The distribution of invertebrate communities in a small South African river

J. M. King

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, South Africa

Keywords: river, aquatic macroinvertebrates, lotic environment, seasonal changes, longitudinal zonation, cluster analysis, multiple discriminant analysis.

Abstract

Monthly samples of macroinvertebrates were collected from the stony-bed and marginalvegetation habitats of a small river in the south western Cape Province, South Africa. Cluster analyses of the samples revealed assemblages of invertebrates (here referred to as 'communities') with clear spatial and temporal distribution patterns in the muer. The species composition of the communities, and their distribution, are described. The relation of the macroinvertebrate distribution to changes in the physico-chemical environment was investigated using stepwise multiple discriminant analysis. The results indicated a strong correlation between the two.

Introduction

Past investigations into the hydrobiology of South African rivers have centred on a few of the longer or more prominent river systems, in particular the Berg (Harrison 1958a, 1958b; Harrison & Elsworth 1958), the Jukskei-Crocodile (Allanson 1961), the Tugela (Oliff 1960a, 1960b, 1963; Oliff & King 1964; Oliff et al. 1965) and the Vaal (Chutter 1963, 1970, 1971; Harrison et al. 1963). These early surveys produced a reasonable understanding of the factors influencing the distribution and abundance of riverine fauna, but subsequent hydrobiological work on the country's rivers has been sparse.

The southern and eastern coasts of South Africa have an abundance of short rivers, none of which have been studied in detail. They rise in coastal hills and drop steeply to narrow coastal plains, and thence to the sea. Most of them have the same longitudinal sequence of physical zones as neighbouring, longer rivers (Noble & Hemens 1978), and are subject to some combination of the same interferences and pollutants (e.g. water extraction, fluvial sediment, organic effluents and agricultural runoff). Their simple profiles and short zones make them particularly suitable systems for studying changes in the biota along a river, and for tracing the factors that cause these changes.

The Eerste River is a short (40 km) river in the south western Cape Province (Fig. 1). The present limnological investigations of its stony-bed section - the upper 26 km - began in March 1975. In this paper, the spatial and temporal changes in species composition of macroinvertebrates of the two major habitats - the stony-bed and marginal vegetation - are described. Distribution of the animals in the river is shown to be related to differences in the physical and chemical character of the river.

The study area

South Africa is subject to seasonal rains, which fall in summer (December to February) over all but the southern and south-western tip of the country. This latter, boomerang-shaped strip of land has a mediterranean climate with a typical

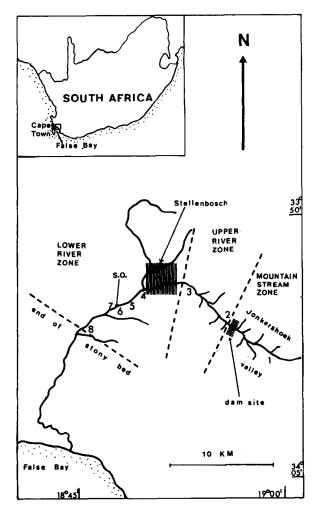


Fig. 1. The Eerste River, showing the eight sampling stations (1-8), the dam, and the sewage outfall (S.O.). The three physical/biotic zones identified in the survey are shown.

winter (June to August) rainfall pattern. Further climatic information is given in Schulze (1965).

The Eerste River lies in the winter rainfall area. It rises in the Dwarsberg Mountains, 60 km east of Cape Town (Fig. 1). Yearly rainfall over its catchment ranges from 3 000 mm on the mountains to 700 mm or less on the coastal plain (Van der Zel 1971), with about 80% of the rain falling in a series of winter downpours, which bring the river down in spate. Only 7% of the annual precipitation occurs between December and March, and as water is continually extracted from the river for urban and rural use, flow may cease in its lower reaches during these months. The upper 26 km of the river, which was the study area, consists of runs, riffles and occasional deep pools, with water less than 1 m deep except during spates. Within the study area there are three distinct physical zones (Fig. 1).

The Mountain Stream is a 7 km stretch from the source to the lower end of the Jonkershoek valley. The stream is 5-7 m wide, with an average gradient of 24 m.km⁻¹. The substrate consists of boulders, large stones and bedrock. Algal growth is sparse and marginal vegetation is confined to occasional clumps of palmiet Prionium serratum. The surrounding mountain slopes form part of a Forestry Reserve; they support fynbos, the indigenous, sclerophyllous flora of the southern and south western Cape, and plantations of Pinus radiata. Several species of tough-leaved, evergreen trees (e.g. Metrosideros angustifolia, Brabejum stellatifolium), most of which are confined to the fynbos biome, line the river. A dam is presently under construction at the lower end of the valley.

The Upper River is a 5 km stretch through foothills covered with vineyards. The average gradient is 12 m/km and the width 7-11 m. Substrate and marginal vegetation are similar to those in the Mountain Stream, and algal growth is sparse except for some Spirogyra in summer. The exotic oak Quercus robur replaces indigenous trees along the banks.

The Lower River is a 14 km stretch onto the coastal plain, through agricultural land and orchards. The substrate consists of stones and pebbles on coarse sand. The river's width increases to 8-18 mand the average gradient drops to 2 m.km⁻¹. Mixed evergreen and deciduous trees line the banks, with Q. robur and another deciduous exotic, *Populus canescens* numerically dominant. Marginal vegetation is abundant and sewage fungus (see Hynes, 1960) covers the rocky substrate in the dry season. Stellenbosch, the only town on the river, is at the junction of the Upper and Lower Rivers. The town has no heavy industry, but winery and sewage effluents enter the Lower River, mostly via a sewage farm situated 3 km below the town.

Methods

Stations

Samples were collected at monthly intervals between March 1975 and April 1976, from eight

stations (1–8) along the river (Fig. 1); Table 1 gives details of the locations. Station 5 was abandoned in October 1975, because of its similarity to stations 4 and 6, while station 8 was created in September 1975, though some samples were collected there earlier.

Physical and chemical variables

Measurements of dissolved oxygen (YSI Oxygen Meter), pH (Beckman Portable pH Meter), water temperature and current speed (Rigosha Small Flow Meter) were taken in the field. Water from the mountain stream was not analysed, but Steer (1966) reported that it was of high quality and free of pollution. Monthly water samples from stations 3, 4, 6, 7 and 8 were tested for nitrite and nitrate using a Technicon autoanalyser; total phosphate-phosphorus, by the Colorimetric Molybdate-Vanadate Technique (Martin & Marais 1975); and total alkalinity using the standard method described by the Am. Pub. Health Ass. (1971). The physical and chemical data were arranged into a number of 'water samples', each corresponding to a faunal sample in time and place of collection, and containing one value for each of the variables.

Sampling the fauna

Stony-bed animals were collected using a squareframed sampler, that sampled 0.25 m^2 of river bed. The upstream and two adjacent sides were covered

with sheeting through which water could flow, while the downstream side held a net with mesh size 0.6 mm. When the sampler was placed on the river bed, a fringe of heavy-duty rubber at its base wrapped around the stones on the edge of the quadrat. The animals in the quadrat were collected, to a depth of 10 cm, and immediately placed in 5% formalin. Two samples were taken at each station, and the animals identified to species where possible, and counted. Data from the two samples were then combined. Animals were collected from an estimated 1 m³ of marginal vegetation, by sweeping a hand-net through the plants. The net had a mesh size of 0.6 mm. Two samples were taken at each station, and treated in the same way as the stonybed samples.

Analysis of data

For each habitat, the relation between faunal samples was investigated using the Bray-Curtis similarity measure (Bray & Curtis 1957). In the analyses, all counts of animal abundance were logtransformed first. The resulting similarity matrices were summarised in two ways: by classification using group-average sorting (Lance & Williams 1967), with the results presented as a dendrogram in which similar samples clustered together; and by ordination using multidimensional scaling (Kruskal 1964), with the samples shown as points on a graph. Using the latter technique, similar samples are clustered together while dissimilar samples are

Table 1. Details of the eight sampling stations on the Eerste River	Table 1.	. Details of	the eight	sampling	stations of	on the	Eerste Rive	r.
---	----------	--------------	-----------	----------	-------------	--------	-------------	----

Zone	Station number	Distance from source (km)	Altitude (m)	Other information
Mountain stream	1	2	382.3	Upstream from all human interference
Upper river	2	7	214.1	2 km below dam site
	3	12	152.9	
Lower River	4	20	76.5	Immediately below Stellen- bosch
	5	22	68.8	
	6 & 7	23	64.2	Above and below sewage farm outfall respectively
	8	26	45.9	Downstream, the substrate changes to coarse sand

further apart. Each method distorts the relationship between samples to some extent, but the two together give a good indication of how robust the clusters are.

