 50km north-east of the Sabie River source, at an altitude of 1 500mAMSL (Chunnett,

Fourie & Partners 1987, 1990) and flows for 125km to its confluence with the Sabie River in the KNP (Figure 2.3), (Chunnett, Fourie & Partners 1987).

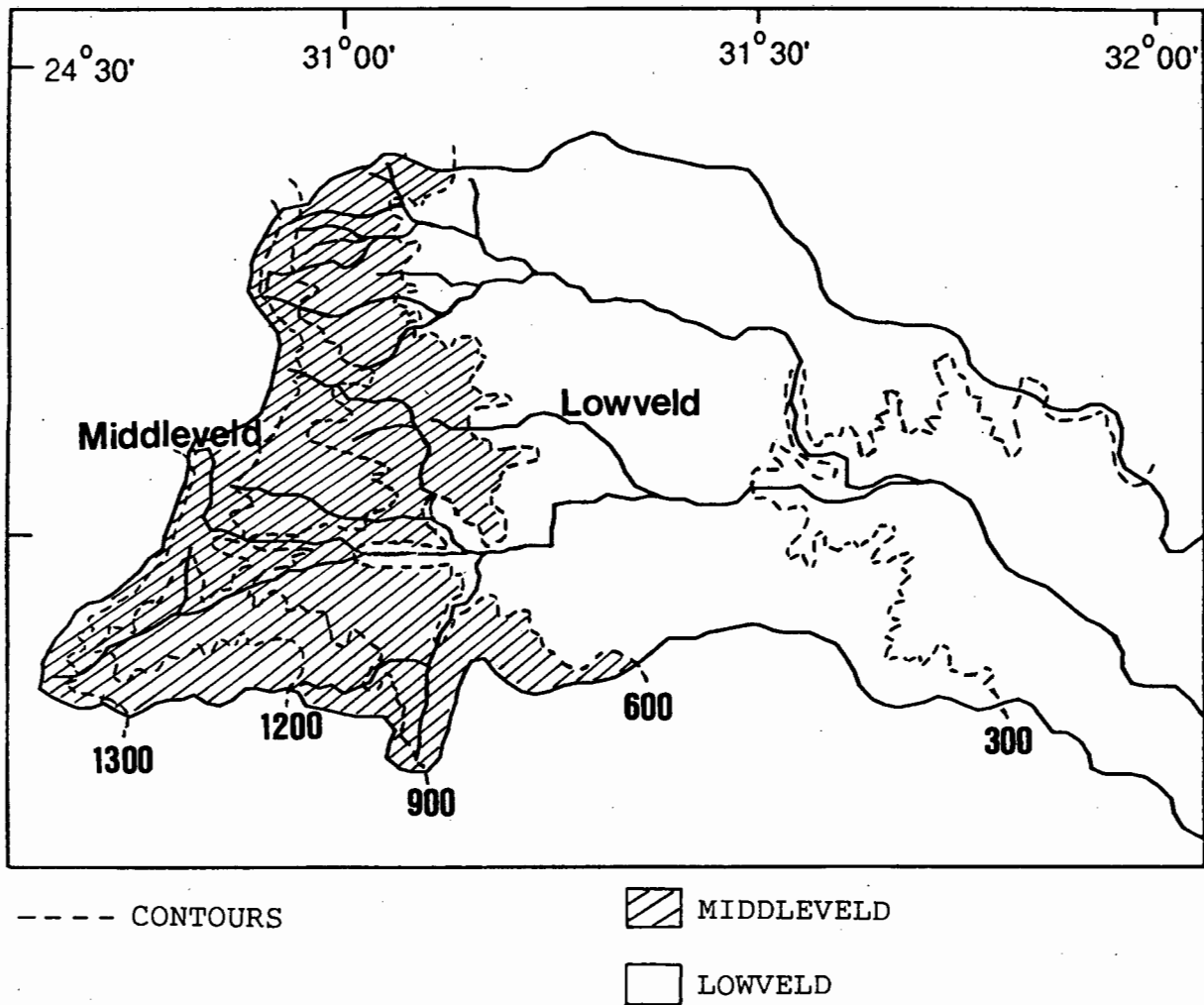


FIGURE 2.3. Map of the Sabie-Sand catchment showing altitudinal contours (mAMS) and topographical regions.

The Sabie-Sand River catchment may be divided into two distinct topographical regions (Figure 2.3): the Middleveld, and the Lowveld regions. The Middleveld Region is

characterised by undulating topography (with slopes generally in excess of 15%), with some mountainous areas towards the Drakensberg (Chunnett, Fourie & Partners 1987, 1990). The Lowveld is characterised by a flat to gently undulating topography, with slopes less than 15% (Chunnett, Fourie & Partners 1987, 1990), except in the vicinity of the Lebombo Mountains. On average, the Lowveld lies about 300mAMSL and can be classified as a pediplain with a gentle slope towards the east (Venter & Bristow 1986). There are no large floodplains, wetlands or swamps within the catchment (Chunnett, Fourie & Partners 1987, 1990).

GEOLOGY AND SOILS

The Sabie-Sand catchment is underlain by three major litho-stratigraphic units (Figure 2.4): the Basement Complex, the Transvaal Sequence and the Karoo Sequence (Chunnett, Fourie & Partners 1987). The Basement Complex occupies the major portion of the catchment from the Drakensberg to the Lebombo Mountains. It comprises granite and granodiorite with minor intrusions of diabase and gabbro in the south west, and a large intrusion of tonalite in the centre. No mineral deposits of economic significance have been noted in the Basement Complex (Chunnett, Fourie & Partners 1990).

The Transvaal Sequence only occupies the extreme western mountainous portion of the catchment and consists of a wide variety of rock formations. In the catchment these consist of shale, quartzite, conglomerate, breccia, diamictite, lava, tuff, dolomite, chert and basalt (Chunnett, Fourie & Partners 1990). Gold deposits occur fairly frequently and

have lead to some mining activity in the Sabie and Graskop area (Chunnett, Fourie & Partners 1990).

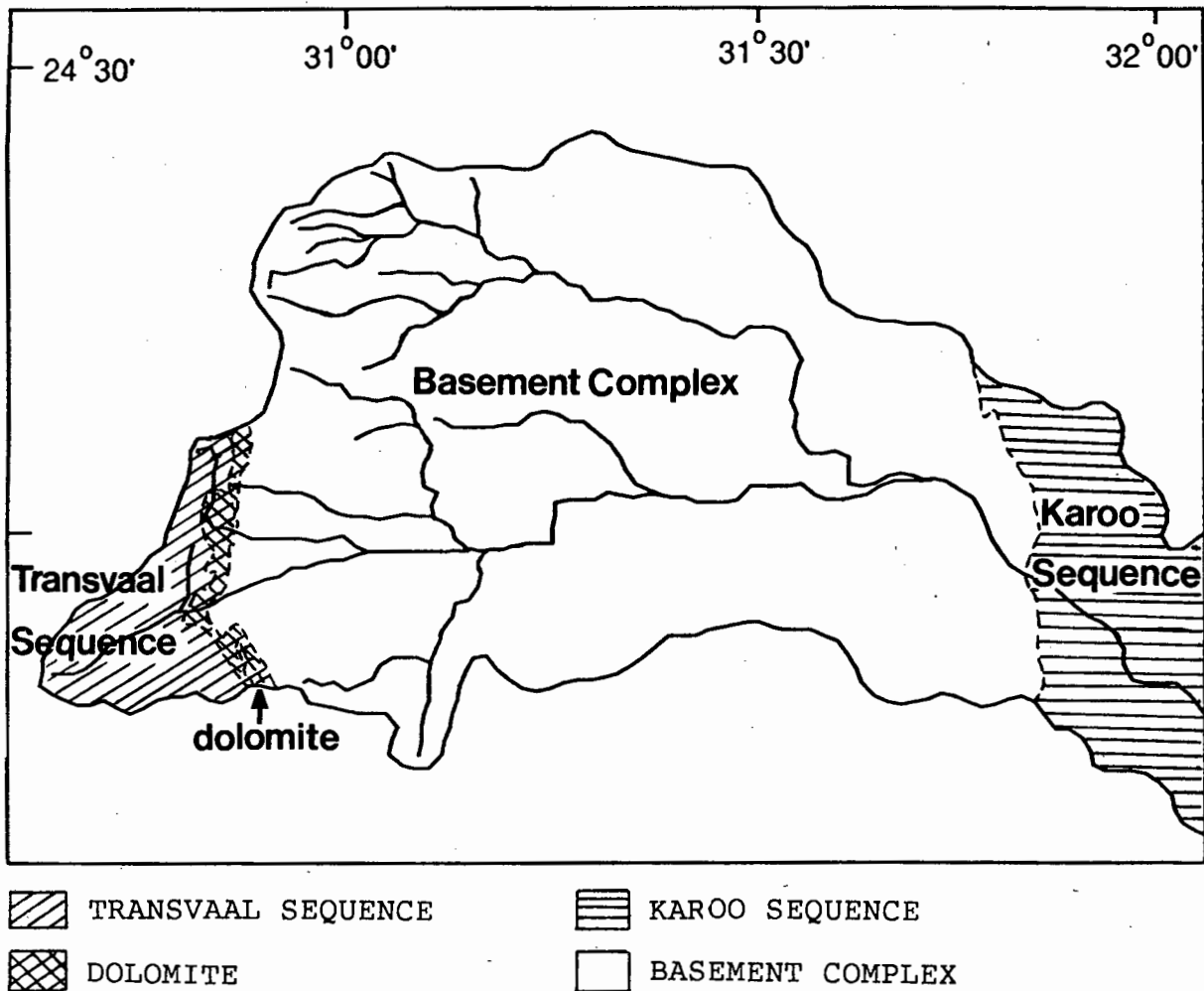


FIGURE 2.4. Map of the Sabie-Sand catchment showing the geology of the area.

The Karoo Sequence occupies the Lebombo Mountain range and vicinity, and mainly consists of basalt and rhyolite of the Lebombo Group; sandstone, shale, mudstone and coal of the Beaufort and Ecca Groups; sandstone and siltstone of the Clarence

formation, and some granophyre and dolerite intrusions (Chunnett, Fourie & Partners 1990). More detailed geology and geomorphology of the KNP itself can be found in Venter & Bristow (1986), and Venter (1990).

Soils outside the KNP are lithosols in the upper catchment, changing to ferrallitic clays and arenosols (O'Keeffe 1985) in the lower catchment. In the KNP, the soils are shallow and sandy on crests, while sodic duplex soils are found in low lying areas. On the western boundary, the river flows through gabbro overlain by black and red clays (O'Keeffe 1985). The soils have a relatively high erosion resistance (and a low erosion risk) compared to other regions in southern Africa, and sediment yields within the catchment vary from 400-600t km⁻² a⁻¹ (Chunnett, Fourie & Partners 1990; see Table 2.1).

A probabilistic study of all past earthquakes in southern Africa has been performed by the Republic of South Africa Department of Mineral and Energy Affairs (Chunnett, Fourie & Partners 1990). It has been inferred that the natural seismic hazard within the catchment is low to moderate (Chunnett, Fourie & Partners 1990).

CLIMATE

The Sabie-Sand River catchment falls within the Eastern Transvaal Lowveld climatic region. It has a warm to hot, subtropical climate, with a somewhat cooler climate prevailing along the escarpment (Chunnett, Fourie & Partners 1987).

Precipitation and evaporation

In the Lowveld region, the mean annual precipitation is 600mm, and towards the Drakensberg, this figure increases to 2 000mm (Table 2.1). The majority of rain falls between November and March, with maximum precipitation occurring in January. The whole of the catchment is prone to tropical cyclonic storms, with orographic rain and mists occurring in the mountainous areas (Chunnett, Fourie & Partners 1987).

The average annual Symon's Pan evaporation varies from 1 700mm in the east of the catchment to about 1 400mm in the west (Chunnett, Fourie & Partners 1987). During the summer months, the average gross evaporation in the Middleveld region is about 40% higher than in the winter months, and about 60% higher in the Lowveld region (Chunnett, Fourie & Partners 1987). A more detailed analysis of rainfall patterns of the KNP and desiccation of the Transvaal Lowveld may be respectively found in Gertenbach (1980) and Pienaar (1985).

Temperature

Generally, temperatures in the catchment decrease with increasing altitude. At Skukuza, typical of the Lowveld region, average temperatures are recorded as follows (Chunnett, Fourie & Partners 1987, 1990):

January - min: 20°C	July - min: 6°C
max: 32°C	max: 26°C.

At Bosbokrand, in the lower Middleveld region, the average temperatures are as follows

(Chunnett, Fourie & Partners 1987, 1990):

January - min: 18°C	July - min: 9°C
max: 28°C	max: 22°C.

At Graskop, which is representative of the upper Middleveld region, they are as follows

(Chunnett, Fourie & Partners 1987, 1990):

January - min: 14°C	July - min: 4°C
max: 23°C	max: 17°C.

Frost is seldom experienced, and is confined to lowlying valleys.

Wind

Winds tend to be fairly light with average wind speeds of less than 12km h⁻¹ for 80% of the time. They mainly blow from the south-southeast and north-northeast. Winds are stronger in the summer months and can reach gale force against the Drakensberg (Chunnett, Fourie & Partners 1987, 1990).

HYDROLOGY

A full hydrological investigation of the Sabie River catchment has been completed (Department of Water Affairs 1990b) giving the basic hydrology of the rivers at various

points which, together with the hydraulic characteristics may be used for the assessment of water requirements for nature conservation. The hydrology of the catchment may be split into three components:

- surface runoff
- geohydrology
- floods

Surface Runoff

The simulated mean annual runoff (MAR) of the Sabie River at the confluence with the Incomati River was 762hm^3 for the period October 1921 to September 1985, of which the Sand River contributed 158hm^3 (Department of Water Affairs 1990b; see Table 2.1). This figure has already been reduced to 633hm^3 by exotic afforestation in the western, upper end of the catchment (Department of Water Affairs 1990b).

Geohydrology

The catchment groundwater resources are insignificant in relation to the surface water resources (Department of Water Affairs 1990b). The only significant source of groundwater, of which the amount of utilisable water is still to be measured, is a dolomitic aquifer in the west of the catchment. Without this, groundwater would only contribute $5\text{hm}^3\text{a}^{-1}$ to the utilizable water resources.

Floods

Approximate flood peaks in the Sabie River at the eastern border of the KNP are:

- 20-year recurrence interval - $2\,200\text{m}^3\text{ s}^{-1}$
- 50-year recurrence interval - $3\,500\text{m}^3\text{ s}^{-1}$
- 100-year recurrence interval - $5\,000\text{m}^3\text{ s}^{-1}$
- 200-year recurrence interval - $7\,000\text{m}^3\text{ s}^{-1}$
- regional maximum flood - $11\,000\text{m}^3\text{ s}^{-1}$
- probable maximum flood - $20\,000\text{m}^3\text{ s}^{-1}$.

For the period from October 1953 to September 1983, at the eastern border of the KNP, the highest recorded flood was $3\,431\text{m}^3\text{ s}^{-1}$, which occurred in January 1958 (Department of Water Affairs 1990b).

WATER QUALITY

An assessment of the water quality of the KNP was carried out by Van Veelen (1990) and Moore *et al.* (1991), and for the Sabie River catchment by Chunnnett, Fourie & Partners (1990). According to Moore *et al.* (1991), no significant detrimental changes in the water quality of the Sabie River have been detected over the period from 1983 to 1989. Therefore, both the surface and groundwater within the Sabie-Sand catchment is suitable for domestic, agricultural and industrial use, and water from both the Sabie and the Sand rivers is highly suitable for irrigation purposes.

Present fixed points of possible point-source pollution are the gold mines in the upper reaches of the Sabie River and the various sewage treatment plants.

RIVER CLASSIFICATION WITHIN THE CATCHMENT

A classification of rivers within the Sabie River catchment can be split into two categories: a physical description and a description of the conservation status of the river.

Physical description

Figure 2.5 shows the longitudinal profiles of the Sabie and Sand rivers and their major tributaries (from their sources to the confluences with other rivers). The Sabie has a steeper gradient in the upper reaches than the Sand River.

Both the Sabie and the Sand rivers may be described in terms of the river zonation of Noble and Hemens (1978). Chunnett, Fourie & Partners (1987, 1990) recognised four zones (Figure 2.6). They are:

- the mountain source and cliff waterfall zone (Sabie River only);
- the mountain stream zone (Sabie and Sand rivers);
- the foothill, sandbed zone (Sand River only), and
- the low, midland stream and river zone (Sabie and Sand rivers).

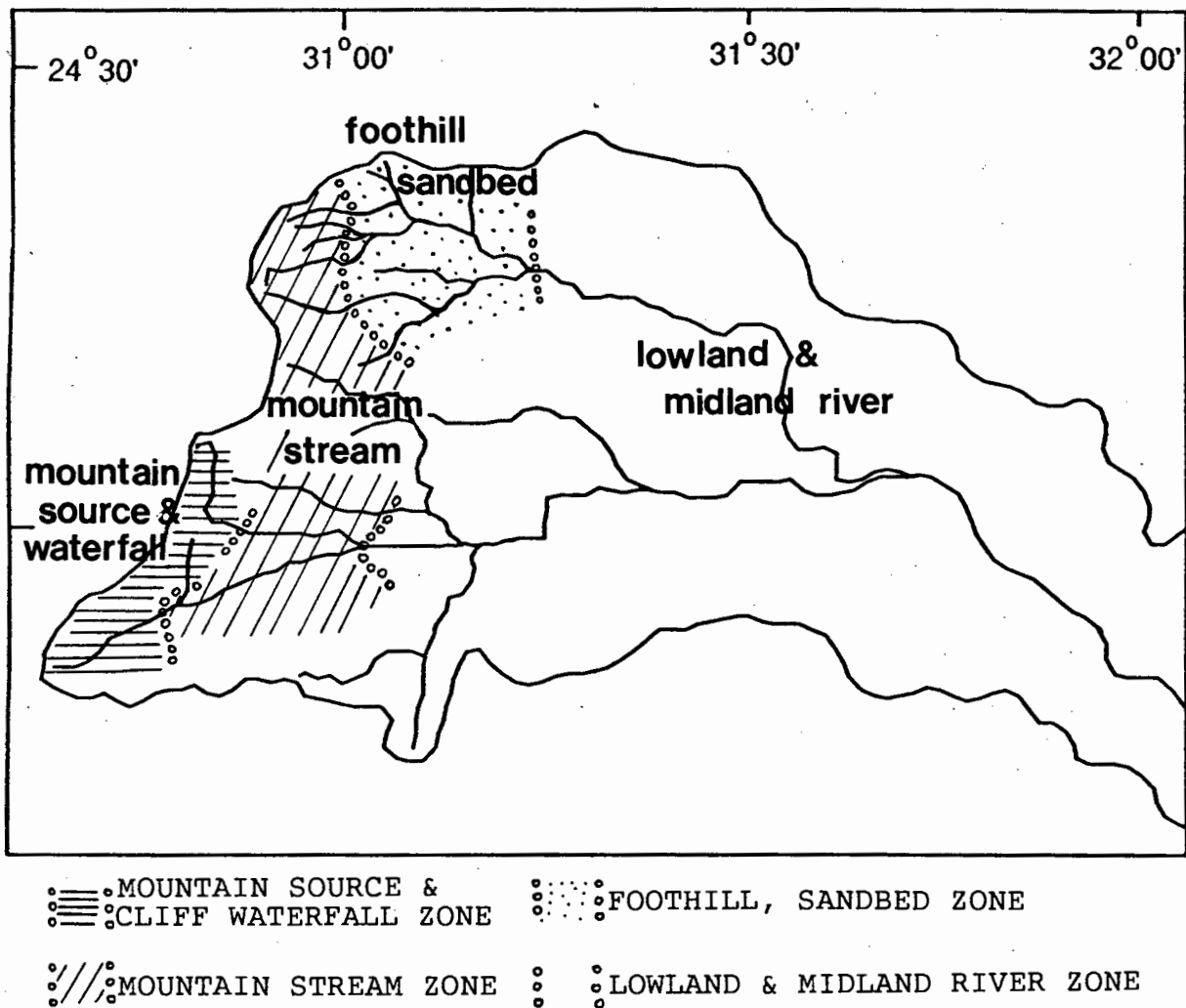


FIGURE 2.6. Map of the Sabie-Sand catchment showing the river zonation.

Conservation status

The conservation of rivers can be determined by assessing various abiotic and biotic factors on a five point scale along the length of a river (Chunnett, Fourie & Partners 1987).

The classification system is as follows:

Class 1: Pristine. Assessed at 100% of potential rating.

Class 2: Largely natural with few modifications. Assessed at 80% to 99% of potential

rating.

Class 3: Modified but primarily natural. Assessed at 60% to 79% of potential rating.

Class 4: Largely modified, but natural in some areas. Assessed at 40% to 59% of potential rating.

Class 5: Very few areas still natural. Assessed at 20% to 39% of potential rating.

Class 6: Completely altered with natural characteristics present in a few isolated instances. Assessed at 1% to 19% of potential rating.

The present status of various reaches in the catchment are given below.

Sabie River from the source to Hazyview: Class 4. Modifications are mainly due to afforestation.

Sabie River within the KNP: Class 3. Modifications are largely due to exotic flora, weirs and bridges.

Sabie River in Moçambique: not classified.

Mac-Mac River: Class 4. Modifications are largely due to afforestation and to other exotic flora.

Marite River: Class 4. Modification is due to afforestation in the upper reaches and to the deforestation of the riparian vegetation.

Sand River upstream of the Sabie-Sand Reserve: Class 4. Modification is due to afforestation in the upper reaches and to denudation of riparian vegetation, weirs, dams and cultivation further downstream.

Sand River in the Sabie-Sand Reserve and KNP: Class 2. Modification is due to exotic flora and small bridges.

Mtlumuvi River: Class 4. Modification in the upper reaches is mainly due to

afforestation, and further downstream it is due to denudation of the riparian vegetation, exotic flora, weirs, dams and cultivation.

In all cases the conservation importance is high (Chunnett, Fourie & Partners 1990). O'Keeffe & Davies (1991) have suggested that, due to this high conservation status, the Sabie-Sand system "...would be more advantageously developed for tourism, recreation, and nature conservation".

CATCHMENT VEGETATION

Natural vegetation

From Acocks (1975) four veld types may be recognised in the catchment (Figure 2.7).

They are:

- north-eastern mountain sourveld (at the headwaters);
- lowveld sour bushveld of inland tropical forest types (in the western portion and Middleveld);
- lowveld tropical bush (in the KNP), and
- savannah (in the KNP) (O'Keeffe 1985).

A more detailed description of the vegetation in the KNP may be found in Gertenbach (1983).

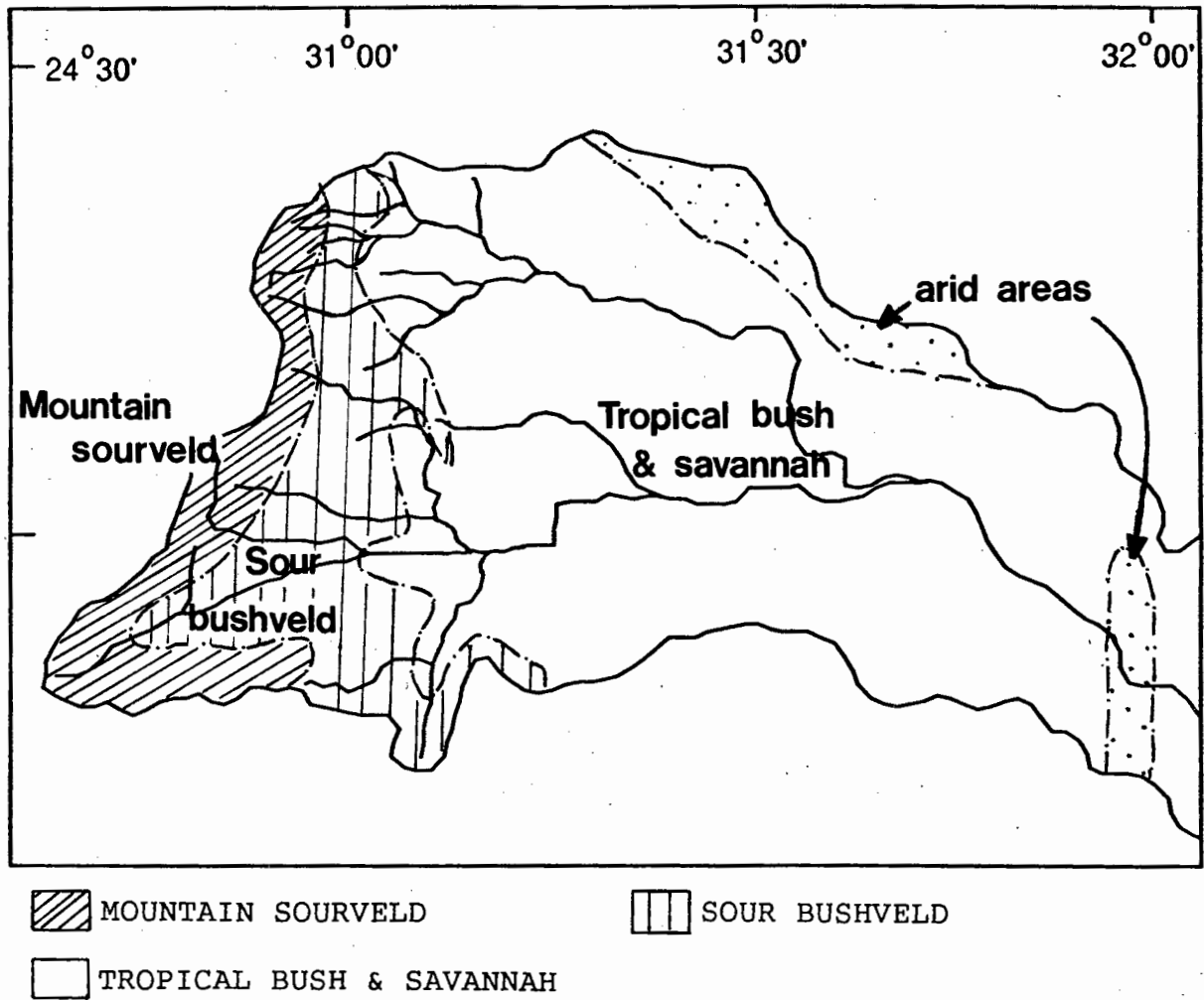


FIGURE 2.7. Map of the Sabie-Sand catchment showing the vegetation types.

Twenty-two endangered plant species have been identified within the catchment (Chunnett, Fourie & Partners 1990; see Table 2.1)

TABLE 2.1. Endangered indigenous plant species found in the Sabie-Sand catchment, and their conservation and endemic status.

SPECIES	CONSERVATION STATUS	ENDEMISM
<i>Aloe simii</i>	vulnerable	endemic
<i>Barleria oxyphylla</i>	indeterminate	endemic
<i>Begonia sonderiana</i>	indeterminate	endemic
<i>Combretum collinum</i>	uncertain	not endemic
<i>Combretum edwardsii</i>	uncertain	not endemic
<i>Cyrtanthus bicolor</i>	rare	not endemic
<i>Disa extinctoria</i>	uncertain	not endemic
<i>Gladiolus calcaratus</i>	rare	endemic
<i>Gladiolus exiguus</i>	rare	endemic
<i>Gladiolus hollandii</i>	rare	not endemic
<i>Gladiolus varius var. micranthus</i>	rare	not endemic
<i>Gladiolus varius var. varius</i>	rare	endemic
<i>Jasminum abyssinicum</i>	uncertain	not endemic
<i>Kalanchoe alticola</i>	rare	not endemic
<i>Kotschya thymodora</i>	rare	not endemic
<i>Melinis drakensbergensis</i>	rare	endemic
<i>Pilea rivularis</i>	rare	endemic
<i>Polystachya albescens</i>	uncertain	not endemic
<i>Streptocarpus decipiens</i>	rare	endemic
<i>Watsonia occulata</i>	rare	not endemic
<i>Watsonia transvaalensis</i>	rare	endemic
<i>Watsonia wilmsii</i>	rare	endemic

Exotic vegetation

The upper catchment has been severely altered by extensive monocultures of pine and eucalyptus forests. The afforested area covers 72 100ha (16% of the total catchment area), 7 600ha of which is in the Sand River sub-catchment (Chunnett, Fourie & Partners 1987; see Table 2.1). The presently established permit limits new afforestation to a further 50 284ha (Chunnett, Fourie & Partners 1990).

Other exotic plants found in the catchment are listed by O'Keeffe (1985). They are *Lantana camara*, *Tagetes minuta* (Khakibos), *Bideirs pilosa*, *Bidens bipinata* (Blackjack), *Xanthium strumarinum* (Kankerbos), *Alternatha sessilis*, *Bauhenia* sp., *Melia azedarach*, *Psidium guajava* (Guava), *Mangifera iondica* (Mango) and the aquatic floating invasive, *Pistia stratiotes* (Nile Cabbage; O'Keeffe 1985).

SOCIO-ECONOMIC AND POLITICAL ENVIRONMENT

The total population dependant on water from the Sabie River catchment was assessed at 417 000 people in 1985 (Chunnett, Fourie & Partners 1987), which is expected to increase to about 691 000 by the year 2010 (Department of Water Affairs 1990a; see Table 2.1). About 205 000 (49.2%) of these people are dependent on the water from the Sand River sub-catchment (Chunnett, Fourie & Partners 1987). In 1985, 80 000 persons outside the catchment boundaries were also dependent upon water from the catchment and this number is expected to increase to about 166 000 in the year 2010 (Department of Water Affairs 1990a; see Table 2.1).

The number of livestock within the catchment has been assessed at 109 000 equivalent-large-stock units (ELSU), including wild game in the KNP and in the Sabie-Sand Reserve (Chunnett, Fourie & Partners 1987; see Table 2.1). The gross density of livestock and game is 5.9ha ELSU⁻¹, which is considered reasonably high.

At present, 11 300ha (1.8%) of the catchment is under irrigation for farming purposes (Chunnett, Fourie & Partners 1987; see Table 2.1). The principal crops under irrigation are banana, avocado, citrus, tobacco, maize and vegetables. It is expected that, by the year 2010, the amount of irrigated land will have increased to 23 100ha (3.6%). Dry-land farming currently occurs over 11 570ha (1.8%) of the catchment (Chunnett, Fourie and Partners 1987; see Table 2.1).

The major industrial developments in the catchment are confined to wood-processing factories and sawmills in the Sabie and Graskop areas. Smaller service industries are concentrated around Mkuhlu, Thulamahaxi, Bosbokrand, Sabie and Graskop, and there is a meat processing factory in the KNP at Skukuza. Mining activity has declined, leaving only five active gold mines in the area.

In terms of the legal and political aspects of water resources management, the Water Act (Act No. 54 of 1956) is applicable in the RSA, and in the Self-governing Territories, but with different amendments. Separate Permanent Water Commissions have been established between RSA and each of the Self-governing Territories. Joint Permanent Technical Committees have been established by RSA, Swaziland and Moçambique, all of which subscribe to the principle of best-joint utilization of water resources, and also

to the principles set out in the Helsinki Rules (Department of Water Affairs 1990a).

WATER REQUIREMENTS AND POSSIBLE DEVELOPMENT SCENARIOS

The potential for irrigation development and afforestation in RSA and in the Self-governing Territories far exceeds the water resources that can be developed to acceptable levels of assurance, while the needs of the increasing population need to be met (Department of Water Affairs 1990a). The present consumptive requirements in the catchment are about $108\text{hm}^3\text{ a}^{-1}$, which is 14.1% of the MAR, while non-recoverable losses are estimated at a further $5\text{hm}^3\text{ a}^{-1}$ (0.7% MAR). These are in addition to the present high-assurance water use of $107\text{hm}^3\text{ a}^{-1}$ (14% MAR) as a result of exotic afforestation (Department of Water Affairs 1990a).

A provisional system, comprising large new dams in the RSA and in the Self-governing Territories, has been identified as being capable of supplying the expected water requirements until the year 2010. As a result of the expected high water requirements in the Sand River sub-catchment, five of the eight possible dam sites so far identified are in this sub-catchment (Chunnett, Fourie & Partners 1987, 1990; see Figure 2.8). These are:

- Acornhoek on the Kleinsand River (Sand River);
- Casteel on the Tlulandziteka River (Sand River);
- Dingleydale on the Nwandlamuhara River (Sand River);

- Zoeknog on the Mohlomobe River (Sand River);
- New Forest on the Mtlumuvi River (Sand River);
- Injaka on the Marite River (Sabie River);
- Waterval on the Marite River (Sabie River), and
- Madras on the Sabie River.

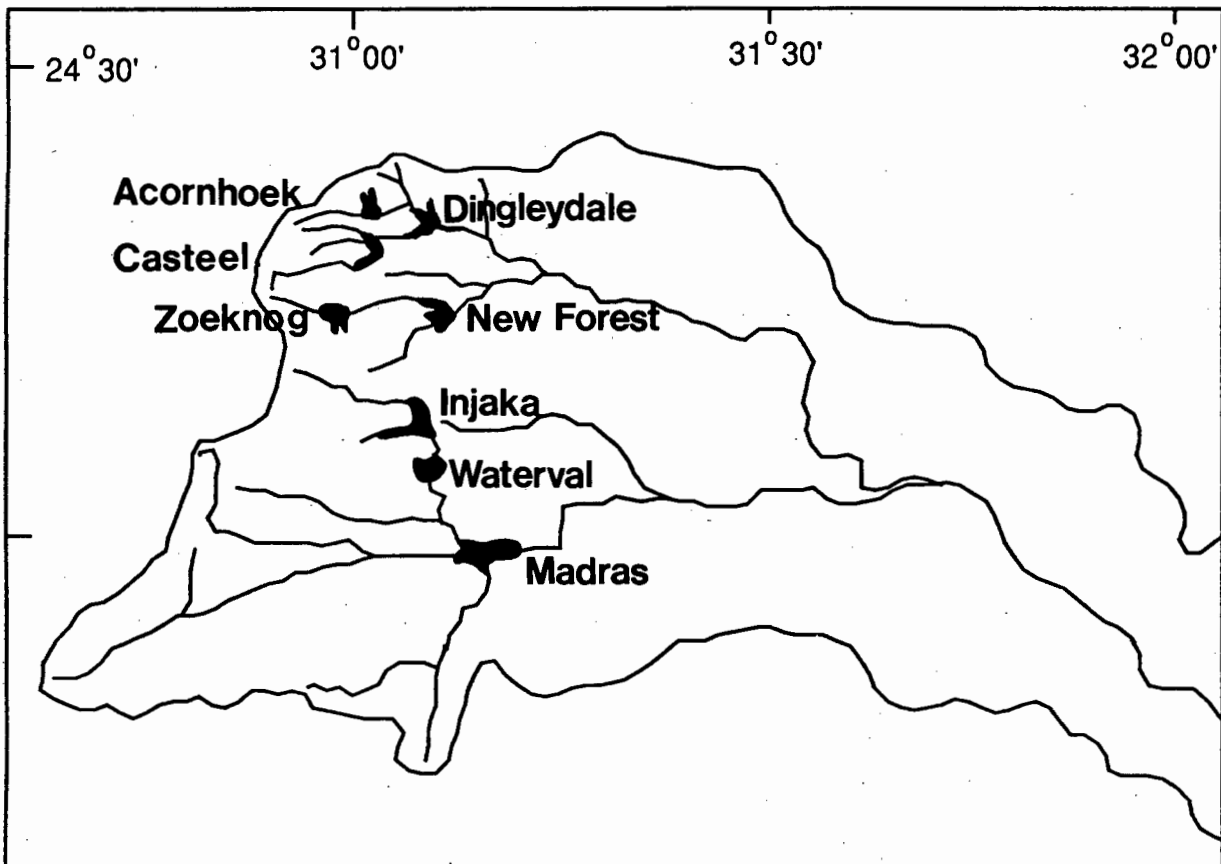


FIGURE 2.8. Map of the Sabie-Sand catchment showing potential dam sites.

