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ON THE ECOLOGY OF THE FAUNA OF STONES IN THE CURRENT IN A SOUTH AFRICAN RIVER SUPPORTING A VERY LARGE *SIMULIUM* (DIPTERA) POPULATION

By F. M. CHUTTER
National Institute for Water Research
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INTRODUCTION

There is a very large population of *Simulium chutteri* Lewis in the Vaal River at and below the village of Warrenton in the north-east of the Cape Province, South Africa. The female of this species attacks man, cattle and horses and had become a pest when the studies described here were made. The first aim of this work was to record the density of the *Simulium* larvae and also of the other invertebrate animals in the river at different times of the year from Warrenton down to Barkly West (Fig. 1). This was done so that when measures were taken to reduce the size of the *Simulium* population, there would be a background of fact about the river fauna, against which the effect of the control measures might be assessed. The planning of the work was very much influenced by this first aim. However, faunal changes may be ascribed to control measures more reliably if the major factors which influence the composition and density of the fauna under natural conditions are known. The studies in the Warrenton area were therefore expanded by the measurement of important environmental variables, and the relationship between the animals collected and these variables, has been investigated. Naturally an important consideration was whether there was any factor with which the occurrence of the unusually large numbers of *Simulium* larvae could be associated.

METHODS AND APPARATUS

(a) *Planning the study*

A preliminary survey of the area showed that the main sites of larval attachment of *Simulium chutteri* were on the stones in the current. There was seldom vegetation trailing in the current, which in other rivers is often an important habitat of *Simulium* larvae. The stones-in-current fauna was studied at several sampling points spaced out between Warrenton and Barkly West, so that when *Simulium* control was attempted it would be possible to establish how far downstream the fauna was affected.

In order that statistical techniques might be used to compare recorded faunal densities, many small samples, instead of single large samples were taken from each sampling point. In the event it turned out that the numbers of animals collected in individual samples varied so irregularly that it was necessary to use non-parametric statistics to compare mean densities of animals, or to investigate the correlation between the occurrence of various pairs of species. Due to distance from the laboratory (775 km) the river was visited only four times in a year, once in each season.

The investigation of water chemistry was planned so that the results were not based on single snap samples, as snap samples can be misleading, particularly when there were to be only four sampling occasions during the course of a year.

(b) *Field methods and apparatus*

The stones in the Vaal River in the Warrenton area are generally large, making it virtually impossible to use several of the more usual quantitative sampling methods for stony biotopes in the current. The stones were too large for the Surber square foot sampler (Surber 1936) and for samples based on the shovel principle (Macan 1958). 'Kicking' methods of sampling (Hynes 1961) and sampling for a standard period were not acceptable because many of the animals adhere closely to the stones. The *Simulium* pupae would not be collected by kicking and they would disrupt the comparison of data collected in a standard time, because a much smaller area would be sampled when animals which have to be picked off stones, rather than rubbed off, were abundant. Sampling methods such as the cone (Wolfe & Peterson 1958) and polythene strip 'traps' (Williams & Obeng 1962) were not suitable as they reveal only the *Simulium* populations and would have required the continuous presence of the author in the field for longer periods than were available to him.

In view of these shortcomings of the more usual sampling methods the fauna of completely submerged individual stones was collected and the animals from each stone were treated as a separate sample. Initially the faunas of twenty stones were collected at each sampling point, though in one instance there were so many Simuliidae on the stones that there was time to sample sixteen stones only. Later the number of stones sampled at each station was reduced to ten. The selection of the stones was important and, on account of the turbidity of the water, it had to be carried out largely by touch. The procedure followed was to feel about among the stones until one considered small enough to be lifted with one hand was found. Really small stones, which were easily encompassed by the fingers, were rejected, but all others that could be lifted were taken. Stones were never taken from parts of the sampling area disturbed by previous sampling on the same day and in this way stones were taken from a large area. Each stone was lifted from the water with a hand net held close behind it and then carried to the bank with the net held below. There it was placed in a bucket of water and the fauna washed and picked off into the bucket until a 3 min inspection revealed no further animals on the stone. The contents of the bucket were then poured through the hand net and the collection of animals transferred to a preserving jar and pickled in formalin. Finally, rough measures of the surface area and volume of each stone were made. For surface area measurements, the stone was placed on the ground with its greatest flat surface downwards, and the length and breadth of the rectangle which most nearly fitted its size, measured. It was then turned on its side and the height measured. The measurements were made with a centimetre cloth tape. The volume of each stone was estimated to the nearest 100 cm^3 by displacement of water in a bucket graduated in half-litres. It will be appreciated that neither the surface area nor the volume measurements were very accurate. However, surface area or volume of the stone sampled are only two of the numerous factors likely to influence the number of individuals collected on a stone, and it was felt that the time used in making accurate measurements, particularly of surface area, would be largely wasted.

The hand net used in sampling consisted of a net 35 cm deep on a strip brass ring 3 cm deep of 25·4 cm (10 in.) diameter mounted on a handle about 2 m long. The net was of bolting silk with 23 meshes/cm and an average aperture between the threads of 0·29 mm.

Current speeds in the stones-in-current biotopes were measured with an Ott Laboratory Minor propeller-driven current meter. Several factors governed the way in which the meter was used. First of all it was obvious, on account of the turbidity of the water, that it would not be possible to measure the current speed in the vicinity of a particular stone with any accuracy. Secondly it is extremely doubtful whether such measurements would be at all meaningful because of the great variation in current speed around a stone in a rapid. The current speed was therefore measured in a large number of places in the rapid to give some idea of the average speed of the water. Differences in the speed from sampling point to sampling point might account for some of the differences in the fauna, but differences in current speed could not be used to account for the differences between the fauna of individual stones at single sampling points. Ideally the current speed should have been measured before the run was disturbed by taking stones from it, but the walking through the run involved in measuring the current speed would have disturbed the fauna. The speed was therefore measured after the biological sampling had been completed.

Water samples for mineral analysis were collected separately from those for analysis of combined nitrogen. The latter were preserved with mercuric chloride according to the method of Hellwig (1964). At each station the water sample for mineral analysis was collected in a 4·5 litre plastic container. This was filled by quarters at roughly equal intervals estimated to cover the whole time that it took to collect the biological samples. Each time water was added to this large plastic bottle a half-litre bottle with mercuric chloride was filled and the pH and temperature of the water were measured. At Station 51 (see below), where only water samples were collected, the interval between one sampling and the next was 10 min. At the other stations the intervals between collecting water samples were always greater than this and often up to 45 min. Samples were collected in this way in order to reduce the possibility of a small batch of unusual water producing a misleading analysis. pH was measured with a Lovibond Comparator. Phenol red, thymol blue and diphenol purple, which together cover a pH range of 6·8–9·6, were the indicators used. Temperature was measured with a mercury thermometer.

(c) *Laboratory methods*

Initially ten, but later five, biological samples were drawn at random from the samples collected at each sampling point, and the animals in these samples were identified as far as possible and counted, using a binocular dissecting microscope. Contrary to the sample counting procedure adopted in the recent past in South African river surveys (Allanson 1961; Chutter 1963, 1967) all the animals were counted in every sample.

The surface area of each stone was then calculated from the dimensions measured in the field and the numbers of animals collected from the stone were converted by direct proportion to the numbers which would have been collected had the stone had a surface area of 1000 cm^2. On one occasion (Station 54, January 1964) the measuring tape was mislaid and only the volumes of the stones were known. For this series of samples the surface area was estimated from a curve fitted by eye to a graphical plot of all the known surface area/volume relationships for stones collected from the same sampling point.

Water samples were analysed within 2 weeks of being brought back to the laboratory. Analysis methods were those adopted by the National Institute for Water Research, a recent description of which is given by Hellwig & Noble (1965).

A GENERAL DESCRIPTION OF THE VAAL RIVER IN THE WARRENTON AREA

A few miles above the village of Warrenton a major part of the flow of the Vaal River is diverted, by means of a weir and a canal system, into a large irrigation scheme in the valley of the adjacent Hartz River (Fig. 1). Above the Vaal Hartz Diversion Weir the

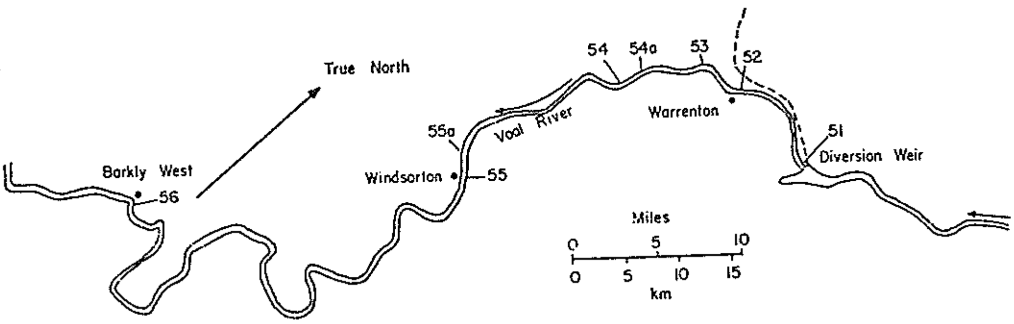


FIG. 1. The Vaal River from the Vaal Hartz Diversion Weir to Barkly West, showing sampling points. - - - -, Irrigation canal.

countryside and rate of fall of the river are extremely flat with the result that the relatively low wall of the weir holds the water of the Vaal River back some 35 km (Fig. 2). From the Weir to Windsorton the river bed is mainly stony and the river falls rapidly, cutting through an escarpment. From Windsorton to Barkly West the countryside is again flat and the bed of the river is mainly sandy. At Barkly West its rate of fall again increases as the river cuts through another escarpment. The steeper falls below the Weir and below Barkly West are analogous to the Rejuvenation Zone in the Tugela River (Oliff 1960a).