Distinct clusters of samples indicate the presence of relatively homogeneous assemblages of macroinvertebrates. While acknowledging that species changes in the biota along a river are usually transitional rather than abrupt, here, for clarity, the faunal assemblages have been treated as representative of separable animal communities in the river. With the communities identified and located, information statistic tests (Field 1969; Velimirov *et al.* 1977) were used to compare those that were spatial or temporal neighbours. Using the tests, species occurring statistically more frequently than expected in one of the two communities are revealed, and the species characteristic of each community thus established.

The correlation between the physical and chemical character of the water and the distribution of animal communities was investigated, using stepwise multiple discriminant analysis (Program BMD P7M, Dixon 1974). Before the analysis, the data for each environmental variable were standardised, using the formula (reading – mean)/(standard deviation); all values were thus expressed in standard deviation units. The water samples were then placed in groups according to the groups formed by cluster analysis of the faunal samples.

The analysis involves computing canonical discriminant functions between groups of water samples and plotting the first two functions to give an optimal two-dimensional picture of the separation of the groups. The resulting scatter diagram contains a multivariate centroid for each group, with the individual water samples indicated as surrounding points. The analysis also reveals the environmental variables which differ significantly (P < 0.05) among groups and produces a classification matrix, in which each water sample is placed in the group to which its probability of belonging is highest. The percentage of water samples in the matrix groups agreeing with the initial grouping of samples (based on the faunal relationships), indicates the degree of correlation between a named animal community and a stated set of environmental conditions.

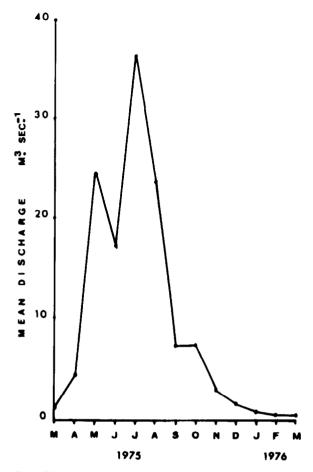


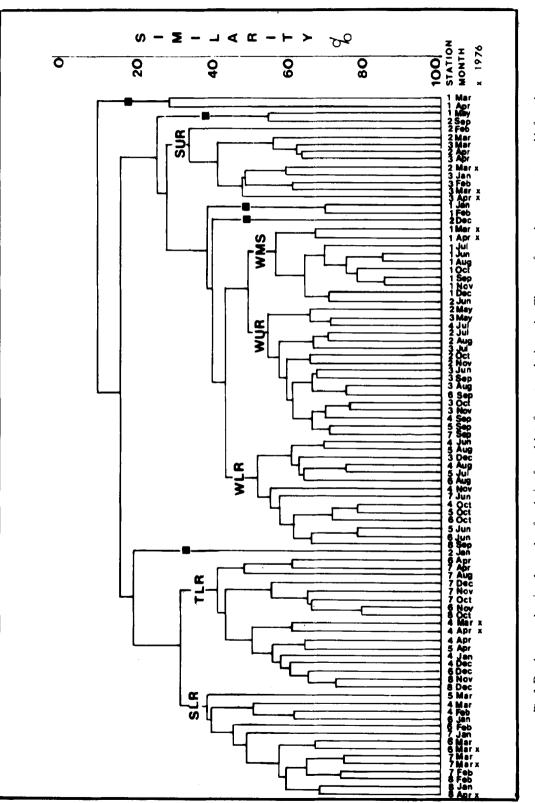
Fig. 2. Discharge of the Eerste River for the period of the survey. Data recorded by the South African Department of Forestry, at a weir below the dam site.

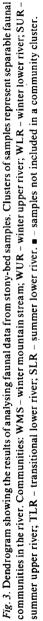
Results

Physical and chemical conditions

Discharge of the Mountain Stream (Fig. 2) was least between December and March (summer to early autumn) and greatest between May and August (late autumn to winter). Major spates occurred in May and July. The low summer discharge coincided with the maximum extraction of irrigation water for the surrounding vineyards and agricultural land.

Summer and winter changes of nine factors of water quality along the river are detailed in Appendix I. Dissolved oxygen levels were high throughout the study area in winter, though generally decreasing downstream (average of all stations:





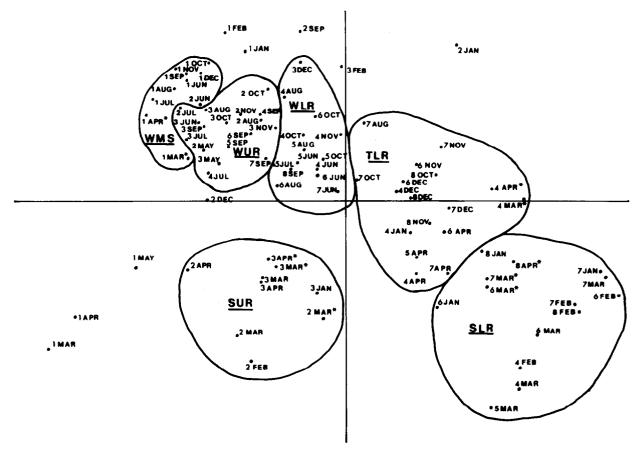


Fig. 4. Two-dimensional ordination showing results of analysing faunal data from stony-bed samples. Scales are arbitrary and arranged to minimise the distortion involved in reducing multidimensional data to two dimensions. Samples are identified as in Fig. 3, and grouped in the same way, except for 3 February which is now separated from SUR. Samples from March and April 1976 are starred; those from March and April 1975 unstarred.

9.7 mg ℓ^{-1} ; the increase between stations 6 and 7 was due to turbulent flow through the sewage outlet. In summer, values decreased considerably downstream, particularly at Stellenbosch (station 4: 6.2 mg ℓ^{-1}) and at the sewage outfall (station 7: 4.2 mg ℓ^{-1}). The high summer levels at station 6 (8.0 mg ℓ^{-1}) were due to photosynthesising algae in stagnant pools.

Similar water temperatures were recorded throughout the study area in winter, with 10 °C and 14 °C the respective minimum and maximum daytime values. Temperatures along the river covered a greater range in summer: 18-21 °C were recorded at stations 1 and 2, and 23-28 °C at stations 3 to 8. pH levels were similar both seasons, and were usually just below neutrality in the Mountain Stream (6.3-6.8) and just above it in the two lower zones (7.0-7.6). In winter, current speeds were measured at least four days after a spate, and were similar at any one time throughout the study area (range $83-286 \text{ cm sec}^{-1}$). Summer speeds were much lower in all three zones (Mountain Stream and Upper River 15-54 cm sec⁻¹, Lower River 0-38 cm sec⁻¹).

Nitrite, nitrate and phosphate values increased from station 3 downstream, with station 7, below the sewage outfall, generally showing the highest levels. In the Lower River, winter levels of these three factors were sometimes higher than the summer ones, despite the greater volume of water; this was at least partially due to agricultural runoff and to incompletely treated sewage being pushed into the river by flood waters. The buffering capacity of the water (total alkalinity) increased downstream and was generally higher in summer than in winter. In both seasons, the highest values were recorded at station 7 (average 124.2 mg l^{-1}). Steer (1964) reported a summer value of 12.5 mg l^{-1} for the Mountain Stream. He concluded (1966) that though the Mountain Stream was free of pollution and the Upper River 'reasonably clean', water quality of the Lower River deteriorated significantly during summer and autumn due to organic pollution and the poor flow. The deterioration continued until the advent of the winter rains. Though showing improvement in winter and spring, conditions deteriorated again each summer, in an annual repeating pattern.

The fauna of the stony bed

The dendrogram resulting from the analysis of stony-bed, faunal data shows that 91% of the samples fell into six main clusters (Fig. 3). In corroboration, the samples separated into the same six clusters, as a result of ordination (Fig. 4), with only one sample (station 3, February) failing to group in the same way as in Fig. 3. Multidimensional scaling revealed, however, that the groups were not as discrete as implied by the dendogram. The groups are considered to be representative of six separable animal communities in the river. These have been named the WMS (winter mountain stream), WUR (winter upper river), WLR (winter lower river), SUR (summer upper river), TLR (transitional lower river) and SLR (summer lower river) communities. In Fig. 4 the X-axis seems to separate the communities along the length of the river, while the Y-axis separates them seasonally.

A diagrammatic representation of the study area (Fig. 5) indicates the location of the six communities. Their distribution along the river divided it into three longitudinal, biotic zones. These coincided with the physical zones described above: the faunal community WMS was confined to the Mountain Stream zone, apart from a brief appearance in the Upper River (station 2) in June; WUR and SUR occurred only in the Upper River, apart from the appearance of WUR in the Lower River (station 4) in July, and again (stations 4–7) in September; WLR, TLR and SLR were characteristic of the Lower River.