It is also envisaged that water be transferred from the Sabie River sub-catchment to the Sand, by means of a rising main in the vicinity of Bosbokrand, and a canal from near Mkuhlu, and that water could also be transferred from the Mtlumuvi tertiary catchment by means of a rising main in the vicinity of Orinoco (Chunnett, Fourie & Partners 1990). With this system, the base flow water requirements in the Sabie and Sand rivers inside the KNP could also be maintained (Chunnett, Fourie & Partners 1990). Further information on water management proposals are found in Department of Water Affairs (1990a) and Chunnett, Fourie & Partners (1990).

It was in the light of these proposed developments, in order to assess the effects that they might have on the system, that this pre-impoundment study of the river was undertaken.

CHAPTER 3

STUDY-SITE SELECTION, SITE DESCRIPTIONS AND COLLECTION METHODS

INTRODUCTION

This chapter deals only with the selection and description of the study sites, the collection of samples in the field, and the processing of samples. Because the subsequent chapters each deal with one aspect of the study, as outlined in Chapter 1, for the sake of continuity, data analysis methodologies are outlined and discussed separately in each chapter.

STUDY-SITE SELECTION

Study-site selection is given high priority within the framework of IFIM (Bovee & Milhous 1978, Bovee 1982) and should be carefully considered when studying any river network. The approach utilised in IFIM involves a breakdown of the river into segments according to certain characteristics (see Bovee & Milhous 1978). On a broad scale, these characteristics include flow régime, channel morphology and channel pattern (Bovee 1982), as well as topography, geology, water quality and species distribution (Bovee & Milhous 1978). Within this project, a similar approach has been used (Figure 3.1). For stratification purposes (see Bovee & Milhous 1978), four variables were selected. They were:

- veld types (see Figure 2.7), as described in Chapter 2 (see also Acocks 1975);
- stream zones (see Figure 2.6), as identified by Chunnnett, Fourie & Partners (1987; also see Chapter 2);
- potential dam sites within the catchment (see Figure 2.8), and
- altitude (see Figure 2.3).

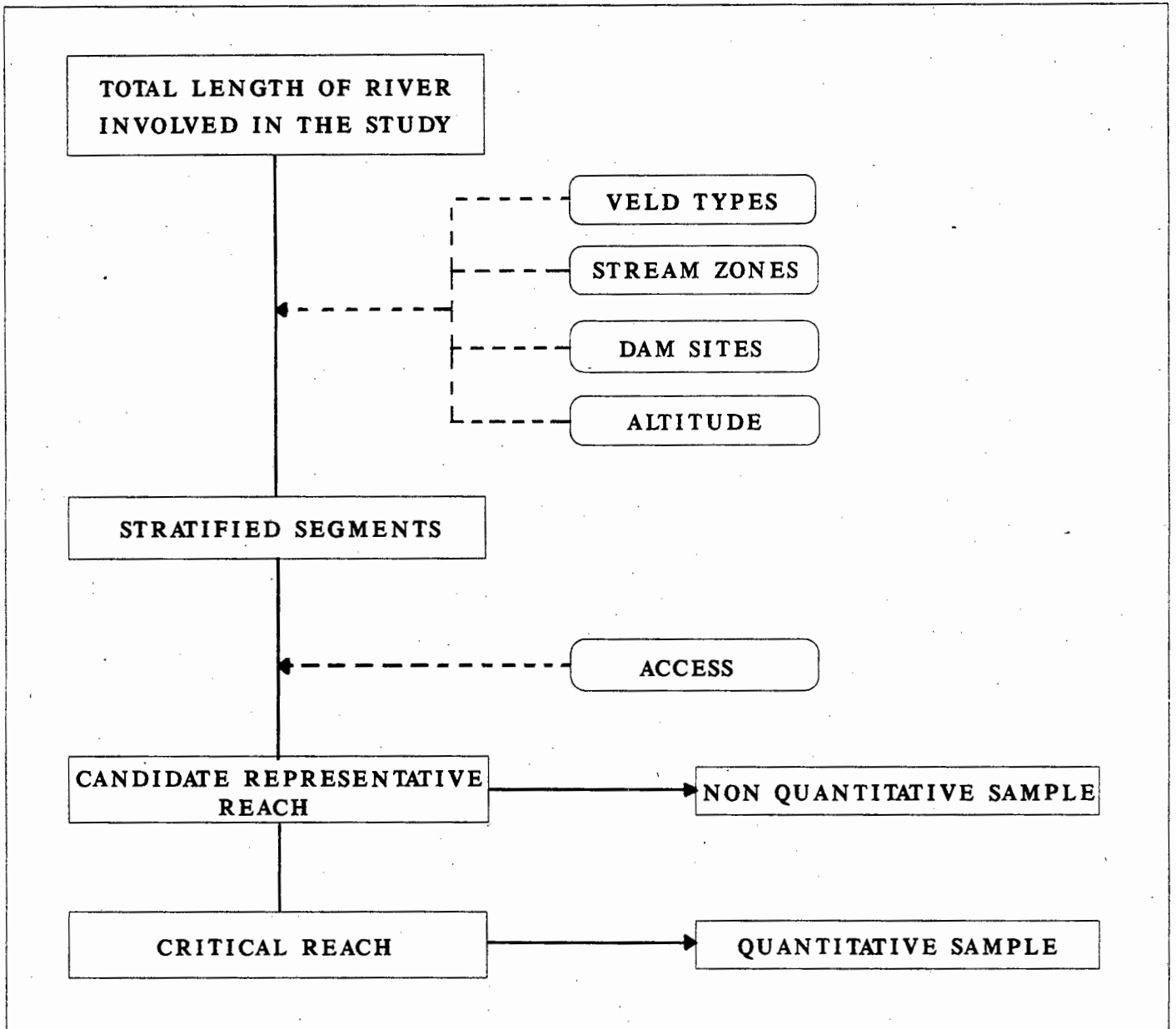


FIGURE 3.1. Model used for the selection of sampling sites and habitats in the Sabie-Sand River catchment.

Thus, stratified segments were identified (Figure 3.1). Access to any site had to be taken into account before positively identifying a candidate reach (Figure 3.1), and all sites eventually selected were accessible using a four-wheel drive vehicle.

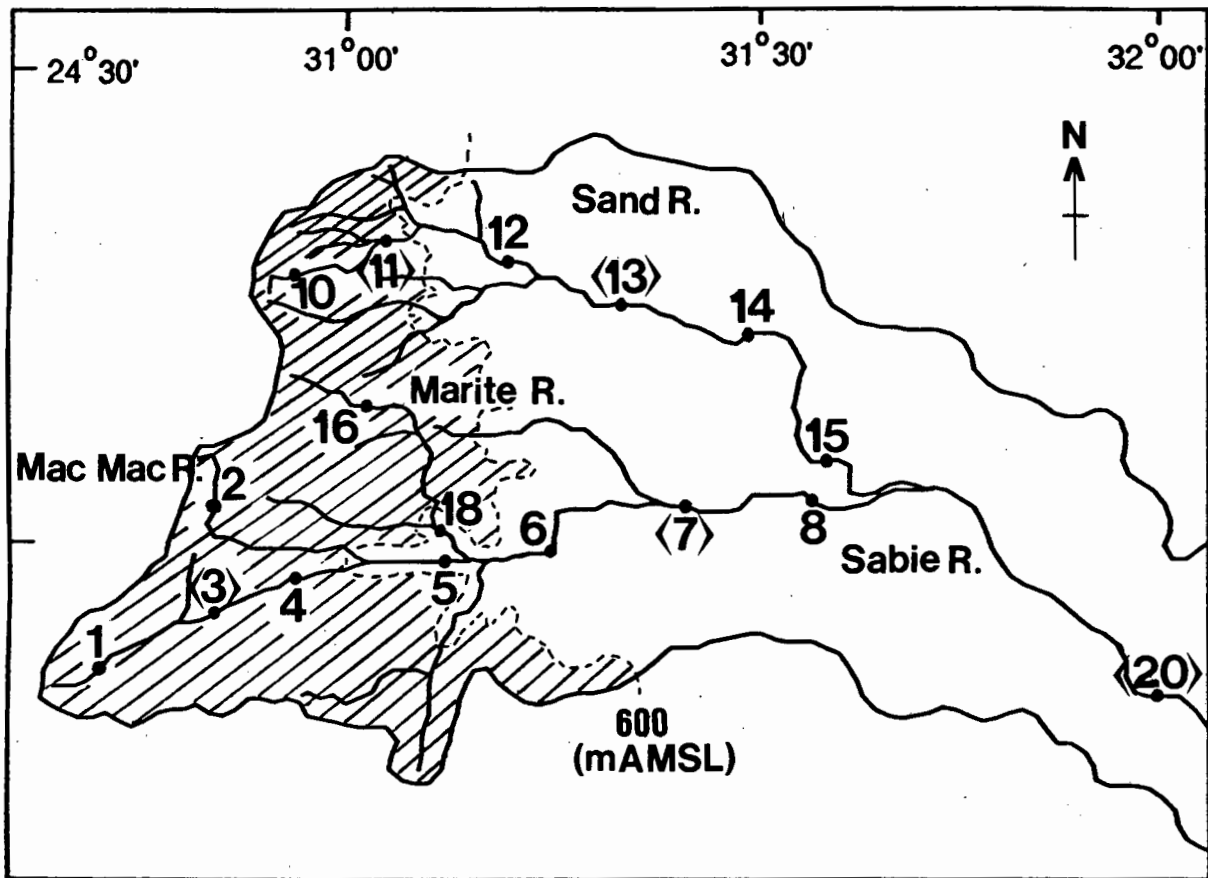
This process gave a selection of "representative reaches" (Bovee & Milhous 1978), each containing different habitat types within which quantitative or non-quantitative sampling could be achieved. In this project, 17 "representative reaches" were selected (Figure 3.2). Table 3.1 gives the exact position of each site, including latitude, longitude, altitude and distance downstream from the source.

These sites were used in a preliminary study (see Chapter 5, and Wells *et al.* in preparation) which was carried out to gain an overall picture of the benthic macro-invertebrate fauna, in relation to the physico-chemistry throughout the catchment. However, only five of them were ultimately selected as suitable sites for the study of biological diversity of the benthic macro-invertebrate fauna (Figure 3.2, and Table 3.1): two on the Sabie River (sites 3 & 7); two on the Sand River (sites 11 and 13); and one below the confluence of the two (site 20). Two of the sites above the confluence (sites 3 and 11) were selected in the upper catchment, above 600mAMSL, in the middleveld region (Figure 3.2). The other three were selected in the lowveld region (Figure 3.2), above (sites 7 and 13) and below (site 20) the confluence (Figure 3.2).

Within the representative reaches, the "critical reach" concept was applied (Figure 3.1; Bovee & Milhous 1978). Any reach is assumed to be "critical" when it represents an area within the stream which is most sensitive to changes. In terms of invertebrate sampling, riffle areas have already been identified as critical reaches (Chutter *et al.* in press). This study, therefore, concentrated on the riffle or rapid habitat as the critical reach in terms of flow; biotic diversity is subsequently considered with regard to this habitat.

TABLE 3.1. Position of sampling sites in the Sabie-Sand River Catchment. Longitude and latitude (both rounded off to the nearest minute), altitude, and distance downstream from the source are all given. Shading highlights the 5 sites which were used to study the biological diversity of the macro-invertebrate riffle fauna

RIVER	SITE NUMBER	LONGITUDE (E)	LATITUDE (S)	ALTITUDE (mAMSL)	DISTANCE DOWNSTREAM (km)
SABIE	1	30°40'	25°09'	1280	3.8
	3	30°52'	25°04'	880	32.3
	4	30°59'	25°02'	620	49.9
	5	31°05'	25°02'	490	61.5
	6	31°15'	25°01'	410	79.8
	7	31°25'	24°58'	320	105.4
	8	31°35'	24°58'	270	127.0
	MAC- MAC	2	30°50'	24°58'	1340
MARITE	16	31°03'	24°51'	800	18.6
	18	31°07'	25°00'	500	59.0
SAND	10	30°56'	24°43'	750	4.8
	11	31°04'	24°41'	540	26.7
	12	31°11'	24°43'	460	41.9
	13	31°21'	24°45'	380	65.4
	14	31°32'	24°47'	320	86.7
	15	31°36'	24°55'	290	109.5
SABIE- SAND	20	32°00'	25°10'	140	187.6



--- CONTOUR
 [Hatched Box] MIDDLEVELD
 [White Box] LOWVELD

FIGURE 3.2. Map of the catchment showing the 17 representative reaches which were used in the preliminary survey. The five sites at which the biological diversity was studied are shown in parentheses.

STUDY-SITE DESCRIPTIONS

Only the five sites at which biological diversity was studied are described here.

Site 3 (30°52'E, 25°04'S)

Site 3 (Figure 3.2) lay on the Sabie River, at an altitude of 880mAMSL, 10km downstream from the town of Sabie. It fell within the "mountain stream zone"

classification of Chunnnett, Fourie & Partners (1987), and was surrounded by exotic forestation. However, the natural riparian forest was dense and extended at least 15m from the water's edge. The banks were steep and access was difficult. No reeds (*Phragmites australis*) were present, though there were some grassy verges.

Figure 3.3A shows a photograph of the site at "medium flow", together with a typical cross-sectional flow profile of the site measured on the same day. Channel width was 14.5m during medium flows. Photographs of the site at the extremes of high and low flow are shown in Figure 3.4A.

The substratum mainly comprised large immovable boulders, although in the side channel, all size-classes of stones were present, from boulders to fine gravel.

Site 7 (31°25'E, 24°58S)

Site 7 (Figure 3.2) was situated on the Sabie River in the KNP, below the confluence of the Saringwa River at an altitude of 320mAMSL. It fell into the "lowland and midland river zone" of Chunnnett, Fourie & Partners (1987), and was surrounded by lowveld tropical bush, with a natural *Phragmites-Mauritianus-Ficus sycamorus* riparian forest, which extended to the water's edge (Figures 3.3B and 3.4B).

Figures 3.3B and 3.4B show photographs of the site at high (Figure 3.4B) and medium flows (Figure 3.3B), with a cross-sectional flow profile of the river at medium flow (Figure 3.3B). The flow profile was measured over a fast flowing rocky area just before a rapid (Figure 3.3B). The channel width at medium flows was 25m.

The substratum in fast flowing areas was smooth bedrock, while in pool areas it was predominantly sand.

Site 11 (31°04'E, 24°41'S)

Site 11 (Figure 3.2) was situated between two potential dam sites on the Sand River, at an altitude of 540mAMSL. It was typical of the "foothill sandbed zone" (Chunnett, Fourie & Partners 1987). The river at this point had indigenous bushveld as the riparian vegetation, with grassy banks and reed encroachment.

Figures 3.3C and 3.4C show the river at this point during high (Figure 3.4C), medium (Figure 3.3C) and low (Figure 3.4C) flows. The flow profile was taken over a very narrow section of the channel, although the channel widened rapidly downstream to about 8m wide during medium flow (Figure 3.3C). The substratum of the riffle areas ranged from cobble to bedrock. Sand was the predominant benthic substratum throughout the remainder of this site.

Site 13 (31°21'E, 24°45'S)

Site 13 (Figure 3.2) was within the Sabie-Sand Reserve at an altitude of 380mAMSL. It, like site 7, occurred in the "lowland and midland river zone" as classified by Chunnett, Fourie & Partners (1987). The surrounding vegetation was tropical bushveld (Acocks 1975), but the river bed comprised vast stands of *Phragmites australis*.

Figures 3.3D and 3.4D show the river at low (Figure 3.4D), medium (Figure 3.3D) and high (Figure 3.4D) flows, together with the cross-sectional profile (Figure 3.3D), which was measured during medium flow over the only riffle/rapid area at the site. The

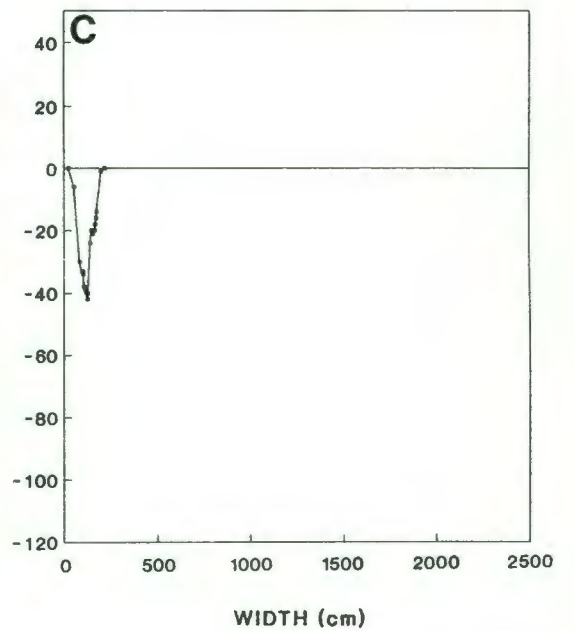
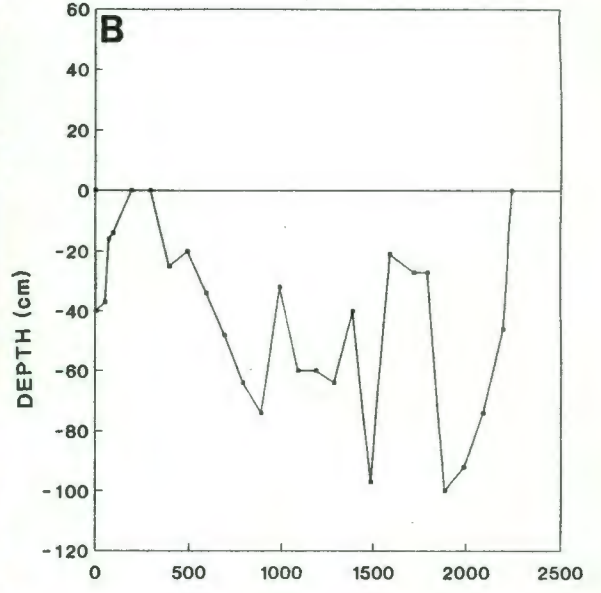
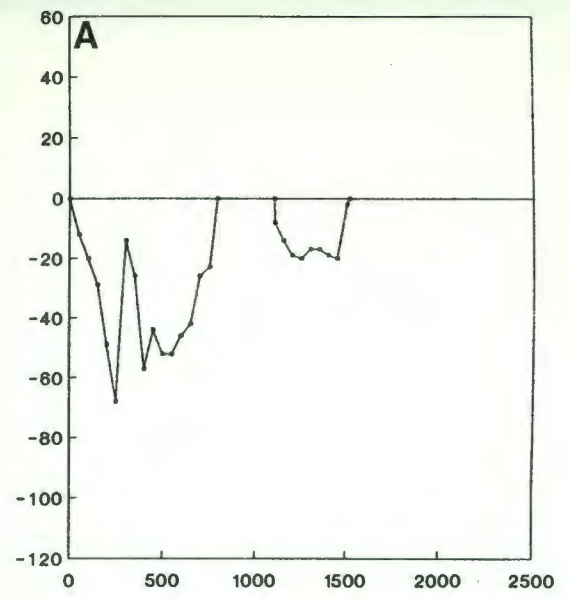


FIGURE 3.3. Photographs and typical flow profiles 7 (B), 11 (C), 13 (D) and 20 (E). Site 20 had no insurmountable (see text). Photographs by Desmond



A
SITE 3



PHOTOGRAPH NOT
AVAILABLE

B
SITE 7



C
SITE 11



FIGURE 3.4. Photographs at sites 3 (A), 7 (B), at low flows (left) and high flows (right). A Photographs by Desmond Weeks.



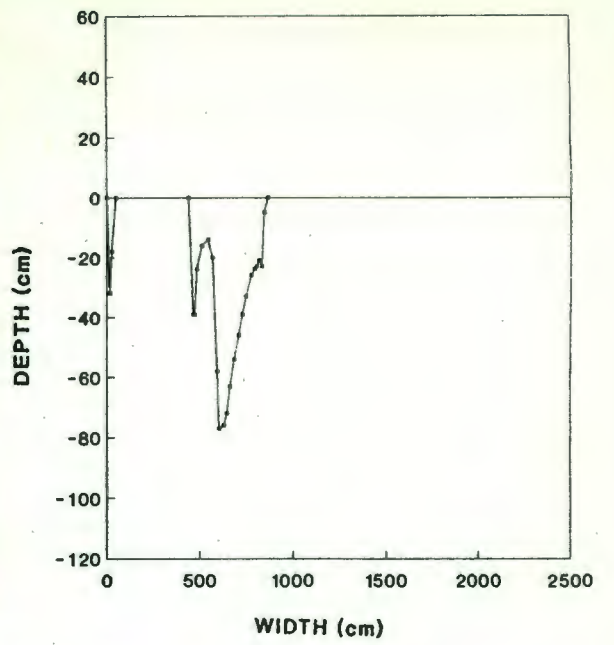
D
SITE 13



E
SITE 20



11 (C), 13 (D) and 20 (E) on the Sabie-Sand river system
photograph was not available for site 7 at low flows.



FLOW PROFILE
NOT AVAILABLE

(facing upstream) at medium flows at sites 3 (A),
flow profile; the logistics of obtaining one were
Weeks.

predominant substratum was sand, while rapids comprised granitic bedrock.

Site 20 (32°00'E, 25°10'S)

Site 20 (Figure 3.2) lay 60km below the confluence of the Sabie and the Sand Rivers within the KNP at an altitude of 140mAMSL, some 5km upstream from the Moçambique border. It occurred in the "lowland and midland river zone" of Chunnett, Fourie & Partners (1987), and was surrounded by tropical bushveld (Acocks 1975).

The river was very braided at this point and it was not possible to sample every channel, thus, one of the most easily accessible channels was sampled (Figures 3.3E and 3.4E). This lay to the north side of the section. The bush and reedbeds on the islands between channels was thick, and wild animals prevented easy access to other channels. No cross-sectional flow profile was taken at this point due to the braided nature of the river and the danger from large mammals and crocodiles.

The substratum of the sample site ranged from roughened bedrock to gravel.

COLLECTION METHODS

Physico-chemistry

Water for chemical analysis of nutrients was collected, filtered through Watman GF/F filters (45 μ m) and preserved on site using a 1% solution of mercuric chloride. These were later analysed for nitrite, nitrate, sulphate, soluble reactive phosphate (SRP) and ammonium using a Technikon Auto-Analyser at the CSIR, Stellenbosch.

Total suspended solids (TSS) were determined by weight difference after passing a known volume of water through a pre-combusted (450°C, 5h), tared Watman GF/F filter and drying at 105°C for a minimum of three hours. The organic fraction was determined after further combustion. Dissolved oxygen and water temperature were measured using an Aqua-lytic Oxi 921 oxygen meter, calibrated against atmospheric pressure. Conductivity was measured using a DiST 3 ATC dissolved solids tester, and pH was measured using a pHep pH meter.

River discharge was measured by setting up a detailed "panel" flow transect at each site. River depth for at least 20 intervals was measured and, at each point, flow velocity was recorded using a Price AA Current Meter. These measurements were converted to discharge down the river by using the equation

$$V = \sum_{i=1}^n (d_i \times w_i \times v_i) \quad (3.1)$$

where i = panel number, according to intervals measured,

d = depth (m),

w = width (m),

v = velocity (m s^{-1}).

Macro-invertebrates

Two sampling procedures were used, one for the preliminary survey of the benthic fauna, and one for the more intensive study at the five sites.

The preliminary survey was carried out, during the medium flow season, in May and June 1990 at the 17 sites within the catchment (Figure 3.2). At each site, 5 macro-invertebrate samples were collected from riffle/rapid and sandy-substrata habitats in the percentage of each habitat type present. For example, at site 3 there was about 75% rocky substratum to 25% sandy substratum, and, therefore, four samples were taken in the riffle/rapid areas and one in the sandy areas. Sampling in riffle areas was done using a Surber Sampler (30cm²; Surber 1936), while sampling in sand substratum areas was achieved with a Van Veen Grab (2 250cm³). All organisms >80µm were retained. The samples were fixed on site with 10% neutralised formalin and stored in the laboratory in 80% alcohol. Laboratory identification to genus level was undertaken where possible, using suitable keys to the different taxa (e.g. Barnard 1931; Crass 1947; Pennak 1953; Crosskey 1960; Usinger 1963; Scott 1974, 1983, unpublished a, b, c; McCafferty unpublished). The data were expressed as the number of organisms m⁻².

Quantitative diversity samples were taken at quarterly intervals at the five sites, over a period of a year, from May 1990 to March 1991. Three replicate samples were taken at each site in the riffle/rapid habitat. On bedrock, sampling was achieved using the 30cm² Surber Sampler, while in other areas, within the riffles, a handnet was used to catch organisms while brushing them off the rock surfaces. In each case an 80µm mesh net was used. When handnets were used, the area of the sampled surface was calculated by measuring rock dimensions and relating these to the surface area of an oblate. The

equation used was:

$$A_{(\text{estimated})} = 2 \pi a(b+c) \quad (3.2)$$

where $a = 1/2 \times \text{height (m)}$,

$b = 1/2 \times \text{width (m)}$,

$c = 1/2 \times \text{depth (m)}$.

Samples were fixed on site with 10% neutralised formalin and stored in the laboratory in 80% alcohol as before. Laboratory identification to genus level was undertaken where possible, using the reference sources cited above, and the data were expressed as the number of organisms m^{-2} .

CHAPTER 4

DEFINITION OF TAXONOMIC, TEMPORAL AND SPATIAL BOUNDARIES

INTRODUCTION

Magurran (1988) has stressed the need to define and to delimit any community under study before measuring diversity. In terms of river ecosystems this incorporates the definition of both spatial and temporal dimensions (Minshall 1988; Wells & Walmsley in preparation). Taxonomic boundaries also need defining, when dealing with little known communities such as the benthic macro-invertebrates. This chapter deals with the definition of these boundaries.

Taxonomic boundaries

Magurran (1988) has stated that the taxonomic level at which biological diversity is studied needs to be constant throughout, and that no diversity measure should be calculated where mixed taxonomic hierarchies are involved. According to Osborne *et al.* (1980), this taxonomic level must be chosen *à priori*.

A significant problem exists with identification of many aquatic organisms (Kaesler & Herricks 1979), and the choice of the taxonomic level at which diversity is to be measured is often constrained by a lack of taxonomic expertise. Numerous orders of aquatic macro-invertebrates have poorly understood taxonomy, and even when systematic relationships are well understood, the limiting factors often include inadequate keys, a shortage of qualified systematists (Kaesler & Herricks 1979), and the time taken to identify organisms. This is true of the situation in South Africa and, in particular, the Sabie-Sand River system.

A number of studies have addressed the problem of measuring the diversity of aquatic macro-invertebrates for different taxonomic levels. Hughes (1978) indicated that the level of Order might be sufficient to determine general trends in benthic macro-invertebrate communities, while Osborne (1977; cited by Osborne *et al.* 1980) indicated that the Family level is more acceptable in this case. On the other hand, Kaesler *et al.* (1978) and Kaesler & Herricks (1979) suggested that for aquatic insects identification to Genus level is acceptable, though they have been directly contradicted by Lenat and Penrose (1980) who, using the same data, argued for identification to Species level. Thus, there is little agreement on an acceptable level of taxonomic identification for the purpose of calculating biological diversity; each study differs and it is up to the individual scientist to determine the level of identification relevant to the study in hand.

In the Sabie-Sand River system the taxonomic knowledge for the identification of invertebrates to genus and species is poor. Thus, one of the aims in this chapter is to determine whether or not it would be applicable to measure the biological diversity of the benthic macro-invertebrate fauna at a Family level of identification.

Temporal boundaries

Wells & Walmsley (in preparation) state that if change in the biological diversity of a community is to be monitored then the minimum time-span of the study should incorporate all natural variation within the community. Temporal variations typical of macro-invertebrate communities are those where seasonal changes are linked to the life-cycles of organisms within the community. At any one time, the biological diversity of a community may be different from that at any other time of the year. It is reasonable, therefore, to suggest that a span of one year is the absolute minimum period necessary

for measuring biological diversity of any benthic macro-invertebrate community. However, variations in the community may also be due to physical variations, which may be inter-annual (e.g. rainfall), or over periods longer than a year (e.g. erosion cycles), and, therefore, although the minimum span is a year there could be greater variations in diversity over a longer period.

One method of testing this is to plot the frequency distribution of species abundance on a log scale. The species abundance of the majority of communities studied by ecologists display a log normal distribution pattern (Magurran 1988). This gives a symmetrical "normal" bell-shaped curve (Figure 4.1). If, however, the data to which the curve is fitted have been derived from a finite sample, the left-hand portion of the curve (representing rare species) will be obscured (Washington 1984; Magurran 1988). This truncation point is known as the "veil line". In smaller samples the veil line will be further from the origin (Figure 4.1).

In communities, where seasonal variation invariably plays a role, the veil line may be further away from the origin if only one season is considered. However, if all seasons are included, the community will tend towards a log normal distribution, and a more complete picture of species diversity may become apparent. The second aim of this chapter is to determine whether or not this is true of the benthic macro-invertebrate communities of the Sabie-Sand River system, by determining where the "veil line" is situated on the frequency distribution plots of species abundance (\log_2) as data from each sampling trip are plotted cumulatively throughout the year.

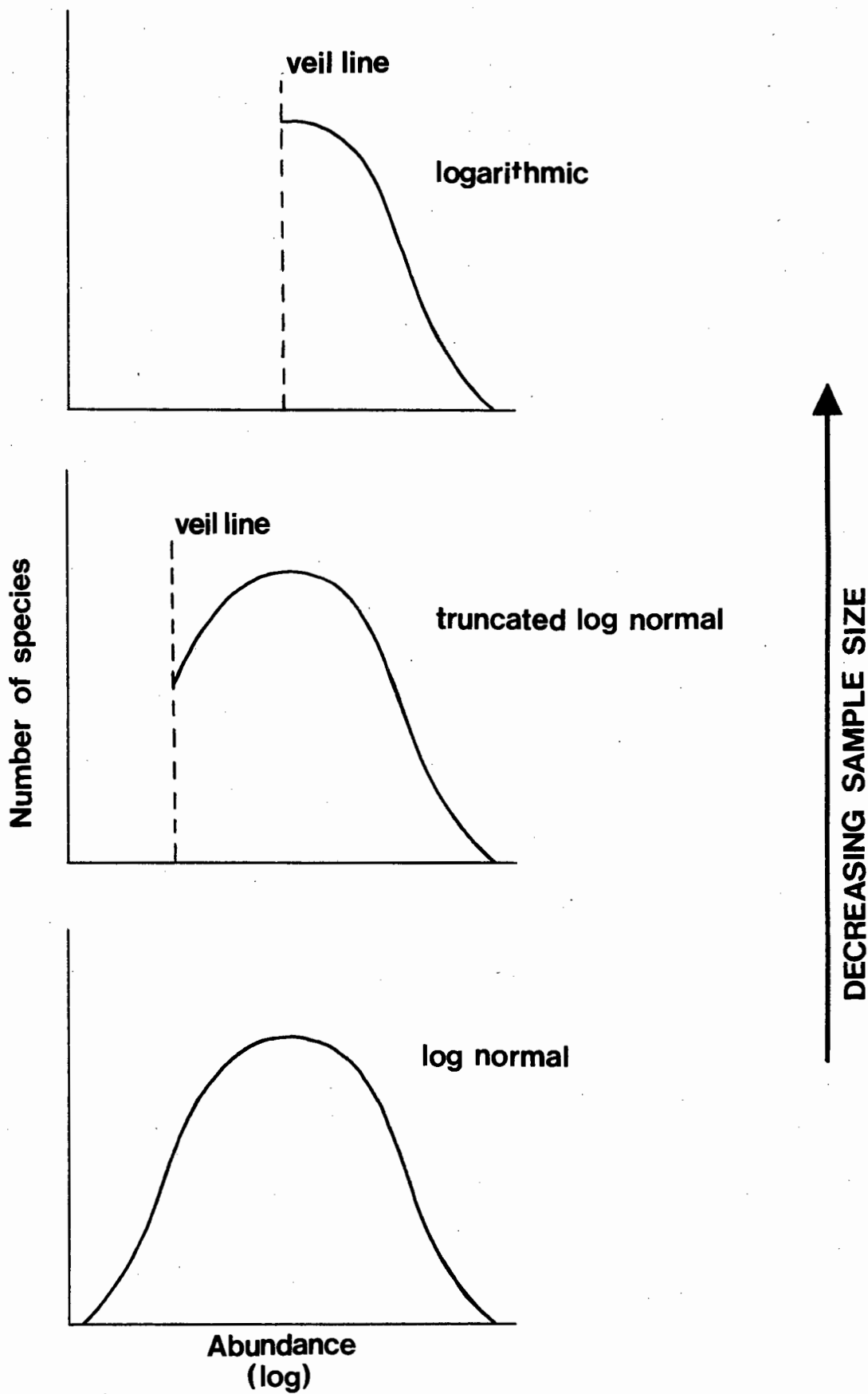


FIGURE 4.1. Hypothetical log normal curves of species abundance showing the veil line effect.