Alluvial diamonds are found in this part of the Vaal River, and consequently the river bed has in the past been considerably disturbed by diamond digging. Rocks and boulders removed from the river bed have been piled in heaps, often forming small islands and leaving holes where workings were sited. During the period of study, disturbance of the river bed on a large scale took place only at Windsorton, where a coffer dam was built through a stony run which had been a sampling point.

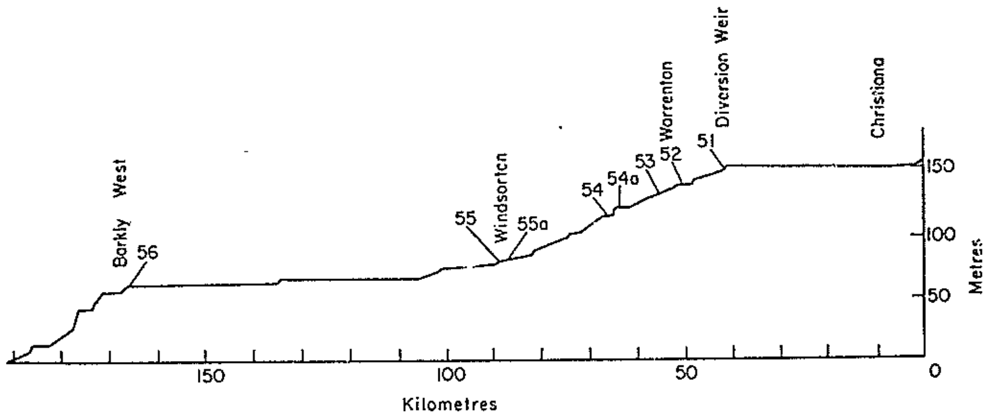


FIG. 2. Profile of the Vaal River in the Warrenton area, showing sampling points. The base-line is 1036 m above sea level.

THE SAMPLING PROGRAMME AND SAMPLING POINTS

Following an exploratory visit to the area in May 1963, the following sampling points were chosen and visited in October 1963, and January, April and August 1964.

Station 51. Immediately below the Vaal Hartz Diversion Weir. The bed of the river was composed of very large boulders here. There was no stony run from which faunal samples might be drawn.

Station 52 (Phot. 1). At the Maria Prinsloo Bridge into Warrenton. The bed of the river was stony at this point and the river sub-divided by a number of small stony islands. The river is of the order of 300 m wide, the bridge about 400 m long.

Station 53. On a farm about 5 km below Warrenton where there was a bone-meal factory about 400 m from the river. The fauna of fringing vegetation was sampled, but the results have not been included as the vegetation was not a *Simulium* larval habitat.

Station 54. On the farm Stonehill about 15 km below Warrenton. At this sampling point the river was divided by a large stony island. The channel containing the stony run from which the fauna was collected was dry on the third and fourth sampling visits and this point was abandoned in favour of Station 54a.

Station 54a. On the farm Witrand about 13 km below Warrenton. Here the main body of water was flowing very fast and cascading in places, and the river was about 40 m wide across the rapids. The fauna was collected from where the water was flowing fast but not cascading. This sampling point was used in April and August 1964, when Station 54 was dry.

Station 55. (Phot. 2). At Windsorton. Here pools in the river were long and the river was about 80 m wide. When the final field trip was undertaken a coffer dam had been built across the biotope previously sampled. The August 1964 samples were therefore collected at the next stony run upstream. This was about 2·5 km above Station 55 and was called Station 55a.

Station 56 (Phot. 3). At Barkly West. The bed of the river was stony here and where sampled it was about 100 m wide.

Water samples for chemical analysis were collected and the temperature and pH of the water were measured at all these sampling points, The stones-in-current fauna was sampled at Stations 52, 54, 54a, 55, 55a and 56.

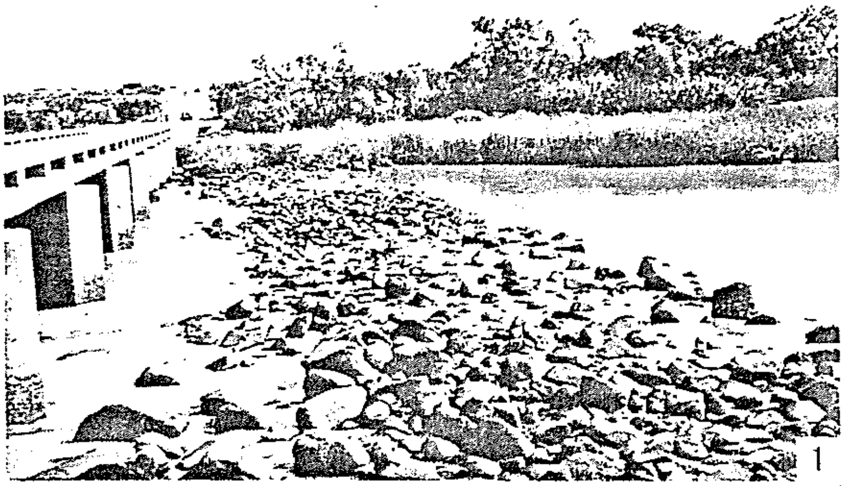
FAUNA—INTRODUCTORY REMARKS AND GENERAL DESCRIPTION

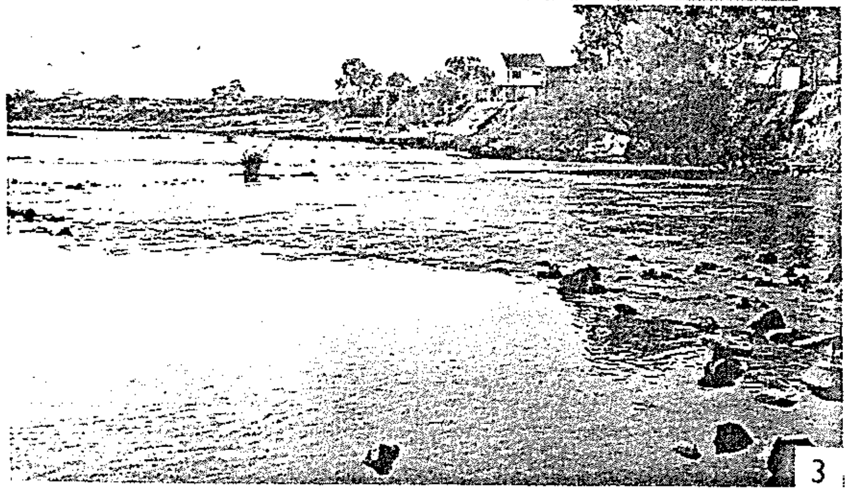
At the beginning of the study, in October 1963, ten faunal samples were drawn at random from the twenty samples collected at each sampling point. The animals in each of these ten samples were identified and counted. When the January 1964 samples came to be analysed it became apparent that there was not time to count the animals on so many stones. In that month and thereafter the fauna of only five stones from each sampling point was analysed. However, because the surface area of the stones collected at Station 54 in January was unknown and had to be estimated from the volume/surface area relationships of the stones collected in October (see above), the animals from ten stones were counted in January at this station, as this would help to cancel out the effect of the estimation of surface areas. (The term 'sample series' has been used here to describe the faunal samples collected during any one of the field trips from any one of the sampling points and subsequently analysed. It is used with the same meaning on several occasions hereafter.)

The mean number of individuals per 1000 cm^2 stone surface, together with the numbers of stones on which they were found, for the commonest stones-in-current animals are shown in Table 1. The densities of animals in sample series were often highly variable and there was then a considerable overlapping of single sample densities in different sample series, whose mean densities differed by fairly large amounts. In view of this it was necessary to use a statistical comparison of density data in pairs of sample series to test whether they came from populations likely to be of the same or of differing sizes. However, the numbers of animals recorded in single sample series could not be fitted to a theoretical distribution and this had two important statistical consequences. Firstly it meant that non-parametric statistics had to be used instead of parametric statistics. Secondly it meant that the reliability of sample means could not be calculated and expressed in the usual forms such as the standard error or the standard deviation.

The Mann–Whitney U Test (Siegel 1956 for theory; Owen 1962 for significance tables) was used to compare sample series. The probability of the samples being drawn from populations with the same density had to be 0·05 or less before it was accepted that the sample means represented populations of different sizes. The Spearman Rank Correlation Coefficient was calculated when correlations were investigated. Correlations were regarded as significant only if their probability was 0·95 or greater.

The commonest stones-in-current animals were the mayflies *Baetis glaucus* and *Neurocaenis* sp., the caddis flies *Amphipsyche scottae* and *Cheumatopsyche thomasseti*, *Simulium chutteri* and Chironomidae of the subfamily Orthocladiinae (Table 1). These and the majority of other common stones-in-current animals were recorded from all the sampling points. However, the density of the different animals varied considerably from





PHOT. 1. Station 52 (Warrenton) showing the stones in current from which animals were collected. Water level low.

PHOT. 2. Station 55 (Windsorton). The stones sampled were between the protruding stones in the centre of the photograph and the bottom left hand corner.

PHOT. 3. Station 56 (Barkly West). The stones sampled were in the centre of the photograph.