The fauna of each zone exhibited different seasonal changes (Fig. 5). WMS was present in the Mountain Stream through most of the year, but was called a winter community because most of its fauna began new life cycles at the beginning of winter. In its absence (March, April, May 1975,

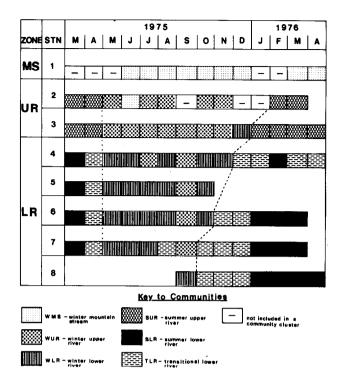


Fig. 5. The location of the six stony-bed communities in the river. The communities are those recognised in Figure 3. The vertical dotted and dashed lines show the appearance of winter and summer communities respectively, at stations 2–8. Zones: MS – mountain stream; UR – upper river; LR – lower river.

January, February 1976) samples from this stretch of river contained very few animals. WUR and SUR occurred in the Upper River in winter and summer respectively, with WUR present for about eight months of the year and SUR for four months. WLR and SLR appeared in the Lower River in winter and summer respectively, with WLR present for approximately six months and SLR for 3-4 months. A transitional community, TLR, occurred between WLR and SLR in both spring and autumn; it remained at station 4 for all but one month (February) of the dry season, but was confined to times of moderate flow (April, October, November, December 1975 - see Fig. 2) at lower stations. TLR has been treated as a summer community because it was more similar to SLR than to the other communities (Fig. 3), and because it occurred at station 4 through most of the summer.

The winter communities appeared almost simultaneously throughout the river as the winter rains began (May), while the switch back to the summer

chrond of the second of the se	I ests										i		
	Test number	-		5		e S		4		s		6	
	Communities compared Number of samples	WMS 10	WUR 17	WUR 17	WLR 14	WUR 17	SUR 10	WLR 14	ŢLR 17	TLR 17	SLR 14	SUR 10	SLR 6
<i>Cnidaria</i> Hydra								0	6xx				
Turbellaria				e	10xx	e	8xx			15xx	9		
<i>Hirudinea</i> Glossiphonia disjuncta				-	8xx								
Mollusca Physa sp. Duranic commissio				-	Ŷ			v	17.0	-	7xx		4x 5
but tupia tapensis Lymnaca columella Bulinus tropicus				-	YO			þ	VV /1	7	7 x		2x 2x 2x
Decapoda Potamon perlatus						7	7хх						
Ostracoda (1 sp.)								0	6xx	9	13xx	0	5xx
Ephemeroptera		Ś											
Aprionyx rubicundus Adenophlebia peringueyella Commentativic contine		10xx 0	2 6x			~~L1	ŗ	7xx 14	- 4	,, y	<	7xx	0
Castanopricona canua Choroterpes elegans				éx x	0	6x 1	101	VV+1	r	YYC	2	r	c
bactis bellus Raetis harrisoni				>	4XX	5	XX/			17××	Ŷ	/ XX 10xx	
Acentrella capensis								11xx	7			7xx	0
Centroptilum sudafricanum						ć	ı	9xx	- •			6xx	0
Centroptilum excisum						• •	x x c	0	4X			5۷	C
Cloeon lacunosum						•	~~~			1	10xx	× 0	5xx
Clocon sp						0	2x						
Afronurus harrisoni Austroraenis en						s	9x 8x x	Χç	0	×	17×	УХХ	0
Ephemerellina barnardi		8x	7	7xx	0	7xx	0			b			
Ephemerellina harrisoni						16xx	0	l4xx	5	5xx	0		

50

Table 2. Results of information statistic tests of stony-bed samples, showing the species which differed significantly in frequency of occurrence between neighbouring communities.

N N S	2x 0 2x 0 5x 2	12xx	0	12xx 0 0	0 2x 3x	0	3x				
ę	6xx 1							3x	0		
		l6x	×	Ібхх	5	8xx	_			5x	0
				7	5 x						
								0	4xx	0	3хх
								- e	8xx 9xx	00	4xx 4xx
								0	3х		
10	0xx 4							0 0	3x 11xx	0	4xx
00 4 4 (1 (1)	8xx 1 4xx 0 4xx 0 2x 0 3x 0			0	2x						
22	10x 13 10xx 9	13x	Ŷ	9xx 5x	0 0	2 5x 3x	9x 1 0	9 3x	12x 0	0 5 x	4xx 0
Ŭ	0 7xx			7xx	0	5x	1				

communities occurred first at the lower stations and progressively later upstream (station 8 - October; station 6 - November; station 4 - December; station 3 - January; station 2 - February) (Fig. 5).

The six communities and the significant faunal differences between them (Table 2), are described below. More detailed information on the contribution of each species to the total macroinvertebrate numbers and standing crop will be given in a future publication.

a) WMS - the winter mountain stream community. WMS was dominated by insects (99.2% of the total invertebrate numbers). The Ephemeroptera, accounting for 37.9% of the numbers, consisted mainly of Leptophlebiidae and Ephemerellidae, with Castanophlebia calida and Lestagella penicillata the most abundant species. Blepharoceridae were numerous in the winter and spring (35.2%), while Trichoptera and Plecoptera were always poor in numbers (2.0% and 5.2% respectively) and in species. The Chironomidae, Rhagionidae and Simuliidae were continually present but not numerous (14.0% combined). Coleoptera of several typical mountain stream families - the Dryopidae, Elmidae, Hydraenidae and Helodidae - were present in small numbers (4.0%). Turbellaria, Oligochaeta and Decapoda were the only non-insect groups (0.8%).

b) WUR – the winter upper river community. Insects comprised 98.8% of the total invertebrate numbers. The Ephemeroptera were again well represented (74.8%), with *Baetis harrisoni, Castanophlebia calida, Lestagella penicillata* and *Ephemerellina harrisoni* the most abundant species. The proportional increase of Ephemeroptera from WMS to WUR was mainly due to the scarcity of Blepharoceridae in WUR. The Diptera as a whole accounted for only 19.1% of the numbers despite an increase in the Chironomidae. WUR had a lower proportion of Trichoptera (1.2%), Plecoptera (2.4%) and Coleoptera (0.7%), and a higher proportion of Oligochaeta (0.9%) than did WMS.

Significant faunal changes as WMS changed to WUR (Table 2, test 1) were the loss, or decreased frequency of several Ephemeroptera, including *Aprionyx rubicundus* and *Ephemerellina barnardi*, Trichoptera, including *Barbarochthon brunneum* and *Cheumatopsyche* spp., the megalopteran *Pla*- *tychauloides* sp., the mountain-stream Coleoptera and the Blepharoceridae. Those species that were absent from WUR may be considered 'indicators' for WMS.

c) WLR - the winter lower river community. Insects comprised 76.1% of the total numbers, with the Ephemeroptera again the dominant group (53.9%). Baetis harrisoni and Castanophlebia calida were common species. Trichoptera, Plecoptera and Odonata were present but scarce, and individuals of other groups (e.g. the Hemiptera and Megaloptera) occurred occasionally. Dipteran numbers (19.6%) were mainly due to the Chironomidae; they included, at station 7, a few individuals of Chironomus spp. the local species group indicative of polluted or disturbed waters. Oligochaeta were the most abundant of the non-insects (20.3%), while the Hirudinea, Mollusca and Turbellaria were present but scarce.

Significant faunal changes as WUR changed to WLR (Table 2, test 2) were a further decrease in the Ephemeroptera, especially *Choroterpes elegans, Ephemerellina barnardi* and *Lestagella penicillata,* and in the Trichoptera, Plecoptera and Rhagionidae. Turbellaria, the hirudinean *Glossiphonia disjuncta,* the mollusc *Burnupia capensis* and *Baetis bellus* increased in frequency.

d) SUR – the summer upper river community. The proportion of insects (85.7%) was lower than in the corresponding winter community (WUR), with the Oligochaeta (10.7%) accounting for most of the increase in non-insect numbers. The Ephemeroptera were again numerous (59.3%), with B. harrisoni still abundant, but the other winter species rare. Characteristic summer species were Afronurus harrisoni (Heptageniidae), Adenophlebia peringuevella (Leptophlebiidae) and Baetis bellus. The latter normally occurs in marginal vegetation, but was forced down onto the river-bed by the falling water level. The Diptera (14.2%) consisted mainly of Chironomidae. Other groups were poorly represented: Trichoptera 7.0%, Plecoptera 0.7%, Coleoptera 2.2%.