Spatial boundaries

Krebs (1985) defines a community as "...a group of populations ...in a given place" and as such, communities are often referred to in terms of their spatial boundaries. Examples of this are: "a community of insects on a bracket fungus" or "a community of plants or animals in a rain forest" (Magurran 1988). Therefore, it is important to delimit the spatial boundaries of a community, and thereby define the scale on which the study is done.

To do this, the concepts of inventory (Whittaker 1977) and differentiation (Pielou 1975; Magurran 1988) diversity can be used (see Chapter 1). Whittaker (1977) distinguishes four levels of inventory diversity:

point diversity - the diversity of a micro-habitat or sample taken from a homogeneous habitat;

alpha diversity - the diversity within a homogeneous habitat;

gamma diversity - the diversity of a larger area within the region, and

epsilon diversity - the overall diversity within a region.

Although Whittaker (1977) matched his categories to fairly precise scales (habitat, geographical area, region), the idea can easily be adapted (Magurran 1988).

The concept of differentiation diversity is closely linked to that of inventory diversity. The levels may be defined as follows (Magurran 1988):

patch diversity - the difference in diversity between areas of point diversity;

beta diversity - the difference in diversity between areas of alpha diversity, and

delta diversity - the difference in diversity between areas of gamma diversity.

A generalised outline of spatial definition for river ecosystems using these two concepts may be found in Wells & Walmsley (in preparation), (see also Figure 1.4, Chapter 1). This also gives the scale which may be applied to the levels of inventory diversity and the associated differentiation diversity. It is this outline on which I shall base the definition of spatial boundaries and the relevant scales for the benthic macro-invertebrate communities.

METHODS

Taxonomic boundaries

For compatibility with other authors (Hughes 1978; Kaesler *et al.* 1978; Lenat & Penrose 1980; Osborne *et al.* 1980) the Shannon diversity index was used. The formula is given as:

$$H' = \sum_{i=1}^n p_i \ln p_i \quad (\text{see eqn. 1.7, Chapter 1})$$

where p_i = proportion of individuals in the i th taxon.

The index value was calculated at five sites for five hierarchical levels: Phylum, Class, Order, Family and Genus. Species level was not included as insufficient organisms were identifiable to this level. Only data from the preliminary survey (May 1990) were used, as they were the only data from samples which had been consistently identified to genus.

The H' values were compared for each hierarchical level using one-way analysis of

variance (ANOVA, Zar 1984). The Student-Newman-Keul's (SNK) *à posteriori* test (Zar 1984) was employed to determine which mean H' values were significantly different from others.

The relationship between diversity at Family and Genus levels was also determined and statistically tested using Pearson's product-moment correlation coefficient (PPMC), (Zar 1984).

Temporal boundaries

Species abundance frequency distributions were plotted for each site using \log_2 frequency classes (Magurran 1988), where each class represents a doubling of species abundances. \log_2 abundance classes were plotted on the x-axis and the number of species per frequency class on the y-axis. A log normal curve was then superimposed on the data and the veil line was identified.

For each site, four such distributions were plotted. They were cumulative plots for:

- 1) the samples from the first field trip (Autumn/Winter; May 1990);
- 2) the samples from the first and second field trips (Autumn/Winter and Spring; May and August 1990);
- 3) the samples from the first, second and third field trips, (Autumn/Winter, Spring and Summer; May, August and November 1990), and
- 4) the samples from all four field trips (Autumn/Winter, Spring, Summer and Summer/Autumn; May, August and November 1990 and February 1991).

Spatial boundaries

The generalised outline of spatial definition for river ecosystems (Figure 1.4, Chapter 1) was adapted so that the terms used for inventory diversity (point, alpha, gamma and epsilon diversity), and differential diversity (patch, beta and delta diversity) were spatially defined. The scales which apply to the levels of diversity were also defined. The results were drawn up on a hierarchical chart similar to Figure 1.4.

RESULTS AND DISCUSSION

Taxonomic boundaries

Figure 4.2 gives values of the Shannon diversity index of five sites on the Sabie and Sand rivers, for five different taxonomic levels. A one-way ANOVA showed that the diversity at the different taxonomic levels was significantly different ($F=7.72$, $p<0.01$, d.f. 4, 65). However SNK tests showed that, although the diversity (H') between Genus, and Class and Phylum levels differed significantly (SNK, $p<0.05$, d.f. 9; see Appendix A), there was no significant difference in diversity between the levels of Genus, Family and Order (SNK, $p<0.05$, d.f. 9; see Appendix A). This can be interpreted to mean that it is acceptable within this study to measure biological diversity at a familial hierarchical level without any significant loss of information.

Though the mean diversity at levels of Family and Genus may not differ significantly, there may be erratic changes in the evenness component of diversity (see definition of diversity in Chapter 1) between the two levels (Lenat & Penrose 1980). Figure 4.3 shows the relationship between the value given by the Shannon index for diversity at Genus

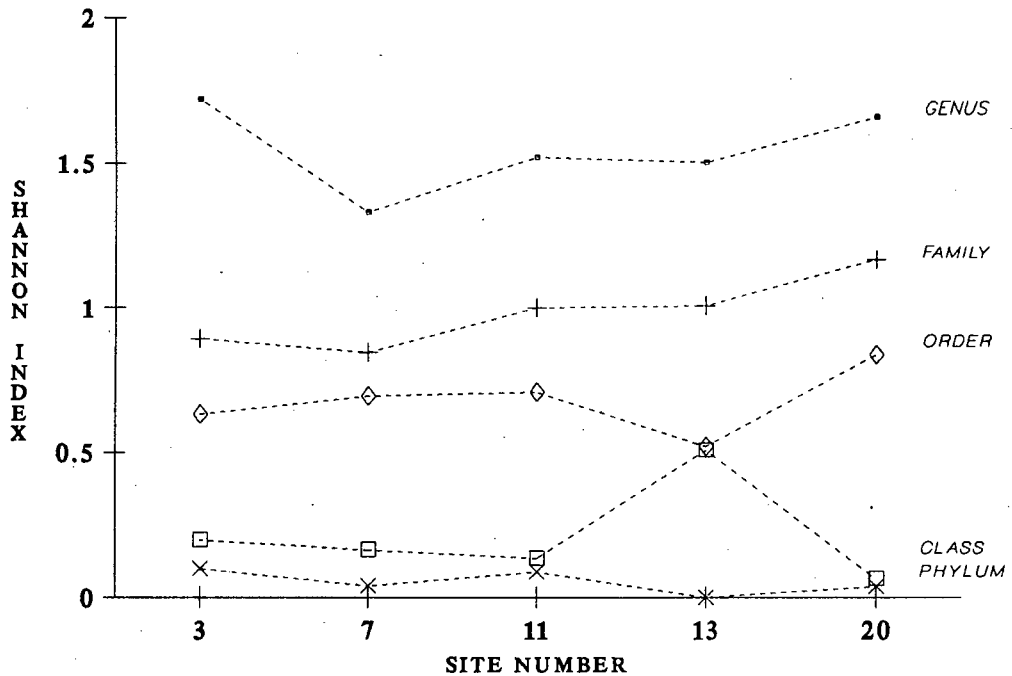


FIGURE 4.2. The Shannon diversity index values calculated from a single data set for five different taxonomic levels for sites 3, 7, 11, 13 and 20.

level and at Family level of samples from the Sabie-Sand River system. The correlation between the two is highly significant (PPMC, $p < 0.005$, $r = 0.941$, d.f. 12), showing that there is a close relationship between the two. They, therefore, have a similar evenness component ($r = 0.94$, $r^2 = 89$; see Kaesler & Herriks 1979); the correlation would not be significant if the communities differed in taxon abundance, that is, if at one level, one taxon dominated while at another level there was an even distribution. From this point of view, using diversity measures at the level of Family is acceptable. The relationship

between the two may be stated by the equation:

$$H'_{\text{Genus}} = 0.85.H'_{\text{Family}} + 0.72 \quad (4.1)$$



FIGURE 4.3. Relationship between Shannon diversity at the Genus Family levels, calculated from individual samples from within the Sabie-Sand River system.

Temporal boundaries

Figures 4.4 - 4.8 show the frequency distribution plots of the abundance of benthic macro-invertebrate families at five sites. At all sites for May (Figures [4.4 - 4.8]A) the veil line is far to the right and the distribution (except at site 20) is essentially logarithmic. For the May/August distribution (Figures [4.4 - 4.8]B) only sites 7 and 13

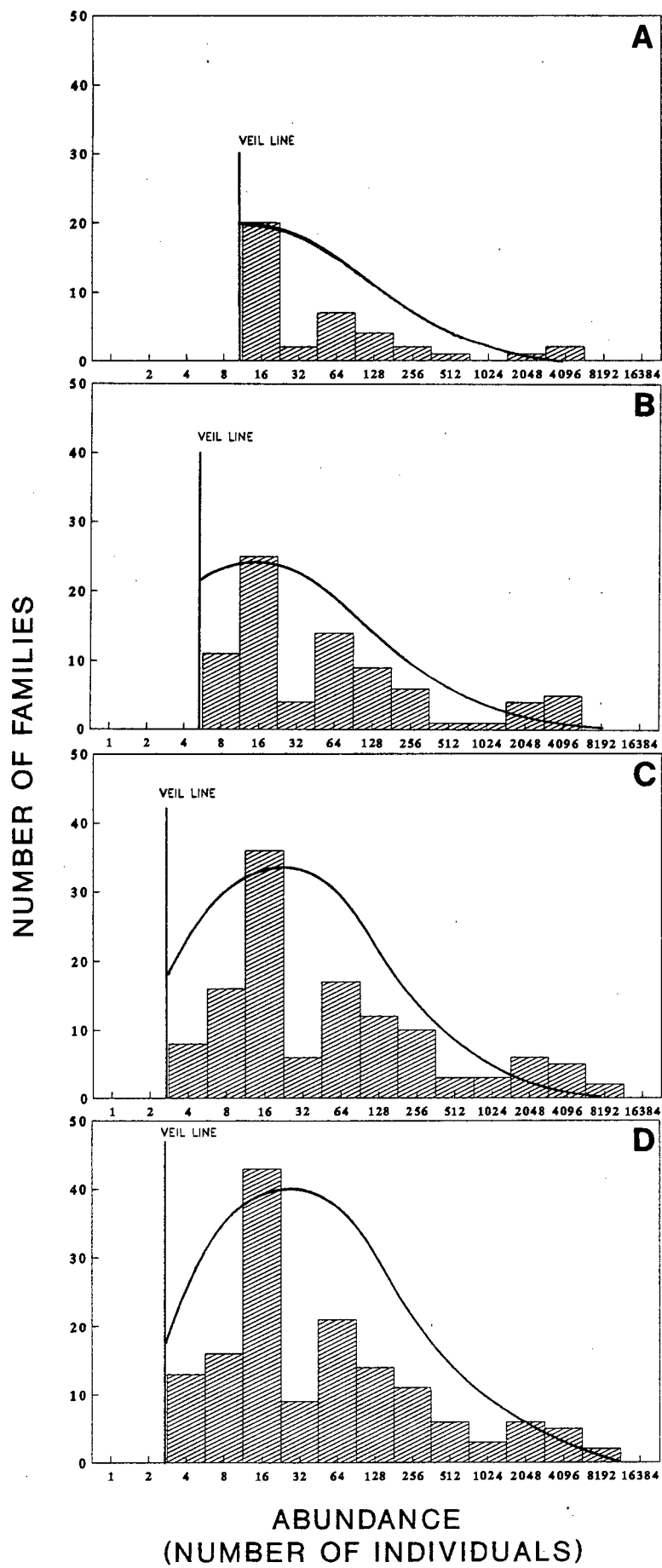


FIGURE 4.4. Family abundance frequency plots for site 3 for A, May; B, May/August; C, May/August/November; D, May/August /November/February.

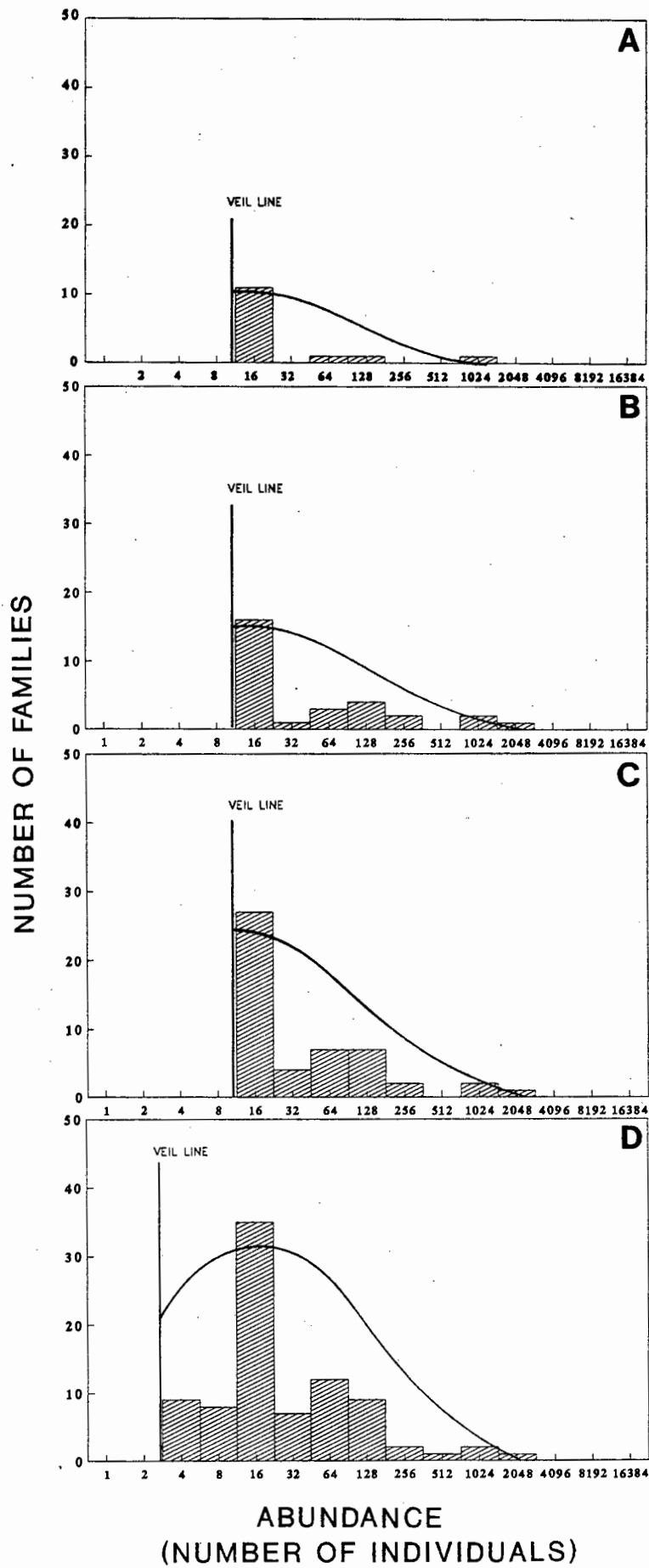


FIGURE 4.5. Family abundance frequency plots for site 7 for A, May; B, May/August; C, May/August/November; D, May/August /November/February.

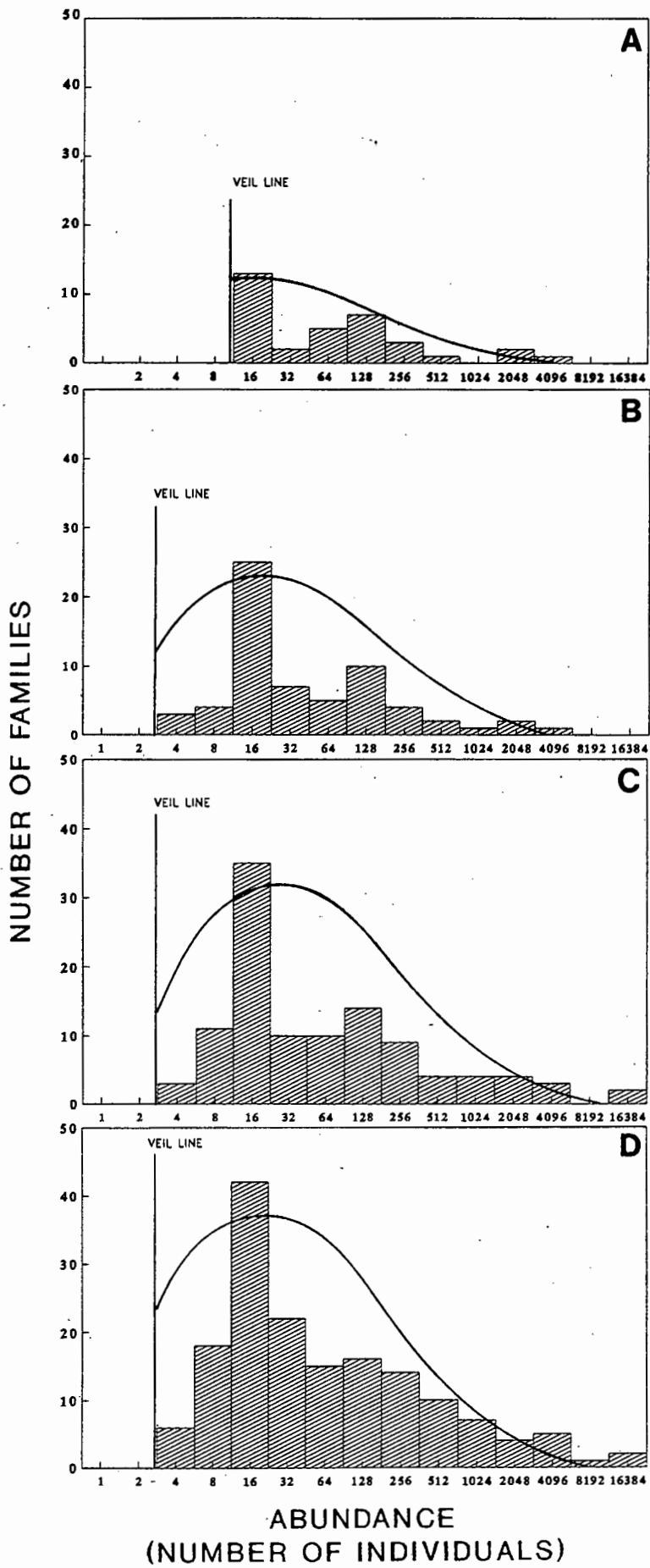


FIGURE 4.6. Family abundance frequency plots for site 11 for A, May; B, May/August; C, May/August/November; D, May/August /November/February.

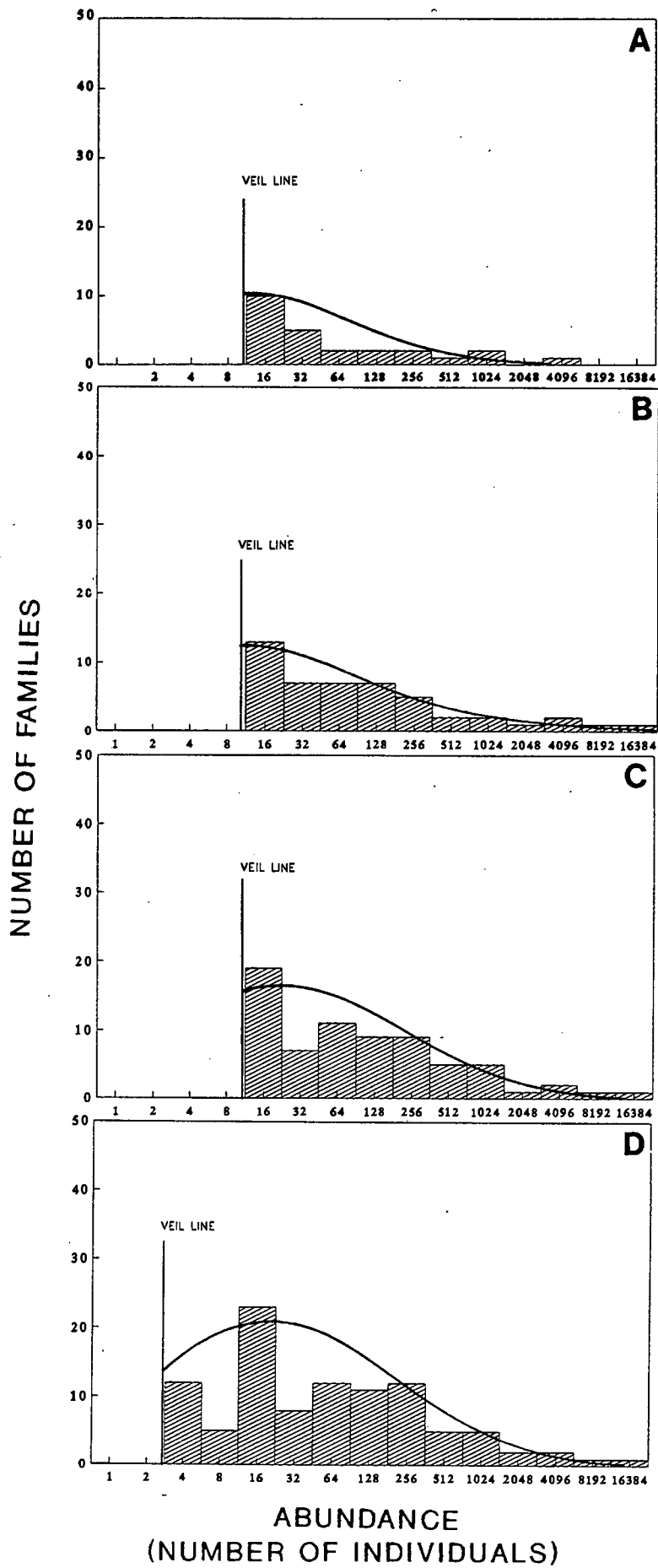


FIGURE 4.7. Family abundance frequency plots for site 13 for A, May; B, May/August; C, May/August/November; D, May/August /November/February.

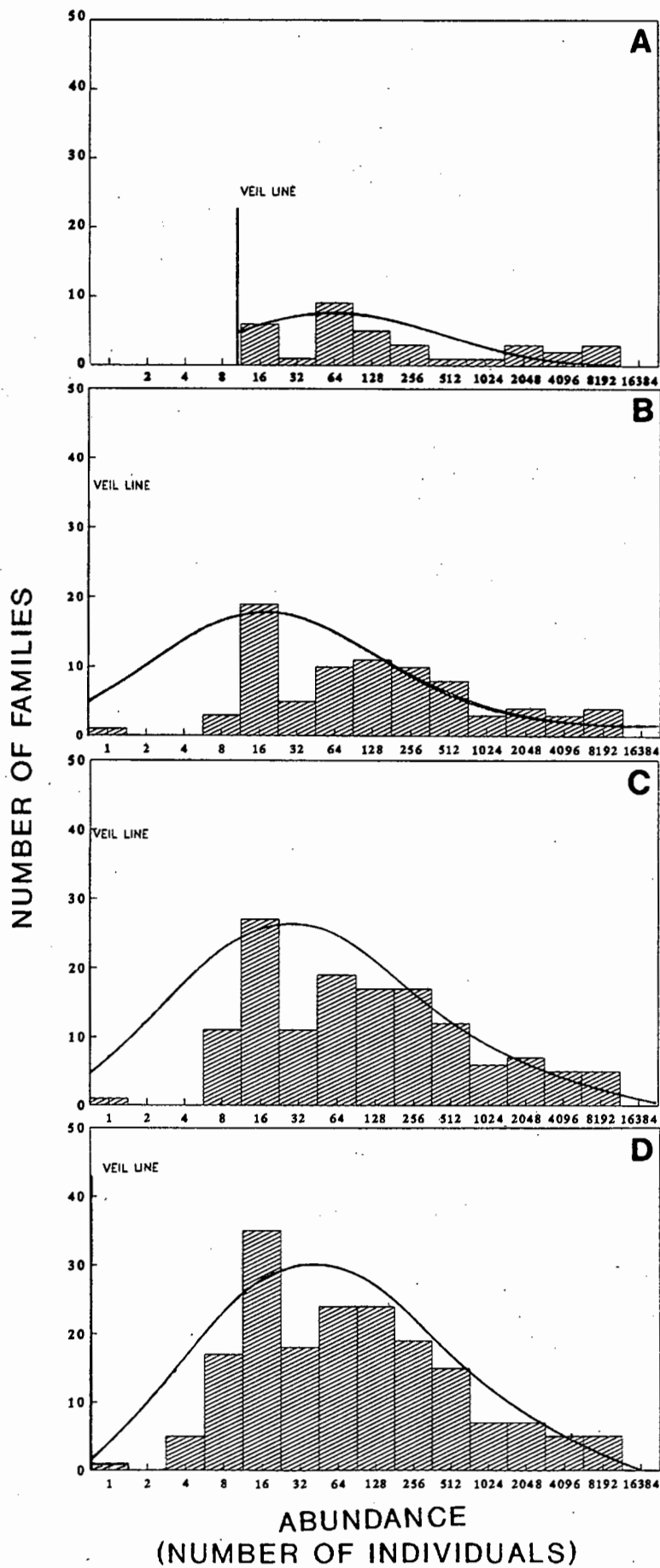


FIGURE 4.8. Family abundance frequency plots for site 20 for A, May; B, May/August; C, May/August/November; D, May/August /November/February.

still show the logarithmic distribution, while the others have a distinctly truncated log-normal distribution. The same is true of the May/August/November distribution (Figures [4.4 - 4.8]C). In Figures [4.4 - 4.8]D, which show the cumulative plots for the whole year at all sites, the distribution patterns are log normal, with only the very left of the curve obscured. These data infer that the calculation of diversity for individual months does not provide a representative description of the community in all spatial and temporal dimensions. However, if the community is considered over a year, the natural variations in community structure due to different life-histories and other cyclic occurrences are taken into account, resulting in a truncated log normal distribution.

Spatial boundaries

Figure 4.9 illustrates a hierarchical outline defining the spatial boundaries of inventory and differentiation diversity within the Sabie-Sand River system. The scale for each type of diversity is shown on the left of Figure 4.9.

The boundaries for inventory diversity in the Sabie-Sand River system may be summarised as follows:

- *point diversity* - the diversity of a single sample in a riffle in an area of one square meter;
- *alpha diversity* - the diversity of the riffle habitat at each of sites 3, 7, 11, 13 and 20, covering an area of about five square meters;
- *gamma diversity* - the diversity of a tributary or section of the river (Sabie River, Sand River or below the confluence of the two), on a scale of 10^4 - 10^5 m, and
- *epsilon diversity* - the diversity of the whole Sabie-Sand catchment, on a scale of 10^5 m.

Spatial
scale(m)

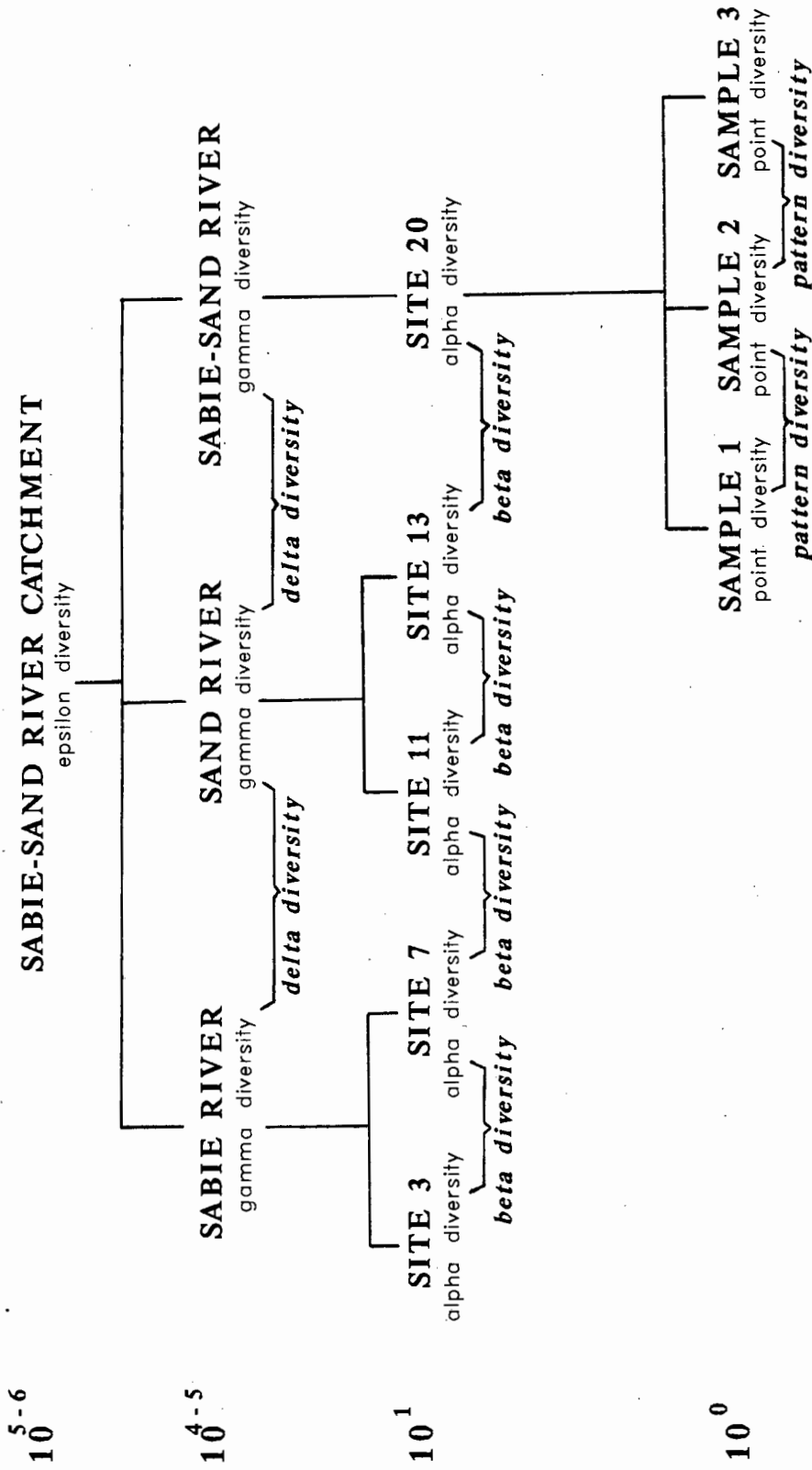


FIGURE 4.9. An outline of the definition of diversity on a spatial scale for the Sabie-Sand River system, using inventory and differentiation diversity.

The boundaries for differentiation diversity for the system may be summarised as follows:

- *pattern diversity* - the difference in diversity between samples in a riffle;
- *beta diversity* - the difference in diversity between sites.
- *delta diversity* - the difference in diversity between tributaries or sections of a river.

CONCLUSIONS

Taxonomic boundaries

In this study, measures of diversity will be determined at a Family level for three reasons:

- the basis for identification to Family level is sound;
- diversity at a generic level is not significantly different from that at a familial level;
- there is a very close relationship between diversity at the levels of Genus and Family.

Temporal boundaries

Magurran (1988) states that only in extensive data collections which cover large areas or time spans will the complete log normal distribution be apparent. However, most data to which the log normal curve is fitted are from smaller samples and, more often than not, the left-hand portion of the curve will be obscured, forming a truncated log normal distribution. The data for the Sabie-Sand system, which spans one year, displays this

more usual form of the log normal distribution and may be considered adequate in terms of sample size. However, if data from separate field trips were analysed this would not be the case, and a full picture of the community diversity would not emerge. Therefore, for the purpose of this study (except the preliminary survey) I shall use mean diversity measures from data collected over one year.

Spatial boundaries

A summary of the spatial boundaries for both inventory and differentiation diversity is set out in the "results and discussion" section of this chapter. Special attention will be paid to alpha, beta, gamma and delta diversity, while point, patch and epsilon diversity will be discussed in order to gain a more complete picture of the biological diversity of the system.

CHAPTER 5

**A PRELIMINARY ANALYSIS OF THE DISTRIBUTION PATTERNS OF THE
BENTHIC MACRO-INVERTEBRATE FAUNA OF THE SABIE-SAND RIVER
SYSTEM IN RELATION TO SEVERAL ENVIRONMENTAL FACTORS.**

INTRODUCTION

Before an assessment of the biological diversity of the benthic macro-invertebrate fauna at select sites can be made, an understanding of the system as an entity needs to be developed. Thus, a preliminary investigation of the benthic macro-invertebrate fauna and some physico-chemical properties of the river system was undertaken. This incorporated the whole of the Sabie-Sand River system, from the headwaters to the Moçambique border in the KNP.

Biological surveys of this magnitude usually result in complex bodies of biotic and environmental data from which patterns and relationships can be extracted (Field *et al.* 1982). There are a number of numerical techniques which may apply to such data, of which many have been used in freshwater studies (e.g. Gauch *et al.* 1977; Green & Vascotto 1978; Culp & Davies 1980; Cushing *et al.* 1980; Gore 1980; Field *et al.* 1982; Townsend *et al.* 1983; Wright *et al.* 1984; Ormerod and Edwards 1987; Warwick *et al.* 1990).

For the purpose of this study I have utilized the approach of Field *et al.* (1982), which is to "...search for patterns amongst the biological variables with an attempt to interpret these in terms of the environmental data", using classification and ordination techniques. An analysis of the distribution patterns of the benthic macro-invertebrate fauna in relation to the physico-chemical properties of the river is presented.

METHODS

Figure 5.1 summarizes the stages of analysis, and includes the relevant mathematical equations for each stage.

Species abundance data (number m⁻²) were aggregated into genera, where possible except in some cases (e.g. Hydracarina and Chironomidae) where, due to a lack of taxonomic expertise, organisms were identified to family. The data were transformed using the root-root transformation of Stephenson & Burgess (1980) (Figure 5.1). The Bray-Curtis measure of dissimilarity, δ (Bray and Curtis 1957), was used on these transformed data (see Figure 5.1), and the similarity was calculated as the complement of dissimilarity (Figure 5.1). These values were used to form a triangular similarity matrix, which could then be used in the cluster and ordination analyses.