(*Facing p.* 536)

Table 1. *The mean number of animals per 1000 cm² of stone surface from stones-in-current biotopes (the numbers of stones on which the animals were found are shown in parentheses)*

Station number	O*	52	54	55	56
	J	52	54	55	56
	Ap	52	54a	55	56
	Au	52	54a	55a	56
FAUNA†					
Porifera	O	P‡(9)	–	P(1)	–
	J	–	–	P(1)	–
	Ap	–	–	–	–
	Au	P(2)	–	P(1)	P(2)
Nematoda					
Mermithidae	O	1(2)	5(8)	1(6)	P(1)
	J	1(2)	P(2)	–	–
	Ap	3(5)	1(1)	–	–
	Au	3(4)	24(5)	6(5)	P(2)
Oligochaeta					
Nais sp.	O	P(1)	–	1(2)	P(1)
	J	–	–	–	–
	Ap	–	P(1)	–	–
	Au	3(4)	1(2)	1(3)	–
Chaetogaster sp.	O	–	–	–	–
	J	–	–	–	–
	Ap	–	–	–	–
	Au	5(1)	1(2)	–	7(3)
Hirudinea					
?*Salifa perspicax* Blanchard	O	3(3)	2(3)	–	4(6)
	J	2(2)	P(1)	–	2(4)
	Ap	–	P(1)	3(2)	1(1)
	Au	–	–	3(3)	–
Cladocera					
Moina sp.	O	1(3)	–	1(6)	15(10)
	J	P(1)	P(2)	–	82(5)
	Ap	P(1)	1(1)	P(1)	30(5)
	Au	–	–	–	–
Ostracoda					
Gomphocythere sp.	O	27(8)	P(2)	P(2)	1(3)
	J	52(2)	P(2)	–	–
	Ap	P(1)	48(2)	19(3)	4(3)
	Au	14(3)	P(1)	5(4)	P(1)
Hydracarina					
Hydrachnellae	O	2(8)	–	P(1)	–
	J	P(1)	P(2)	P(1)	P(1)
	Ap	P(1)	P(1)	–	–
	Au	P(2)	P(1)	P(1)	–
Ephemeroptera					
Baetis glaucus Agnew	O	56(10)	60(10)	120(10)	79(10)
	J	65(5)	54(10)	63(5)	17(5)
	Ap	74(5)	68(5)	48(5)	88(5)
	Au	22(5)	69(5)	18(5)	107(5)

Table 1 (*continued*)

Centroptilum medium Crass	O	–	–	–	–
	J	4(2)	–	3(4)	P(2)
	Ap	–	P(1)	–	–
	Au	–	–	–	–
Baetid juveniles	O	3(4)	1(2)	5(4)	P(1)
	J	7(5)	11(9)	25(5)	7(5)
	Ap	3(4)	13(5)	23(5)	10(5)
	Au	13(5)	9(5)	14(5)	6(5)
Choroterpes (*Euthraulus*) sp.	O	4(4)	1(3)	1(4)	3(8)
	J	5(2)	8(3)	3(2)	8(5)
	Ap	P(1)	7(1)	2(2)	8(5)
	Au	17(3)	4(5)	79(5)	11(5)
Neurocaenis sp.	O	74(10)	2(4)	19(10)	420(10)
	J	38(5)	9(8)	30(5)	96(5)
	Ap	171(5)	37(5)	11(5)	202(5)
	Au	–	–	–	–
Caenid—?*Caenodes* sp.	O	56(10)	–	–	25(5)
	J	19(3)	1(3)	3(2)	7(5)
	Ap	1(3)	16(1)	6(4)	29(4)
	Au	35(4)	1(2)	39(4)	4(5)
Afronurus sp.	O	4(8)	P(1)	P(3)	3(7)
	J	3(4)	1(4)	5(4)	1(3)
	Ap	4(3)	P(1)	4(4)	1(2)
	Au	5(4)	3(4)	2(3)	3(4)
Plecoptera					
Neoperla spio (Newman)	O	1(4)	–	–	P(1)
	J	1(2)	P(1)	–	–
	Ap	P(1)	P(1)	1(1)	–
	Au	2(3)	1(2)	4(3)	–
Neuroptera					
?*Sisyra* sp.	O	5(9)	–	P(1)	–
	J	–	–	3(1)	–
	Ap	–	–	–	–
	Au	P(1)	–	2(1)	P(1)
Trichoptera					
Amphipsyche scottae Kimmins	O	6(8)	P(1)	20(10)	112(10)
	J	7(4)	P(1)	3(4)	9(5)
	Ap	4(4)	–	5(5)	52(5)
	Au	1(2)	–	1(2)	12(4)
Cheumatopsyche thomasseti (Ulmer)	O	60(10)	9(8)	25(10)	210(10)
	J	7(4)	5(9)	16(5)	27(5)
	Ap	14(5)	26(5)	34(5)	214(5)
	Au	29(5)	5(3)	71(4)	129(5)
Hydropsyche sp.	O	1(3)	2(5)	21(10)	–
	J	2(3)	–	4(5)	–
	Ap	3(5)	27(5)	4(5)	P(1)
	Au	1(1)	3(3)	3(3)	–
Macronema capense Walker	O	6(9)	–	–	–
	J	6(4)	–	–	–
	Ap	P(1)	2(1)	–	–
	Au	6(4)	–	–	–

Table 1 (*continued*)

Hydropsychid juveniles	O	50(10)	5(6)	43(10)	66(10)
	J	3(2)	2(4)	6(5)	10(5)
	Ap	11(4)	10(4)	12(5)	128(5)
	Au	2(2)	–	–	–
Catoxyethira n. sp.	O	12(10)	–	–	P(2)
	J	5(3)	–	2(4)	–
	Ap	9(3)	12(3)	1(2)	15(5)
	Au	20(5)	16(5)	–	8(3)
Orthotrichia sp.	O	2(4)	1(4)	4(9)	P(4)
	J	2(3)	2(6)	3(4)	1(4)
	Ap	1(1)	7(4)	–	2(3)
	Au	3(5)	6(5)	6(5)	5(3)
Coleoptera Elmid larvae (probably *Stenelmis godes* Hinton)	O	7(6)	–	P(1)	4(5)
	J	4(4)	–	–	P(1)
	Ap	–	8(1)	P(1)	2(2)
	Au	3(2)	–	1(1)	1(2)
Diptera					
Simulium adersi Pomeroy (larva and pupae)	O	P(1)	–	–	–
	J	–	–	–	P(1)
	Ap	6(5)	–	–	12(5)
	Au	2(4)	P(1)	–	26(5)
S. chutteri Lewis (pupae)	O	2(5)	1358(10)	33(9)	2(4)
	J	7(4)	76(10)	2(3)	P(1)
	Ap	55(5)	430(5)	2(2)	18(5)
	Au	4(5)	43(5)	12(4)	P(1)
S. chutteri Lewis (larvae)	O	1(5)	648(10)	24(10)	2(6)
	J	8(4)	45(10)	1(3)	1(3)
	Ap	52(5)	311(5)	1(2)	7(4)
	Au	8(5)	81(5)	33(5)	1(1)
S. damnos:':a Theobald (larvae and pupae)	O	5(7)	P(1)	1(4)	–
	J	–	–	–	–
	Ap	15(3)	3(3)	–	1(1)
	Au	18(5)	2(4)	1(2)	P(2)
S. mcmahoni de Meillon (larvae and pupae)	O	2(4)	P(1)	1(2)	14(10)
	J	P(1)	P(1)	–	1(3)
	Ap	39(5)	6(4)	5(3)	1(2)
	Au	38(5)	16(5)	2(3)	36(5)
Simulium spp. larvae	O	87(10)	4310(10)	476(10)	33(10)
	J	423(5)	496(10)	241(5)	38(5)
	Ap	862(5)	1164(5)	48(5)	96(5)
	Au	514(5)	1134(5)	926(5)	23(5)
Simulium spp. larvae parasitized by Nematoda (?Mermithidae)	O	1(5)	22(10)	3(5)	–
	J	10(4)	2(4)	–	–
	Ap	7(4)	P(1)	–	–
	Au	14(5)	84(5)	72(5)	2(2)
All Simuliidae together	O	100(10)	6339(10)	537(10)	49(10)
	J	448(5)	619(10)	243(5)	41(5)
	Ap	1036(5)	1913(5)	55(5)	135(5)
	Au	599(5)	1361(5)	1045(5)	89(5)

Table 1 (*continued*)

Chironomini	O	13(9)	6(8)	2(7)	7(7)
	J	2(3)	1(6)	1(2)	2(3)
	Ap	2(2)	18(5)	1(4)	5(3)
	Au	30(5)	68(5)	22(4)	16(2)
Tanytarsini	O	P(1)	P(1)	P(1)	P(2)
	J	P(2)	P(3)	1(2)	–
	Ap	–	13(5)	1(2)	3(3)
	Au	1(2)	1(3)	P(1)	1(1)
Orthocladiinae	O	13(9)	21(10)	5(8)	3(6)
	J	8(5)	1(5)	1(2)	–
	Ap	15(5)	121(5)	1(3)	2(2)
	Au	280(5)	122(5)	36(5)	99(5)
Mollusca					
Burnupia sp.	O	53(10)	P(1)	13(8)	8(8)
	J	30(5)	P(2)	33(5)	13(5)
	Ap	16(5)	15(5)	33(5)	4(2)
	Au	16(5)	13(5)	28(5)	9(5)
Corbicula sp.	O	1(4)	–	–	1(3)
	J	8(3)	–	–	–
	Ap	–	P(1)	1(1)	9(4)
	Au	–	–	1(2)	P(1)
Pelecypod juveniles	O	3(3)	–	–	–
	J	3(1)	–	–	4(4)
	Ap	–	1(1)	–	–
	Au	–	–	–	–
Whole fauna with number of samples counted in parenthesis	O	576(10)	6469(10)	824(10)	1018(10)
	J	737(5)	719(10)	451(5)	332(5)
	Ap	1372(5)	2376(5)	275(5)	956(5)
	Au	1116(5)	1712(5)	1395(5)	515(5)

* O, October 1963; J, January 1964; Ap, April 1964; Au, August 1964.