Most of the significant faunal differences between SUR and WUR centred around the Ephemeroptera (Table 2, test 3), with the characteristic species of one community rare in, or absent from, the other. The winter community had a higher frequency of Leptophlebiidae and Ephemerellidae, while the summer one contained mainly Baetidae, Heptageniidae and Caenidae. Other differences included a higher frequency of Turbellaria, and *Potamon perlatus*, and a lower frequency of *Athripsodes* (bergensis group) and *Aphanicerca* spp., in SUR.

e) TLR – the transitional lower river community. Insects comprised a larger part of the fauna (85.7%)than in the corresponding winter community (WLR), mainly because of a drop in the proportion of Oligochaeta (8.7%). The insects consisted almost entirely of Ephemeroptera (40.7%) and Diptera (44.9%), with the Trichoptera, Plecoptera, Megaloptera and Coleoptera virtually or completely absent. B. harrisoni accounted for about threequarters of the ephemeropteran numbers, the remainder being remnants of the summer species (in autumn) and winter species (in spring). The high dipteran numbers were entirely due to Chironomidae and Simuliidae; these occurred in roughly equal numbers, and usually the numbers of one group were high when those of the other were low. Chironomus spp. was more frequent than in WLR. Non-insects, other than Oligochaeta, were present in similar proportions to WLR, with the additional presence of Ostracoda (1.1%) and Hydra. Though Hydra were usually scarce, a short-lived 'bloom' in November briefly raised their numbers to 5 600 m⁻² and 74 000 m⁻² at stations 6 and 7 respectively. Because of the brief life of these 'blooms' and the enormous numbers involved, Hydra has not been included in the above calculations of percentage composition.

TLR was the transitional community between the summer and winter ones in the Lower River, its fauna representing a halfway stage between the seasonal extremes. Significant faunal changes as WLR changed to TLR (Table 2, test 4) included a decrease in the winter ephemeropterans Castanophlebia calida and Ephemerellina harrisoni and of those species more typical of the upper river (Acentrella capensis, Centroptilum sudafricanum, Afronurus harrisoni and Adenophlebia peringueyella), and the appearance of the still-water species Centroptilum excisum. Other changes included an increased frequency of the mollusc Burnupia capensis, the algal-cased trichopteran Hydroptila capensis and Chironomus spp. plus the appearance of Hydra and the ostracods.

f) SLR – the summer lower river community. Insect numbers were at their lowest in SLR (55.7%) due to the virtual absence of the Ephemeroptera (3.7%). Those species present, Cloeon lacunosum, Centroptilum excisum and Austrocaenis sp. were rare and generally occurred only upstream of the sewage outfall. The Diptera (49.2%) consisted mainly of Chironomidae, with Chironomus spp. the most common species. Simuliidae were present but rare. The corixids Sigara contortuplicata and Micronecta scutellaris, and several different dytiscid larvae, comprised the remainder of the insect fauna (2.7%). Among the non-insects, the Ostracoda (26.5%), Mollusca (7.6%) and Hirudinea (2.6%)were more common than in TLR, while the proportion of Oligochaeta remained about the same. Though Hydra were rare, a second 'bloom' in January, at station 7 only, briefly raised their numbers to 44 700 m^{-2} .

As TLR changed to SLR (Table 2, test 5) there was a further loss of winter Ephemeroptera (C. calida, B. harrisoni, E. harrisoni) and a build-up of still-water species (Cloeon lacunosum, Austrocaenis sp.). The Corixidae, Gerridae and Notonectidae increased in frequency, as did the Mołłusca, Ostracoda, hydrophilid and dytiscid Coleoptera and Chironomus spp.

The summer communities of the Upper (SUR) and Lower (SLR) Rivers were quite different (Table 2, test 6), with the characteristic species of one community usually completely absent from the other. While SUR was typified by a variety of Ephemeroptera, SLR contained mostly Ostracoda, Mollusca, Hemiptera, Dytiscidae and *Chironomus* spp.

Seven of the eight stony-bed samples excluded from community clusters (Figs. 3 & 4) were collected as one community was replacing another (Fig. 5). Their exclusion from the clusters was probably due to their low faunal numbers, and the consequent lack of information with which to classify them. The eighth sample (Sept. – station 2) was collected shortly after a heavy input of sediment into the river occurred between stations 1 and 2. Sediment blanketed the river bed at station 2 in September, and animals were scarce. In the same month, the faunal community WUR appeared at all stations downstream, except station 8 (Fig. 5). In the following months, faunal numbers remained low at station 2 (hence the poorly recorded changeover from WUR to SUR), while the normal communities reappeared in the Lower River. WUR overshadowed WLR in the Lower River in September because the communities were similar and distinguished largely by a reduction of species as WUR changed to WLR. As the WUR fauna drifted downstream that month they made good the deficiency, briefly turning WLR to WUR.

The fauna of the marginal vegetation

Results of the cluster analyses of marginalvegetation samples, using classification and ordination, are shown in Figures 6 and 7 respectively. The three broad clusters of samples in Fig. 6 are enclosed by boundary lines in Fig. 7.

Attempts to split the groups further were unsuccessful, as small clusters within the main ones in Fig. 6 were not necessarily mirrored by similar groupings in Fig. 7; when they were, their pattern of occurrence in the river often made no sense. The complex boundary lines in Fig. 7 indicate that even the three main groups of samples were not discrete.

To preserve continuity, the three communities have been named the MSV (mountain stream vegetation), URV (upper river - vegetation) and LRV (lower river - vegetation) communities. The titles, however, indicate only the communities' main areas of occurrence (Fig. 8); for instance, three samples grouped in the mountain stream community were collected at stations 4, 6 and 7. Because of the broad grouping of samples, the marginal vegetation communities appeared to exist over larger temporal and spatial ranges than did comparable stony-bed communities. MSV was present at both stations 1 and 2, URV at stations 3 and 4 and LRV at stations 4 to 8. In the Mountain Stream and Upper River the marginal-vegetation habitat was only available when water levels were

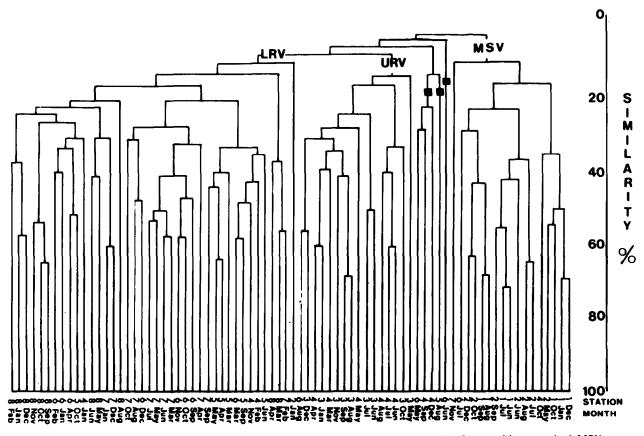


Fig. 6. Dendrogram showing the results of analysing faunal data from marginal-vegetation samples. Communities recognised: MSV – mountain stream (vegetation); URV – upper river (vegetation); LRV – lower river (vegetation). - samples not included in a community cluster.

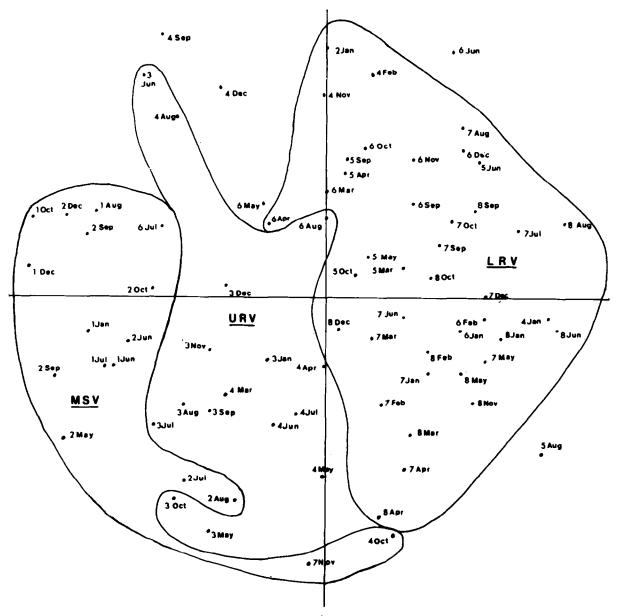


Fig. 7. Two-dimensional ordination showing results of analysing faunal data from marginal-vegetation samples. Samples are identified as in Fig. 6, and grouped in the same way.