Cluster analysis and multi-dimensional scaling

Clustering was achieved by an hierarchical agglomerative method, employing group-average linking, the results of which were displayed in a dendrogram. Ordination was by non-metric multi-dimensional scaling (MDS) of Shepard (1962). This method was chosen as it has several conceptual advantages over other methods (Clarke & Green 1988). It has flexibility of its definition, which principal component analysis (PCA) does not have (Jongman *et al.* 1987; Ludwig & Reynolds 1988). Also, unlike PCA and principal co-ordinates analysis (PCoA) its rationale is the preservation of the relationships in low-dimensional ordination space (Ludwig & Reynolds 1988; K.R. Clarke & R.M. Warwick, Plymouth Marine Laboratory, U.K., pers comm.) The theory of MDS also recognises the essential arbitrariness of the absolute similarity values used in detrended correspondence analysis (DECORANA; Gauch 1982) and thus makes use of relative values. The ordination produced a scatter plot in which each replicate sample was represented by a point. The distances between points were then compared with the corresponding similarities by fitting a general monotonic (increasing) regression (Field *et al.* 1982). The extent to which the relationship could adequately be represented in two or three dimensions is summarised

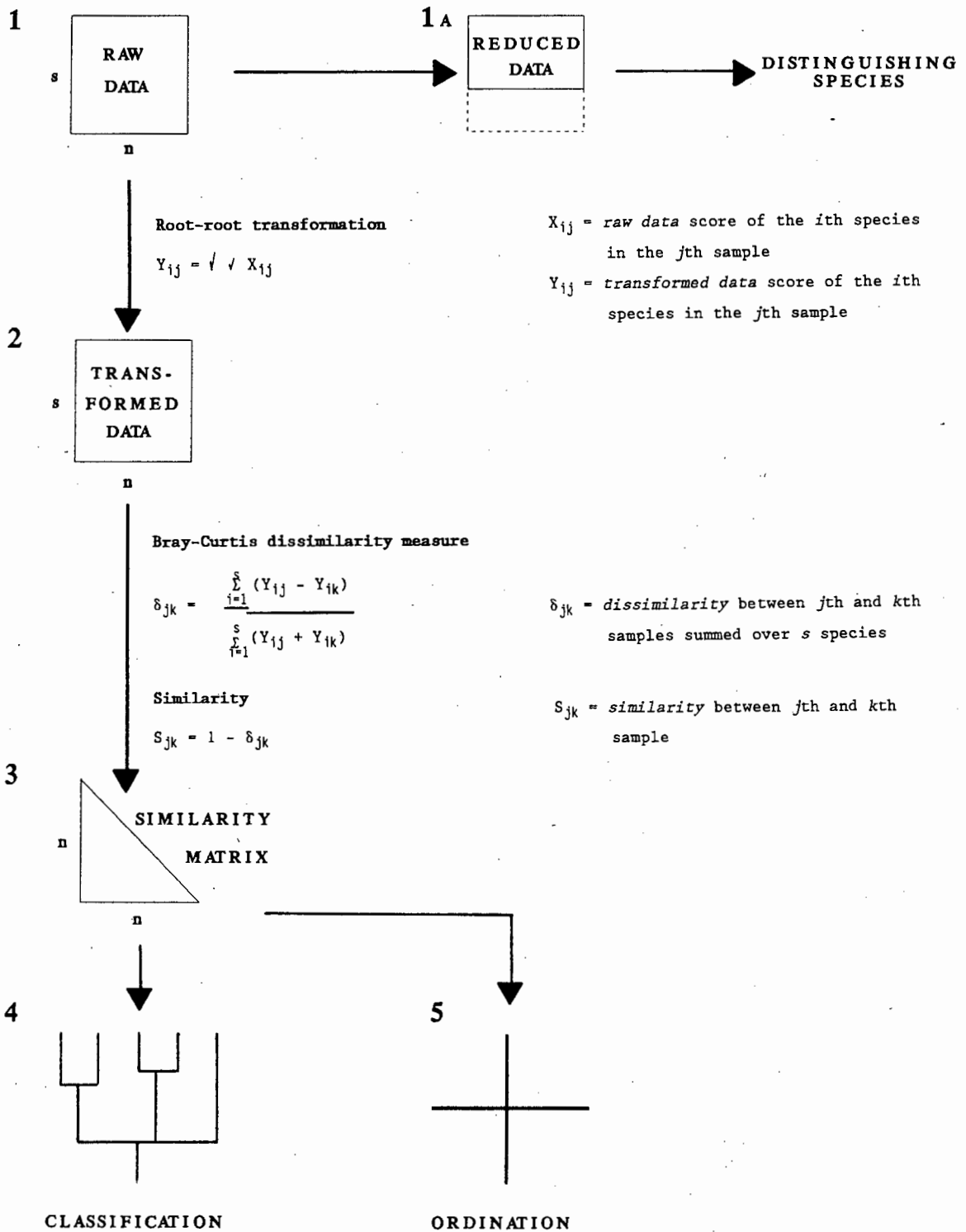


FIGURE 5.1. Diagrammatic summary of the stages leading to classification and ordination of samples and the determination of distinguishing species or taxa (adapted from Field *et. al* 1982).

by a "stress" coefficient:

$$\text{Stress 1} = \frac{\sum_j^n \sum_{k>j}^n (\delta_{jk} - \hat{\delta}_{jk})^2}{\sum_j^n \sum_{k>j}^n \delta^2_{jk}} \quad (5.1)$$

where $\hat{\delta}_{jk}$ = distance estimated for the regression, corresponding to dissimilarity.

Groups of samples were then identified by concurrent examination of both the dendrogram and the ordination plot. Environmental variables were superimposed upon the plots and the apparent variation between the groups was tested for statistical significance using one-way ANOVA (Zar 1984).

Species analysis

Before the raw data were analysed for distinguishing taxa, all those that contributed less than 4% of the total abundance in each sample were removed, in order to eliminate any taxon whose occurrence is due to chance (K.R. Clarke & R.M. Warwick, Plymouth Marine Laboratory, U.K., pers. comm.). Thereafter, the taxa responsible for the observed discrimination were ascertained by dissection of the Bray-Curtis dissimilarity matrix (see Warwick *et al.* 1990). For each pair of groups, and separately for each taxon, a mean of contributions to the average dissimilarity ($\bar{\delta}$) between all possible pairs of replicates was computed. These means were then ranked across taxa to develop the sequence of taxa, from the most to the least important, which determined the group differences. The percentage contribution of each taxon to the overall dissimilarity was determined and

cumulated across taxa.

RESULTS

Cluster Analysis and Multi-dimensional Scaling

The dendrogram, depicting sample similarities (Figure 5.2), may be split into 6 groups, A, B, C, D, E and an outlier group D'. Group B may be divided into B1 and B2. These groupings are reflected in the 2-dimensional ordination (Figure 5.3). The stress value of the 2-dimensional ordination is 0.21. Experience shows that this is a reasonably accurate summary of the similarity matrix in two dimensions, but that there is some distortion of detail in "compressing" the picture (K.R. Clarke & R.M. Warwick, Plymouth Marine Laboratory, U.K., pers. comm.). This is confirmed by the slightly decreased stress of 0.17 for the 3-dimensional ordination.

Identification of Distinguishing Taxa

The taxa principally responsible for the differences in community structure between Groups A, B1, B2, C, D and E, as measured by the Bray-Curtis dissimilarity measure, are listed in Table 5.1. This table includes only comparisons between adjacent groups in the ordination, rather than all 15 possible paired combinations.

The difference between A and B1 may mainly be attributed to the greater abundance of *Baetis* species and Chironomidae in B1, whereas B1 and B2 are distinguished by greater abundance of *Caenis* spp. in B2 and the greater abundance of *Baetis* spp. in B1.

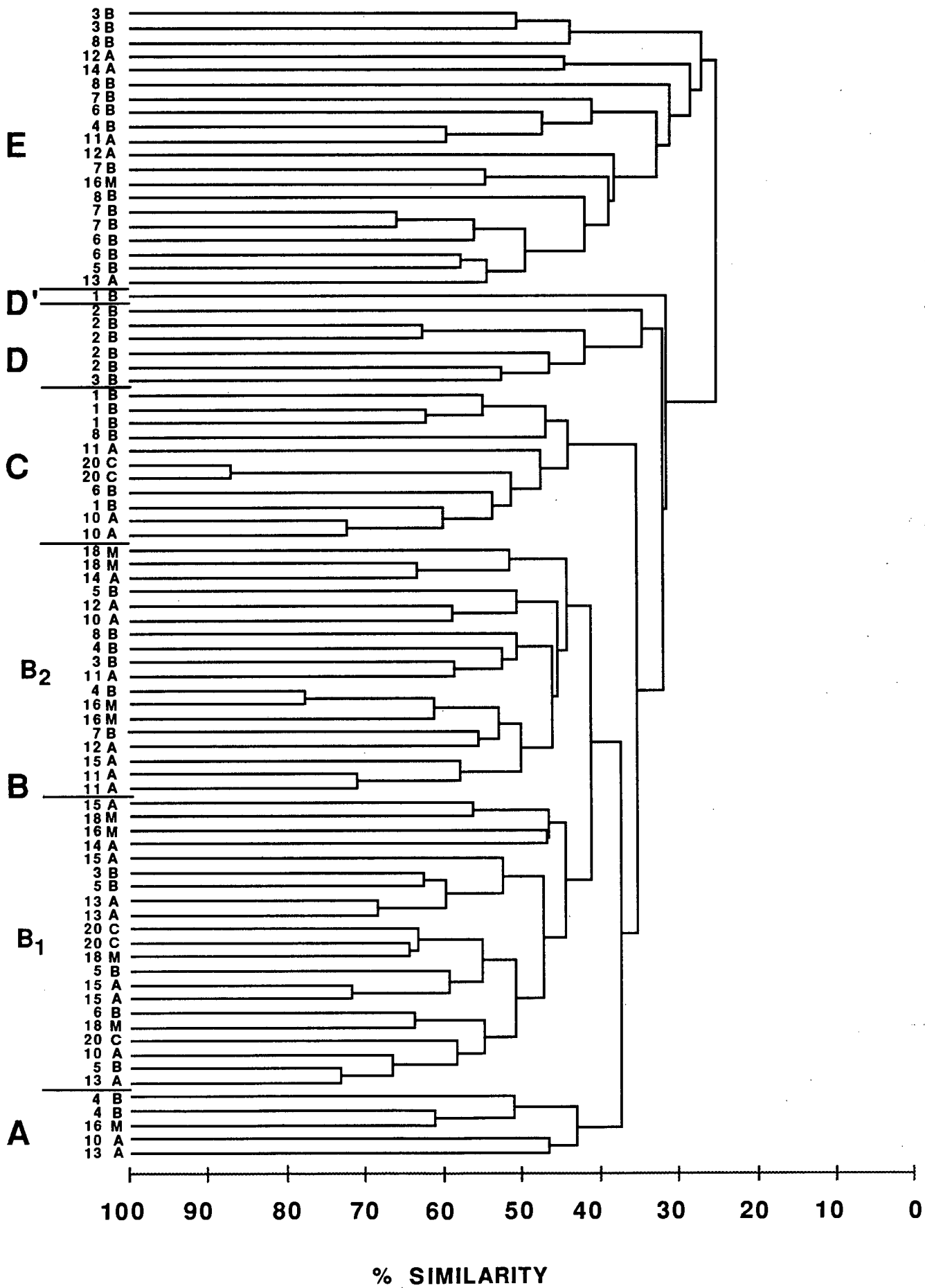


FIGURE 5.2. Dendrogram showing the classification of 82 samples at 17 sites in the Sabie-Sand catchment. Site numbers and rivers sampled (B=Sabie, A=Sand, M=Marite, C=below confluence).

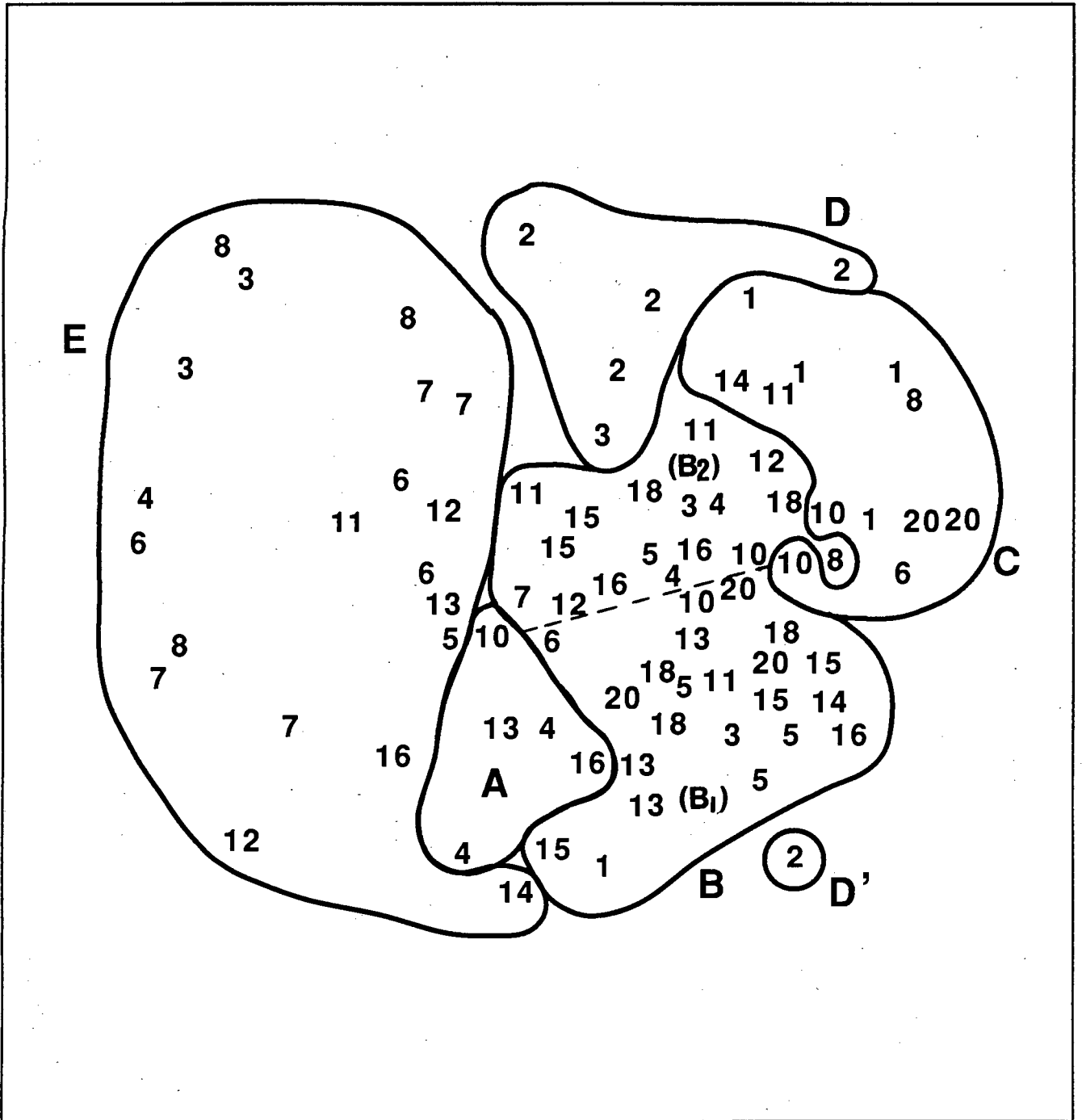


FIGURE 5.3. Ordination of 82 samples at 17 sites in the Sabie-Sand catchment in 2-dimensions, using multi-dimensional scaling. Each sample is represented by the site number.

TABLE 5.1. SIMPER comparison in mean species abundance (m^{-2}) between groups. δ_i is the contribution of the i th taxon to the average Bray-Curtis dissimilarity, $\bar{\delta}$, between two groups, which is also expressed as cumulative percentage ($\Sigma\delta_i\%$). Taxa are listed in decreasing order of importance in contribution to $\bar{\delta}$, with a cutoff at $\leq 50\%$ of $\bar{\delta}$. The higher taxon abundance is listed in bold type

Average dissimilarity between A and B1, $\delta = 58.8$				
Taxon	Mean abundance m^{-2}		δ_i	$\Sigma\delta_i\%$
	Group A	Group B1		
<i>Baetis</i> spp.	15.3	136.1	5.64	9.59
Chironomidae spp.	887.8	4249.9	5.36	18.71
Baetidae sp.A. (juv.)	15.6	297.8	4.73	26.76
Tipulidae sp.B.	26.5	26.9	4.20	33.90
<i>Simulium</i> spp.	15.4	201.8	4.04	40.77
Diptera sp. A.	6.9	63.2	3.59	46.87
Average dissimilarity between B1 and B2, $\delta = 54.87$				
Taxon	Mean abundance m^{-2}		δ_i	$\Sigma\delta_i\%$
	Group B1	Group B2		
<i>Caenis</i> spp.	4.5	257.8	4.04	7.36
<i>Baetis</i> spp.	297.8	10.0	3.67	14.04
Baetidae sp.A. (juv.)	136.1	47.7	2.99	19.49
Chironomidae spp.	4250	3792.1	2.90	24.77
Hydracarina spp.	10.9	109.5	2.84	29.95
<i>Simulium</i> spp.	201.8	36.4	2.76	34.98
Elmidae sp.A.	6.3	96.5	2.46	39.45
Tipulidae sp.B.	61.9	7.7	2.45	43.92
<i>Bezzia</i> sp.	2.6	39.3	2.33	48.17
Average dissimilarity between B2 and C, $\delta = 56.81$				
Taxon	Mean abundance m^{-2}		δ_i	$\Sigma\delta_i\%$
	Group B2	Group C		
<i>Cheumatopsyche</i> spp.	34.1	433.0	3.18	5.59
<i>Choroerpes</i> complex	5.1	333.2	3.05	10.96
<i>Simulium</i> spp.	36.4	560.9	2.64	15.61
<i>Baetis</i> spp.	47.7	439.7	2.44	19.91
<i>Dugesia</i> sp.	7.6	72.0	2.39	24.11
Baetidae sp.A. (juv.)	10.0	504.0	2.37	28.28
<i>Neurocaenis</i> spp.	3.1	721.5	2.37	32.46
Chironomidae spp.	3792.1	4641.3	1.93	35.86
<i>Athripsodes</i> spp.	0.7	180.3	1.92	39.24
<i>Caenis</i> spp.	257.8	96.7	1.87	42.53
Elmidae sp.A.	78.3	134.8	1.84	45.78
<i>Acentrella</i> spp.	96.5	59.0	1.78	48.92

Table 5.1 continued

Average dissimilarity between C and D, $\delta = 59.85$				
Taxon	Mean abundance m ⁻²		δ_i	$\Sigma\delta_i\%$
	Group C	Group D		
<i>Cheumatopsyche</i> spp.	433.0	2.4	3.21	5.36
<i>Baetis</i> spp.	439.7	0.0	3.09	10.52
Chironomidae spp.	4641.3	1195.4	2.76	15.12
<i>Choroterpes</i> complex	333.2	114.6	2.75	19.71
<i>Dugesia</i> sp.	72.0	1.2	2.39	23.71
Baetidae juv. spp.	504.0	17.8	2.33	27.60
<i>Neurocaenis</i> spp.	721.5	0.0	2.29	31.42
<i>Simulium</i> spp.	560.9	40.4	2.21	35.11
<i>Cloeon</i> complex	46.2	95.2	2.10	38.62
<i>Athripsodes</i> spp.	180.3	0.0	1.87	41.76
Elmidae sp.A.	59.0	207.4	1.84	44.84
<i>Acentrella</i> spp.	87.4	114.0	1.80	47.85
Average dissimilarity between B2 and D, $\delta = 60.72$				
Taxon	Mean abundance m ⁻²		δ_i	$\Sigma\delta_i\%$
	Group B2	Group D		
Chironomidae spp.	3792.1	1195.4	3.83	6.31
<i>Cloeon</i> complex	0.0	95.2	3.46	12.01
Diptera sp.A.	107.6	0.4	3.32	17.48
<i>Acentrella</i> spp.	24.7	114.0	3.09	22.57
Elmidae sp.A.	96.5	207.4	2.73	27.07
<i>Hydrocena</i> sp.	5.2	160.4	2.58	31.33
<i>Caenis</i> spp.	257.8	83.0	2.40	35.28
Hydracarina spp.	109.5	255.4	2.13	38.79
Tipulidae sp.B.	7.7	110.8	2.05	42.18
<i>Oecetis</i> spp.	1.3	41.8	2.04	45.54
<i>Baetis</i> spp.	47.7	0.0	2.02	48.86
Average dissimilarity between D and E, $\delta = 71.94$				
Taxon	Mean abundance m ⁻²		δ_i	$\Sigma\delta_i\%$
	Group D	Group E		
Culicidae sp.A.	95.2	0.0	5.11	7.10
Elmidae sp.A.	207.4	11.7	4.77	13.74
Hydracarina spp.	255.4	8.0	4.65	20.20
<i>Acentrella</i> spp.	114.0	1.1	4.58	26.56
Chironomidae spp.	1195.4	221.2	4.25	32.47
<i>Hydrocena</i> spp.	160.4	0.3	4.07	38.13
<i>Simulium</i> spp.	40.4	0.0	3.65	43.20
Tipulidae sp.B.	110.8	0.6	3.57	48.17
Average dissimilarity between B1 and E, $\delta = 74.70$				
Taxon	Mean abundance m ⁻²		δ_i	$\Sigma\delta_i\%$
	Group B1	Group E		
Chironomidae spp.	4249.9	221.2	9.92	13.28

A comparison between group C and groups B2 and D shows that C has large numbers of *Cheumatopsyche* spp., *Choroterpes* spp., *Simulium* spp., *Baetis* spp. and *Dugesia* sp. A large contribution to the difference between B2 and D is the presence of *Cloeon* complex species in D. Group E is distinguished from groups B1, B2 and D by the reduced abundance of the principal differentiating taxa in E. The high abundances of the Chironomidae and their importance in distinguishing between the groups in all cases cannot be ignored. However, due to the lack of differentiation between genera, caution must be observed before putting too much reliance on discriminating between groups using the Chironomidae. The group which is notably lacking in chironomids is Group E.

In addition to the taxa that distinguish the groups A to E, taxa that differentiate the Sabie River from the Sand River, and those that differentiate the sand-substrata samples from rock-substrata samples, were examined. The taxa which principally distinguish the Sabie River from the Sand River are listed in Table 5.2. The variation between the two faunal groups was not significant (ANOSIM, $p > 0.05$, Clarke 1988). However, the sand-substrata samples were significantly more depauperate than the rock substrata samples (ANOSIM, $p < 0.05$, Clarke 1988), (see Figure 5.3 for the list of taxa).

Relation of Sample Groups to the Environment

Figure 5.4 is a map of the catchment upon which the sample groups (A, B, C, D and E) have been superimposed. Group D samples are only found at altitudes $> 1200\text{mAMS}$ L (predominantly at site 2 on the Mac-Mac River), while Group C is predominantly found at altitudes $> 1200\text{mAMS}$ L, and Groups A, B and E are scattered throughout the catchment. Sites 15 and 18 consist only of group B samples, while site 2 consists only of group D samples.

TABLE 5.2. SIMPER comparison of mean species abundance (m^{-2}) between the Sabie and Sand rivers. δ_i is the contribution of the i th taxon to the average Bray-Curtis dissimilarity, $\bar{\delta}$, between two groups, which is also expressed as cumulative percentage ($\Sigma\delta_i\%$). Taxa are listed in decreasing order of importance in contribution to $\bar{\delta}$, with a cutoff at $\leq 50\%$ of $\bar{\delta}$. The abundance shown in bold type is the more abundant of the two

Average dissimilarity between Sabie and Sand R., $\delta = 64.23$				
Taxon	Mean abundance m^{-2}		δ_i	$\Sigma\delta_i\%$
	Sabie R.	Sand R.		
Chironomidae spp.	1666.7	3196.5	5.20	8.10
<i>Caenis</i> spp.	89.8	89.5	3.11	12.94
<i>Baetis</i> spp.	57.2	76.4	3.10	17.77
<i>Simulium</i> spp.	101.3	139.9	3.07	22.54
Tipulidae sp.B.	33.0	47.7	3.00	27.22
Hydracarina spp.	58.3	52.9	2.88	31.07
<i>Cloeon</i> complex	99.4	49.5	2.86	36.15
Diptera sp.A.	16.4	27.6	2.72	40.39
<i>Dugesia</i> sp.	46.0	28.2	2.35	44.05
<i>Bezzia</i> sp.	9.8	16.0	2.33	47.67

TABLE 5.3. SIMPER comparison of species abundance (m^{-2}) between sand and rock substratum. δ_i is the contribution of the i th taxon to the average Bray-Curtis dissimilarity, $\bar{\delta}$, between two groups, which is also expressed as cumulative percentage ($\Sigma\delta_i\%$). Taxa are listed in decreasing order of importance in contribution to $\bar{\delta}$, with a cutoff at $\leq 50\%$ of $\bar{\delta}$. The abundance shown in bold type is the more abundant of the two

Average dissimilarity between sand and rock, $\delta = 71.87$				
Taxon	Mean abundance m^{-2}		δ_i	$\Sigma\delta_i\%$
	sand	rock		
Chironomidae spp.	891.0	4199.3	8.65	12.03
Baetidae sp.A. (juv.)	0.8	248.2	4.97	18.95
<i>Baetis</i> spp.	2.2	99.6	4.94	25.82
<i>Simulium</i> spp.	1.8	66.9	4.30	31.81
Diptera sp.A.	9.1	63.1	3.96	37.33
Tipulidae sp.B.	3.1	42.7	3.69	42.47
<i>Caenis</i> spp.	51.7	96.9	3.41	47.21

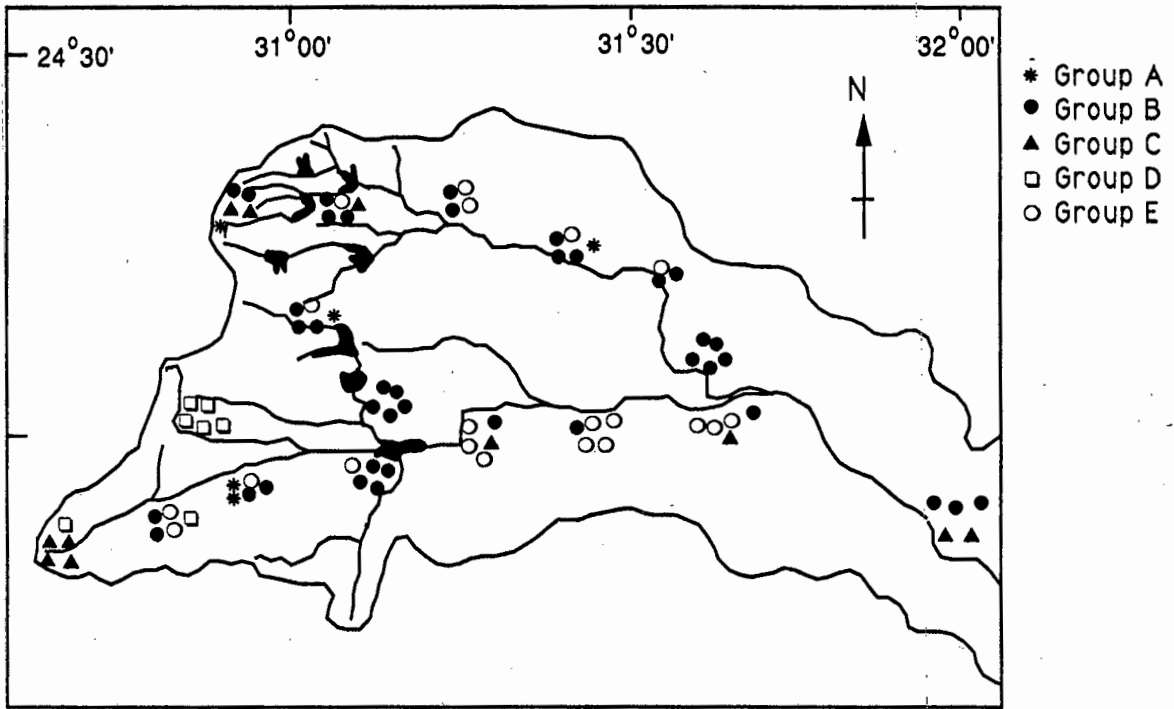


FIGURE 5.4. Map of the Sabie-Sand catchment showing the distribution of sample groups A, B, C, D and E as distinguished by the classification and ordination analyses.

Physical and chemical variables were superimposed upon the ordination (Figures 5.5 and 5.6). The physical variables (Figure 5.5) were:

- a) the river from which the sample was taken (Sabie, Sand, Marite and Sabie-Sand below the confluence), - this can also be considered a site variable;
- b) altitude (mAMSL);
- c) substratum type (rock or sand), and
- d) discharge (cumecs).

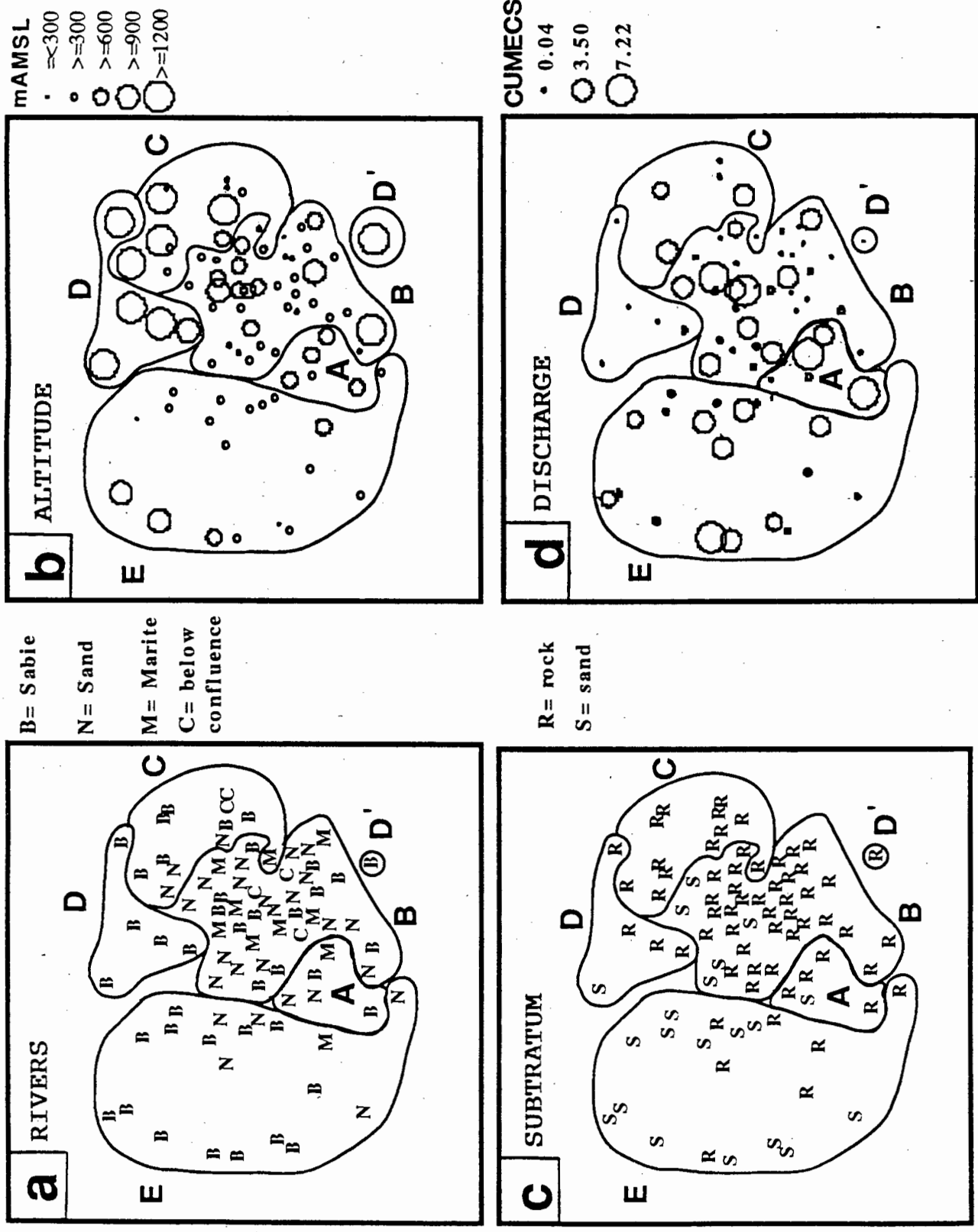
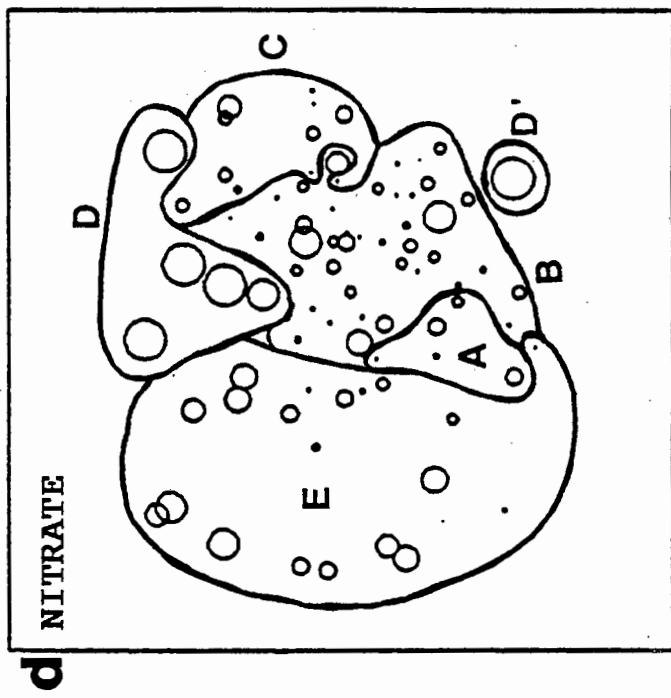
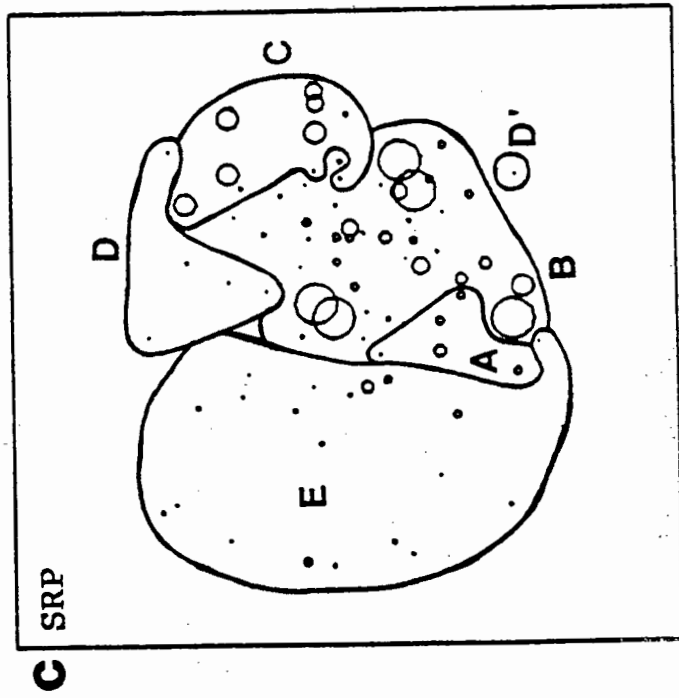
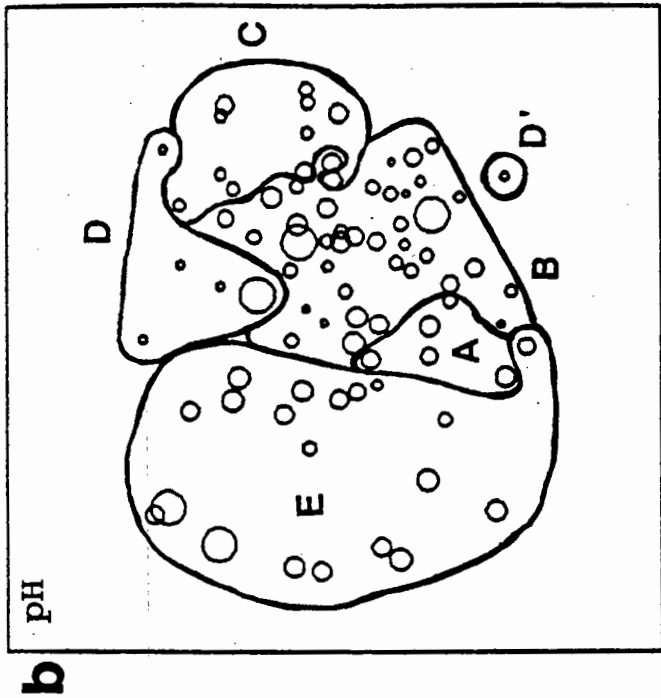
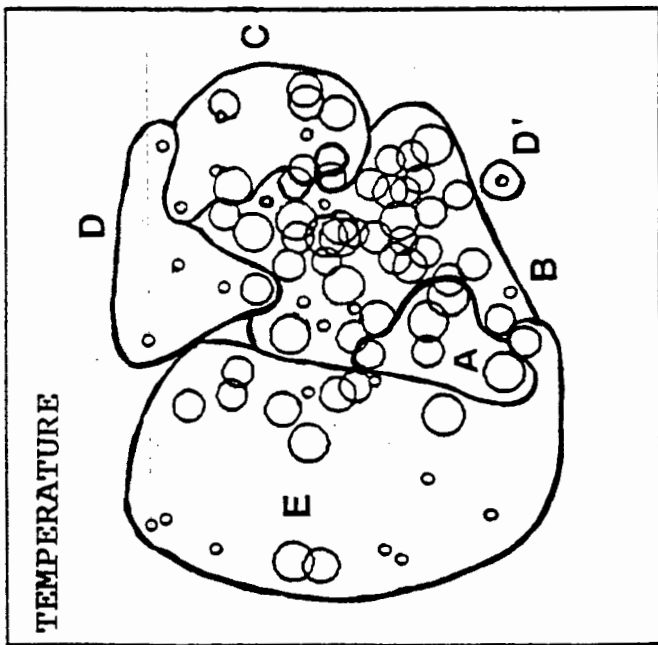


FIGURE 5.5. Relation of sample groups, as distinguished by the classification and ordination analyses, to physical environmental factors: a) rivers, b) altitude c) substratum and d) discharge. Relevant keys and the range of the discharge values are given to the right of each plot.