† This table includes only animals which were found in more than half the samples at any one sampling point in any month and which had a mean density > 2/1000 cm^2. The other animals are shown in Table 2.

‡ P stands for 'present', meaning that the mean number of individuals was < 0·5, except in the case of Porifera where P simply means present.

sampling point to sampling point and also from season to season. For example the greatest numbers of Simuliidae were found at Stations 54 and 54a, and *Simulium* densities were rather low in January. *Neurocaenis* and *Cheumatopsyche thomasseti* densities were highest at Station 56. In the sections which follow, the variation in the fauna is related to the variation in environmental and biotic factors.

The rarer stones-in-current animals are shown in Table 2.

THE FAUNA IN RELATION TO THE NON-BIOLOGICAL ENVIRONMENT

(a) *Size of stone sampled*

The variation in surface area of the stones whose fauna is described is summarized in Table 3. Correlations between stone-size and density/1000 cm^2 of the species found on half or more of the stones in any sample series were estimated using the Spearman Rank Correlation test. All the results could not be lumped together for the test as seasonal

Table 2. *The occurrence of animals not shown in Table* 1

Group	Sampling point						Month			
	52	54	54a	55	55a	56	October	January	April	August
Coelenterata										
Hydra sp.	+	.	.	.	.	+	+	+	.	.
Turbellaria										
Planariidae	+	.	+	.	.	.	.	.	.	+
Nematoda										
?Rhabditidae	+	.	.	.	+	+	+	.	+	+
Oligochaeta										
Lumbricid	.	+	.	.	.	.	.	+	.	.
Tubificid	+	.	.	.	.	.	+	.	.	+
Limnodrilus sp.	.	.	.	.	.	+	+	+	.	.
Pristina sp.	.	.	.	.	.	+	+	+	+	.
Naididae	+	+	.	.	.	+	+	+	+	+
Cladocera										
Daphnia sp.	+	.	.	.	.	.	.	.	.	+
Simocephalus spp.	.	+	.	+	.	+	+	.	.	+
Macrothrix sp.	.	.	.	+	.	.	.	+	.	.
Diaphanosoma sp.	.	.	.	.	.	+	.	+	.	.
Bosmina sp.	.	.	.	.	.	+	+	.	.	.
Chydorus sp.	.	+	.	.	.	.	+	.	.	.
Copepoda										
Diaptomus sp.	.	.	.	.	.	+	.	+	.	.
Cyclops sp.	+	+	+	+	.	+	+	+	+	+
Paracyclops sp.	.	.	.	.	+	.	.	.	.	+
Ostracoda										
Cypridopsis sp.	+	+	+	+	.	+	+	+	+	+
?*Megalocypris* sp.	+	.	.	.	.	+	+	.	.	.
Pionocypris sp.	+	.	.	.	.	+	+	.	.	.
Stenocypris sp.	+	.	.	.	.	.	+	.	.	.
Ilyocypris sp.	+	+	.	+	.	+	+	.	.	.
Cyprilla sp.	+	+	.	+	.	+	+	.	.	+
Decapoda										
Caridina nilotica (P. Roux)	.	.	.	.	.	+	.	.	+	.
Ephemeroptera										
Ephoron sp.	.	.	.	+	.	.	+	.	.	.
Baetis bellus Barnard	.	.	.	+	.	+	+	.	+	.
Centroptilum excisum Barnard	+	+	+	+	+	+	+	.	+	+
C. ?*flavum* Crass	.	.	.	+	.	.	.	+	.	.
Centroptiloides ?*bifasciatum* (Lestage)	.	+	.	.	.	.	.	+	.	.
Pseudocloeon maculosum Crass	+	+	.	+	+	+	+	+	+	+
Baetid sp. nov.	.	.	.	+	.	.	.	+	+	.
Prosopistoma ?*crassi* Gillies	+	.	.	+	+	+	+	.	+	+
Hemiptera										
Nychia marshalli (Scott)	+	.	.	.	.	.	+	.	.	.
Micronecta sp.	.	.	.	+	.	.	+	.	.	.
Trichoptera										
Aethaloptera ?*maxima* Ulmer	+	+	.	+	.	+	+	+	+	.
Ecnomus sp.	+	.	.	+	.	.	+	.	+	+
?*Trichosetodes* sp.	+	.	.	.	.	.	+	.	.	.
?*Athripsodes* sp.	.	.	+	.	.	+	.	+	.	+
Pseudoleptocerus sp.	+	.	+	+	+	+	+	+	+	+
Leptocerid	.	.	.	+	.	.	.	.	+	.
?*Adicella* sp.	.	.	.	.	.	+	+	.	.	.
Polycentropid	.	.	.	+	.	.	.	+	.	.
Coleoptera										
Helminthopsis elongata Delève	.	.	.	.	.	+	.	+	.	.
Pachyelmis rufomarginata nigra Delève	+	+	+	.	+	.	+	+	+	+
?*Pachyelmis* larvae	+	+	+	.	+	+	+	+	+	+
Stenelmis gades Hinton	+	+	+	+	+	+	+	+	+	+
Aulonogyrus sp. larvae	+	+	.	+	.	+	+	+	+	+
Hydraenid	.	.	+	.	.	.	.	.	.	+
Hydraenid larvae	.	.	+	.	.	+	.	.	.	+
Diptera										
Simulium gariepensis de Meillon	.	.	.	.	.	+	.	.	+	.
S. nigritarsis Coquillet	+	.	.	.	.	.	.	.	.	+
Pentaneura sp.	+	+	+	.	+	+	+	+	+	+
Corynoneura sp.	+	+	+	+	+	+	+	+	+	+
Atrichopogon type larvae	+	.	.	+	.	.	+	.	.	.
Bezzia type larvae	+	.	.	.	.	+	+	.	.	.
Empididae	.	.	.	.	.	+	.	.	.	+
Ephydrid	.	.	+	.	.	.	.	.	+	.
?*Limnophora* sp.	.	.	.	.	.	+	+	.	.	.
Mollusca										
Pisidium sp.	+	.	.	+	+	+	+	+	+	+

changes in density and changes in density due to sampling point could not be eliminated. Because Station 54 was not in a permanent stony run and had a peculiar fauna (see below), data from this sampling point were not used in correlation tests. For each species there was therefore a maximum of fourteen sample series (four each for Stations 52 and

56, two for Station 54a, three for Station 55 and one for Station 55a) in which the correlation between stone size and numbers/1000 cm² could be tested.

Table 3. *The surface area (square centimetres) of the stones whose fauna was counted*

Station no.	Mean	Range
52	792	392–1264
54	648	280–1080
54a	615	331–1167
55	855	400–1408
55a	791	570–1154
56	875	328–1698

The species whose densities were significantly correlated with surface area of stones in any of the correlation tests are shown in Table 4. In all animals shown in Table 4 the proportion of correlation tests with significant results was too low to warrant a conclusion that the density of any species was related to the surface area of the stones.

Table 4. *The correlation between surface area of stone and number of individuals per* 1000 *cm² of stone surface for species showing significant* ($P>0{\cdot}95$) *correlations*

Species	No. of correlation tests	No. of significant positive correlations	No. of significant negative correlations
Baetis glaucus	14	0	1
Choroterpes (*Euthraulus*) sp.	7	2	0
?*Caenodes* sp.	10	0	1
Amphipsyche scottae	10	1	2
Cheumatopsyche thomasseti	14	0	2
Hydropsychid juveniles	9	0	2
Orthotrichia sp.	10	1	0
Elmid larvae—?*S. gades*	5	0	1
All Simuliidae	14	1	0
Orthocladiinae	11	1	1
Burnupia sp.	13	1	1
Whole fauna	14	0	1

Such is the nature of the available data and the test used that had any species density often shown a significant correlation with stone surface area, then surface area would have been an unusually important factor in the species' choice of habitat. It would have meant that surface area was more important than, for instance, current speed, shape of stone and the way the stone was resting on the river bed. In South African rivers there certainly are animals such as the large mayflies *Centroptiloides bifasciatum* (Lestage) and the Oligoneuriidae which are found mainly under large stones, but these stones, being too large to lift from the water single-handed, were not included in the present study.

(b) *Stone shape*

In the field *Caenodes* sp., *Choroterpes* (*Euthraulus*) sp. and *Gomphocythere* sp. were found mainly on those stones with a cavity under the side away from the direction of flow. The observation that these three species tended to occur together was confirmed by the data for Station 52, in which the correlation between numbers of individuals belonging to the three groups was positive and significant in sample series. At other sampling points

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one or other of these three animals was usually rare but correlations between pairs from the three groups were always significant and positive. *Choroterpes* (*Euthraulus*) is very similar in body form to the European *Habroleptoides modesta* (Hagen) which Ruttner (1963, p. 239) illustrates as an example of a cavity dweller. In the Vaal Dam Catchment (Chutter 1967) *Choroterpes* (*Euthraulus*) was often extremely abundant under the stones out of the current. Other animals were not obviously affected by the shapes of the stones.

(c) *Temperature*

All readings of water temperature were made in obviously moving but not broken water, except at Station 53 where readings were made in a large pool about a yard from the bank. The water temperatures are summarized in Table 5. Comparable records are so few that definite conclusions about water temperature changes along this stretch of the river can not be drawn, though temperatures at Station 56 tended to be higher than those at Stations 51 and 52.