high, and was always occupied by the same fauna, at any one station. In the Lower River the habitat was continually available, but seasonal changes did not show up in the cluster analyses. The three communities are described below. Because of the poor separation of samples into clusters, information statistic tests have not been applied to the data.

a) MSV – the mountain stream (vegetation) community. The community was dominated by

insects (97.1%), with the different groups present in proportions similar to those in the corresponding stony-bed community, WMS. The Ephemeroptera (31.7%) and Diptera (36.3%) were most common, followed by the Trichoptera (15.9%), Plecoptera (5.7%), Coleoptera (4.6%) and Odonata (2.9%). Characteristic ephemeropterans were Castanophlebia calida, Baetis harrisoni, Baetis bellus and Centroptilum sudafricanum. The most common trichopterans were Athripsodes (bergensis group)

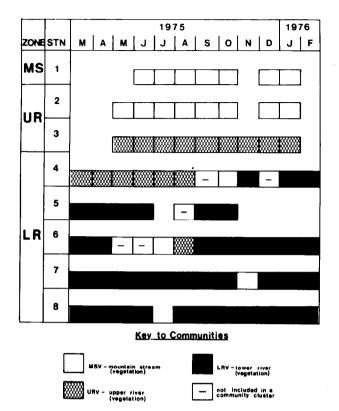


Fig. 8. Location of the three marginal-vegetation communities in the river. The communities are those recognised in Figure 6. Spaces left at stations 1-3 indicate periods when the water level was too low for a marginal-vegetation community to exist. Spaces at stations 5 and 8 in July indicate spoiled samples. Zones: MS – mountain stream; UR – upper river; LR – lower river.

and Barbarochthon brunneum, and odonate was Pseudagrion salisburyense. The Coleoptera were a mixture of Gyrinidae, Dytiscidae and the mountain-stream families (Elmidae, Helodidae, Hydraenidae, Dryopidae). Simuliidae and Chironomidae were the main dipterans, with occasional Rhagionidae, Culicidae, Tipulidae and Blepharoceridae. The non-insects (2.9%) were Turbellaria, Oligochaeta and, at station 2, a few weak-shelled molluscs.

b) URV – the upper river (vegetation) community. Insects accounted for 94.4% of the numbers. The Ephemeroptera were most common (51.2%) and included species typical of both summer and winter. The same species were present as in the corresponding stony-bed communities (WUR and SUR), but characteristic stony-bed species such as *Castanophlebia calida* and *Ephemerellina harrisoni*

were less frequent, while Centroptilum sudafricanum and Baetis bellus were more common, especially at station 3. The same trichopterans, odonates and coleopterans were present as in MSV, with the exception of the mountain-stream Coleoptera. Those Hemiptera present (2.1%) were largely confined to station 4, and to the summer and autumn; they included Gerris zuqualana, Rhagovelia infernalis africana, Sigara contortuplicata and Enithares sobria. Chironomidae were the most common dipterans, with an occasional recording of Chironomus spp. at station 4. The non-insects (5.6%) included the winter and spring presence of Oligochaeta, and the summer and autumn presence of the hirudinean Glossiphonia disjuncta and the molluscs Lymnaea columella, Burnupia capensis and Physa sp.

c) LRV – the lower river (vegetation) community. As with the corresponding stony-bed communities, the proportion of insects was low (76.3%). The Ephemeroptera (22.4%) were mostly *Baetis harri*soni and *Baetis bellus*, with some *Cloeon lacuno*sum in summer; leptophlebiids were rare. The Diptera (49.1%) were mostly Chironomidae, with some Simuliidae at station 7. Other insects were rare: Trichoptera 0.6%, Odonata 0.8%, Hemiptera 2.3%, Coleoptera 1.0%. The non-insects (23.7%) were mainly Mollusca (13.1%), Ostracoda (6.2%) and Oligochaeta (2.8%).

The correlation between the physicochemical quality of the water and faunal distribution

Sixty-six water samples were complete, in that they contained a value for each of the variables dissolved oxygen (mg l^{-1}), dissolved oxygen (percent saturation), pH, water temperature and current speed; of these, 54 also contained values for nitrite, nitrate, total phosphate and total alkalinity (no chemical analyses had been done for stations 1 or 2). The water samples were arranged according to the cluster-analysis groups of stony-bed faunal samples, and given the same six group names (WMS, WUR, WLR, SUR, TLR, SLR) with an additional 'W' to indicate 'water sample'. The stony-bed clusters were chosen in preference to those of the marginal vegetation because they were more distinct. Table 3 gives the mean values of the variables for each group of water samples (and thus

Variable		Group					
		WMSW	WURW	WLRW	SURW	TLRW	SLRW
Dissolved oxygen	Mean	9.14	8.82	8.18	7.86	6.95	5.20
mg l ⁻¹	Standard error	0.46	0.34	0.55	0.56	0.52	0.81
Dissolved oxygen	Mean	100.22	96.20	89.90	88.14	76.27	53.56
% saturation	Standard error	3.27	0.85	1.90	2.52	3.04	5.47
рН	Mean	6.7	7.0	7.7	7.1	7.4	7.3
	Standard error	0.2	0.1	0.2	0.1	0.1	0.2
Water °C	Mean	13.1	13.8	14.9	19.3	19.4	23.5
Temperature	Standard error	0.8	0.6	1.3	1.4	1.1	0.9
Current Speed	Range	34-	35-	30-	4-	4–	0-
cm sec ⁻¹		154	286	189	36	157	35
Nitrite	Mean	-	0.008	0.027	0.008	0.048	0.076
mg l ⁻¹	Standard error		0.001	0.012	0.002	0.021	0.038
Nitrate	Mean	-	0.091	0.329	0.089	0.744	0.210
mg ℓ ⁻¹	Standard error		0.007	0.074	0.028	0.296	0.072
Total phosphate	Mean	-	0.463	1.648	0.547	1.800	3.098
mg l ⁻¹	Standard error		0.058	0.622	0.075	0.261	0.763
Total alkalinity	Mean	-	8.6	38.6	17.5	39.5	119.4
mg ^{g-1}	Standard error		1.1	17.4	4.4	5.9	15.7

Table 3. Mean values and standard errors of the environmental variables for the six groups of water samples.

for each stony-bed faunal community).

The discriminant analysis was initially performed on the 66 samples containing data on the five variables dissolved oxygen (mg l^{-1}), dissolved oxygen (% saturation), pH, water temperature and current speed; these samples represented all sections of the study area (Table 3). The degree of agreement between the initial grouping of water samples (as based on the faunal clusters) and the grouping indicated in the discriminant analysis was 56.1% (Table 4). Distinctive groups (e.g. SURW) had a higher level of agreement than indistinct groups (TLRW). Most reclassifications involved placing a water sample in a group that was a neighbour in space or time. For instance, of the four samples reclassified from WMSW, two were placed in WURW and two in SURW. In the scatter diagram (Fig. 9) the groups of water samples blended one into another, as one would expect, considering the continual nature of the sampling medium. The group centroids were, however, in a logical sequence, with WMSW and SLRW at opposite extremes of the plot. Variables that differed significantly between the groups of water samples (and thus between the stony-bed communities), were dissolved oxygen (% saturation), pH and water temperature. Interpretation of the results is thus confined to these three variables. The groups were separated mainly on canonical variable 1, and formed a series of decreasing dissolved oxygen and increasing water temperature from the Mountain Stream (WMSW) to the Lower River in summer (SLRW); details are given in Table 3. Midwinter samples from the Mountain Stream (station 1: June - August) and late summer/autumn samples from the sewage outfall (station 7: February – March) predictably occurred at opposite extremes of the plot. The Mountain Stream (WMSW) and the Lower River in winter (WLRW) were separated from the other groups on canonical variable 2, and had the lowest (6.7) and highest (7.7) mean pH values respectively.

A second analysis was performed on the 54 samples containing data on nine environmental variables; added to the variables already analysed were nitrite, nitrate, total phosphate and total

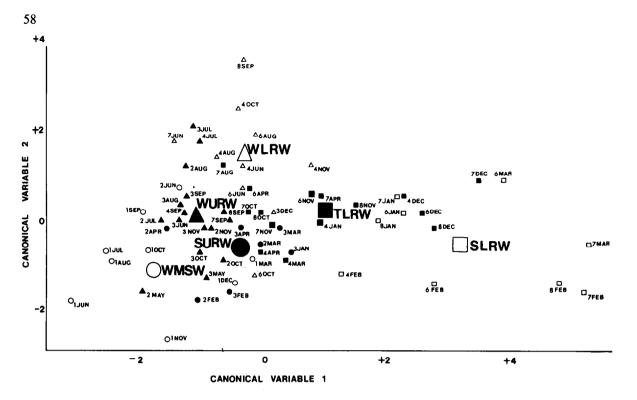


Fig. 9. Scatter diagram resulting from the stepwise, multiple discriminant analyses of 66 water samples, each of which contained data on five environmental variables. The water samples were pre-grouped according to the clusters of stony-bed samples (Fig. 3), and given the same group names, with an additional 'W' to denote water samples. The diagram is a two-dimensional picture of the separation of the groups. Large symbols – multivariate centroids of the groups. Small symbols – individual water samples, identified by station number and month of collection.