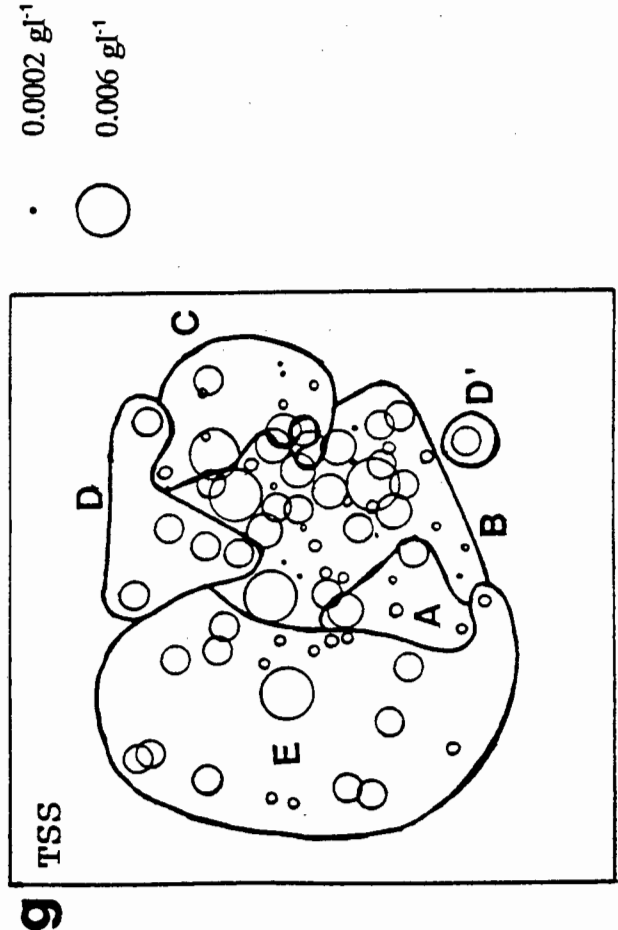
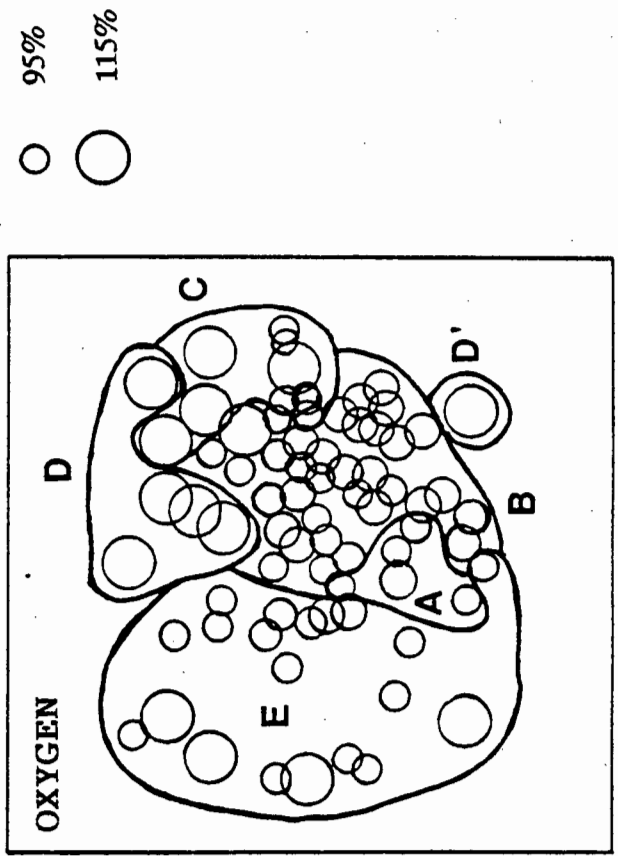
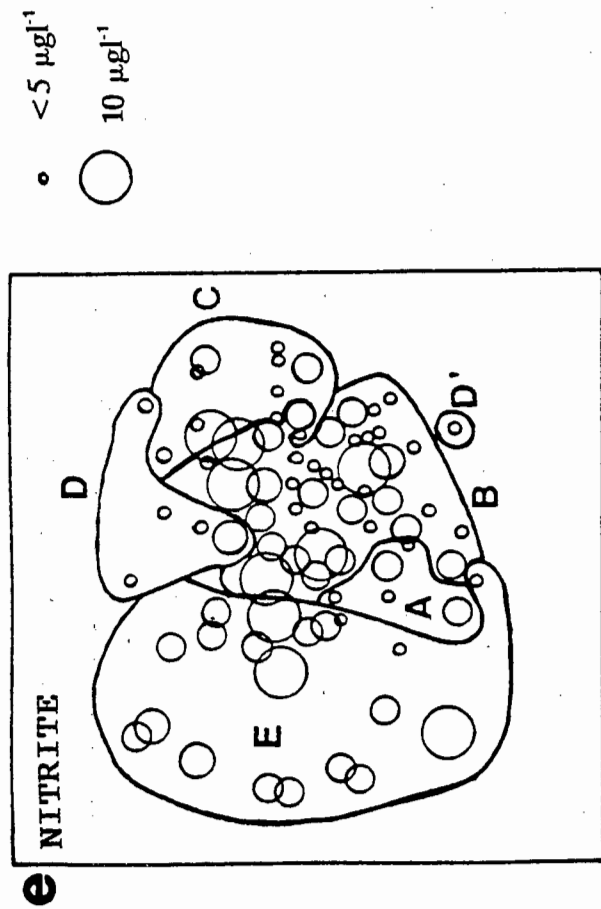
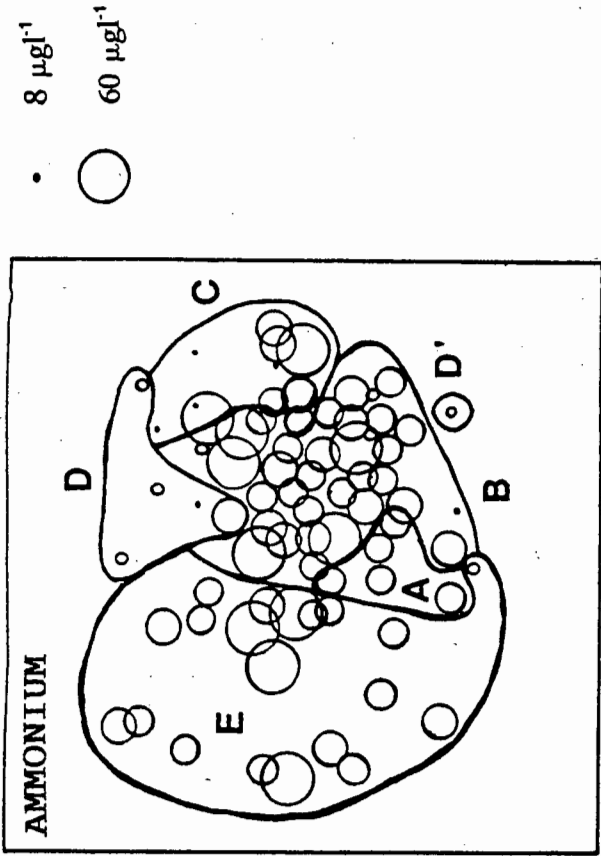


FIGURE 5.6. Relation of sample groups, as distinguished by the classification and ordination analyses, to chemical environmental factors: a) temperature, b) pH, c) soluble reactive phosphate, d) nitrate, e) nitrite, f) ammonium, g) TSS and h) oxygen (%). The range of values are given to the right of each plot.

The majority of the Sand River samples were clustered in groups A and B (Figure 5.5A), while the Sabie River samples were scattered throughout the groups. There was a significant difference among the groups with respect to altitude (Kruskal-Wallis, $F=20.99$, $p<0.001$, d.f. 4, 77), (see Figure 5.5B), with the greatest statistical difference between groups B and D (Tukey test, $p<0.05$). Figure 5.5C shows the substratum type from which the samples were taken. Groups A, B and D were predominantly rock substratum samples; group C had only rock substratum samples; and group E was mostly sand substratum samples. Groups A and D were too small to be used in a χ^2 analysis. However, χ^2 tests on B, C and E showed that B and C were not significantly different from each other in terms of substratum ($\chi^2 = 1.28$, $p<0.001$, d.f. 1), while E was significantly different from both B ($\chi^2 = 18.18$, $p>0.05$, d.f. 1) and C ($\chi^2 = 16.9$, $p>0.05$, d.f. 1). Discharge down the river (Figure 5.5D) was significantly different among the groups, at the 95% confidence level (1-way ANOVA, $F=3.180$, $p<0.05$, d.f. 4, 77), with group A being significantly different from group D (Tukey test, $p<0.05$).

The chemical parameters that were superimposed on the ordination diagrams (Figure 5.6) were: temperature ($^{\circ}\text{C}$), pH, soluble reactive phosphate (SRP; $\mu\text{g}\ell^{-1}$), nitrate ($\mu\text{g}\ell^{-1}$), nitrite ($\mu\text{g}\ell^{-1}$), ammonium ($\mu\text{g}\ell^{-1}$), TSS ($\text{mg}\ell^{-1}$), and percentage oxygen content. There was a significant difference among the 5 groups with respect to temperature (1-way ANOVA, $F=4.417$, $p<0.005$, d.f. 4, 77), (see Figure 5.6A), with D differing significantly from A (Tukey test, $p<0.05$). The groups were also significantly different with respect to pH (Kruskal-Wallis, $F=16.67$, $p<0.005$, d.f. 4, 77) (Figure 6B), with group D, once again, differing significantly from group A (Tukey test, $p<0.05$). The groups were not, however, significantly different from each other with respect to TSS and percentage oxygen content (1-way ANOVA, $p>0.05$, df. 4, 77).

Nutrients also affected the grouping of the samples (Figure 5.6C and 5.6D). The 5 groups were significantly different with respect to nitrate (1-way ANOVA, $F=21.021$, $p<0.00001$, d.f. 4, 77), with D differing significantly from the other groups (Tukey test, $p<0.05$). They also differed significantly with respect to SRP (1-way ANOVA, $F=3.906$, $p<0.01$, d.f. 4, 77), with group C being significantly different from D (Tukey test, $p<0.05$). However, they were not significantly different to each other with respect to ammonium and nitrite (1-way ANOVA, $p>0.05$, d.f. 4, 77).

Table 5.4 is a summary of the environmental properties of groups A, B, C, D and E. Groups A and B shared many characteristics such as substratum, discharge, temperature, pH, nitrate and SRP. Group D had the most distinct characteristics, some of which are shared with C. Group E was a diffuse group with a range of characteristics, the most distinctive having been the small number of the rock substrata samples and the low SRP concentrations.

DISCUSSION

For the sake of simplicity, this study took place over a short time span, effectively reducing temporal variations to a minimum. Even so, the complexity of the system is such that cause and effect relationships are not easily identifiable.

From both the dendrogram (Figure 5.2) and the ordination (Figure 5.3) the percentage similarity among the groups was high and they were clustered close together. It was, originally, hypothesised that the Sabie and Sand rivers, each rising in different sub-catchments, may harbour two distinct faunal groups. This was due to the different

TABLE 5.4. Environmental properties of groups A, B, C, D and E (as determined by the cluster analysis). Similar properties are shaded in the same manner. For example, A and B are similar in many respects and thus share a similar shading pattern, while D stands out as dissimilar from the rest except for two variables which it shares with C. Ammonium, nitrite, TSS and oxygen were not included in the table because of their similarity across the board

GROUP	A	B	E	C	D
NO.OF SAMPLES PER RIVER	2 Sabie 2 Sand 1 Marite	11 Sabie 17 Sand 8 Marite 3 Sabie-Sand	14 Sabie 5 Sand 1 Marite	6 Sabie 2 Sand 2 Sabie-Sand	7 Sabie
ALTITUDE	> 600m	> 100m	> 100m	> 1200m	> 1200m
SUBSTRATUM	80% rock	68% rock	30% rock	100% rock	80% rock
DISCHARGE	high - low	high - low	medium	medium	v.low
TEMP.	high - medium	high - medium	high - medium	medium	low
pH	medium	medium	medium	medium	low
NITRATE	high - low	low - medium	medium	medium	v.high
SRP	high - low	high - low	v.low	medium	v.low

characteristics of the two sub-catchments, of which the most prominent differences are:

- gradient - the Sabie River has a steeper gradient than the Sand for most of its length (see Chapter 2);
- river zones - the zones within the rivers are not the same; the Sabie River lacks the foothill, sandbed zone of the Sand, and the Sand River lacks the mountain source zone of the Sabie (see Chapter 2).
- utilisation of the water - the Sand River is mainly situated in the Self-Governing Territories of Gazankulu and Lebowa, where the water

is used predominantly for domestic needs and subsistence agriculture, while the water from the Sabie is extracted for industrial use and for large-scale agriculture;

- discharge - the Sand River has significantly less water flowing down it than does the Sabie River.

However, the community structure was not statistically different (ANOSIM, $p > 0.05$, Clarke 1988). Except at very high altitudes, the groups seemed to have a fairly random distribution throughout the catchment (Figure 5.4), indicating of a fairly homogeneous (at a 30% similarity level) benthic macro-invertebrate faunal component. This was confirmed in Table 5.3 by the similarity between the two rivers in the taxa present and their abundances. This is a rather surprising result, considering the differences between the two rivers, and *may* have been an artifact of two factors. They were:

- 1) the limited time frame within which this survey was completed, which takes no account of seasonal variations in species composition and physico-chemical properties, and
- 2) the lack of species definition due to limited taxonomic knowledge. Identification to species would allow a more detailed analysis and a deeper understanding of the functioning of the macro-invertebrate communities (see Chapter 8 for a more detailed discussion).

Distinguishing Taxa

From Table 5.1 it appears that the presence or absence of a taxon depends mainly on micro-habitat availability, where micro-habitat may be defined as the area in which organisms occur, where varying conditions affect individual organisms differently. Micro-habitat may vary considerably over a small area (e.g. on a cobble substratum with varying

water velocities) or be consistent over a large area (e.g. on granite bedrock with a constant flow). A good example of the effect of micro-habitat is found in group C, which had distinguishing taxa that were recognised as organisms adapted to fast flowing waters, such as the *Cheumatopsyche* spp., *Choroterpes* complex, *Simulium* spp., *Baetis* spp. and *Dugesia* sp. Groups A, B1 and B2 were not dominated by any group of organisms which are preferential dwellers in any specific habitat, and these groups were, therefore, distributed throughout the catchment. However, this may also be due to the lack of species definition as mentioned above (see also Chapter 8).

This effect of micro-habitat availability on the benthic fauna was confirmed by the fact that the differences between the fauna of the sand and rock substrata were large. The observed differences were not in the number of taxa, but rather in the abundance of species present. The sand-substrata fauna had a lower species abundance than the rock-substrata fauna. The exact reason for this phenomenon is not known, and in this case supposition cannot replace research!

Group E comprised a depauperate fauna, which may explain the diffuse grouping of the samples. This may also be due to the group E samples being mainly from sand substrata. Group D was anomalous in many respects, with a distinct fauna and environment. It is a group which was mainly found at site 2, above the Mac-Mac Falls on the Mac-Mac River, in an area where there were no fish predators (Mr D. Weeks, Zoology Department, Rhodes University, Grahamstown, pers. comm.). This lack of fish predators may be the reason for the distinct community at site 2.

Relation of Sample Groups to the Environment

Wright *et al.* (1984) have stated that the macro-invertebrate assemblages of running waters can accurately be predicted from the environmental data alone. However, often the edges are blurred due to environmental interactions, which may or may not have synergistic effects.

From this analysis it appears that groups A - E were not differentiated from each other significantly with respect to any one dominant environmental factor. Rather, some groups have one or more distinct environmental characteristic which distinguish them from the others (Table 5.4). For example, group E consisted mainly of low altitude sand-substratum samples, with very low SRP levels, while groups C and D were predominantly from rock substrata, and both occurred at high altitudes. However, D was distinguished from C by the relatively high nitrate levels and low discharge. On the other hand, groups A and B were distinguished by medium to low altitudes and rocky substrata.

Temperature, which is considered to be one of the major factors influencing macro-invertebrate community structure (e.g. Ward & Stanford 1979b; Ward 1985), did not exert a strong influence. This lack of influence may be explained by the fact that temperature was taken as a spot measure, and may have been influenced by wide diurnal variation (e.g. Ward 1985).

The lack of dominance of any one factor and the small range of each environmental variable (Figures 5.5 and 5.6) is indicative of a balance, characterising a pristine system. If the system had been severely disturbed in any way, either by regulation or by pollution, one or more of the physico-chemical parameters might have been altered to a level

above that normally experienced by the organisms, causing a change in the community. Because physico-chemical variables are considered to be macro-habitat variables (see Bovee 1982), a disturbed system would be "macro-habitat dominated". However, in the Sabie-Sand River system it seems that micro-habitat determines the structure and functioning of the benthic macro-invertebrate communities (i.e. "micro-habitat dominance"). This is confirmed by the fact that the largest differences in communities were those between the sand-substrata fauna and the rock-substrata fauna; substratum being considered a micro-habitat variable (Bovee 1982). Thus, the Sabie-Sand River system may be considered a relatively undisturbed system (see also Chapter 8).

CHAPTER 6

**INVENTORY DIVERSITY OF THE BENTHIC MACRO-INVERTEBRATE
RIFFLE/RAPID FAUNA OF THE SABIE-SAND RIVER SYSTEM**

INTRODUCTION

The evaluation of biological diversity can be approached from two perspectives. The first is to assess each habitat, site or area as an entity on its own (inventory diversity). The second uses the concept of diversity along a gradient, or turnover in diversity between two communities (differentiation diversity).

This chapter deals with the first approach. Inventory diversity is used to provide a characterisation of community structure within a system. It is useful in determining the fundamental ecological patterns (Kempton 1979) and for monitoring community changes due to disturbance. Each community can then be compared statistically as independent units with others .

In this chapter, point, alpha, gamma and epsilon diversity are assessed within the restrictions of the spatial boundaries, as defined in Chapter 4. A mathematical description of the biological diversity of the benthic macro-invertebrate riffle communities of the Sabie-Sand River system is provided, and the differences in point and alpha diversity between areas are statistically examined. Using point diversity index values the relationship between the two conditions of biological diversity, richness and evenness (or dominance), within the Sabie-Sand system, is examined.

METHODS

Point diversity

At each of the five sites identified for the measurement of biological diversity (see Chapter 3), three samples were taken in the riffle/rapid habitat (see Chapter 3). The diversity of any one sample is defined as the point diversity. For each sample the log series, α (see Taylor *et al.* 1975; Kempton & Wedderburn 1978; Shepard 1984; Magurran 1988), was fitted to the data, taking the form:

$$\frac{\alpha x}{1}, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3} \dots \frac{\alpha x^n}{n} \quad (\text{see eqn. 1.5, Chapter 1})$$

where αx = number of families with one individual,

$\alpha x^2/2$ = number of families with 2 individuals etc.

In the above equation, x , where $0.9 < x < 1.0$, was estimated using the equation:

$$S/N = [(1-x)/x][-\ln(1-x)] \quad (6.1)$$

where S = total number of families,

N = total number of individuals.

The number of observed and expected families in each abundance class was compared using a goodness of fit χ^2 test (Zar 1984).

Three diversity indices were calculated to describe the abundance and dominance components of diversity.

1. Species richness (abundance)

$$S = \text{number } m^{-2} \quad (\text{see eqn. 1.1, Chapter 1}).$$

2. Margalef index (abundance)

$$D_{mg} = (S-1)/\ln N \quad (\text{see eqn. 1.3, Chapter 1})$$

where S = number of families recorded,

N = total number of individuals.

3. Berger-Parker index (dominance)

$$d = \frac{N_{max}}{N} \quad (\text{see eqn. 1.6, Chapter 1})$$

where N_{max} = number of individuals in the most abundant species.

Statistical differences in point diversity between sites and between sections of the river for α , S , D_{mg} and d were tested using ANOVA and *à posteriori* Student-Newman-Keuls (SNK) tests (Zar 1984).

Alpha diversity

Because all samples were taken in riffles/rapids, each of the five sites on the Sabie and Sand rivers were treated as five habitats (as defined in Chapter 4). Rank abundance graphs were plotted for all five sites using the mean abundance of families over one year.

The log of abundance was plotted against family sequence.

Alpha diversity was calculated for each site using the same methods as outlined for point diversity, with the samples combined by site. Statistical differences in alpha diversity, for α , S, D_{mg} and d, between the three river sections were tested using ANOVA and SNK tests (Zar 1984).

Gamma diversity

Gamma diversity was assessed for three sections of the river system. They were:

- the Sabie River above the confluence with the Sand River (i.e. sites 3 and 7)- referred to as the Sabie section;
- the Sand River above the confluence with the Sabie River (i.e. sites 11 and 13) - referred to as the Sand section;
- the Sabie River below the confluence with the Sand River (i.e. site 20) - referred to as the Sabie-Sand section.

Rank abundance graphs were plotted for all three sections as outlined for alpha diversity.

Biological diversity was calculated for each section using the same methods as outlined for point diversity. No statistical analysis between sections was possible as there were no replicates for gamma diversity within sections.

Epsilon diversity

Epsilon diversity was assessed as the biological diversity of the system calculated from combining the samples at all five sites. A rank abundance graph was plotted and the

diversity indices calculated, using the same methods as outlined for point and alpha diversity.

Relationship between richness and dominance

The relationship between the richness and the dominance components of the biological diversity within the system was examined by plotting the Berger-Parker index against the Margalef index for every point diversity sample. For each site, and for all the samples together, the correlation between the two was statistically examined using the Pearson's product-moment correlation coefficient (PPMC), r (Zar 1984).

RESULTS

Point diversity

Figure 6.1A shows the mean point diversity index values calculated for all five sites. The indices shown are:

- richness (S), which, in this case is family richness;
- α , giving the biological diversity as described by the log series distribution fitted to the model (χ^2 goodness-of-fit, $P > 0.001$, d.f. 14);
- the Margalef index (D_{mg}), which is a measure of the richness, and
- the Berger-Parker index (d), which is a measure of the dominance (or the inverse of evenness).

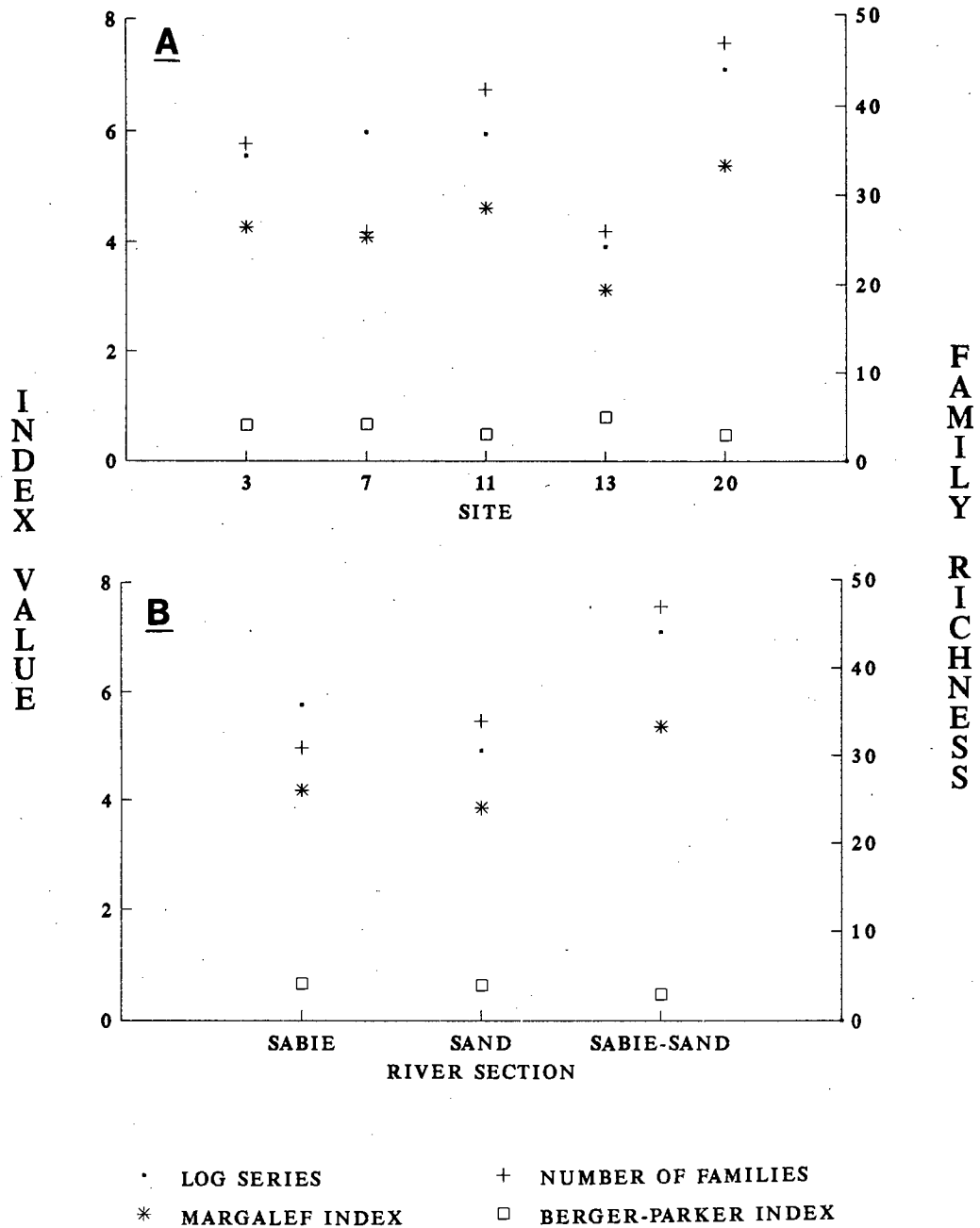


FIGURE 6.1. Mean point diversity index values calculated for sites (A) and river sections (B).

In order of highest to lowest values, sites 20, 11 and 3 have the greatest α , Margalef and family richness values (Figure 6.1B). However, site 20 has the lowest Berger-Parker value (Figure 6.1B), while site 13 has the lowest α and Margalef values and the highest Berger-Parker value (Figure 6.1B), and site 7 has the lowest α , Margalef and family richness

values next to site 13, and the second lowest Berger-Parker value (Figure 6.1B).

A one-way ANOVA showed that there was a significant difference among the sites for the α value (1-way ANOVA, $F=5.89$, $p<0.01$, d.f. 54, 4), the Margalef index (1-way ANOVA, $F=3.91$, $p<0.01$, d.f. 54, 4), and the number of families (1-way ANOVA, $F=3.42$, $p<0.01$, d.f. 54, 4). SNK tests were used to determine which sites caused this difference in each case, and revealed that for family richness, sites 3, 11 and 20 were not significantly different from each other (SNK, $p>0.05$, d.f. 54, see Appendix A), and neither were sites 7 and 13 (SNK, $p>0.05$, d.f. 54, see Appendix A), but that there was a significant difference between the two groups - sites 3, 11, and 20; and sites 7 and 13 (SNK, $p<0.05$, d.f. 54, see Appendix A). For the Margalef index, site 20 had a significantly higher value than sites 3 and 7 (SNK, $p<0.05$, d.f. 54, see Appendix A). For α , site 20 had a significantly higher value than site 13 (SNK, $p<0.05$, d.f. 54, see Appendix A). There was no significant difference among the sites for the Berger-Parker index values (1-way ANOVA, $F=2.12$, $p>0.01$, d.f. 54, 4). These statistics suggest that sites 20, 3 and 11 are more diverse than sites 7 and 13.

The mean point diversity index values calculated for all three river sections are presented in Figure 6.1B. The indices are the same as those described above. The Sabie and the Sand sections had very similar mean point diversity values for all the indices, while the Sabie-Sand had higher α , Margalef index and family richness values, and a lower Berger-Parker value. However, there was no significant difference, in terms of point diversity, among the three river sections, for any of the four diversity indices (ANOVA, $F<5.01$, $p>0.01$, d.f. 56, 2).

Alpha diversity

The rank-abundance plots for sites 3, 7, 11, 13 and 20 (Figure 6.2), when compared to the hypothetical rank abundance plots of Magurran (1988; see Chapter 1, Figure 1.2), all fit a typical log normal distribution.

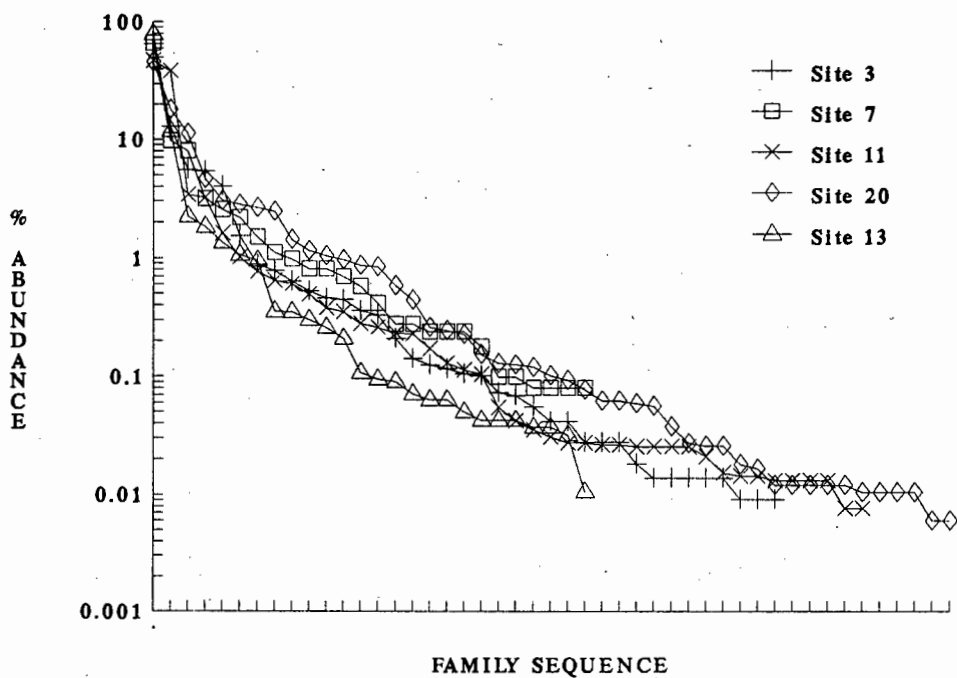


FIGURE 6.2. Rank abundance plots for five sites on the Sabie-Sand River system.