Table 5. *Summary of day-time water temperatures (°C) in the Vaal River between the Vaal Hartz Diversion Weir and Barkly West*

(a) The range of temperatures recorded on field trips

Field trip	Minimum	Maximum
October 1963	20	23
January 1964	23	27
April 1964	14	18
August 1964	9·7	13

(b) Comparable temperature records

Station	Date	Time (hours)	Temperature (°C)
51	15 October 1963	17.00	24·3
53	16 October 1963	17.00	23·3
56	17 October 1963	17.00	22·4 (cloudy weather)
51	28 January 1964	17.30	25·5
52	29 January 1964	17.30	25·0
53	29 January 1964	16.30	26·7
56	30 January 1964	17.30	25·9
52	30 January 1964	09.30	23·0
54	29 January 1964	09.30	24·2
56	31 January 1964	09.30	24·3
51	28 April 1964	16.30	14·8
52	29 April 1964	16.30	16·3
56	30 April 1964	16.30	17·5

The South African Weather Bureau maintains weather stations at Kimberley and in the Vaal Hartz irrigation area. Station 56 (Barkly West) is about 30 km west of Kimberley, and the Vaal Hartz weather station is about 20 km north of Warrenton. Comparison of air temperature data (obtained from the Monthly Weather Reports issued by the South African Department of Transport) from these two weather stations showed that:

(a) the mean normal monthly temperature was about 0·5° C higher at Kimberley than at Vaal Hartz,

(b) the minimum average daily temperature per month and the lowest temperatures recorded each month were about 2° C lower at Vaal Hartz than at Kimberley, and,

(c) there was little difference in the maximum average daily temperatures per month or the highest temperatures recorded each month.

This means that air temperatures probably did not fall quite as low at Station 56 as they did at Station 51 and the other stations close to Warrenton. However, maximum air temperatures were probably about the same along the whole of this stretch of the river. This small difference in air temperatures indicates that water temperature differences are unlikely to be large.

The seasonal occurrence of animals is often ultimately due to the seasonal variation of the temperature, but the point to be considered here is whether or not the station to station variation in the fauna can be ascribed to temperature changes along the river. Since temperature changes in this restricted stretch of the Vaal River were small it is best to compare the fauna of the uppermost sampling point, Station 52, with that of the lowermost, Station 56, to assess whether faunal differences may have been due to temperature.

Of the animals shown in Table 1, *Macronema capense* was the only species not recorded at both stations. In the upper Vaal River (Chutter 1967) and in the rest of southern Africa (K. M. F. Scott, personal communication) the distribution of this species is patchy and not apparently related to temperature. Among the animals found at both stations there were several which were far more abundant at one station than at the other. *Moina* sp., *Neurocaenis* sp., *Amphipsyche scottae*, *Cheumatopsyche thomasseti* and *Simulium adersi* were all more abundant at Station 56, where the water was probably warmer, than at Station 52. However, all these animals were recorded in large numbers in the upper Vaal River (Chutter 1963, 1967) where temperatures were considerably lower than they were at Station 52, so that temperature was not the factor restricting the numbers of these animals at Station 52. Species more abundant at Station 52 than 56 were *Gomphocythere* sp., *Simulium chutteri*, *S. damnosum* and *Burnupia* sp. There is some evidence (Chutter 1968) that *Gomphocythere* and *Burnupia* numbers were related to the amount of silt and sand in the river bed. *Simulium damnosum*, having been recorded in tropical Africa (Wanson & Henrard 1945; Le Berre 1966), lives in warmer water than that at Station 56. The largest numbers of *S. chutteri* were found at sampling points between Stations 52 and 56 (Table 1). They were consequently thriving at sampling points where the temperature was very close indeed to that at Station 56 and it hardly seems likely that the low numbers of *S. chutteri* at Station 56 were due to unfavourable temperature.

It may therefore be concluded that temperature differences were unlikely to have been responsible for the observed considerable variation in the stones-in-current fauna in this part of the river.

(d) *Rainfall, flow and water level fluctuations*

The seasonal distribution of the rainfall at the Kimberley and Vaal Hartz weather stations is the same, though the Kimberley normal annual rainfall (420 mm) is about 20 mm less than that at Vaal Hartz. The area is one of summer rainfall (Fig. 3) and during the study period there were heavy rains in April and November 1963 and in March 1964.

The flow of the river (Fig. 4) followed the rainfall cycle, the greatest flows being recorded in the summer. However, local rainfall is not responsible for the major flow fluctuations in this part of the river. They are largely governed by the rate at which water is released from Vaal Dam, about 580 km upstream. There is, however, an important local influence on the flow of the river. Little irrigation takes place during week-ends, and the unwanted water is allowed to flow down the river instead of being diverted to the irrigation scheme. Consequently there are peak flows in the Vaal on Saturdays (Fig. 5) followed by a sudden drop in the flow on Sundays as water is diverted to meet the

Monday irrigation demand. This weekly pattern of daily flow was masked by high flows and was not apparent when there was very little irrigation during the week (Fig. 4). It was, however, apparent for the greater part of the time that the river was being studied. Such a pattern is unusual in South African rivers in the summer rainfall area, as their flow is relatively stable in the dry season.

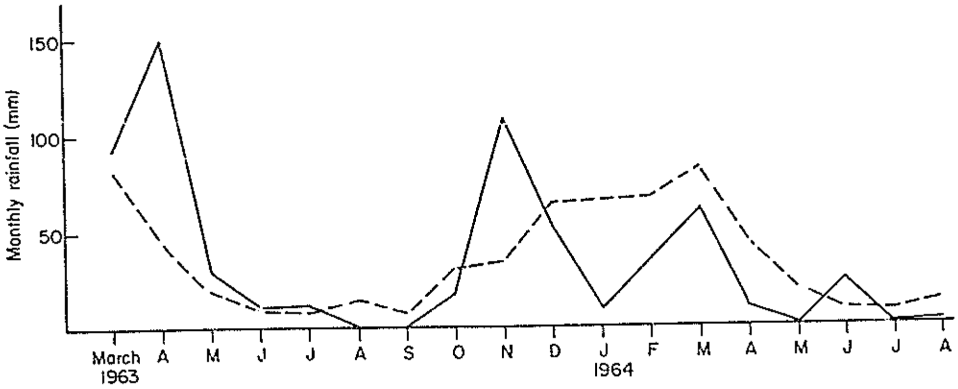

FIG. 3. The rainfall at the Vaal Hartz weather station. ——, Actual rainfall; - - - -, normal rainfall.

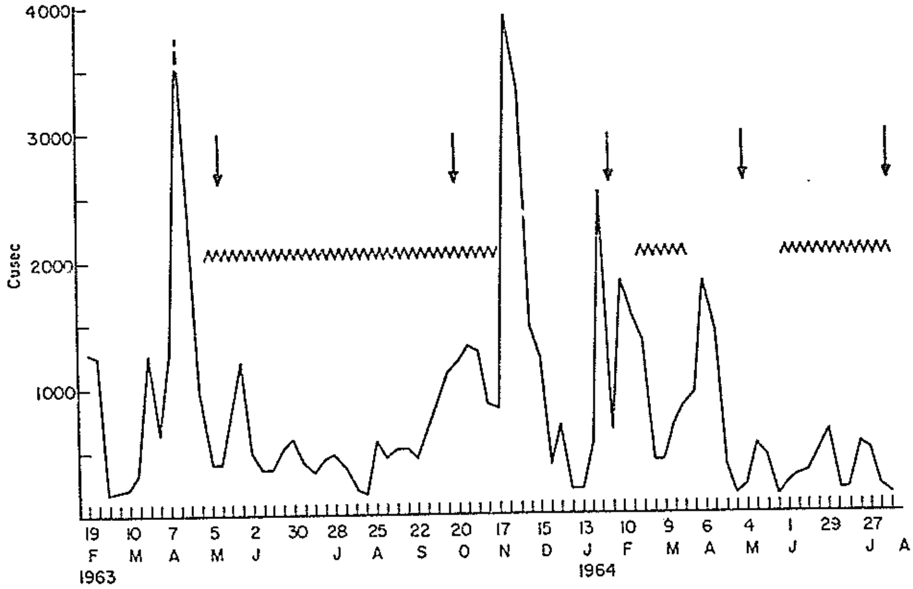

FIG. 4. The average daily rate of flow, week by week, of the Vaal River at the Vaal Hartz Diversion Weir, based on daily readings at 8 a.m. VVV, periods with a peak week-end flow, arrows show when field trips were undertaken.

The river was widest at Station 52, narrowest at Station 54a and of intermediate width at Stations 55, 55a and 56 (descriptions of sampling points, p. 535). Changes in water level due to the weekly fluctuation in daily flows would be greatest where the river was narrowest (Station 54a) and least where the river was widest (Station 52).

The difference between the rainfall at Kimberley and Vaal Hartz was very small and therefore unlikely to account for faunal differences in the Vaal River. Due to the unusual flow pattern there are three important aspects to the relationship between flow and fauna. Firstly there is the fluctuation in water level due to the weekly flow pattern, which is best examined by comparing the fauna of Stations 52 and 54a. Secondly there is water level fluctuation due to seasonal changes in flow. This results in biotopes, such as that at Station 54, which are aquatic only in some seasons. Thirdly there are floods.