Group	%		Samples	Reclassified				
	Correct		SLRW	TLRW	WLRW	WURW	SURW	WMSW
SLRW	55.6		5	3	0	0	1	0
TLRW	33.3		3	5	1	3	3	0
WLRW	70.0		0	0	7	1	2	0
WURW	50.0		0	0	2	8	3	3
SURW	100.0		0	0	0	0	7	0
WMSW	55.6		0	0	0	2	2	5
Mean	56.1	Total	8	8	10	14	18	8

Table 4. Discriminant analysis classification matrix - all six groups of water samples, five variables.

alkalinity. WMSW was excluded from the analysis for lack of samples, and SURW represented by only four samples, from station 3. The initial grouping of water samples showed 79.6% agreement with the classification matrix (Table 5), with SURW again having the highest level of correspondence and TLRW the lowest. Pooling similar groups (SLRW with TLRW, WURW with WLRW) increased the agreeing classification to 87.3%. Variables differing significantly between groups were dissolved oxygen (% saturation), total alkalinity and pH. In the scatter diagram (Fig. 10), the group centroids showed the same sequence as in Fig. 9. Horizontally (canonical variable 1), the groups formed a series of decreasing dissolved oxygen and increasing total alkalinity from the Upper River in winter (WURW) to the Lower River in summer (SLRW). Vertically (canonical variable

Group	% Correct		Samples	reclassified			
	Correct		SLRW	TLRW	WLRW	WURW	SURW
SLRW	88.9		8	1	0	0	0
TLRW	66.7		0	10	1	0	4
WLRW	70.0		0	0	7	0	3
WURW	87.5		0	0	2	14	0
SURW	100.0		0	0	0	0	4
Mean	79.6	Total	8	11	10	14	11

Table 5. Discriminant analysis classification matrix - five groups of water samples, nine variables.

2), the Lower River in winter (WLRW) was again separated from the other groups, and had a higher value for pH.

Discussion

The aquatic macroinvertebrates of the Eerste River undergo spatial and temporal changes in their species composition (Figs. 5 and 8). These changes are predictable, in that the same group of species occurs in the same season and place each year (pers. obs. in years following original survey). Such phenomena are by now well documented. Among those who have described longitudinal and/or seasonal changes in the species of lotic macroinvertebrates are: Harrison & Elsworth (1958), Chutter (1963), Hynes (1961, 1968, 1970), Harrison (1965), Egglishaw & MacKay (1967), Minshall (1968), MacKay (1969), MacKay & Kalff (1969), Bishop (1975), Minshall & Minshall (1978), Andrews & Minshall (1979a, 1979b), Towns (1979) and Gore (1980). Often the described changes have been based on differences between pooled groups of

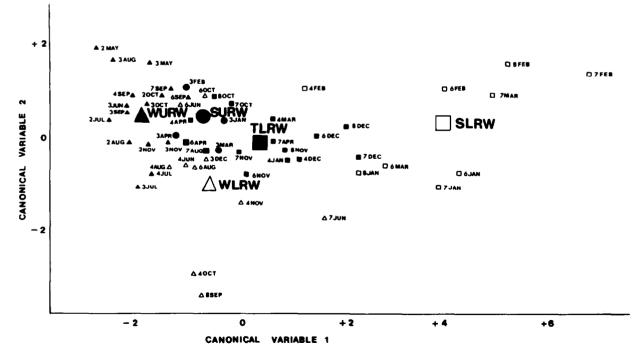


Fig. 10. Scatter diagram resulting from the stepwise multiple discriminant analysis of 54 water samples, each containing data on nine environmental variables. Pre-grouping and identification of samples as in Fig. 9.

faunal samples, each group representing a preconceived 'zone' or 'season' in the river. In this investigation, through cluster analysis of the faunal samples, the fauna themselves have pinpointed the times and places of their changes in community structure.

The analyses indicated that the stony-bed communities were more limited in distribution than the marginal-vegetation ones (Figs. 5 & 8). Kemp *et al.* (1976) found the marginal vegetation fauna less satisfactory to classify than the stony-bed fauna, and attributed this to the greater variability of the marginal-vegetation habitat. Chandler (1970) concluded that animals from the stony-bed habitat were most useful for pollutional studies, as they were most sensitive to changes in their environment.

Further discussion below has been confined to the stony-bed communities, because of their clear distribution pattern in the river.

Three biotic zones, each with a distinctly different fauna, were identified in the study area (Fig. 5). The biotic zones corresponded to obvious physical zones. In terms of Illies' (1961) system of river zonation, the Mountain Stream was equivalent to the upper rhithron, the Upper River to the lower rhithron and the Lower River to the upper potamon. Harrison (1965) recognised these and others of Illies' zones in several southern African rivers.

Seasonal changes in the fauna differed in the three zones (Fig. 5). In the Mountain Stream, the single, year-long community (WMS) was dominated by insects, which first appeared in late autumn/early winter, and grew slowly to emerge as winged adults in summer. In 1976, WMS appeared earlier (March) than in 1975 (June), and contained smaller animals (unpublished data). Possibly the young animals begin their life cycles deep in the substrate sometime before appearing at the substrate surface (see Coleman and Hynes (1970) for discussion on vertical migration of benthic fauna down into the river-bed), and thus are smaller the earlier they migrate upwards. Very few animals were found in the months between successive WMS communities (March - May, 1975; January -February, 1976); those present were late-maturing remnants of the old community, and some individuals of the ephemeropteran Aprionyx peterseni. Hynes (1970) states that if, after the winter species have emerged, the remaining summer season is too

short for a species to complete its life cycle, it will not occur. The brief gaps between WMS communities appear to be unsuitable for the establishment of a summer community.

In the Upper River, the winter community (WUR) was present twice as long (8 months) as the summer one (SUR 4 months). The two communities were quite different in species structure, though both contained a high percentage of insects. In both, numbers were initially high, as eggs hatched, and finally low, as animals emerged as winged adults. Hynes (1970) describes such a pattern for streams dominated by insects.

Of the three winter communities, the one in the Lower River, WLR, was present the shortest time (5-7 months). WLR had a high percentage of insects and, as with the Upper River communities, faunal numbers were initially high and finally low. The summer community, SLR, was present for 3-4 months. Non-insects, especially ostracods and molluscs, were abundant in SLR, and total animal numbers continued to increase until the winter rains began. Hynes (1970) describes this pattern as typical of streams dominated by multivoltine snails or Peracarida. TLR, the transitional community, occupied the Lower River for the remaining months of the year, occurring both in spring and in autumn. Its species composition was intermediate between the extremes of WLR and SLR. The summer buildup of molluscs, ostracods, Chironomus spp. and others began when TLR appeared in spring, and the last remnants of these species were in TLR when it reappeared at the time of the first light rains. Similarly, winter species were present as latematuring individuals in spring, and as newly-hatched larvae and nymphs in autumn. Where TLR did not give way to SLR, but remained through the summer (station 4), the fauna was characterised by a lower concentration of the summer species present at stations 6-8, and a higher concentration of stillwater ephemeropterans.

The trend through the study area was of winter communities occupying the stony-bed habitat longer, the nearer they occurred to the source of the river. As these communities disappeared, summer communities replaced them where possible. The Mountain Stream supported only the winter community each year, while both the Upper and Lower Rivers supported summer and winter ones. Because of the different durations of the winter communities, the summer community of the Lower River was present longer than that of the Upper River. (TLR was not a third community being squeezed into the Lower River, but a summer community that would have persisted there if the physicochemical environment had not deteriorated so drastically.) The three winter communities shared several common, univoltine species whose aquatic lives were as long as the duration of their respective communities (unpublished data). Animals of the same winter species were thus present longer in, and emerged later from, the Mountain Stream than the Lower River. Additionally animals from the Mountain Stream were smallest at emergence, while those from the Lower River were largest. These different levels of secondary productivity along the river will be the subject of a subsequent paper.