Site 13 tends towards the log distribution which indicates a lower diversity, while site 20 tends towards the broken stick distribution which indicates a higher diversity. Sites 7 and 13 have a smaller number of families than do the other three sites.

The log series model was used to describe the data sets. This is acceptable as the log

normal distribution which the data sets follow is in its truncated form and is, thus, almost indistinguishable from the log series (see Magurran 1988). χ^2 goodness-of-fit tests (Magurran 1988) were applied to establish whether or not the log series appropriately described the data. At all five sites, the expected values for the log series models were not significantly different from the observed values (χ^2 goodness-of-fit, $P > 0.001$, d.f. 14).

The alpha diversity index values were calculated for all five sites (Figure 6.3A). For the Margalef and family richness indices, sites 13 and 7 had the lowest values, while sites 11 and 20 had the highest. For the Berger-Parker index the opposite occurred, with sites 13 and 7 having the highest values and sites 11 and 20 the lowest. For the log series model, site 13 had the lowest value, site 20 the highest and sites 3, 7 and 11 exhibited similar mid-range values.

The same index values were calculated for all three river sections (Figure 6.3B). For the log series distribution and the Margalef index, the Sand section had the lowest values, and the Sabie-Sand the highest. The Sabie-Sand section was the most family rich, while the Sabie section had the fewest families, in terms of alpha diversity. For the Berger-Parker index, the Sabie-Sand section had the lowest mean index value, and the Sabie had the highest. However, there was no significant difference between the three river sections for any of the indices (1-way ANOVA, $F < 19.0$, $p > 0.05$, d.f. 2,2).

Gamma diversity

The rank-abundance plots for the three sections all fit a typical log normal distribution (Figure 6.4), with the Sabie-Sand tending towards the broken stick model (see Chapter

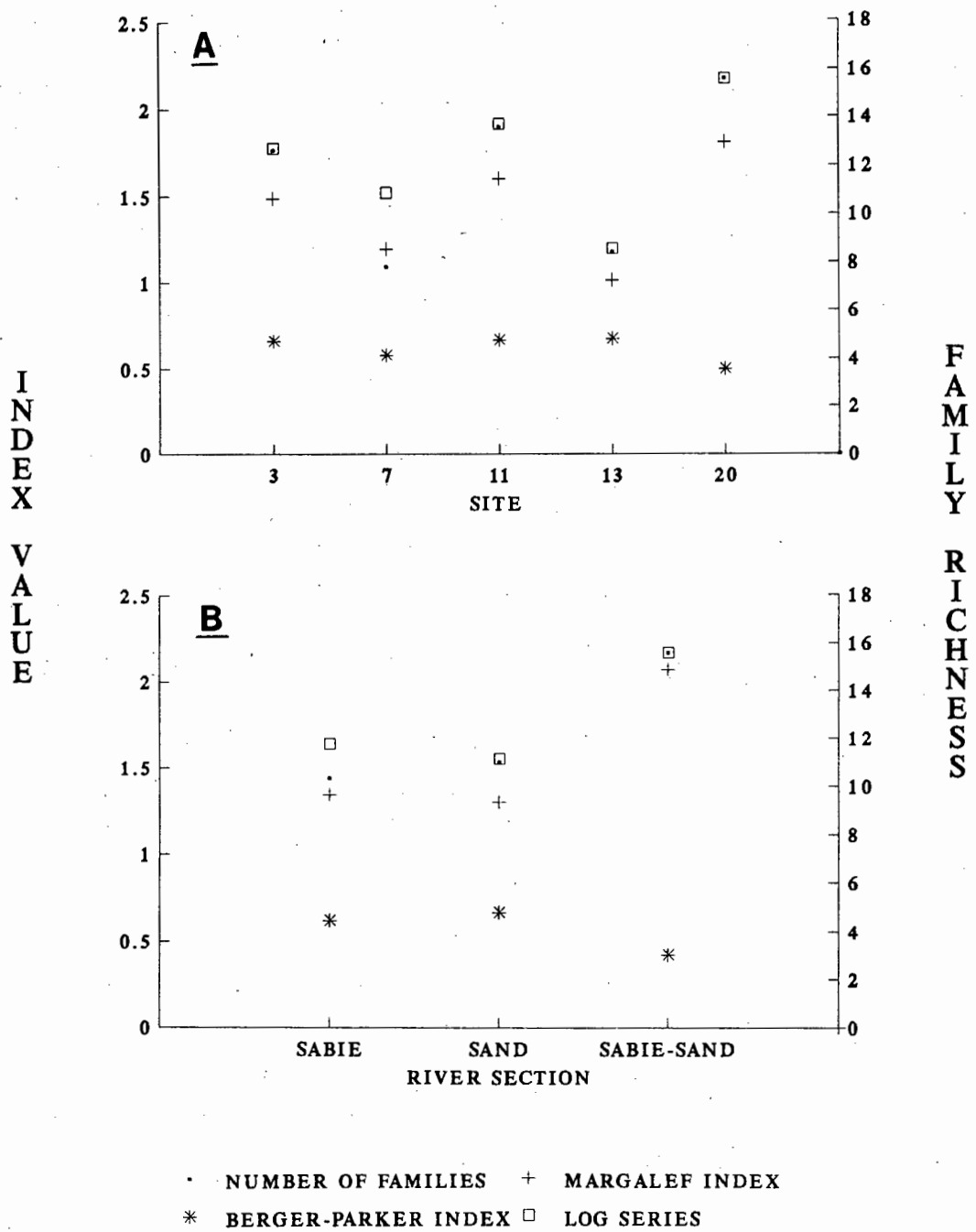


FIGURE 6.3. Mean alpha diversity index values calculated for sites (A) and sections (B).

1, Figure 1.2). The Sabie and the Sand rivers followed very similar distributions.

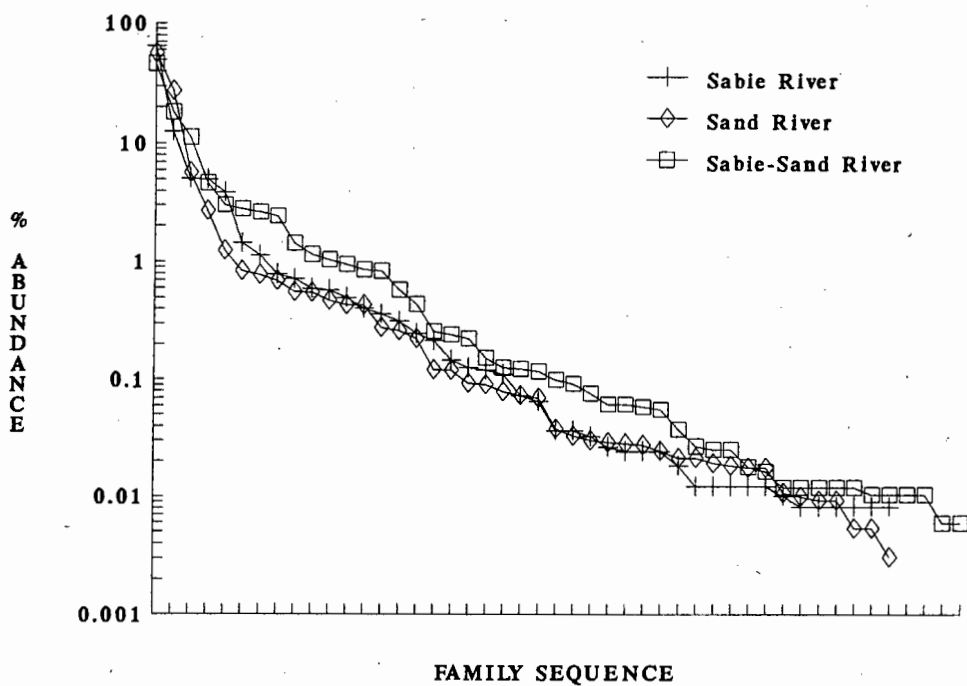


FIGURE 6.4. Rank abundance plots for three sections of the Sabie-Sand river system.

The log series model was used to describe the data sets, and in all three river sections the expected values for the log series models were not significantly different from the observed values (χ^2 goodness-of-fit, $P > 0.001$, d.f. 14).

The gamma diversity index calculated for the three river sections are presented in Figure 6.5. For the log series distribution and the Margalef index the Sand had the lowest values, and the Sabie-Sand had the highest. The Sabie-Sand section was the most family rich, with the lowest Berger-Parker index value, while the Sabie was poor in terms of number of families and had the highest Berger-Parker index value.

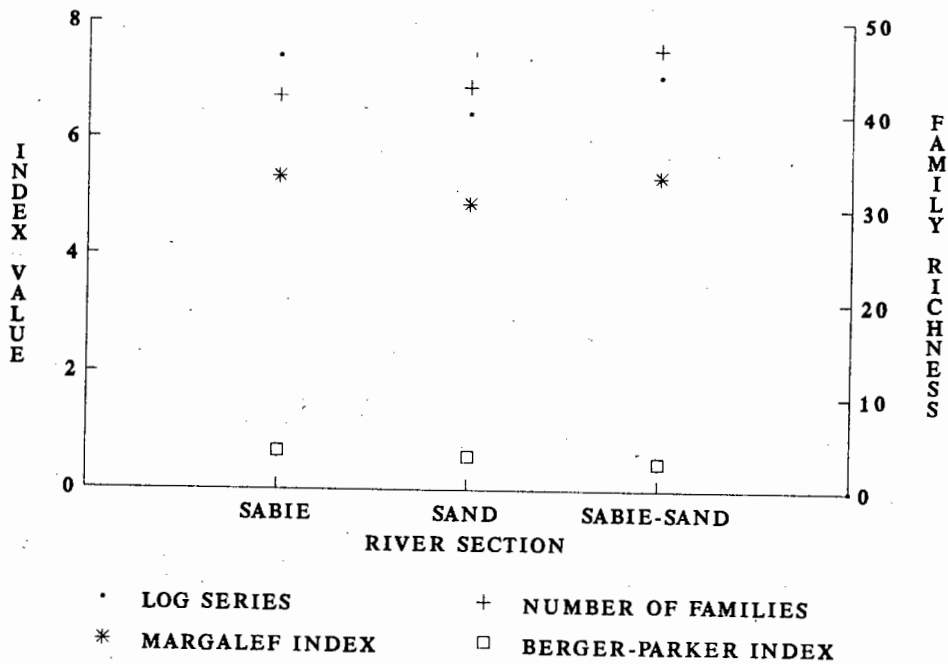


FIGURE 6.5. Gamma diversity index values calculated for the three river sections.

Epsilon diversity

The rank-abundance plot of the combined data from the Sabie-Sand River system is illustrated in Figure 6.6. The plot follows a log normal distribution to which the log series model has been fitted.

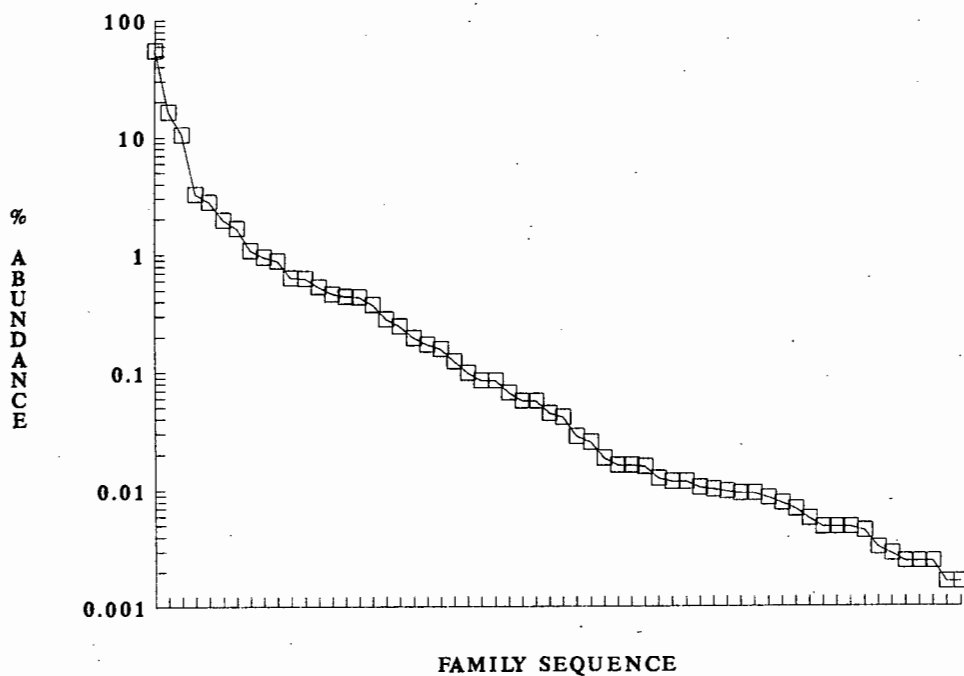


FIGURE 6.6. Rank abundance plot of the combined data from the Sabie-Sand River system.

Table 6.1 gives the diversity index values (α , D_{mg} , d and S) for alpha, gamma and epsilon diversity as a comparison between the three types of inventory diversity.

TABLE 6.1. Diversity index values for alpha, gamma and epsilon diversity in the Sabie-Sand River system

DIVERSITY	AREA	α	S	D_{mg}	d
α	SITE 3	5.54	36	4.26	0.65
	SITE 7	5.96	26	4.07	0.66
	SITE 11	5.91	42	4.58	0.47
	SITE 13	3.88	26	3.10	0.78
	SITE 20	7.05	47	5.33	0.46
γ	SABIE	7.41	42	5.34	0.65
	SAND	6.41	43	4.88	0.56
	SABIE-SAND	7.05	47	5.33	0.46
ϵ	SABIE-SAND CATCHMENT	10.13	61	7.19	0.55

The comparison between point, alpha, gamma and epsilon diversity for all four diversity indices is shown on Figure 6.7. The slopes of three graphs form power curves, indicating that diversity does not increase indefinitely with increasing area. In all cases, the graphs have reached an asymptote by the level of epsilon diversity. A regression analysis on the log-transformed data showed that the correlation between the number of samples (representing all forms of diversity), and the index values, was significant for α (PPMC, $r=0.823$, $p<0.05$, d.f. 2), the Margalef index (PPMC, $r=0.825$, $p<0.05$, d.f. 2), the Berger-Parker index (PPMC, $r=0.821$, $p<0.05$, d.f. 2) and family richness (PPMC, $r=0.887$, $p<0.05$, d.f. 2).

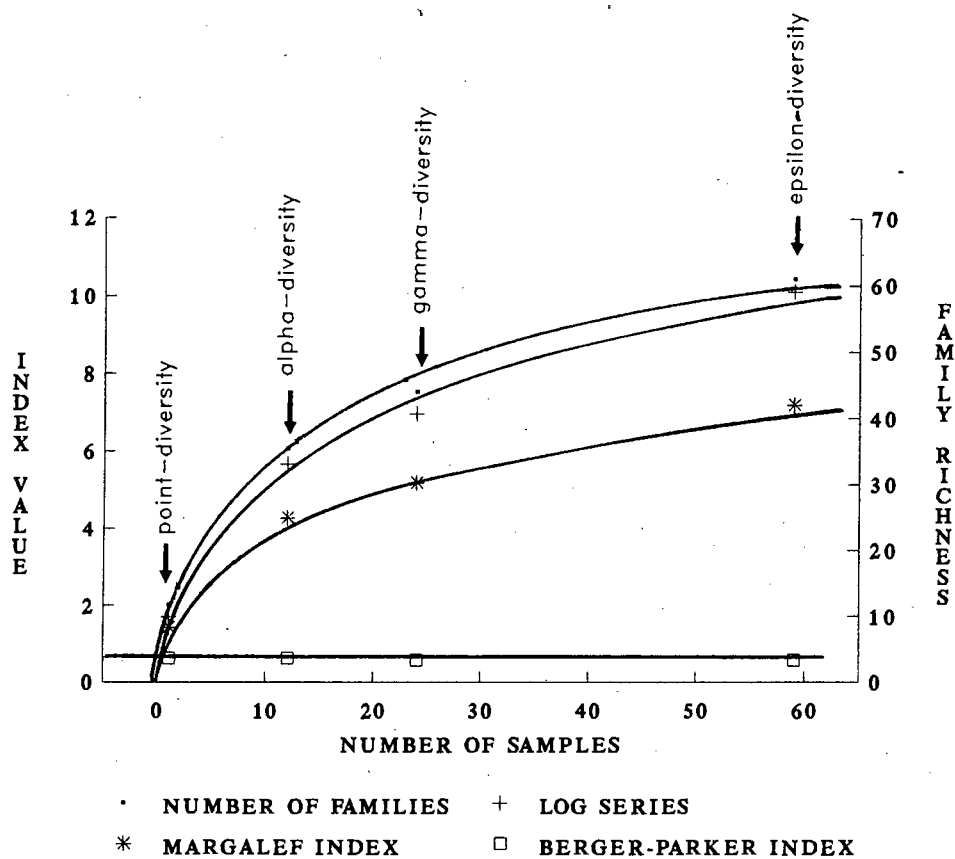
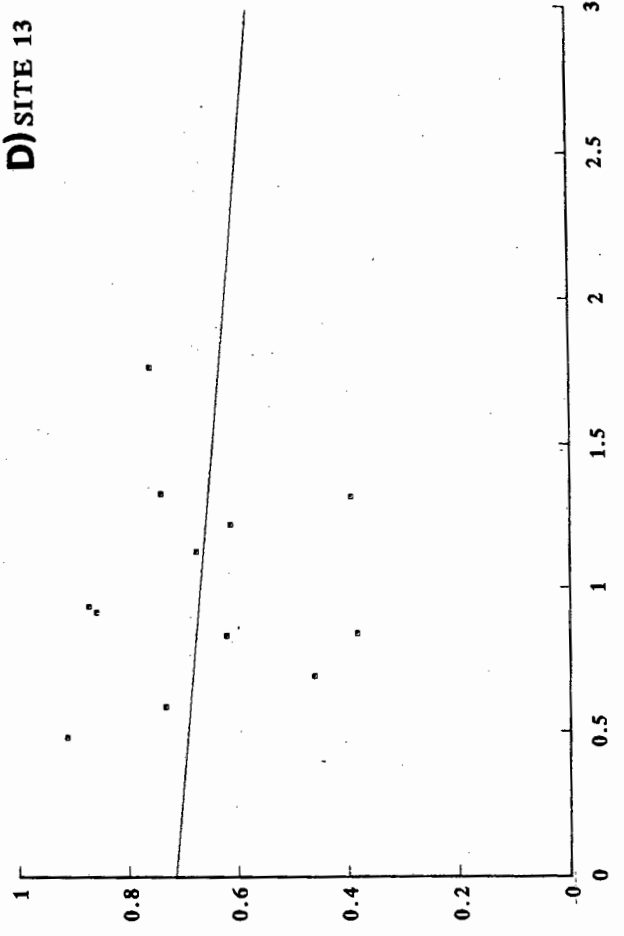
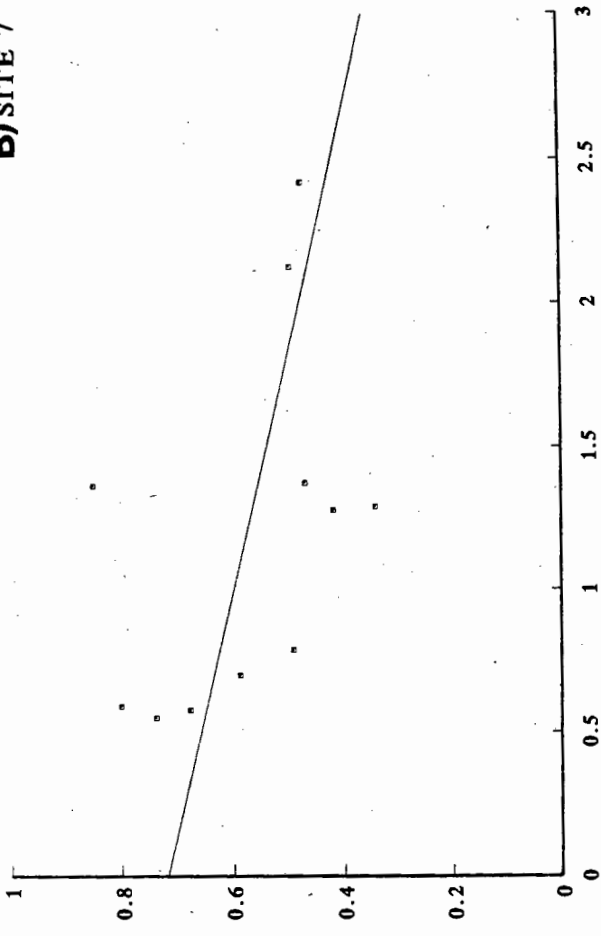
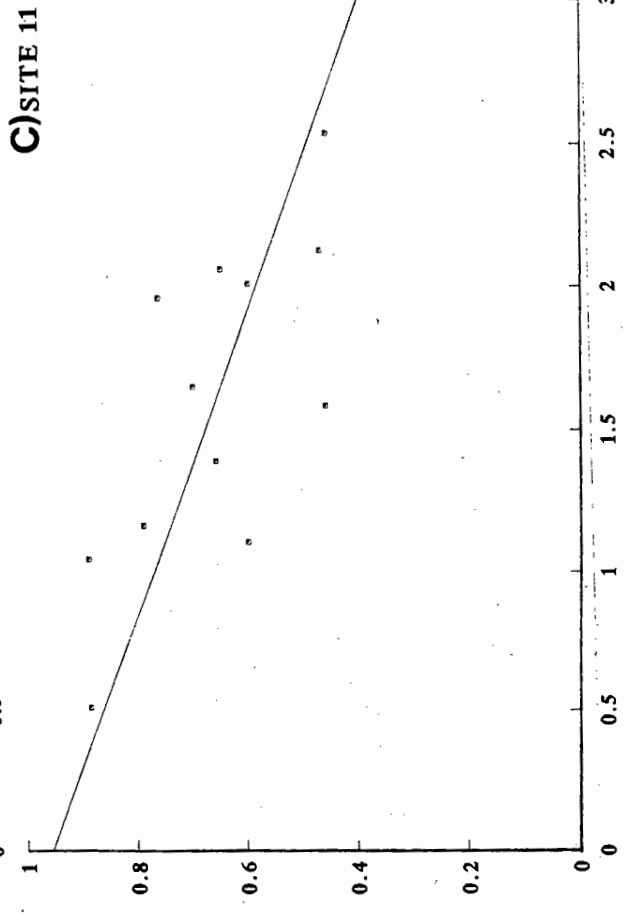
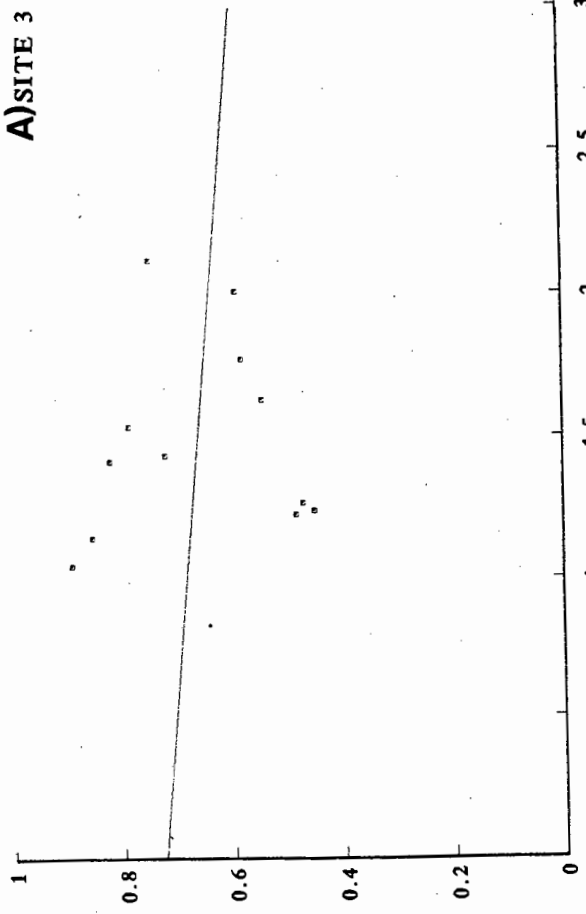


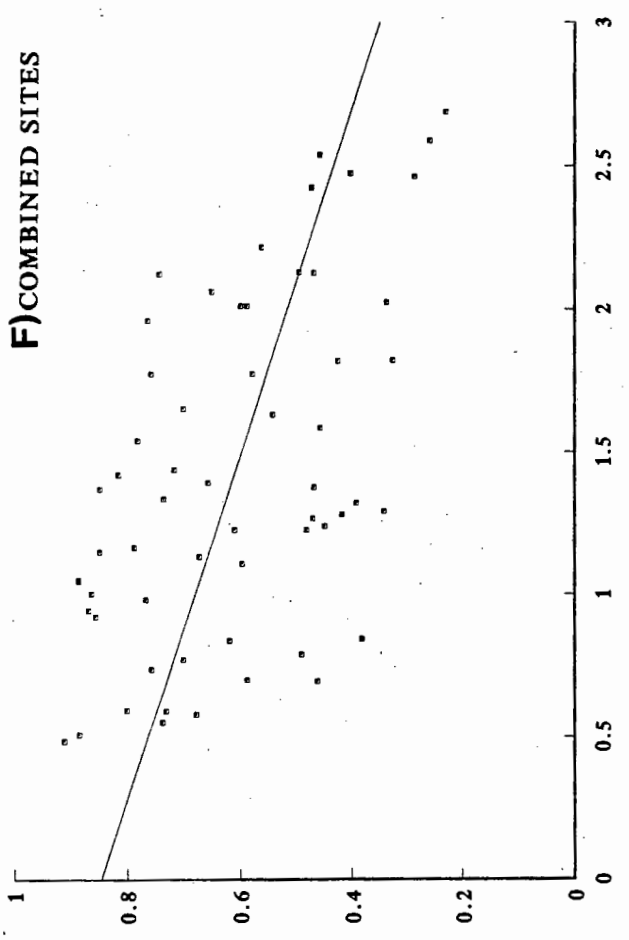
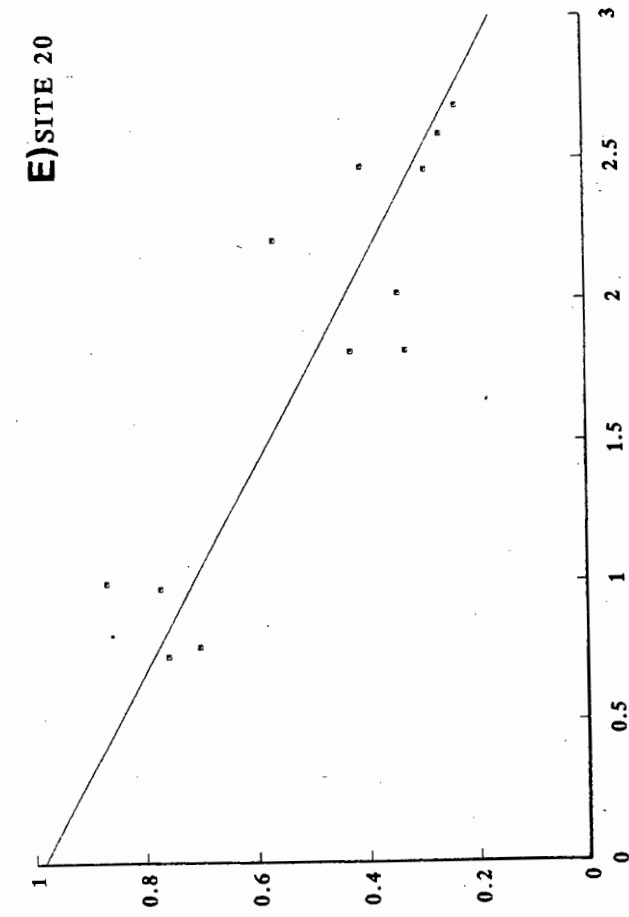
FIGURE 6.7. Relationship between the index values and the number of samples, representing point, alpha, gamma and epsilon diversity.

Relationship between richness and dominance

Figure 6.8 illustrates the relationship between the Margalef index (richness) and the Berger-Parker index (dominance) for site 3 (A), site 7 (B), site 11 (C), site 13 (D), site 20 (E) and all the sites together (F). Each data point represents one sample (i.e. point diversity). All graphs show a negative correlation between the two variables. The correlation between the two is not significant at site 3 (PPMC, $r=0.097$, $p>0.05$, d.f. 10),

BERGER-PARKER INDEX





MARGALEF INDEX

FIGURE 6.8. Relationship between the Berger-Parker and the Margalef indices in the Sabie-Sand River system for A, site 3; B, site 7; C, site 11; D, site 13; E, site 20, and F, combined sites.

site 7 (PPMC, $r=0.457$, $p>0.05$, d.f. 9) and site 13 (PPMC, $r=0.094$, $p>0.05$, d.f. 10). However, the correlation between the two is significant at both sites 11 (PPMC, $r=0.695$, $p<0.05$, d.f. 10) and 20 (PPMC, $r=0.892$, $p<0.05$, d.f. 10). When the data for all the sites are plotted on the same graph (Figure 6.8F) the negative correlation between the two variables is significant (PPMC, $r=0.538$, $p<0.05$, d.f. 57).

DISCUSSION

Measures of biological diversity, whether in the form of abundance plots or indices, are used primarily to provide a better characterisation of community structure within a system (Kempton 1979). A basic tenet of population ecology is that communities have characteristic species abundances that remain stable, despite changes in species composition. In Chapter 5, I discussed the similarities between areas within the system by analysing the individual taxa present in each community. However, a study of community structure may be more fruitful in displaying more fundamental ecological patterns (Kempton 1979; see Chapter 8), and a combination of the two will give a deeper understanding of the communities.

Within-habitat (site) diversity

Abundance plots such as illustrated in Figure 6.2 are valuable for the visual comparison of habitats. The patterns seen are a fundamental feature of community structure independent of component species (Samways 1983). They also provide information on the dominance pattern without reducing the information to a single statistic. From the

alpha diversity abundance plots, (Figure 6.2), it can be seen that site 20 is the most diverse, with a high number of families and a gently sloping graph (high equitability). Sites 7 and 13, on the other hand, are the least diverse, with a small family richness and, in the case of site 13, a steep graph gradient. Using visual cues the sites can be put in order of decreasing diversity as follows:

$$20 > 11 > 3 > 7 > 13.$$

On examination of mean point diversity (Figure 6.1A) and alpha diversity (Figure 6.3A) at each site, the sites can be placed in the same order of decreasing diversity. Both these figures contain four diversity measures. The Margalef index and the family richness are both measures of richness/abundance and do not stand on their own if the two requirements of the definition of diversity are to be fulfilled - that is, species richness and evenness of distribution. However, the Berger-Parker index is a measure of the dominance component within the community. This is effectively the opposite of equitability, and therefore, if the community has a low dominance, it is considered to be more diverse. These three indices provide a great deal of basic information, and when supplemented by the log series, α , a full picture of richness and equitability emerges. The log series, α , is the only single statistic used here that encompasses both richness and equitability. Its usefulness lies in the fact that it is robust to any moderate deviations from the log-series model (Kempton 1979), and has a high discriminating ability for "between-site" variation. The Shannon index was not used as the "...only reason for using the ... function is its popularity" (Vandermeer 1981).

Statistically, only the family richness index showed that sites 3, 11 and 20 differed from

sites 7 and 13. For the Margalef index, site 20 differed from sites 7 and 13, and for the log series, only sites 20 and 13 were significantly different from each other. There was no significant difference in dominance. This suggests that there was a significant difference in diversity between sites 20 and 13, but not between each of these two and the other three sites. The statistical differences found for the Margalef index and family richness are the differences between only one component of diversity, whereas α incorporates both components and is better used in discriminating between areas.

The difference in diversity between sites can be attributed to site and habitat characteristics. Site 20 was below the confluence of the Sabie and Sand rivers. Thus, the increase in diversity may be due to the "boundary effect" (Naiman *et al.* 1988). However, the question of the distance that the boundary extends downstream arises. Site 20 was 60km below the confluence. Intuitively one may feel that this distance is too far for any "boundary effect" to play a role. However, in Chapter 5 it was determined that there was not a significant difference in taxa between site 20 and the other sites, which suggests that there is a conglomerate community at site 20, of which some families were found in the Sand and some in the Sabie River. Therefore, it is possible that the "boundary effect" extended that far downstream, and is a feature of the longitudinal movement found in river ecosystems and not in terrestrial ecosystems.

Site 13 was characterised by large boulders of granitic bedrock, and the "stones-in-current" habitat was missing. Thus, the substratum was more homogeneous and there were few interstices in which the organisms could have found refuge. This may account for the lack of diversity at this site.

Site 7 had a similar aspect to site 13, and accordingly the two sites are very similar in diversity. Sites 11 and 3, on the other hand, had diversities intermediate to site 20, and sites 13 and 7, and were located in the upper catchment. Thus, they did not "suffer" from either the "boundary effect" or extreme substratum homogeneity.

Diversity within geographic areas

The rank abundance plots for the three river sections (Figure 6.4) show the Sabie-Sand to be most diverse. This is as would be expected from the within-habitat diversity results discussed above; the Sand and the Sabie sections showed little difference in diversity. An examination of the mean alpha (Figure 6.3B) and gamma diversities (Figure 6.5) for each section, identifies the Sabie-Sand section as the most diverse, followed in order by the Sand and the Sabie. In terms of richness, the Sabie was more diverse than the Sand, but the evenness component was low (the Berger-Parker value is high) and, thus, biological diversity was lower in the Sabie. However, statistical differences among the three areas were not significant. Therefore, in areas of gamma diversity, the mean diversity was very similar.

Catchment diversity

The abundance plot for epsilon diversity (Figure 6.6) had a log-normal distribution, with a high family richness. This, and the high index values, showed that the diversity within the Sabie-Sand system is high (Table 6.1) (Magurran 1988).

Because only five sites were sampled, there is the question of whether or not the epsilon diversity values given here are truly representative of the whole catchment. The point,

alpha, gamma and epsilon diversity values for all four indices are presented in Figure 6.7. The fitted curves were power curves, except in the case of the Berger-Parker index which decreased only slightly. At the point which represents epsilon diversity, each curve was at the asymptote, which means that for a greater number of samples the diversity would not have risen significantly. Thus, the diversity of all five sites can be considered as representative of the catchment diversity of the benthic macro-invertebrate riffle/rapid fauna.