The main differences between the fauna of Stations 52 and 54a were that *S. chutteri* and *Hydropsyche* sp. were more abundant at Station 54a, and *Simulium adersi*, *S. damnosum*, *S. mcmahoni* and *Macronema capense* were more abundant at Station 52 (Table 1). *Amphipsyche scottae* was found in low numbers at Station 52, but was not recorded at Station 54a. These animals were all Simuliidae or Hydropsychidae and all strain their food from the water. (The only other animal in which there was a regular and

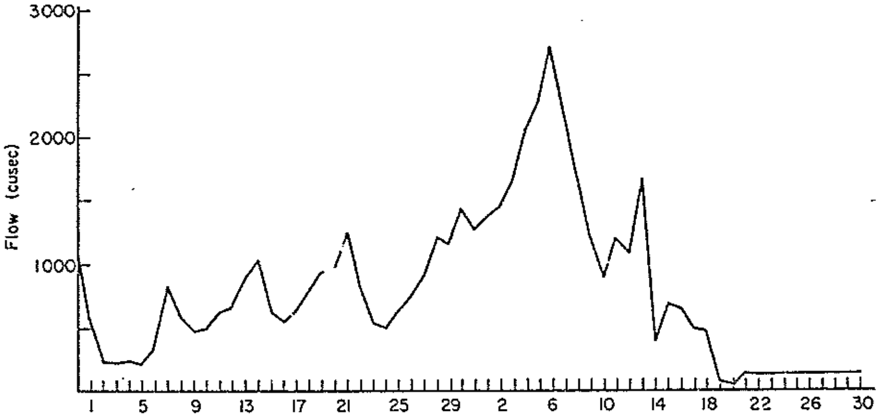

FIG. 5. The flow of the Vaal River at the Vaal Hartz Diversion Weir at 08.00 hours in March and April 1964.

consistent large difference in mean density at the two sampling points was *Neurocaenis* sp. However, the stone to stone variability in the numbers of *Neurocaenis* was so great that the difference in mean numbers was not significant when tested using the Mann–Whitney U Test.) The only large environmental difference between the two stations appeared to be the amount of water level fluctuation and these faunal differences may be associated with this.

The densities of the animals at the sampling points further downstream than Station 54a, where the fluctuation in water levels would be expected to be intermediate between those at Stations 52 and 54a, were not intermediate between those recorded at these two stations. Possibly these sampling points were sufficiently far away from Stations 52 and 54a for other factors, such as distance from the Diversion Weir (which one would expect to affect the amount of microplankton in the water), and turbidity (which affects algal growth and hence the food resources of the biotopes) to have an appreciable effect on the fauna.

The biotope sampled at Station 54 was part of a side channel of the river which dried up when flows were low. There was a strong flow of water at this sampling point in October 1963 and January 1964, but it was dry in April and August 1964. From a consideration of the flow pattern of the river prior to these field trips (Fig. 4) it was estimated that in October 1963 water could have been permanently flowing over the stones for a maximum of 2 months, while in January 1964 it could have been permanently flowing for only 2 weeks. During these 2 weeks there was a minor flood.

The fauna recorded at Station 54 in both October and January (Table 1) was unusual and its composition reflected the temporary flow there. In October *Simulium chutteri*, *Baetis glaucus* and Chironomidae were the only abundant animals and many animals which were widespread or abundant elsewhere, such as the other Ephemeroptera, the caddis flies and the Mollusca, were rare or not recorded. The community therefore resembled that recorded during the early stages of recolonization of an intermittently flowing stream in the Western Cape, where Simuliidae, *Baetis* spp. and Chironomidae were the important early re-invaders (Harrison 1958a, Table 40). Among the rarer animals at Station 54 the leech ?*Salifa perspicax* and the parasitic Nematoda (Mermithidae) are of interest. ?*S. perspicax* was found to eat *Simulium* larvae and the Mermithidae were *Simulium* parasites, so their presence was mainly related to the very large numbers of *Simulium* larvae.

In January the fauna was similar to the October fauna in that *Baetis glaucus* and Simuliidae were the only really abundant animals, but *Simulium chutteri* was very much less abundant than in October. The lower numbers in January could have been due either to the short period that the water had been flowing in the run, to the flood that occurred during that short period, or possibly to a reduction in the amount of food available which is discussed below (p. 551). The most important point shown by the fauna at Station 54 is that rapids in temporarily flowing parts of the river bed may be important sites of massive *S. chutteri* larval development.

An interesting observation was that *Baetis glaucus* was an early re-invader of this temporary biotope. Among the animals recorded at Warrenton, *B. glaucus* stood out as the species whose numbers were least variable from stone to stone in single sample series. It was the animal whose numbers varied least in Chutter & Noble's (1966) Surber sampler study. Waters (1965) found that a large part of the invertebrate 'drift' in American streams was made up of a *Baetis* species. It is therefore not at all unlikely that *B. glaucus* 'drifts' on a large scale in South African streams. An animal which readily 'drifts' might be expected to be comparatively evenly distributed in biotopes in the current, and also to colonize newly covered parts of the river bed.

The effect of floods on the stony run fauna has often been described in South Africa (Allanson 1961; Oliff 1960a, b, 1963; Oliff & King 1964) and elsewhere (Allen 1951; Jones 1951). The conclusion, based on field observations made with various sampling techniques, of these workers was that floods drastically reduce the faunas of stones in flowing-water biotopes. Macan (1963, pp. 122, 130–1) found it hard to believe that floods would wash animals out of stable stony runs, since he would expect them to crawl into places suitably protected from the increased velocity of flood waters. In the Vaal at Warrenton high flows occurred in the latter part of November 1963 and in the week before sampling in January 1964 (Fig. 4). Significant decreases in density of several species or groups of animals were found after the floods (Table 1) but species showing a decrease at one sampling point often showed either no significant change or even sometimes a significant increase in density at other sampling points. The only species and groups which had a January density significantly smaller than the October density at all sampling points were *Simulium damnosum*, Chironomini and hydropsychid juveniles. Several other species had significantly smaller populations in January than in October only at the sampling points where they were most abundant. These were *Neurocaenis* sp. (Station 56), *Amphipsyche scottae* (Stations 55 and 56), *Cheumatopsyche thomasseti*

(Stations 52 and 56), *Hydropsyche* sp. (Station 55), *Catoxyethira* sp. (Station 52) and *Simulium mcmahoni* (Station 56). Because of the 3-month interval between samples, it is impossible to ascribe any of these significant changes in density solely to the floods, since the life-cycle of the species might in any case result in a mid-summer larval population smaller than the spring population. Indeed this would appear to be the case in *Cheumatopsyche thomasseti*, thousands of adults of which were present at Station 56 in January. Such numbers of adult *C. thomasseti* were not seen on other sampling visits.

Floods could not be shown to have had any effect on the density of *Simulium chutteri* populations. At Station 52 the January density was significantly larger than the October density, in spite of the minor flood during the fortnight before the January field trip (Fig. 4), but at Station 55 the January *S. chutteri* density was significantly smaller than the October density. Densities at Station 54 were markedly influenced by the temporary nature of the biotope (see above) and therefore contribute nothing to the effect of floods on the *S. chutteri* densities. According to local information the numbers of adult *S. chutteri* were high from before the October sampling trip until the end of November, when there was a period of cooler, rainy weather lasting nearly a fortnight. In January the number of adult flies seen near the river was not high.

Table 6. *Current speeds (cm/sec) recorded in stony runs in the Vaal River from Warrenton to Barkly West*

Station		October	January	April
52	Maximum	114	112	68
	Minimum	33	33	41
	Mean	71	63	56
54	Maximum	152	76	–
	Minimum	36	33	–
	Mean	79	53	–
54a	Maximum	–	–	73
	Minimum	–	–	21
	Mean	–	–	53
55	Maximum	112	104	73
	Minimum	46	56	21
	Mean	89	81	56
56	Maximum	89	96	66
	Minimum	31	41	24
	Mean	56	66	48

The meter was defective in August.

(e) *Current speed*

The current speed (Table 6) at most sampling points followed the flow of the river (Fig. 4), higher mean speeds being recorded when the flow was greater. Thus the flow was greatest in October, lower in January, and lowest in April, and at all sampling points except Station 56 the highest mean current speed was recorded in October and the lowest in April. To judge by the flows (Fig. 4) current speeds were even lower in August than they were in April.

The recorded speeds were variable but suggest that the fastest overall speed was at Station 55 and the lowest at Station 56. It was not possible, on account of the variability of the available measurements, to arrange the remaining stations in order of current speed.

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In October and January current speeds at Station 55 were higher than elsewhere. *Hydropsyche* sp. density at this station appeared to be related to current speed. In October and January this animal was most abundant at Station 55, less abundant at Station 52 and not recorded at Station 56. In October this density change followed current speed changes between the three sampling points, but even in January the correlation began to break down as the current speed at Station 56 was of the same order as that at Station 52, but *Hydropsyche* was present at Station 52 and not recorded at Station 56. However, as will be discussed later, the density of this species followed that of *Simulium chutteri* and there was no evidence that *S. chutteri* numbers were highest where current speeds were highest.

Current speeds were variable at Station 56, but in October they were a lot, and in April a little, slower than elsewhere (Table 6). The mean densities of *Amphipsyche scottae*, *Cheumatopsyche thomasseti* and *Neurocaenis* sp. were higher at Station 56 than elsewhere. However, counts of these animals often varied considerably from stone to stone. At Station 56 in October the mean number of *Cheumatopsyche thomasseti*/1000 cm^2 was 210 (Table 1), but this was largely due to one stone with 1329 individuals per 1000 cm^2. Without this stone the mean density of *C. thomasseti* in this sample series was seventy-seven per 1000 cm^2. The Mann–Whitney U Test consequently showed that there was no significant difference between the size of the populations at Stations 52 and 56. In *Amphipsyche scottae* the density in October was highest at Station 56, but then higher at Station 55 than at Station 52, so that density was not inversely related to current speed. It is therefore unlikely that current speed was the most important factor bringing about the high densities of these animals at Station 56.