The three winter communities (WMS, WUR, WLR) were similar, while the summer ones above (SUR) and below (TLR, SLR) Stellenbosch were quite dissimilar (Figs. 3 and 4). SUR, with its high proportion of insects, resembled the winter communities more than TLR and SLR. These faunal associations were reflected in the associations of the water samples, which can be 'visually judged' (Green & Vascotto 1978) in Figs. 9 and 10; Table 3 indicates the reasons for the similarity. The physicochemical quality of the water was more uniform through the study area in winter than in summer. For instance, mean water temperature between the Mountain Stream and the Lower River increased by only 1.8 °C in winter, but by 10.4 °C in summer. Mean dissolved oxygen (% saturation) showed a corresponding downstream decrease of 10.3% in winter and 46.7% in summer. The Upper River was above the major sources of pollution, and thus did not exhibit the same summer deterioration in water quality as the Lower River. Values of some environmental variables for the Upper River in summer (e.g. dissolved oxygen, water temperature) were more extreme than for any winter sample, while values of other variables (e.g. pH, nitrite, nitrate, phosphates) were similar to those for the Upper River in winter. This was reflected in the positioning of SURW near to, but to one side of, the winter groups of water samples in the scatter diagrams (Figs. 9 & 10).

Discriminant analyses revealed that the variables differing significantly between groups of water samples (and thus between stony-bed faunal communities) were dissolved oxygen (% saturation), water temperature, pH and total alkalinity. The over-riding importance of dissolved oxygen, and to a lesser extent of the allied variable water temperature, can be appreciated when noting that levels of the nutrients nitrite, nitrate and phosphate were sometimes higher in winter than in summer (details in Appendix I), yet the winter fauna did not show the same drastic, downstream changes in species composition as the summer fauna. The cold, turbulent winter flow presumably maintained a sufficiently high dissolved oxygen level for the winter fauna to cope with organic pollutants without undergoing such a complete change of species. Total alkalinity and pH, both of which showed increased values downstream, may have been influencing factors in the establishment of the three biotic zones.

Grouping of water samples, based on the clustering of faunal samples, appears to have considerable validity (Tables 4 & 5). Depending on the number of variables included in the discriminant analysis, 56.1% (5 variables) or 79.6% (9 variables) of the water samples were correctly grouped in this way. Reclassified samples were usually placed in a group that was a spatial or temporal neighbour. For instance, the sample reclassified from SLRW to TLRW (Table 5) was collected at station 4 in February 1976. Fig. 5 shows that TLR was in fact the prevalent faunal community at station 4 throughout that summer. Similarly, of the two samples reclassified from WURW to WLRW (Table 5) one was collected at station 4 in July 1976. As suggested by the reclassification, the faunal community WLR normally occurred at station 4, but had been replaced by WUR that one month (Fig. 5).

In both the above examples, the fauna changed briefly, while the water samples remained similar to others taken at the same place and time of year. There are a number of possible explanations for this, including high sensitivity of the fauna to small environmental changes and reaction of the fauna to environmental changes which were not monitored. The high level of agreement between groups of faunal samples and groups of water samples, however, indicates that environmental changes are usually quickly reflected by changes in the species composition of the fauna. While acknowledging that a much wider range of chemical analyses would be necessary to establish the predictive value of this 62

relationship, the results do indicate a strong correlation between faunal distribution and the physical and chemical quality of the water.

In conclusion I feel that hydrobiological studies of rivers such as the Eerste River, with their miniature zones and simple profiles, can advance our understanding of rivers in general. Longitudinal changes in their macroinvertebrate fauna would probably be simple, one-way trends in such factors as species composition and secondary productivity, and relatively few samples would be necessary to monitor such changes. A more limited number of external factors would be implicated in the trends than in longer and more complex river systems. The spatial and temporal distribution pattern of the macroinvertebrates of the Eerste River clearly revealed their reactions to the seasonal cycle and the changing physicochemical quality of the water along the river. This information will provide a valuable base-line when monitoring future changes in the river, especially those following the completion of the Jonkershoek dam.

Summary and conclusions

1. Faunal samples collected from the stony-bed and marginal-vegetation habitats of the stony-bed section (upper 26 km) of a small (40 km) South African river, were used to investigate spatial and temporal changes in the species composition of the macroinvertebrates. Cluster analyses of the samples revealed the presence of assemblages of invertebrates, which were treated as representative of separable animal communities in the river.

2. Stony-bed communities were found to be more clearly and restrictively distributed than marginalvegetation communities, and further discussion was confined to the former.

3. Spatial distribution of the stony-bed communities divided the river into three, longitudinal biotic zones, which corresponded with obvious physical zones: the Mountain Stream (7 km), Upper River (5 km) and Lower River (14 km) zones.

4. Temporal changes in the species composition of the fauna were different in the three zones. In the Mountain Stream a slow-growing, insect-dominated community appeared at the beginning of winter and took approximately one year to grow to maturity. It was then replaced by another similar community. In the Upper River, winter and summer communities alternated, occupying the habitat for eight months and four months respectively. The two communities had different species compositions, but both were dominated by insects. Winter and summer communities, each lasting roughly six months, also occurred in the Lower River. While the winter community was similar in species composition to the winter ones of the two higher zones, the summer community had a high percentage of non-insects, particularly molluscs and ostracods. The trend through the study area was of winter communities persisting longer, the closer they occurred to the source of the river; as they disappeared, summer communities replaced them where time allowed.

5. There were downstream changes in the physical and chemical quality of the water. While the Mountain Stream was free of pollution and the Upper River 'reasonably clean', water quality of the Lower River fluctuated from 'poor' in the summer (low dissolved oxygen and flow, high water temperature and nutrient levels) to 'improved' in the winter (high dissolved oxygen and flow, low water temperature, but still occasional high nutrient levels). The annual deterioration of the Lower River was mainly due to poor summer flow, combined with the continued input of organic effluents from Stellenbosch.

6. Correlations between changes in the physical and chemical quality of the water and changes in the faunal communities were investigated using multiple discriminant analysis. The results indicated a strong correlation between the two. Environmental variables that differed significantly between faunal communities were dissolved oxygen, water temperature, pH and total alkalinity.

7. I conclude that studies of short rivers with simple profiles, such as the Eerste River, can advance our understanding of rivers in general. The distribution pattern of macroinvertebrates in the Eerste River, and its relation to changes in the physicochemical quality of the water, provide baseline information for monitoring future changes in the river's ecology.

Acknowledgements

My sincere thanks to Drs G. Branch, T. Crowe, B. Davies, J. Day, J. Field and R. Siegfried, for

Variable	Zone:	Mountain Stream	.ii	Upper River	liver					Lower River	iver				
	Station:	_		2		3		4		6		2		∞	
		s	3	s	M	s	×	Ś	×	S	M	s	×	S	×
Dissolved Oxygen	Mean	8.4	11.2	8.3	10.1	8.3				8.0	8.6	4.2	9.2	4.7	1
mg l ⁻¹	Standard error	0.1	0.3	0.1	0.1	0.3	0.4	0.5	0.2	1.6	0.4	0.8	0.2	0.7	J
Dissolved Oxygen	Mean	94.2	102.5	93.7	0.06	93.2				91.6	88.0	49.9	93.5	54.9	I
Percent saturation	Standard error	0.5	3.7	0.3	0.8	0.7				17.4	2.4	10.2	2.8	9.0	
PH	Mean	6.8	6.3	7.2	7.2	7.2				7.4	7.4	7.5	7.6	7.6	I
	Standard error	0.1	0.1	0.3	0.1	0.2				0.2	0.2	0.4	0.2	0.1	I
Water temperature	Mean	19.7	11.0	20.2	11.7	21.8				25.5	12.2	24.3	12.3	24.5	I
°C	Standard error	0.7	0.3	0.9	1.2	0.9	1.2	0.8		1.8	0.6	0.9	0.7	0.8	I
Current Speed															
cm sec ⁻¹	Range	2054	116-167	15-33	83-185	18-28	ò	0-24	102-177	0-15	124-189	538	108-286	4-35	ı
Nitrite	Mean	ł	1	т э	I	0.005	0.010	0.012	0.011		0.042		0.108	0.160	0.059
$mg \ \ell^{-1}$	Standard error	I	I	I	I	0.002	0.001	0.005	0.001	0.008	0.029	0.076	0.038	0.055	0.012
Nitrate	Mean	I	I	ı	I	0.165	0.119	0.122	0.291		0.394		0.825	1.010	0.728
mg ℓ ^{-l}	Standard error	ı	1	I	I	0.038	0.024	0.025	0.076		0.060		0.517	0.860	0.179
Total Phosphate	Mean	I	I	I	I	0.680	0.482	1.000	0.801		1.241		3.510	1.773	1.162
$mg \ l^{-1}$	Standard error	ı	I	ſ	I	0.040	0.185	0.200	0.100		0.193		1.781	0.542	0.319
Total alkalinity	Mean	I	i	ı	I	20.00	7.66	54.33	18.33	Ξ	18.33	-	125.00	90.67	33.30
$mg \ l^{-1}$	Standard error	I	I	I	ļ	2.89	2.67	19.54	1.67		1.67		40.41	23.35	7.26
Appendix I. Summer (S) and Winter (W)	ner (S) and Winte		values of nine factors of water quality, along the river. Mean values and standard errors are given, except for 'current speed'	factors (of water q	uality, al	ong the r	iver. Mea	in values	and stanc	lard erroi	rs are givei	1, except fc	n 'curren	t speed'

where the range is shown. Measurements of current speed were taken at least four days after a spate.

critically reviewing various drafts of the paper. The following specialists kindly verified faunal identifications: J. D. Agnew (Ephemeroptera), H. Bertrand (Coleoptera), M. W. Mansell (Megaloptera), J. Omer-Cooper (Dytiscidae), J. H. Oosthuizen (Hirudinea), F. de Sallier Dupin (Hemiptera), K. M. F. Scott (Trichoptera) and B. C. Wilmot (Odonata).