Relationship between richness and evenness

From Figure 6.8F it appears that as richness increases, so dominance decreases; that is, as the richness component of biodiversity increases, so does the evenness component. This may lead to two assumptions, both of which may be erroneous. Firstly, one might assume that a high number of taxa automatically means that the community is more diverse and secondly, one might assume that the community is more stable. However, the positive correlation between richness and evenness is tenuous. At sites 3, 7 and 13 (Figure 6.8A, B & D) the correlation between the two was not significant, whereas for the other two sites it was. Thus, there is no consistency within the different habitats, though the clumped data (Figure 6.8F) showed a significant correlation. Also the link between diversity and the stability of a community is still under debate (Magurran 1988), and, thus, assumptions cannot be made in this regard. Therefore, before making any assumptions, the relationship between the two components requires definition for each habitat, and high species richness does not necessarily imply either high diversity or a stable community.

CHAPTER 7

**DIFFERENTIATION DIVERSITY OF THE BENTHIC MACRO-INVERTEBRATE
RIFFLE/RAPID FAUNA OF THE SABIE-SAND RIVER SYSTEM**

INTRODUCTION

Differentiation diversity is a measure of how different a range of samples, habitats or areas are in terms of the variety and abundances of species (Magurran 1988). The common approach to differentiation diversity is to look at the change in species along an environmental gradient. However, the study of differentiation diversity is moving beyond this traditional description (Wilson and Schmida 1984) and is being used to compare species composition and abundance of different communities at different spatial scales (i.e. patch, beta and delta diversity).

The concept of differentiation diversity has three important features which have been outlined by Wilson and Schmida (1984):

- it indicates the degree to which habitats have been partitioned by species;
- the values of differentiation diversity can be used to compare the habitat diversity of different systems;
- differentiation diversity and inventory diversity together measure the overall diversity or biotic heterogeneity of an area.

Thus, to complement Chapter 6, where the inventory diversity of the Sabie-Sand River system has been discussed, and to achieve a full picture of the overall diversity, this chapter covers the differentiation diversity of the system. In particular, the patch, beta and delta diversity (as defined in Chapter 4) of the benthic macro-invertebrate riffle fauna are assessed.

METHODS

Beta diversity

Beta diversity was calculated as the change in family composition of the macro-invertebrate riffle fauna at five sites (3, 7, 11, 13 and 20) on the Sabie and Sand rivers. Whittaker's measure of beta diversity (Magurran 1988) was calculated between all possible pairs of sites using the equation:

$$\beta_w = S/\alpha - 1 \quad (\text{see eqn. 1.8, Chapter 1})$$

where S = the total number of families recorded in the system,

α = the average sample diversity where each sample is a standard size
and the diversity is measured as family richness.

The data were presented in the form of a matrix.

For the purpose of assessing the degree of association between sites, Sorensen's similarity coefficient for quantitative data was calculated for every pair of sites. The equation takes the form:

$$C_N = \frac{2jN}{(aN + bN)} \quad (\text{see eqn. 1.9, Chapter 1})$$

where aN = total number of individuals at site A,

bN = total number of individuals at site B,

jN = the sum of the lower of the two abundances recorded for families found at both sites.

A dendrogram was drawn from these data using the group-average cluster technique (Field *et al.* 1982).

Delta diversity

Delta diversity was considered to be the change in family composition of the benthic macro-invertebrate fauna between the three sections of the Sabie and Sand rivers as outlined in Chapter 6. It was calculated using Whittaker's index in the same way as for beta diversity.

Patch diversity

Patch diversity was defined as the change in species composition and abundance between samples. The change in families, or family turnover, within sites and within the different river sections was measured using patch diversity.

It was calculated between successive samples using the equation:

$$\beta = (a + b).(1 - C_N) \quad (\text{see eqn. 1.10, Chapter 1})$$

where C_N = similarity coefficient calculated using Sorensen's index,

a = number of families in sample A,

b = number of families in sample B.

Frequency histograms of the patch diversity values were drawn up for each site and for each of the three river sections.

The difference between the within-site and within-section family turnover was measured statistically using a one-way ANOVA and *à posteriori* SNK tests (Zar 1984).

RESULTS

Patch diversity

The frequency distributions of the patch diversity for the five sites (Figure 7.1) gave a visual description of the turnover of species within a site. The more skewed to the left the frequency is, the higher the turnover of species is between samples. Site 13 (Figure 7.1D) had a distribution which is skewed to the right and a low mean family turnover (8.43), while Sites 7 and 3 (Figure 7.1A & B) had distributions which follow normal curves, with very similar mean turnover values to each other (higher than site 13), although site 3 had a broader range of turnover values than site 7. Sites 11 and 20 had distributions which are skewed to the left, and both have a high mean family turnover rate between samples, with site 20 having the highest mean turnover rate of all the samples (20.87).

An ANOVA of the mean patch diversity showed that there was a significant difference among the five sites (one-way ANOVA, $F=7.05$, $p<0.05$, d.f. 48, 5). The *à posteriori* SNK tests showed that sites 3, 7 and 13 did not differ significantly from each other (SNK,

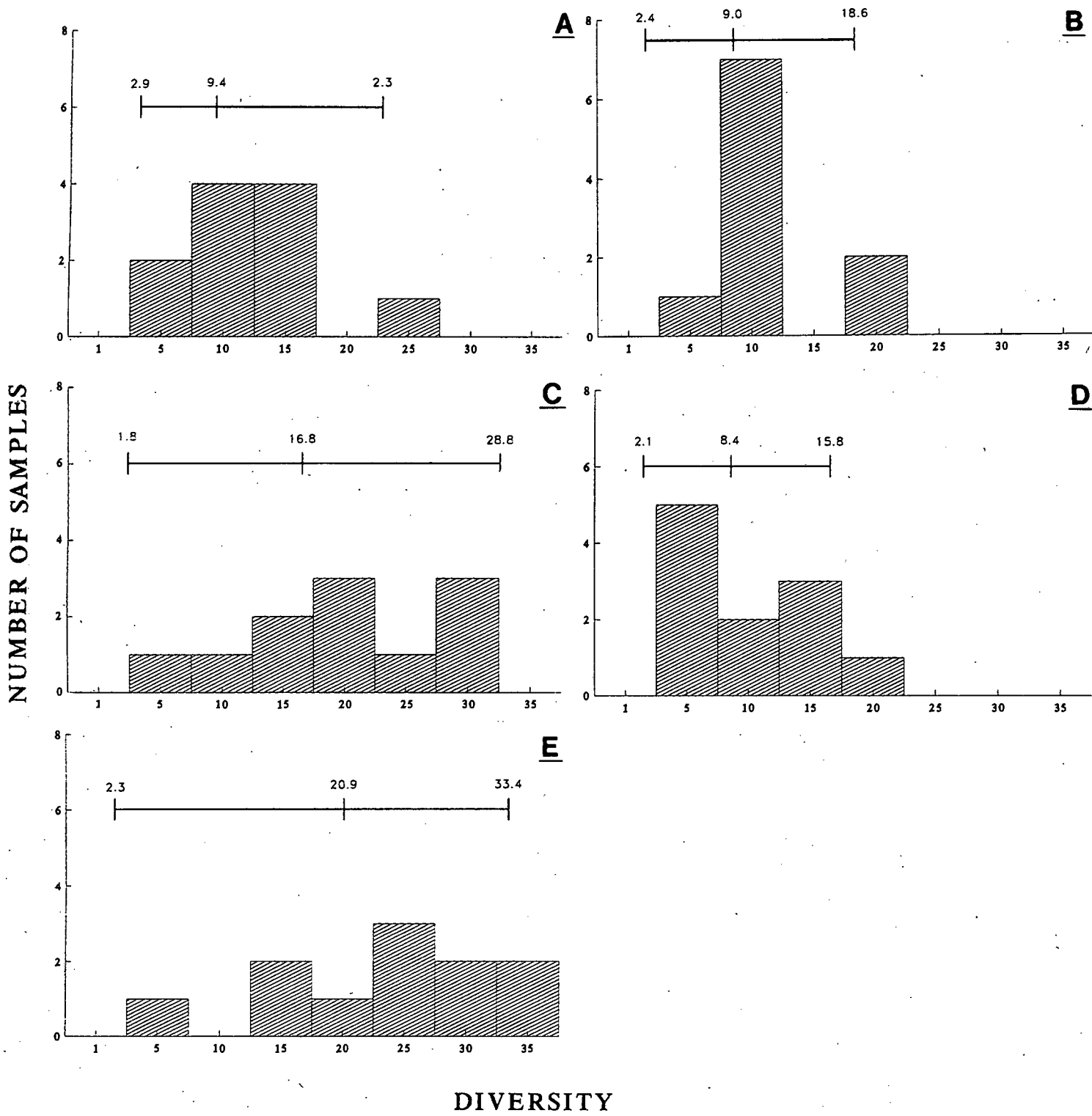


FIGURE 7.1. Frequency distributions of the patch diversity at A, site 3; B, site 7; C, site 11; D, site 13, and E, site 20.

$p > 0.05$, d.f. 48, see Appendix A), and that sites 11 and 20 did not differ from each other (SNK, $p > 0.05$, d.f. 48, see Appendix A), but that sites 3, 7 and 13 differed significantly from sites 11 and 20 (SNK, $p < 0.05$, d.f. 48, see Appendix A).

The frequency distributions of the patch diversity in the three sections of the Sabie-Sand River system are presented in Figure 7.2. In the Sabie section, the distribution followed a normal curve which was slightly skewed to the right and had a mean turnover of 9.23. The distribution of the Sand section, on the other hand, was also skewed to the right but had a mean turnover of 12.61, and that of the Sabie-Sand section was skewed to the left with a mean turnover of 20.87.

An ANOVA on these data showed that there was a significant difference in mean turnover among samples in these three river sections (one-way ANOVA, $F = 9.541$, $p < 0.05$, d.f. 52, 3). The Sabie-Sand section was significantly different from the Sand and Sabie (SNK, $p < 0.05$, d.f. 52, see Appendix A), while the Sabie and Sand did not differ significantly from each other (SNK, $p > 0.05$, d.f. 52, see Appendix A).

Beta diversity

The matrix of Whittaker's beta diversity values for the turnover in diversity between all possible pairs of sites (Table 7.1) indicates that the highest beta diversity values were between sites 7 and 13 (69% family turnover), followed by sites 20 and 7 (42% turnover), sites 20 and 13 (37% turnover), and sites 3 and 7 (35% turnover). The lowest family turnover was recorded between sites 3 and 11 (3% turnover), and between sites 20 and 11 (21% turnover).

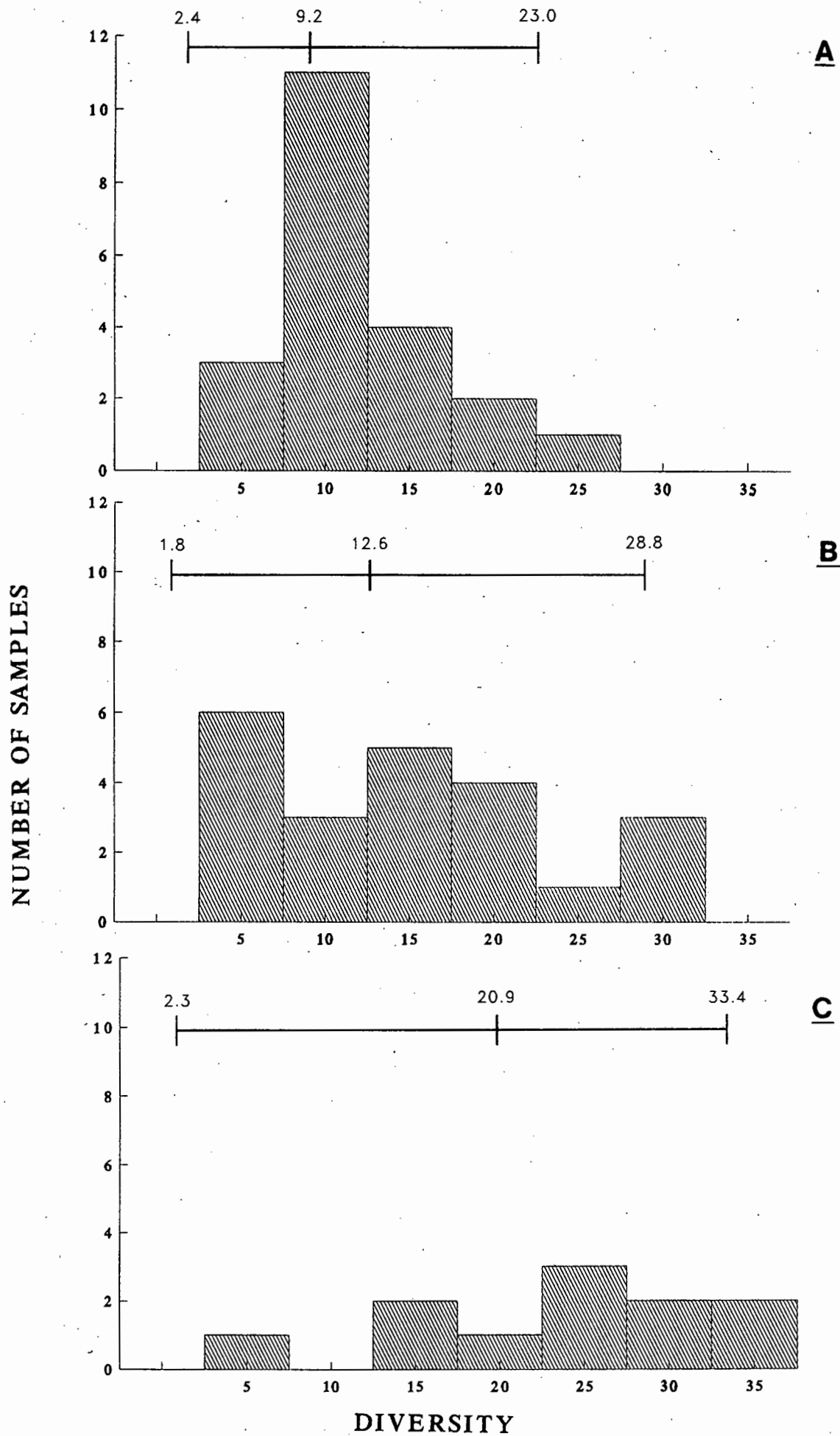


FIGURE 7.2. Frequency distributions of the patch diversity in the A, Sabie section; B, Sand section, and C, Sabie-Sand section (see Figure 7.1E).

TABLE 7.1. Matrix of Whittaker's index values for all possible pairs of sites

SITE NO.	3	7	11	13
7	0.35			
11	0.03	0.29		
13	0.22	0.69	0.26	
20	0.28	0.42	0.21	0.37

Figure 7.3 is a dendrogram showing the similarity in organisms between sites as calculated using Sorenson's similarity coefficient. Three groups can be identified:

1. sites 3 and 11,
2. sites 13 and 20 (as the two most similar), and
3. site 7.

Delta diversity

Table 7.2 is a matrix of Whittaker's index values for the turnover in diversity for all possible pairs of river sections, indicating that the turnover in families between the Sabie and the Sand sections was the highest, though this was relative to the intermediate and low turnover values of beta diversity. The turnover between the Sand section and the Sabie-Sand section was the lowest (19% turnover), while between the Sabie and the Sabie-Sand it was intermediate (24% turnover).

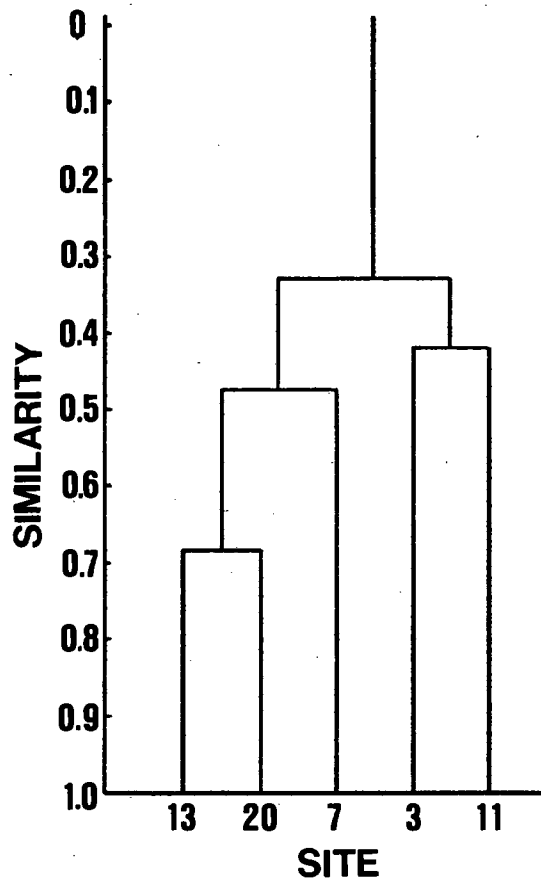


FIGURE 7.3. Dendrogram showing the classification of the five sites on the Sabie-Sand River system. Sites were compared using Sorenson's similarity coefficient on the untransformed quantitative data, and the dendrogram formed by group average sorting.

TABLE 7.2. Matrix of Whittaker's index values for all possible pairs of river sections

RIVER SECTION	SABIE	SAND
SAND	0.27	
SABIE-SAND	0.24	0.19

DISCUSSION

Magurran (1988) defines differentiation diversity (specifically beta diversity) as "...a measure of how different (or similar) a range of habitats or samples are in terms of variety (and sometimes the abundances) of species found in them", while Wilson and Shmida (1984) define it as the "...extent of species replacement". Herein lies the essential difference between differentiation and inventory diversity. Inventory diversity deals with community structure of which there are two components, variety of species and evenness of distribution. Differentiation diversity only deals with the variety of species - it measures the turnover of species (or families) between two areas but does not measure the change in equitability. Therefore, for a better understanding of community structure and functioning it is essential to measure both types of diversity concurrently.

Patch diversity

The concept of patch dynamics within lotic ecosystems has been dealt with in detail by Pringle *et al.* (1988) and it is not my intention to go into the theory behind it. It suffices to say that any environment is a mosaic of heterogeneous components or patches (Pringle *et al.* 1988), within which are found a diversity of species. In fact Pringle *et al.* (1988) define a "patch" in terms of the organisms themselves, stating that a "patch" is a spatial unit determined by the organisms. One would expect that a high species variability between patches is synonymous with a high biotic diversity.

Between-patch variability, known as patch diversity, was measured for all five sites in the Sabie-Sand River system (Figure 7.1). Sites 20 and 11 had the highest mean patch

diversity (site 20 having the highest), and a wide range of patch diversity values. Thus, patches range from being highly heterogeneous with each other to homogeneous. Chapter 6 showed that the alpha diversity at these sites is high. Site 3 had a lower mean patch diversity to sites 20 and 11, similar to that of site 7, while site 13 had the lowest mean patch diversity. These data correspond to those in Chapter 6, where site 20 was considered to be the most diverse, followed by sites 11, 3, 7 and 13 in order of decreasing diversity. Therefore, the diversity at any site corresponds to the between-patch variability.

Patch variability is also a reflection of the habitat. Sites 20 and 11 have highly heterogeneous substrata on which the organisms are found. Therefore, the patch diversity, and consequently the alpha diversity were both high.

Figure 7.2 shows the mean patch diversity for the three river sections of the Sabie-Sand system. The patch diversity was significantly higher in the Sabie-Sand section, which also had the highest gamma diversity value (see Chapter 6). A similar connection was seen between the Sand and the Sabie sections, and the respective gamma diversity values of the two (see Chapter 6). Therefore, the gamma diversity of a system also depends on the micro-habitat and patch diversity.

Beta diversity

Beta diversity is the turnover of species between habitats (in this case, sites). It can be measured in two complementary ways. The first is by measuring a change in the diversity, where only the species richness component is taken into account. Whittaker's measure

of beta diversity does this, and is considered to be a straightforward measure which conforms to the four criteria of "good" performance set out by Wilson and Shmida (1984):

- conformity with the intuitive notion of community turnover;
- additivity along a gradient;
- independence from alpha diversity, and
- independence from sample size.

Table 7.1 shows that family turnover was highest between sites 13 and 7 (69% turnover rate). Both are characterised by the same substratum; granitic bedrock, and therefore, it is surprising that they did not support the same species. This may be due to differential colonisation at the sites. The environment on the granitic rock surface is harsh, and temporal turnover of species may be high due to drift. Thus, colonisation will take place at a higher rate than in areas of high substratum heterogeneity, where the organisms are more protected. The families recolonising at each of these sites may differ, creating a high beta diversity between the sites. Table 7.1 also indicates that a higher family turnover occurred between those sites which have a high alpha diversity (sites 3, 11 and 20; see also Chapter 6) and those which had a low alpha diversity (sites 7 and 13; see also Chapter 6). This may not be due to a large change in family composition between the high diversity and the low diversity sites *per se*, but rather due to an additional array of families found at the high diversity sites. This would create a larger difference between the sites as far as species composition is concerned.

The lowest family turnover occurred between the sites with the highest alpha diversity.

Whittaker (1975) has stated that a high beta diversity value is a consequence of a high habitat diversification and that there must be a saturation point at which the habitat cannot become more diverse. The low turnover at these diverse sites may be a consequence of habitat saturation. All three sites have a high substratum heterogeneity as discussed in Chapter 6, which leads to the "nook and cranny effect" (see Pielou 1975) and, consequently, to a high diversity. With a high substratum heterogeneity, these sites may all have reached saturation point as far as niche space and new families are concerned, and turnover will be minimal.

The second method of assessing beta diversity was by measuring the similarity of the habitats by directly comparing the organisms present. This was achieved by using Sorenson's similarity coefficient and constructing a dendrogram using the group average cluster technique (see Figure 7.3). One would expect from the high turnover between sites 13 and 20 that they would not be clustered together. However, this grouping suggests that site 20 had an array of families not found at site 13, but the majority of families found at site 13 were also found at site 20. The same might apply to site 7 and site 20. The fact that sites 3 and 11 are clustered together may be due to their similar substratum type and physico-chemical characteristics (see Chapter 5). Therefore, beta diversity between sites is a function of the cumulative variety of species present at the sites and the number of common species, both of which are influenced by environmental parameters.

Delta diversity

Table 7.2 indicates that the two lowest delta diversity values are between the Sabie-Sand section of the river and the other two sections. This may be due to the former sharing species with both the Sand and the Sabie sections, and so the turnover between either of the two and the Sabie-Sand section is not high. This concept fits well with the concept of the "boundary effect" which I discussed in detail in Chapter 6. The turnover between the Sabie and the Sabie-Sand section is the lowest. This could be due to the fact that below the its confluence with the Sand River, the Sabie River becomes superficially more morphologically characteristic of the Sand River than the Sabie (Prof. B.R. Davies, Freshwater Research Unit, U.C.T., Cape Town, pers. comm.). If this is so then it explains why the Sabie-Sand section would share more common elements with the Sand section.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

INTRODUCTION

Magurran (1988) has stated that the major applications of diversity measurement are in nature conservation and environmental monitoring, and in both cases, diversity is considered to be synonymous with environmental quality. Diversity measures are, therefore, used extensively in gauging the effects of environmental disturbance. In the case of the Sabie-Sand River system, which is soon to be regulated by a number of dams, determining the biological diversity of the system before impoundment could provide a useful basis for further, post-impoundment monitoring.

The aims of this study were, therefore, threefold:

- to carry out a preliminary survey of the benthic macro-invertebrate riffle fauna, and to determine the influence of environmental factors on these communities;
- to measure the biological diversity in different reaches over a seasonal cycle, with special reference to determining the difference in diversity among reaches, and between the Sabie and the Sand rivers, as well as below their confluence, and
- to assess the applicability of accepted measures of biological diversity to river ecosystems.

The results of the preliminary survey, combined with the study of biological diversity, give an overall picture of the structure of the benthic macro-invertebrate communities of the Sabie-Sand system and the environmental factors which influence them, and will be dealt with concurrently. The assessment of the applicability of measures and a discussion on the ecological significance of biological diversity are dealt with under two

separate headings.

BIOLOGICAL DIVERSITY AND DISTRIBUTION PATTERNS OF THE BENTHIC MACRO-INVERTEBRATES IN RELATION TO SOME ENVIRONMENTAL VARIABLES

The most striking feature of the Sabie-Sand system was the fact that the benthic macro-invertebrate community did not differ significantly between the two rivers, or below the confluence. This is apparent from three analyses:

- i) *Classification and ordination analysis* - The six groups of macro-invertebrate communities distinguished by the classification and ordination analyses were aggregated on the two-dimensional ordination (see Figure 5.3, Chapter 5). This, and the fact that the groups had a fairly random distribution throughout the catchment (see Figure 5.4, Chapter 5), indicated a fairly homogeneous benthic macro-invertebrate faunal component at the Genus level of identification.

- ii) *Analysis determining distinguishing taxa* - This showed that all the macro-invertebrate groups distinguished by the ordination analysis had very similar dominant taxa at the Genus level of identification (except the Chironomidae and Hydracarina; see Table 5.1, Chapter 5). The same applied to a comparison between samples from the Sabie and Sand rivers (see Table 5.2, Chapter 5).

The dominant taxa throughout the system were:

Diptera:	Ephemeroptera:	Coleoptera:
Chironomidae	<i>Baetis</i> spp.	Elmidae sp.A
Tipulidae sp.B.	<i>Cloeon</i> complex	
<i>Bezzia</i> sp.	<i>Cheumatopsyche</i> spp.	
<i>Simulium</i> spp.	<i>Acentrella</i> spp.	
	<i>Neurocaenis</i> spp.	

iii) *Calculation of biological diversity* - The calculation of gamma diversity at the Family level (Chapter 6), indicated that there was no significant difference in diversity between the rivers (Figures 6.4 and 6.5, and Table 6.1). This was verified by the low delta diversity values (Table 7.2, Chapter 7), which indicated a slight difference in families between rivers.

Power *et al* (1988) have suggested that variation in biotic dynamics and interactions within the river ecosystem are inextricably linked to variations in abiotic factors. Therefore, distribution patterns of taxa and the structure of the fauna in the Sabie-Sand system should be influenced by abiotic environmental factors. However, the relationship between biotic and abiotic factors is complex, and though many studies have tried to isolate the most dominant factor (e.g. Gore 1980; Scullion *et al.* 1982; Townsend *et al.* 1983; Furse *et al.* 1984; Bunn *et al.* 1986; Ormerod & Edwards 1987; King *et al.* 1988; Ormerod 1988; Bennison *et al.* 1989; McElravy *et al.* 1989; Wright *et al.* 1989), there is no uniformity in results due to the innate differences of the systems under study. Thus, each system differs in

terms of the overriding influential abiotic factors; for example, in one system, pH may be the dominant variable (e.g. Townsend *et al.* 1983), while in another, discharge is the dominant variable (e.g. Bunn *et al.* 1986; McElravy *et al.* 1989).

King *et al.* (1988) have suggested that there are two types of variable which characterise a river system, driving variables and passive variables. Driving variables are related to the major natural forces that shape the character of rivers (e.g. geomorphology, climate, topography, geochemistry, hydrology), while passive variables usually relate to the river itself (e.g. water chemistry, discharge, substratum) and result from higher controlling forces. Both these terms are, in essence, misnomers, as driving variables may not necessarily be active (e.g. geomorphology), while passive variables may not necessarily be passive (e.g. nitrate, nitrite and ammonium). However, for the purposes of this discussion these definitions will be adhered to. The passive variables may be sub-divided into macro-habitat variables (e.g. discharge and chemistry), which affect, for example, life cycles, growth patterns and food availability, and micro-habitat variables (e.g. substratum heterogeneity; see Chapter 5), which may influence factors such as niche partitioning, and protection against predators and physical stress.

In the Sabie-Sand system, the interaction between combinations of environmental factors, both driving and passive, have determined the macro-invertebrate community structure within the Sabie-Sand River system. King *et al.* (1988) have stated that one of the problems facing scientists is that none of the analytical techniques give an indication of which

variables are the primary determinants, and which are correlated to distribution. This was also the case for the Sabie-Sand system.

One of the variables significantly correlated ($p < 0.001$) to the distribution patterns of the Sabie-Sand system was altitude, a variable which has also been correlated to macro-invertebrate distribution patterns in Australia (e.g. Davis *et al.* 1988; Edward *et al.* 1988; Bennison *et al.* 1989) and in England (Furse *et al.* 1984). However, in the Sabie-Sand system, this trend seemed to be due to the combined interactions of the other environmental variables as well. For example, in the ordination diagram (Figure 5.3, Chapter 5), groups C and D not only consisted of samples which were predominantly collected from high altitudes, but were also the most distinctive groups, both environmentally and taxonomically (see Figure 5.3, Chapter 5).

The dominant variable influencing the macro-invertebrate faunal distribution was the substratum type, which is a micro-habitat variable. This was evident from both the biological diversity of different reaches, and the abundances of the taxa on different substrata. Magurran (1988) has stated that habitat diversity and species, or family, diversity are directly proportional to one another. Thus, the low patch and alpha diversity at sites 7 and 13 may have been a result of low habitat diversity (see Chapter 6). At these sites the substrata from which the samples were taken were homogeneous granitic bedrock, whereas at sites 3, 11 and 20, which were more biologically diverse, a variety of substrata were observed. Thus, in this case, habitat diversity was directly linked to substratum diversity.

The *abundance* of any taxon in the Sabie-Sand system also depended on the substratum type, or the micro-habitat available. An example of this was the difference in faunal abundance between the samples from sand and rock substrata (see Table 5.3, Chapter 5). The sand substratum fauna had a lower abundance than the rock substratum fauna, though similar taxa were found in both.

These trends suggest that, at the time of the study, the system was in equilibrium (see Resh *et al.* 1988). Any major disturbance (see Reice 1985; Resh *et al.* 1988) could upset this equilibrium and result in a decrease in the diversity of the system. Over the next few years the greatest disturbance to the Sabie-Sand catchment will be impoundment of the river. Therefore, it is imperative to discuss the possible implications of the regulation of the Sabie and Sand rivers for the distribution of the macro-invertebrate fauna, and the biological diversity of the system, particularly in the light of the apparent uniqueness of the system (e.g. O'Keeffe *et al.* 1989a; O'Keeffe & Davies 1991).

The first modification to consider is the alteration of the hydrological régime. If, as has happened in other rivers of the KNP (Bruwer in press) and globally (e.g. Ward & Stanford 1979a; Lillehammer & Saltveit 1984a; Petts 1984; Craig & Kemper 1987; Gore & Petts 1989; Petts *et al.* 1989), the mean annual discharge decreases, certain niches, currently available to the organisms, will no longer be available, and diversity will decrease with concomitant alteration of present macro-invertebrate distribution patterns. If, on the other hand, hydrological alterations take the form of dampening seasonal flow fluctuations (e.g.

Hellawell 1988), the changes in the distribution of the fauna may be localised (e.g. say at the dam wall), but the overall diversity will probably decrease due to the lack of variability (see the Intermediate Disturbance Hypothesis and the related Serial Discontinuity Concept; respectively, Connell 1978; Ward & Stanford 1983a, b)

Other probable modifications are changes in chemical (e.g. Armitage 1984; Newbold 1987; Ward & Stanford 1987a; Byren & Davies 1989; Palmer & O'Keeffe 1990a; O'Keeffe *et al.* 1990) and thermal régimes (e.g. Ward & Stanford 1982; Armitage 1984; Ward 1985). Alteration of these variables might cause changes in, for example, life cycles, reproductive capability and growth rates (Ward 1985), and affect both distribution *and* biological diversity of the macro-invertebrate fauna. Whether the effects will be adverse, or not, can only be determined after impoundment. However, it is probable that, due to such modifications, the diversity will decrease after impoundment. Thus, the post-impoundment macro-invertebrate communities will be a result of a combination of changes in the physical and chemical properties of the river.

ASSESSMENT OF THE MEASUREMENT OF BIOLOGICAL DIVERSITY IN RIVER ECOSYSTEMS

One of the aims of this study was to assess of the applicability of commonly used diversity measures to river ecosystems. I shall approach this *à posteriori*, assessing the approach that

I took in this study and identifying areas of weakness.

Ensuring representative sample sizes

The recommended approach includes the use of an accepted collection method, such as a grab or surber sampler, combined with a statistically valid number of replicates (Magurran 1988). This approach may be adequate, although a possible problem involves the spatial scale on which one is working. Minshall (1988) has stated that in many cases, the scale at which stream ecologists work appears to be outside the dimensions of a given ecological interaction.

The important question to be answered in this study was whether or not five sites would be representative of the whole Sabie-Sand catchment. Although the answer was "yes" for the Sabie-Sand (Chapter 6), this might not necessarily be the case for studies of other systems. It is also debatable as to whether or not three samples per site is a statistically valid "replication"; five or more would give a more accurate representation of the site. Although time and money often take preference, a preliminary investigation of acceptable sample sizes is recommended for each study.

Definition of spatial and temporal boundaries

Although a general framework may be given to assist the researcher (see Chapter 4), spatial and temporal definitions depend on the system under study, together with the aims of the project and the time span over which the project is running.

Spatial definition relies largely on the definition of terms. Scales similar to those used in this study (see Chapter 4) may be acceptable for other macro-invertebrate studies, especially if comparisons are to be made. However, these scales would probably not be suitable for research on fish or the riparian vegetation for example, and re-definition of the terms (alpha, beta, delta diversity etc.) would be essential.

In this study, the temporal dimensions were defined on a short-term basis, due to the length of the study, and practical considerations made it necessary to sample quarterly during the year that the study was in progress. This was sufficient in the Sabie-Sand system as one of the features of the system that was recognised by Moore & Chutter (1988), is that there is very little seasonal change in the macro-invertebrate populations. However, although this gives an understanding of the Sabie-Sand system before impoundment, a more continuous, medium-term sampling programme (1-5 years) may be more valuable for management purposes.