Slow current speeds probably played a part in the appearance of a profusion of epiphytic growths in August (see below). Although the numbers of several types of animals increased, this was in nearly every case related to the increase in the epiphytes (see p. 552). However, the August increase in the numbers of Mermithidae and *Simulium* larvae parasitized by Mermithidae was not directly associated with the increase in the epiphytes, for the numbers of these animals increased at Station 55a where there was no large increase in the epiphytes. It is therefore possible that the large numbers of Mermithidae then were due to lower current speeds, though it should be stressed that it is equally possible that this seasonal change in abundance was related to the mermithid life-cycle.

(f) *Water chemistry*

Sampling points used during the preliminary survey (May 1963) did not all coincide with those used later, and replicate water samples were not taken. However, certain results were of interest and are shown in Table 7. By comparison with the Great Berg River (Harrison & Elsworth 1958) and with the Tugela River (Oliff 1960a) nitrate and Kjeldahl nitrogen figures were unusually high. It is obvious from the analyses that the source of these large amounts of nitrogenous compounds was above the Vaal Hartz Diversion Weir. The concentration of total nitrogen did not increase as the river passed Warrenton. Free and saline ammonia increased in concentration from Station 51 to Station 54 and organic nitrogen decreased sharply but less evenly. However, these changes were not substantiated in later sample series and they were therefore probably the chance outcome of snap sampling.

The concentrations of forms of nitrogen found during the main study (Table 8) were far lower than those recorded during the preliminary survey (Table 7). Apart from one

Table 7. *Concentration (ppm) of forms of nitrogen in water samples taken during a preliminary survey of the Vaal River at Warrenton in May* 1963

	Station 51	Just above Warrenton Village	Just below Warrenton Village	Station 53	Station 54a	Station 54
Ammonia–N	ND	ND	0·1	0·3	0·5	1·0
Nitrites	Trace	ND	ND	ND	ND	ND
Nitrates	1·74	1·58	1·66	1·74	1·90	1·85
Kjeldahl–N	1·07	1·30	0·60	1·10	0·90	1·10
Total nitrogen (Kjeldahl–N + NO_2 + NO_3)	2·81	2·88	2·26	2·84	2·80	2·95
Organic nitrogen (Kjeldahl–N less ammonia–N)	1·07	1·30	0·50	0·80	0·40	0·10

ND, not detectable.

Table 8. *A summary of water analysis results for the Vaal River from the Vaal Hartz Diversion Weir to Barkly West*

(a) Mean figures for all four sampling occasions

	All sampling points	Station 51	Station 56
Free and saline ammonia–N (ppm N)	0·11	0·12	0·10
Nitrites (ppm N)	0·003	0·005	0·001
Nitrates (ppm N)	0·12	0·19	0·03
Organic–N (ppm N) (Kjeldahl–N less ammonia–N)	0·59	0·71	0·42

(b) Mean figures based on analyses in January, April and August 1964

	All sampling points	Station 51	Station 56
Total alkalinity (ppm $CaCO_3$)	92	89	94
Total hardness (ppm $CaCO_3$)	134	131	142
Ca-hardness (ppm $CaCO_3$)	85	87	86
Chloride (ppm Cl^-)	20	18	21
Sodium (ppm Na^+)	26	24	29
Potassium (ppm K^+)	6	6	6

(c) Figures for separate sampling months

	Sampling month	Mean for All sampling points	Station 51	Station 56
Total nitrogen (Kjeldahl–N + NO_2 + NO_3) (ppm N)	Oct.	0·90	1·08	0·43
	Jan.	0·65	0·71	0·50
	April	0·86	1·16	0·55
	Aug.	0·87	1·16	0·68
Turbidity (ppm SiO_2)	Oct.	86	103	55
	Jan.	52	74	44
	April	155	234	120
	Aug.	32	36	22
Total dissolved solids (ppm)	April	181	151	208
	Aug.	235	246	280
Sulphate (ppm SO_4^{--})	Jan.	135	145	130
	April	16	11	24
	Aug.	47	46	52

instance when the replicate nitrate analysis figures were 0·11, 0·04, 0·06 and 1·47 ppm, there was very little variation in the results obtained from the four separate water samples taken on each visit to each sampling point. Between Stations 51 and 56 there were no regular increases or decreases in the concentrations of the various forms of nitrogen. However, the concentrations of all forms of nitrogen were lower at Station 56 than they were at Station 51. In January, after a minor flood (Fig. 4), the concentrations of all forms of nitrogen were lower than at other times, and this is reflected in the total nitrogen figures (Table 8c). The pH of the water was rather high (Table 9) and varied little, indicating with the high total alkalinity (Table 8) that the water was well buffered. Turbidities were high in October, January and April, but at all times the turbidity of the water decreased between Station 51 and Station 56 (Table 8). This decrease was sufficient to be noticed in the field without directly comparing water samples. Sulphates were recorded in very much higher concentrations in January 1964 than in April and August. They probably originated in the gold mining areas of the southern Transvaal, whence high sulphate waters are known (Chutter 1963, Table 1). Sampling was too infrequent to arrive at more detailed conclusions and the main purpose of Table 8 is to give an idea of the type of water in this part of the Vaal River.

Table 9. *The pH in the Vaal River from the Vaal Hartz Diversion Weir to Barkly West, based on field readings in October* 1963, *January, April and August* 1964

Station No.	Maximum	Mean	Minimum
51	8·6	8·5	8·4
52	8·6	8·4	8·3
53	8·8	8·6	8·4
54/54a	8·8	8·6	8·5
55/55a	8·6	8·5	8·4
56	8·5	8·4	8·3

A large part of the total nitrogen in the water was in the form of organic nitrogen (Table 8) indicating that there may have been rather large amounts of microplankton in the water. The impoundment behind the Vaal Hartz Diversion Weir would provide suitable sheltered conditions for this to develop. Harrison (1958b) found that mild organic pollution led to the development of large *Simulium* populations some way downstream from the source of the polluting material, and this he ascribed to the development of large quantities of microplankton on which the *Simulium* were feeding. It is therefore distinctly possible that the large *Simulium* populations from Stations 52 to 55 (Table 1) developed because there was an ample food supply. At Station 56 where the amount of organic nitrogen in the water was lowest *Simulium* populations tended to be smallest. However, the availability of microplankton food was obviously not the only factor governing the abundance of the Simuliidae for the sampling point nearest to the Diversion Weir (Station 52) did not have the largest *Simulium* populations.

Total nitrogen concentrations were lowest in January possibly due to the floods of the previous fortnight (Fig. 4). There were no really large *Simulium* larval densities in January and it could be that suitable food was less abundant then than at other times.

No clear relationships between the other chemical features and the fauna were found. However, the low turbidity of the water in August, a physical characteristic shown with the chemical features in Table 8, was very important as the greater transparency of the water then helps to account for the appearance of large growths of epiphytic algae, which did affect the fauna.

(g) *Silt and sand*

The amount of silt and sand moving down the Vaal River in the study area was not measured. However, the Vaal Hartz Diversion Weir could act as a large silt and sand trap and there is probably little silt and sand carried down the river immediately below the weir. The river bed is mainly stony at Warrenton but from Windsorton to Barkly West it is sandy. While this change is undoubtedly related to the river profile (Fig. 2), it does seem reasonable to assume that the further away from the Weir the greater will be the amount of silt and sand moving down the river bed due to local soil erosion.

There is considerable evidence that the occurrence of certain animals is related to the presence of large or small amounts of silt and sand (Chutter 1968). It is likely that the very large numbers of *Neurocaenis* at Station 56 were associated with the larger amounts of silt and sand there. There is unfortunately no evidence on whether the Simuliidae are or are not affected by the amount of silt and sand passing through their habitat.

BIOTIC FACTORS AND THE COMPOSITION OF THE FAUNA

(a) *Life history*

In the aquatic insects with aerial stages it frequently happens that the developmental stages are present in rivers only at certain times of the year. The life histories of very few African aquatic insects are known, but there were certain insects in the lower Vaal River whose seasonal changes in abundance were probably primarily related to life history phenomena. *Neurocaenis* sp. was not found at all in the samples collected in August (Table 1) and this was probably due to its life history, as it also vanished from the Berg River (Harrison & Elsworth 1958, Table 16 as *Tricorythus*) and from the Tugela River (Oliff 1960a, Fig. 8a) in the winter. *Centroptilum medium* was found mainly in January and not at all in October and August. This pattern of occurrence was also found in other parts of the Vaal River (Chutter 1963, 1967) and is therefore probably due to life history.

The scarcity of hydropsychid juveniles in August (Table 1) suggests that the Hydropsychidae encountered in this part of the river do not have winter-hatching eggs. In January very large numbers of adult Hydropsychidae were found. This, taken with the rather low numbers of *Amphipsyche scottae*, *Cheumatopsyche thomasseti* and hydropsychid juveniles occurring then, suggests that the greater part of the population was in the adult stage at this time. Porifera had numerous gemmules in October, were very scarce in January, not recorded in April, and were found at three of the four sampling points in August, when a few gemmules were found in only one colony. It would therefore appear that the scarcity of Porifera in January and their absence in April was due to a life-cycle in which the summer and autumn are spent in the resting (gemmule) stage. As would be expected ?*Sisyra* sp. (Neuroptera, Sisyridae) larvae were found only where Porifera were found. The cladoceran *Moina* sp. was not recorded anywhere in August 1964, and this is typical of the seasonal occurrence of this animal in South African rivers, where it has previously been recorded mainly in the summer (Chutter 1963). It is perhaps surprising to find this cladoceran in a stony run fauna: its presence was almost certainly due to its being swept through the stony runs, rather than living there permanently.