The research was supported financially by the Council for Scientific and Industrial Research, and the University of Cape Town. The S.A. Department of Forestry allowed me to work in the Jonkershoek Nature Reserve.

References

- Allanson, B. R., 1961. Investigations into the ecology of polluted inland waters. Hydrobiologia 18: 1-76.
- American Public Health Association 1971. Standard methods for the examination of water and waste water. 13th edition, Washington, D.C.
- Andrews, D. A. & G. W. Minshall, 1979a. Distribution of benthic invertebrates in the Lost streams of Idaho. Am. Midl. Nat. 102: 140-148.
- Andrews, D. A. & G. W. Minshall, 1979b. Longitudinal and seasonal distribution of benthic invertebrates in the Little Lost River, Idaho. Am. Midl. Nat. 102: 225-236.
- Bishop, J. E., 1973. Limnology of a Small Malayan River Sungai Gombak. Dr W. Junk B.V., The Hague.
- Bray, J. R. & Curtis, J. J., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.
- Chandler, J. R., 1970. A biological approach to water quality management. Wat. Poll. Control 4: 415-422.
- Chutter, F. M., 1963. Hydrobiological studies on the Vaal River in the Vereeniging area. Part I. Introduction, water chemistry and biological studies on the fauna of habitats other than muddy bottom sediments. Hydrobiologia 21: 1-65.
- Chutter, F. M., 1970. Hydrobiological studies in the catchment of Vaal Dam, South Africa. Part I. River zonation and the benthic fauna. Int. Rev. ges. Hydrobiol. 55: 445-494.
- Chutter, F. M., 1971. Hydrobiological studies in the catchment of Vaal Dam, South Africa. Part 2. The effects of stream contamination on the fauna of stone-in-current and marginal-vegetation biotypes. Int. Rev. ges. Hydrobiol. 56: 227-240.
- Coleman, M. J. & Hynes, H. B. N., 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. 15: 31-40.
- Dixon, W. J. (ed.), 1975. Biomedical Computer Programs: University of California Publications in Automatic Computation, No. 5. Berkeley: University of California Press.
- Egglishaw, H. J. & MacKay, D. W., 1967. A survey of the bottom fauna of streams in the Scottish Highlands. Part III. Seasonal changes in the fauna of three streams. Hydrobiologia 30: 305-334.

- Field, J. G., 1969. The use of the information statistic in the numerical classification of heterogeneous systems. J. Ecol. 57: 565-569.
- Gore, J. A., 1980. Ordinational analysis of benthic communities upstream and downstream of a prairie storage reservoir. Hydrobiologia 69: 33-44.
- Green, R. H. & Vascotto, G. L., 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12:583–590.
- Harrison, A. D., 1958a. Hydrobiological studies on the Great Berg River, Western Cape Province, Part 2. Quantitative studies on sandy bottoms, notes on tributaries and further information on the fauna, arranged systematically. Trans. Roy. Soc. S. Afr. 35: 227-276.
- Harrison, A. D., 1958b. Hydrobiological studies on the Great Berg River, Western Cape Province, Part 4. The effects of organic pollution on the fauna of parts of the Great Berg River system and of the Krom Stream, Stellenbosch. Trans. Roy. Soc. S. Afr. 35: 299-329.
- Harrison, A. D., 1965. River zonation in Southern Africa. Arch. Hydrobiol. 61: 380-386.
- Harrison, A. D. & Elsworth, J. F., 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part I. General description, chemical studies and main features of the flora and fauna. Trans. Roy. Soc. S. Afr. 35: 125-226.
- Harrison, A. D., Keller, P. & Lombard, W. A., 1963. Hydrobiological studies on the Vaal River in the Vereeniging area. Part 2. The chemistry, bacteriology and invertebrates of the bottom muds. Hydrobiologia 21: 66-89.
- Hynes, H. B. N., 1960. The biology of polluted waters. Liverpool University Press.
- Hynes, H. B. N., 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344-388.
- Hynes, H. B. N., 1968. Further studies on the invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 65: 360-379.
- Hynes, H. B. N., 1970. The ecology of running waters. Liverpool University Press.
- Illies, J., 1961. Versuch einer allgemeinen biozönotischen Gliederung der Fließgewässer. Int. Rev. ges. Hydrobiol. 46: 205-213.
- Kemp, P. H., Chutter, F. M. & Coetzee, D. J., 1976. Water quality and abatement of pollution in Natal rivers. Part V. The rivers of southern Natal. Natal Town and Regional Planning Report Vol. 13.
- Kruskal, J. B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29: 1–27.
- Lance, G. N. & Williams, W. T., 1967. A general theory of classificatory programs. I. Hierarchical systems. Comput. J. 9: 373-380.
- Mackay, R. J., 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. J. Fish. Res. Bd Can. 26: 1157-1183.
- Mackay, R. J. & Kalff, J., 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. Ecology 50: 101-109.
- Martin, K. A. C. & Marais, G. v R., 1975. Kinetics of enhanced phosphorus removal in the activated sludge process. University of Cape Town, Department of Civil Engineering Research Report No. W14.

- Minshall, G. W., 1968. Community dynamics of the benthic fauna in a woodland springbrook. Hydrobiologia 32: 305-339.
- Minshall, G. W. & Minshall, J. N., 1978. Further evidence on the role of chemical factors in determining the distribution of benthic invertebrates in the River Duddon. Arch. Hydrobiol. 83: 324-355.
- Noble, R. G. & Hemens, J., 1978. Inland water ecosystems in South Africa – a review of research needs. South African National Scientific Programmes Report No. 34. 150 pp.
- Oliff, W. D., 1960a. Hydrobiological studies on the Tugela River System. Part I. The main Tugela River. Hydrobiologia 14: 281-385.
- Oliff, W. D., 1960b. Hydrobiological studies on the Tugela River System. Part 2. Organic pollution in the Bushman's River. Hydrobiologia 16: 137-196.
- Oliff, W. D., 1963. Hydrobiological studies on the Tugela River System. Part 3. The Buffalo River. Hydrobiologia 21: 355-379.
- Oliff, W. D., Kemp, P. H. & King, J. L., 1965. Hydrobiological studies on the Tugela River System. Part 5. The Sundays River. Hydrobiologia 26: 189-202.
- Oliff, W. D. & King, J. L., 1964. Hydrobiological studies on the Tugela River System. Part 4. The Mooi River. Hydrobiologia 24: 567-583.
- Schulze, B. R., 1965. Climate of South Africa, Part 8. General Survey. WB28 Weather Bureau, Pretoria.

- Steer, A. G., 1964. Pollution survey of the Berg and Eerste Rivers. Intensive survey of the Eerste River. National Institute for Water Research Progress Report No. 2. Typescript.
- Steer, A. G., 1966. Pollution survey of the Eerste River including the Krom and Plankenbrug Rivers. National Institute for Water Research Report No. 13. Typescript.
- Towns, D. R., 1979. Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. Freshw. Biol. 9: 251-262.
- van der Zel, D. W., 1971. 'n Hidro-ekonomiese waardebepaling van die bosboubedrijf in de opvangebied van die Eersterivier. Unpub. M.Sc. thesis. University of Stellenbosch.
- Velimirov, B., Field, J. G., Griffiths, C. L. & Zoutendyk, P., 1977. The ecology of kelp-bed communities in the Benguela upwelling system. Helgoländer wiss. Meeresunters 30: 495-518.

Received September 11, 1980.

Authors Address: Zoology Department University of Cape Town Private Bag Rondebosch 7700 South Africa