Definition of taxonomic boundaries

A factor which almost certainly affected the result of the analyses discussed earlier was the taxonomic levels at which the analyses were executed. In Chapter 4, it was stated that the definition of taxonomic boundaries depends on the organisms under study and the extent of taxonomic knowledge. The approach taken in this study, to determine whether or not identification to Family level was adequate, is acceptable for the determination of biological diversity, as long as these boundaries are determined *à priori*. However, although Kaesler

& Herricks (1979) and Furse *et al.* (1984) have stated that for ordination and classification analyses meaningful patterns could be obtained with either generic or familial data, considerable debate has sprung up concerning the acceptability of this approach (Lenat & Penrose 1980; Dr J.A. Day, Zoology Department, University of Cape Town, Rondebosch, pers comm.; Dr J.H. O'Keeffe, Zoology Department, Rhodes University, Grahamstown, pers comm.). Moore & Chutter (1988) and Moore (1991), in their study of the KNP rivers, suggested that the lack of taxonomic detail may have masked significant trends in their data. This may also explain partly the surprising lack of trends found in the Sabie-Sand system, and the similarity among sections. It must, therefore, be left up to the researcher to determine the acceptable taxonomic level at which the study is executed, although community functioning cannot be determined significantly at a level above Genus. In other words, such taxonomic levels tell us little of ecological functioning and importance.

Measuring diversity

The accurate measurement of diversity is based on the choice of index or diversity measure. In Chapter 1, guidelines on the use of a few measures which might be applicable to river ecosystems were presented. Table 8.1 gives an assessment of the performance and characteristics of the diversity measures used in this study.

Four main points of interest concerning the diversity measures used, are given below:

1. Abundance plots and the log series, α , can stand alone as descriptions of biological diversity, and are valuable tools for statistical comparisons of communities within and

TABLE 8.1. A summary of the performance and characteristics of a range of diversity measures. These assessments are partly subjective, and the intention is not to give a definite classification of diversity measures but rather to show their relative merits and shortcomings. Classification and ordination analyses are included as an alternative to Sorenson's similarity coefficient

DIVERSITY MEASURE	SENSITIVITY TO SAMPLE SIZE	RICHNESS OR EVENNESS DOMINANCE	STATISTICAL DISCRIMINATORY ABILITY	EASE OF CALCULATION	INDEPENDANT FROM OTHER MEASURES?
ABUNDANCE PLOTS	low	neither	good	simple	yes
LOGSERIES α	low	neither	good	simple	yes
NUMBER OF SPECIES	high	richness	good	simple	no
MARGALEF INDEX	high	richness	good	simple	no
BERGER-PARKER INDEX	low	evenness	poor	simple	no
WHITTAKER'S INDEX	low	neither	good	simple	no
SORENSEN'S SIMILARITY COEFFICIENT	low	neither	good	simple	no
FREQUENCY PLOTS	high	richness	poor	simple	no
CLASSIFICATION AND ORDINATION	low	neither	good	complex	no

between systems.

2. Species richness, the Margalef index and the Berger-Parker index do not stand on their own as measures of diversity, but need to be calculated as complementary to each other.
3. Although the calculations are simple, the Sorenson's similarity coefficient is not as powerful as ordination and classification analyses for determining differences in communities. In this study, more information might have been gained by using ordination and classification analyses on the data from the five sites.
4. Frequency plots of differentiation diversity add no information not already gained by the other measures. They are also not a measure of the turnover in diversity, and give more information on the inventory diversity of the system than the differentiation diversity. They may be considered extraneous in the measurement of the differentiation diversity of a system.

From these results it may be ascertained that the best descriptions of inventory diversity were abundance plots and the α log series used in conjunction with each other. They provide a good visual representation, they can be analysed statistically, they are not sensitive to sample size and they give a measure of both evenness and richness. For inventory the best description of turnover was Whittaker's measure, while cluster analyses provided an understanding of the effect of environmental parameters on the communities.

ECOLOGICAL SIGNIFICANCE OF MEASURING BIOLOGICAL DIVERSITY AND FUTURE RESEARCH NEEDS

Ecological significance

Ecological communities are a reflection of their environment (Wright 1984, 1989) and, as stated earlier, biological diversity is synonymous with environmental quality. Thus, the measurement of biological diversity is useful as a monitoring and comparative tool. It may also be viewed as favourable in South Africa, where managers need quick and easy answers, and guidelines for river management.

Biological diversity measures can give an indication of the relative degradation of the system by using inventory and differential diversity. The latter gives an indication of the change in taxa. In this case identification of the species present would determine the type of change that has taken place.

This is where the usefulness of measuring biological diversity is stretched to the limit, especially if it has been measured at the Family level. Diversity measures can tell us that there has been a change, and even what the change is, but they do not give any information on the functioning of the communities or the system under study (Kempton 1979). Without knowledge of the functioning of a system, management cannot take appropriate steps to counteract detrimental changes.

To comprehend the functioning of any system, the functioning of individual communities requires understanding (i.e. aspects such as predation, competition, mutualism and

symbiosis). This certainly cannot be done at a Family or Genus level of identification. Many con-familial and con-generic species have vastly different characteristics and habitat requirements. For example, Palmer (1991) has described the preferred habitat of *Choroterpes elegans* as "riffles and stony backwater biotopes", while *Choroterpes nigrescens* is found exclusively in "depositional backwater biotopes" (Palmer 1991).

One of the problems of studying macro-invertebrate community functioning, especially in the Sabie-Sand, is systematics. As mentioned in Chapter 4, many of the species in the Sabie-Sand River system are as yet undescribed, and little is known as to whether or not many of them are conspecific or con-generic. Cook (1991) studied the systematics of the fairly well known amphipod genus, *Paramelita*, and found, through the use of gel electrophoresis, that populations which were thought to be con-specific were, in fact, con-generic. If little is known of the systematics of organisms in a community, then even less will be known of their biological functioning

One way of circumventing the taxonomic problem is by splitting the organisms into functional guilds. One such example is of the functional feeding groups (FFGs; Vannote *et al.* 1980). The FFG concept, which links the origin and fate of organic matter in streams to the feeding of macro-invertebrates, emphasizing the role played by feeding activities in the mediation of stream processes, has been tested by Palmer (1991) with positive results. Thus, the study of FFGs, where organisms can be placed into guilds without identification to species, can give a greater insight into community and stream functioning.

Thus, the usefulness of biological diversity measures seems to be in their survey import. However, when it comes to ecological management, the *concept* of diversity, linked to a functional approach, may provide a powerful and complete management tool. Unfortunately very little is known of the functioning of communities and the resultant effect on diversity. This brings us to the research needs appertaining not only to the Sabie-Sand River system, but to other South African rivers and also globally.

Research needs

In the light of the above discussion, five areas of research can be identified concerning the Sabie-Sand River system.

1. This study only covered a relatively short pre-impoundment period. For management purposes it might be advantageous for a medium-term pre- and post-impoundment monitoring programme to be set up. If, as Magurran (1988) suggests biological diversity is synonymous with environmental quality, the measurement of biological diversity over a longer period will give an indication of the degradation, if any, of the system. A comparison of the Sabie-Sand system with other systems may also give a good indication of relative quality and be useful as a conservation tool.
2. The biological diversity of other organisms in the Sabie-Sand River system (i.e. fish, macrophytes, riparian vegetation) has not yet been calculated. For monitoring purposes this is important, as post-impoundment changes of environmental variables may effect other biota differently to macro-invertebrates.
3. The greatest, single stumbling block in this study was the lack of taxonomic knowledge of the fauna of the system. Thus, research into the systematics of the organisms is vital,

and until such time as the species are described, unknown species should be coded consistently for comparability (see Davis *et al.* 1988).

4. Research on systematics may be linked with detailed research concerning the functioning of the macro-invertebrate communities, and especially how functioning is linked to the diversity of the system. This information together with the measurement of biological diversity would be a powerful management tool for river ecosystems.
5. Magurran (1988) has stated that "...diversity is rather like an optical illusion. The more it is looked at, the less clearly defined it appears to be and viewing it from different angles can lead to different perceptions of what is involved...", and, especially in terms of river ecosystems, and the Sabie-Sand in particular, research into biological diversity and the concepts involved is required.

SUMMARY

The Sabie-Sand River system is the only river system in the Kruger National Park that remains unregulated and perennial, and has been identified as the most important river for nature conservation in South Africa (Chutter & De Moor 1983; Moore & Chutter 1988). However, eight dam sites have been identified for future development, and consequently, a pre-impoundment survey of the catchment was initiated under the auspices of the Kruger National Park Rivers Research Programme. This study was incorporated in that survey with several objectives:

- to determine benthic macro-invertebrate distribution patterns in relation to several environmental variables;
- to determine the biological diversity of the benthic macro-invertebrate riffle fauna in different reaches and river sections, and
- to assess the applicability of accepted measures of biological diversity to river ecosystems.

Two approaches were utilised in this study. The first was a preliminary survey, using classification and ordination analyses to determine the distribution of the benthic macro-invertebrate fauna in the system with respect to select environmental variables. Distinguishing taxa were also identified using an analysis outlined in Warwick *et al.* (1990).

The second approach was the measurement of the benthic macro-invertebrate diversity within the system. The macro-invertebrate riffle/rapid fauna was sampled over one year, in five representative reaches, and the inventory and differentiation diversity was calculated at a familial taxonomic level. The measures of diversity used in the study were later assessed as to their applicability in river ecosystems.

The results showed that the benthic fauna did not differ significantly between either the Sabie and the Sand rivers or below the confluence of the two. This may be due to the fact that there was no dominant macro-habitat variable which influenced the fauna, or the fact that taxonomic detail was insufficient to determine distinct trends. Substratum, a macro-habitat variable, was the dominant factor influencing biological diversity and faunal distribution.

It is concluded that:

- the Sabie-Sand River system was in equilibrium, due to the fact that it was micro-habitat, and not macro-habitat dominated;
- the measures used to determine biological diversity were adequate for the use in river ecosystems if the spatial, temporal and taxonomic boundaries are defined rigorously;
- abundance plots and the α log series were the preferred measures for inventory diversity, while Whittaker's index and cluster analyses best described the differentiation diversity, and
- biological diversity, linked with the functional biology of communities, provides a powerful management tool.

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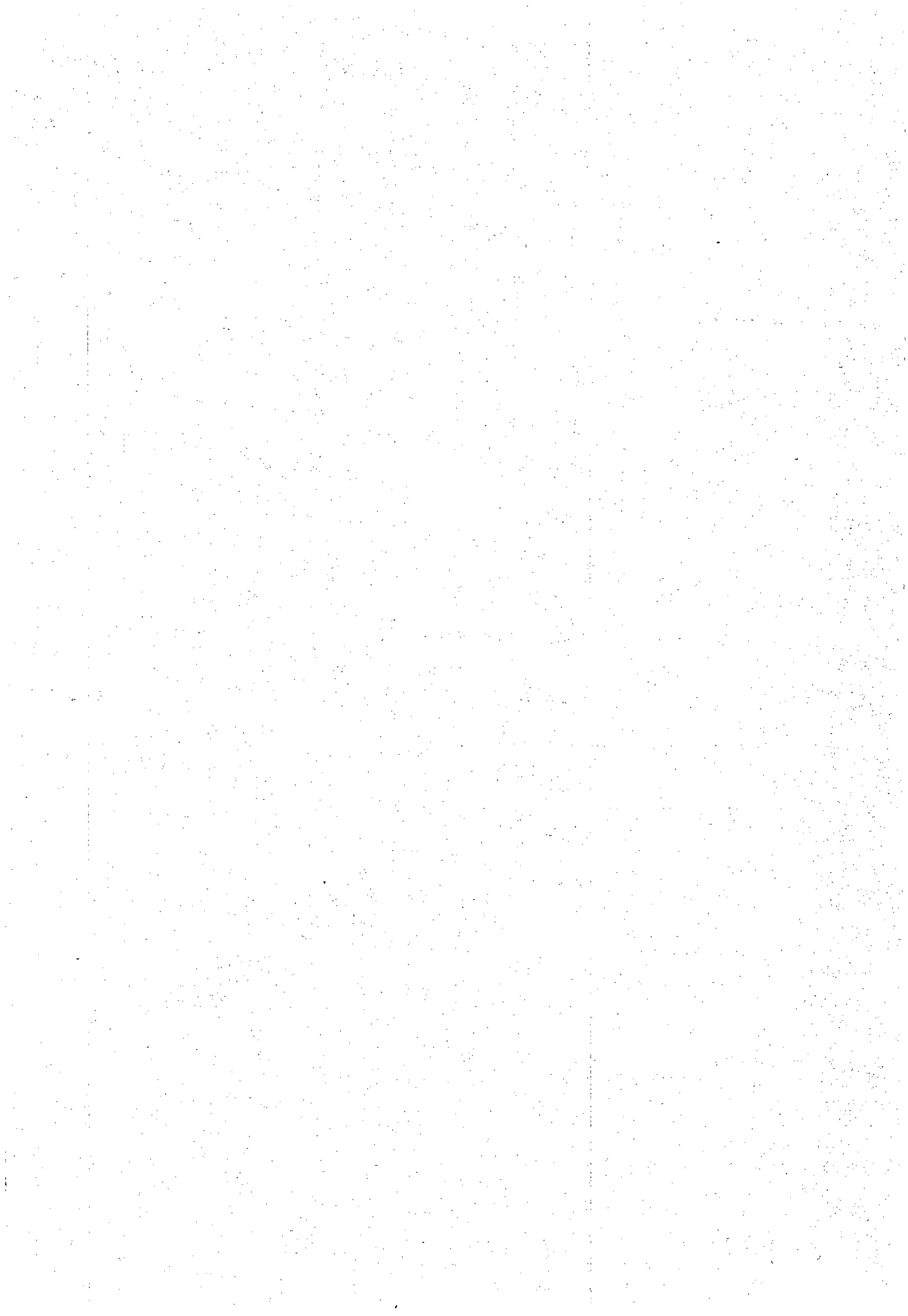
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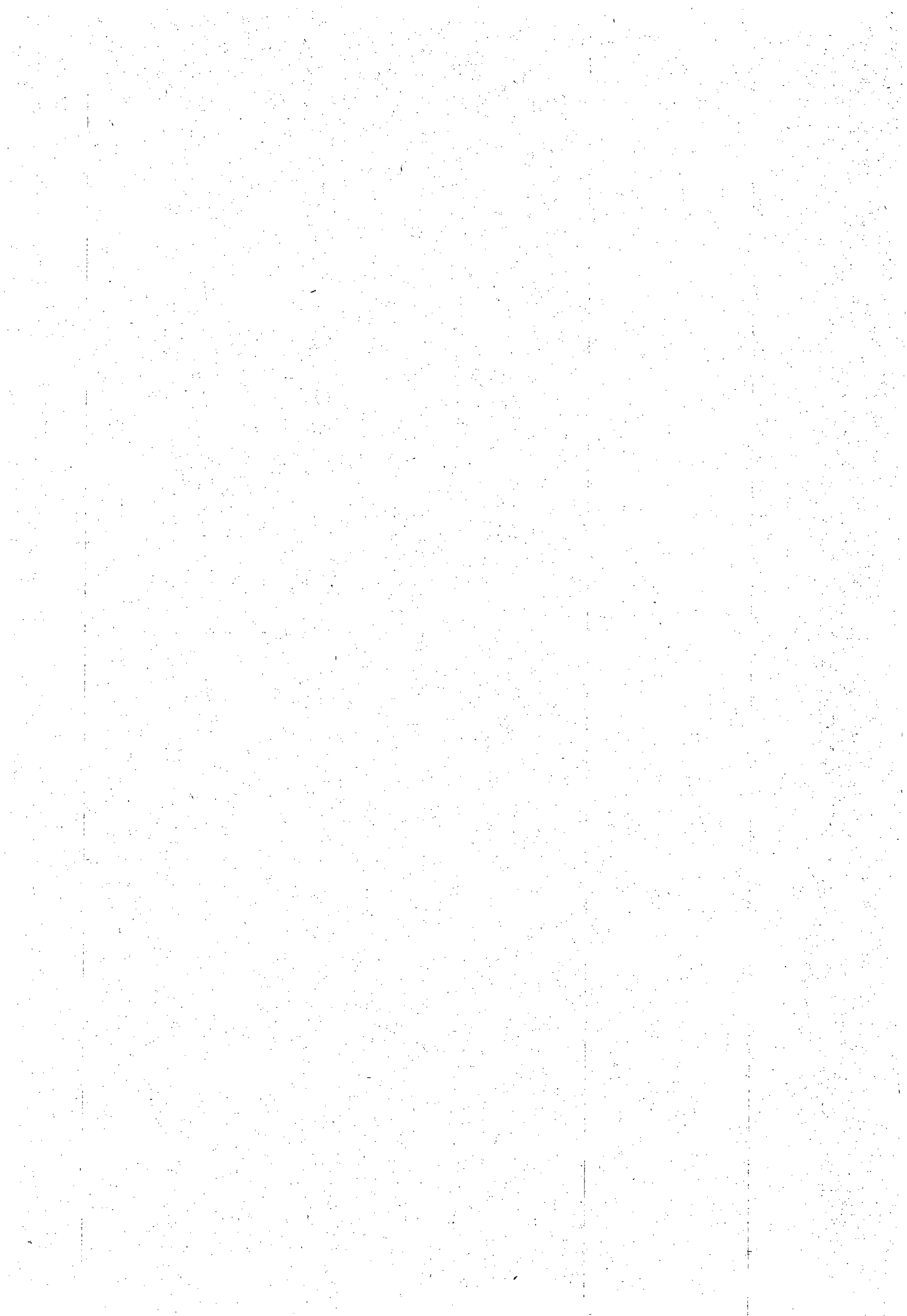
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APPENDIX A



STUDENT-NEWMAN-KEULS STATISTICAL TEST

A full explanation of the test and the relevant calculations may be found in Zar (1984).

CHAPTER 4

Student-Newman-Keuls test to determine which mean Shannon index values for Phylum, Order, Class, Family and Genus level of identification differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3	4	5
TAXON:	Phylum	Class	Order	Family	Genus
MEAN:	0.00539	0.13942	0.7273	0.9200	1.5619
SAMPLE SIZE:	14	14	14	14	14

COMPARISON	DIFF.	SE	q	p	q(0.05,65,p)	CONCL ^a
5vs1	1.56	0.32	4.875	5	3.977	reject H_0
5vs2	1.42	0.32	4.438	4	3.737	reject H_0
5vs3	0.83	0.32	2.594	3	3.399	accept H_0
5vs4	0.64	0.32	2.000	2	2.829	accept H_0
4vs1	0.91	0.32	2.844	4	3.737	accept H_0
4vs2	0.78	0.32	2.438	3	3.399	accept H_0
4vs3	0.20	0.32	0.625	2	2.829	accept H_0
3vs1	0.72	0.32	2.250	3	3.399	accept H_0
3vs2	0.59	0.32	1.844	2	2.829	accept H_0
2vs1	0.13	0.32	0.406	2	2.829	accept H_0

RESULT:

Phylum	*	.
Class	*	*
Order	*	*
Family		*
Genus		*

Asterisks which are not aligned with each other, either horizontally or vertically, identify the groups which are significantly different from each other (i.e. Family and Phylum; Genus and Phylum). Those which are aligned identify the groups which are not

significantly different from each other (i.e. Phylum, Class and Order; Genus, Family, Order and Class)

CHAPTER 6

Student-Newman-Keuls test to determine which mean family richness values for sites 3, 7, 11, 13 and 20 differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3	4	5
TAXON:	SITE 7	SITE 13	SITE 3	SITE 11	SITE 20
MEAN:	7.818	8.417	12.670	13.580	15.580
SAMPLE SIZE:	11	12	12	12	12

COMPARISON	DIFF.	SE	q	p	q(0.05,54,p)	CONCL ⁿ
5vs1	8.03	1.40	5.736	5	3.977	reject H_0
5vs2	7.16	1.37	5.226	4	3.737	reject H_0
5vs3	2.91	1.37	2.120	3	3.399	accept H_0
5vs4	2.00	1.37	1.460	2	2.829	accept H_0
4vs1	5.76	1.40	4.110	4	3.737	reject H_0
4vs2	5.16	1.37	3.766	3	3.399	reject H_0
4vs3	0.91	1.37	0.66	2	2.829	accept H_0
3vs1	4.85	1.40	3.460	3	3.399	reject H_0
3vs2	4.25	1.37	3.104	2	2.829	reject H_0
2vs1	0.60	1.40	0.428	2	2.829	accept H_0

RESULT:

Site 7 *
 Site 13 *
 Site 3 *
 Site 11 *
 Site 20 *

Student-Newman-Keuls test to determine which mean Margalef index values for sites 3, 7, 11, 13 and 20 differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3	4	5
TAXON:	SITE 13	SITE 7	SITE 3	SITE 11	SITE 20
MEAN:	1.007	1.188	1.487	1.594	1.798
SAMPLE SIZE:	12	11	12	12	12

COMP AR-ISON	DIFF.	SE	q	p	q(0.05,54,p)	CONCL ⁿ
5vs1	0.790	0.159	4.961	5	3.977	reject H_0
5vs2	0.610	0.163	3.744	4	3.737	reject H_0
5vs3	0.311	0.159	1.951	3	3.399	accept H_0
5vs4	0.203	0.159	1.275	2	2.829	accept H_0
4vs1	0.587	0.159	3.686	4	3.737	accept H_0
4vs2	0.406	0.163	2.495	3	3.399	accept H_0
4vs3	0.107	0.1590	0.674	2	2.829	accept H_0
3vs1	0.480	0.163	2.946	3	3.399	accept H_0
3vs2	0.299	0.159	1.877	2	2.829	accept H_0
2vs1	0.181	0.163	1.150	2	2.829	accept H_0

RESULT:

Site 13 *
 Site 7 *
 Site 3 * *
 Site 11 * *
 Site 20 *

Student-Newman-Keuls test to determine which mean α -log series index values for sites 3, 7, 11, 13 and 20 differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3	4	5
TAXON:	SITE 13	SITE 7	SITE 3	SITE 11	SITE 20
MEAN:	1.188	1.512	1.768	1.903	2.164
SAMPLE SIZE:	12	11	12	12	12

COMP AR-ISON	DIFF.	SE	q	p	q(0.05,54,p)	CONCL ⁿ
5vs1	0.975	0.201	4.842	5	3.977	reject H_0
5vs2	0.652	0.206	3.163	4	3.737	accept H_0
5vs3	0.396	0.201	1.964	3	3.399	accept H_0
5vs4	0.261	0.201	1.036	2	2.829	accept H_0
4vs1	0.714	0.201	3.546	4	3.737	accept H_0
4vs2	0.391	0.206	1.897	3	3.399	accept H_0
4vs3	0.135	0.201	0.669	2	2.829	accept H_0
3vs1	0.594	0.201	0.201	3	3.399	accept H_0
3vs2	0.270	0.206	1.310	2	2.829	accept H_0
2vs1	0.324	0.206	1.571	2	2.829	accept H_0

RESULT:

Site 13	*
Site 7	*
Site 3	*
Site 11	*
Site 20	*

CHAPTER 7

Student-Newman-Keuls test to determine which mean patch diversity values for sites 3, 7, 11, 13 and 20 differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3	4	5
TAXON:	SITE 13	SITE 7	SITE 3	SITE 11	SITE 20
MEAN:	8.429	9.046	9.406	16.795	20.870
SAMPLE SIZE:	11	10	11	11	11

COMP AR- ISON	DIFF.	SE	q	p	q(0.05,48,p)	CONCL ⁿ
5vs1	12.44	2.10	5.92	5	4.008	reject H_0
5vs2	11.82	2.15	5.50	4	3.764	reject H_0
5vs3	11.46	2.10	5.46	3	3.420	reject H_0
5vs4	4.07	2.10	1.94	2	2.875	accept H_0
4vs1	8.37	2.10	3.98	4	3.764	reject H_0
4vs2	7.75	2.15	3.60	3	3.420	reject H_0
4vs3	7.39	2.10	3.52	2	2.875	reject H_0
3vs1	0.98	2.10	0.47	3	3.420	accept H_0
3vs2	0.36	2.15	0.17	2	2.875	accept H_0
2vs1	0.62	2.15	0.29	2	2.875	accept H_0

RESULT:

- Site 13 *
- Site 7 *
- Site 3 *
- Site 11 *
- Site 20 *

Student-Newman-Keuls test to determine which mean patch diversity values for the Sabie, Sand and Sabie-Sand sections of the river differ from any of the others.

$H_0: \mu_1 = \mu_2$ (for each pair of samples)

$H_1: \mu_1 \neq \mu_2$

RANK:	1	2	3
TAXON:	SABIE	SAND	SABIE-SAND
MEAN:	9.225	12.612	20.870
SAMPLE SIZE:	22	22	11

COMPARISON	DIFF.	SE	q	p	q(0.05,52,p)	CONCL ⁿ
3vs1	11.64	01.90	6.12	3	3.420	reject H_0
3vs2	8.20	1.90	4.30	2	2.844	reject H_0
2vs1	3.39	1.56	2.17	2	2.844	accept H_0

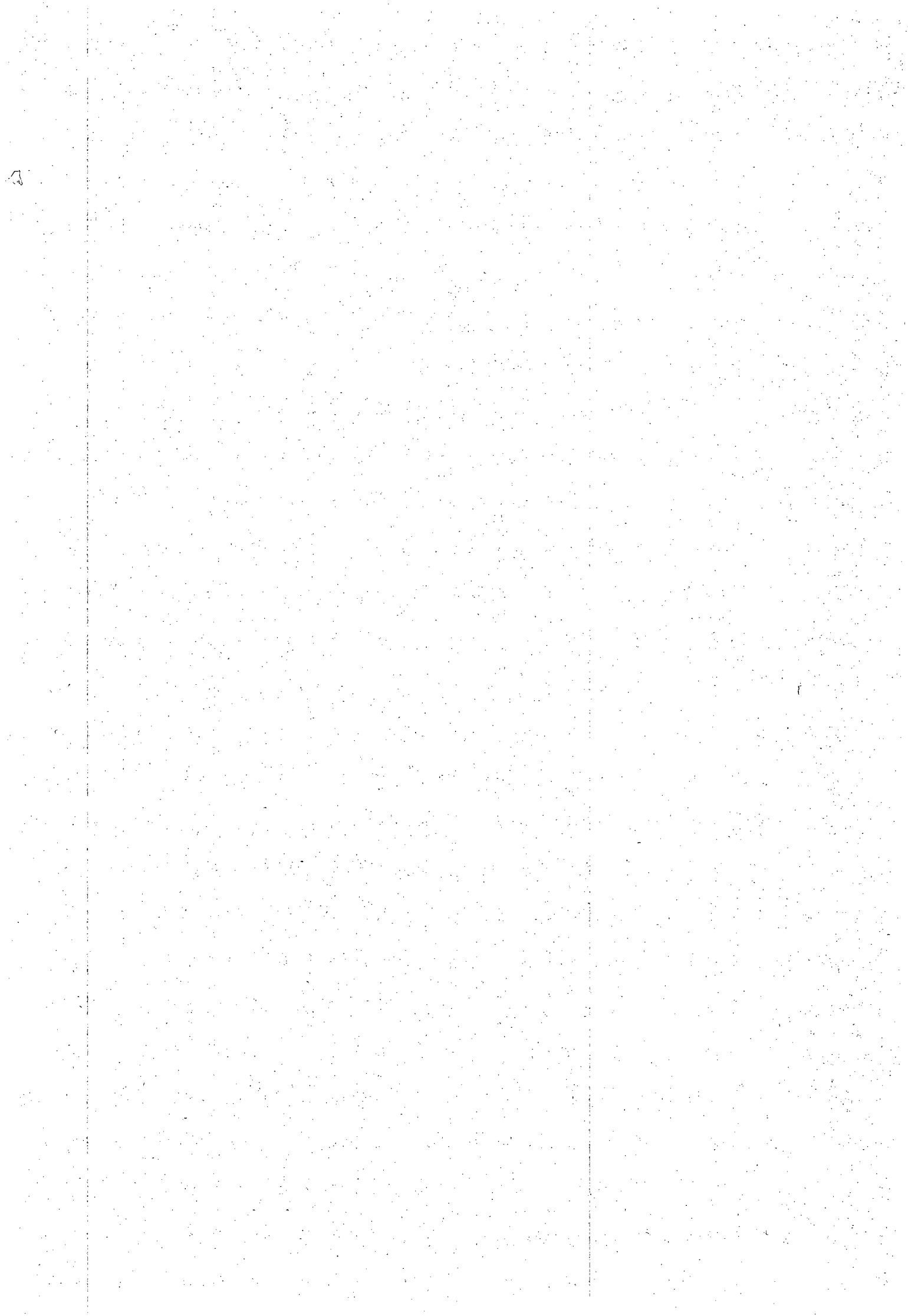
Result:

Sabie section *

Sand section *

Sabie-Sand section *

APPENDIX B



List of benthic macro-invertebrate taxa identified from the Sabie-Sand River system,
Eastern Transvaal.

COELENTERATA
CNIDARIA
HYDROZOA
Hydra sp.

MOLLUSCA
GASTROPODA
PLANORBIDAE
Gyraulis sp.
Biomphalaria sp.
Heliosoma sp.
HYDROCENIDAE
Hydrocena sp.
ANCYLIDAE
Ferrisia sp.
THIARIDAE
Melanoides sp.
PHYSIDAE
Bulinus (Pyrogophysa) sp.
Bulinus (Physopsis) sp.
LYMNAEIDAE
Succinea sp.
Lymnaea sp.
HYDROBIIDAE
Tomichia sp.

BIVALVA
SPHAERIDAE
Sphaerium sp.
Pisidium sp.
UNIONIDAE
Caelatura sp.
CORBICULIDAE
Corbicula sp.

PLATYHELMINTHES
TURBELLARIA
Dugesia sp.

ANNELIDA
HIRUDINEA
GLOSSIPHONIIDAE
OLIGOCHAETA
NAIDIDAE
TUBIFICIDAE
LUMBRICULIDAE
NEMATODA

NEMERTEA

ARTHROPODA

CRUSTACEA

MACRURA

Caridina sp.

BRACHYURA

Potamonautes sp.

OSTRACODA

COPEPODA

CONCHOSTRACA

CLADOCERA

DIPTERA

PSYCHODIDAE

CHIRONOMIDAE

TANYTARSINI

CHIRONOMINAE

ORTHOCLADINAE

TIPULIDAE

Pupa - sp.A.

Pupa - sp.B.

SIMULIIDAE

Prosimulium (Paracnephia) sp.

Simulium (Pomeroyellum) spp.

Simulium (Metomphallus) spp.

Simulium (Edwardsellum) sp.

Simulium (Anasolen) spp.

Simulium (Nevermannia) spp.

CERATOPOGONIDAE

Bezzia sp.

CULICIDAE

sp.A.

DIXIDAE

ATHERICIDAE

DOLICHOPODIDAE

HELEIDAE

EMPIDIDAE

RHAGIONIDAE

TABANIDAE

ANTHOMYIIDAE

sp. A. "worm with a bulb"

COLLEMBOLLA

SMYNTHURIDAE

Smynthurnis sp.

ISOTOMATIDAE

TRICHOPTERA

ECNOMIDAE

Ecnomus spp.

HYDROPSYCHIDAE

Hydropsyche sp.

Cheumatopsyche spp.

Leptonema sp.

Macrostemum sp.

juveniles

PHILOPOTAMIDAE

Dolophilodes(*Thylakion*) sp.

Chimarra sp.

HYDROPTILIDAE

Hydroptyla sp.

Orthotrichia sp.

Oxyethira sp.

juveniles

POLYCENTROPODIDAE

Nyctiophylax sp.

PSYCHOMYIIDAE

Tinodes sp.

LEPTOCERIDAE

Oecetis sp.

Athripsodes sp.

Leptocerus sp.

Trichosetodes sp.

Setodes sp.

Triaenodes sp.

Pseudoleptocerus sp.

juveniles

DIPSEUDOPSISIDAE

Dipseudopsis sp.

GLOSSOSOMATIDAE

sp.A.

HEMIPTERA

NAUCORIDIDAE

SALDIDAE

NEPIDAE

COROXIDAE

NOTONECTIDAE

VELIIDAE

PLEIDAE

CICADELLIDAE

HEBRIDAE

GERRIDAE

LEPIDOPTERA

PYRALIDAE

PSOCOPTERA

EPHEMEROPTERA

TRICHORYTHIDAE

Neurocaenis sp.

Machadorythus sp.

Ephemerythus sp.

LEPTOPHLEBIIDAE

Adenophlebia sp.

Choroterpes complex

Thraulius sp.

Aprionyx sp.

BAETIDAE

Demoulina complex

Afroptilum sp.

Rithrocloeon sp.

Acentrella sp.

Cloeon complex

Centroptiloides sp.

Baetis spp.

Pseudopannota sp.

Centroptilum sp.

Afrobaetodes sp.

Acanthiops sp.

Afroptilum complex

sp. A. (juv.)

juveniles

POLYMITARCYIDAE

Exeuthyplocia sp.

OLIGONEURIDAE

Elassoneuria sp.

CAENIDAE

Austrocaenis sp.

Caenis sp.

Caenodes sp.

Caenospella sp.

PROSOPISTOMATIDAE

Prosopistoma sp.

HEPTAGENIIDAE

Afronurus sp.

Composoneuriella sp.

PLECOPTERA

COLEOPTERA

DYTISCIDAE

Hydaticus sp.

Yola sp.

HYDROPORINAE sp.

HYDRAENIDAE

PSEPHENIDAE

GEORYSSIDAE

Georyssus sp.

ELMIDAE

larva A

larva B

larva C

Narpus sp.

Peloriolus sp.

Pachyelmis sp.

Leptelmis sp.

Helminthocharis sp.

Potamogethes sp.

Microdinodes sp.

Leielmis sp.

Stenelmis sp.

HELODIDAE

GYRINIDAE

NOTERIDAE

HYDROPHYLIDAE

ODONATA
LIBELLULIDAE

Trithemis sp.
Zygonyx sp.

Acisoma sp.
Tholymis sp.

GOMPHIDAE

Ictinogomphus sp.
Lestinogomphus sp.
Onychogomphus sp.
Phyllogomphus sp.
Crenigomphus sp.
Notogomphus sp.
Paragomphus sp.
Microgomphus sp.

AESHNIDAE

Aeshna sp.
Hemianax sp.
Anax sp.

CORDULIIDAE

Syncordulia sp.
Hemicordulia sp.
Macromia sp.

PROTONEURIDAE

CALOPTERIGIDAE

Phaon sp.

PLATYCNEMIDIDAE

COENAGRIONIDAE

CHLOROCYPHIDAE

Platycypha sp.

ARACHNIDA

HYDRACARINA

UNKNOWN spp.