(b) *Algae and diatoms*

Algae were not seen on the two sampling visits paid to Station 54. At the other stations short dense growths of algae were present on top of at least some of the stones in October

1963, January and April 1964. These growths consisted mainly of *Cladophora*, *Stigeoclonium* and an alga belonging to the Oedogoniales. In August 1964 there were thick brown mat-like growths of algae on top of all the stones at Stations 52 and 54a; at Station 55a the stones were covered with a very thin, extremely slimy layer, presumably diatoms, and at Station 56 the mat-like growths were again found. Trailing or conspicuous green algae were not observed at Stations 52 and 55a, but they were present at Station 54a and were abundant at Station 56. The brown mat-like growths at Stations 52, 54a and 56 were made up largely of the diatoms *Cymbella* sp. and *Synhedra* sp., while *Stigeoclonium* sp. was also found at all three stations. At Station 56 there was a lot of *Cladophora* sp. and some *Spirogyra* sp. *Cocconeis pediculus* Ehrenberg, a diatom seldom recorded in South Africa, was abundant at Station 56 where it was growing epiphytically on the *Cladophora*. Cyanophyta, mainly *Oscillatoria* sp., were present at all three sampling points but were not abundant.

Environmental changes which help to explain the appearance of algae and diatoms in large quantities in August were the low turbidity of the water (Table 8) and the small flow of the river (Fig. 4). The small flow would result in lower current speeds and shallower water which together with the low turbidity provided suitable conditions for the algae and diatoms. The massive growths had disappeared by October, probably due to increasing turbidity and flows. There was no obvious reason why the algae were not as abundant at Station 55a as they were at the other sampling points.

The short tufty growths of algae found in months other than August were the habitat of the caddis *Catoxyethira* sp. n. and Chironomini. As a result of this preference for alga-covered stones there was a significant positive correlation between the densities of *Catoxyethira* and Chironomini from series of samples analysed at single sampling points on the same day. However, the Orthocladiinae, even though their density increased sharply in August when thick mats of diatoms and algae appeared, were equally abundant on stones with and without algae at other times of the year.

Animals found on and in the growths in August were *Nais* sp., *Chaetogaster* sp., *Catoxyethira* sp. n., Chironomini and Orthocladiinae and the numbers of these animals were consequently higher at Stations 52, 54a and 56 than they were at other times of the year (Table 1). Although some of these animals (*Catoxyethira*, Chironomini and Orthocladiinae) are herbivores, it is obvious that there was a vast unexploited food supply in August. This may be because it developed at the end of winter, which may be a time when most animals are in advanced juvenile stages, but few are in the reproductive stage. If this is true, late winter would be a time of little recruitment to larval populations and the herbivores would consequently not be in a position to increase rapidly in response to the increased food supply.

Simulium larvae and pupae were not found attached to the growths, which means that in August the area available for *Simulium* attachment was lower than at other times. It seems likely that *Simulium* larval populations would have been larger in August had the stones not been covered by algae and diatoms.

(c) *Mermithidae and* Simulium chutteri

Most of the Mermithidae recorded during this study probably left their *Simulium* hosts only in the sample bottle, for free-living specimens were not seen in the field and pickled material included many *Simulium* larvae with the parasites breaking out of their bodies. Large Mermithidae may easily be seen inside *Simulium* larvae and parasitized larvae were counted separately from the normal larvae (Table 1). Larvae were not dissected to look for Mermithidae and the numbers of parasitized larvae given in Table I represent the numbers of large *Simulium* larvae with large Nematoda inside them. Mermithidae were not found in *S. adersi*, *S. damnosum* or *S. mcmahoni* larvae, all the parasitized larvae belonging to *S. chutteri*.

No parasitized larvae had developed pupal respiratory histoblasts, which is in keeping with the observations of Anderson & De Foliart (1962) and Anderson & Dicke (1960) that Mermithidae prevent the pupation of most parasitized larvae. At Station 52 and 54/54a the proportion of *S. chutteri* pupae to the total numbers of Simuliidae fell as the proportion of Mermithidae rose (Fig. 6), suggesting that the Mermithidae were preventing the pupation of *S. chutteri* larvae. Mermithidae and parasitized larvae were most abundant in August. In April at Station 54a there were 1·38 *S. chutteri* pupae present for

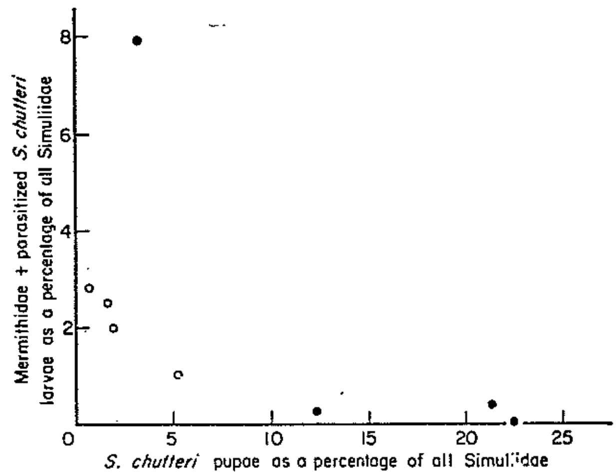

FIG. 6. The relationship between the numbers of *Simulium chutteri* pupae, *Simulium* larvae and Mermithidae at Stations 52 (○) and 54/54a (●), based on data given in Table 1.

every *S. chutteri* larva. Had the ratio between larvae and pupae been the same in August at this sampling point then 120 pupae would have been recorded and not forty-three (Table 1). It may be concluded that in August the Mermithidae were considerably influencing the size of the *S. chutteri* population. There are some instances of Nematoda eliminating Simuliidae on record in the literature. Phelps & De Foliart (1964) found that on two occasions there was a virtual elimination of *Simulium* larvae due to nematode parasites and Rubtsov (1963) reported that high infections of the parasites were sometimes followed by an almost complete disappearance of the Simuliidae for several years.

(d) *Predators of* Simulium *larvae*

The potential predators of *Simulium* larvae in the invertebrate fauna of the stones in the current were mainly Hydropsychidae. The feeding habits of these caddis larvae have not been studied in South Africa, but there are several studies from other parts of the world. Slack (1936) and Scott (1958) showed that net building Hydropsychidae are omnivorous. Kaiser (1965) found that the younger *Hydropsyche* larvae are plankton feeders, and that the older are predators with a preference for larger prey. From Kaiser's description of the feeding habit of the young larvae it is obvious that their diet is microplankton. Both the *Cheumatopsyche* and the *Hydropsyche* larvae recorded by Hynes & Williams (1962) in Uganda had eaten *Simulium* larvae. Peterson & Davies (1960) observed

Hydropsyche and *Cheumatopsyche* larvae actively preying on *Simulium* larvae and concluded that the larvae of *Hydropsyche* were the most important predators of *Simulium* larvae in Algonquin Park, Canada. Ussova (1964, p. 247) found that there were few *Simulium* larvae where there was a large number of Trichoptera.

It is perhaps at first difficult to understand how an animal which builds a net and then passively waits for food material to be swept into the net can be put forward as a predator of *Simulium* larvae which, when seen in the field, are usually firmly attached to stones or other substrata. However, *Simulium* larvae do move about a lot in the stones in current, one of the most frequently employed methods being to attach a thread to the substratum and then to drift downstream on the end of the thread. Such drifting larvae could easily be carried into a hydropsychid net. The extent to which simuliid larvae move about may be seen from the success with which various *Simulium* traps, all of which depend on larvae attaching themselves to an artificial substratum, have been developed (Wolfe & Peterson 1958; Williams & Obeng 1962).

A simple investigation of the diet of the hydropsychid larvae encountered in the study area was made by examining the foregut contents of large specimens collected in analysed samples. *Macronema capense* has a strongly toothed gizzard and the gut of the specimens examined contained large amounts of insect exoskeleton. It was concluded that large larvae of this species are mainly carnivorous and would probably readily eat *Simulium* larvae. The gizzard of *Amphipsyche scottae* was moderately strongly toothed. Its gut contained mainly exoskeletal fragments, but there were some algae present too. The gut contents of *Hydropsyche* sp. were similar to those of *Amphipsyche scottae* but its gizzard was more weakly toothed. These two animals were omnivores, possibly eating more animal food than plant food. *Cheumatopsyche thomasseti* had a weakly toothed gizzard and its gut contents were mainly algal filaments and diatoms. There were, however, also fragments of orthoclad head capsules, ?Entomostraca and ?baetid cerci. *C. thomasseti* was therefore also an omnivore, probably eating more plant food than animal food. It may be concluded that, given the opportunity, all the Hydropsychidae found in this lower part of the Vaal River would feed on *Simulium* larvae.

Other potential predators of *Simulium* larvae were the leech ?*Salifa perspicax*, the plecopteran larva *Neoperla spio* and the gyrinid larva *Aulonogyrus* sp. *Neoperla spio* and *Aulonogyrus* are known carnivores. A dissected specimen of ?*Salifa perspicax* contained numerous Simuliidae. These three predators were, however, very much less abundant than the Hydropsychidae (Tables 1 and 2).

(e) *Biotope preferenda of the fauna*

In this section correlations between the mean densities of pairs of the more abundant species or groups of animals are described (Table 10). Here the point in question is not whether certain species preferred the same stones or different stones, but whether there were particular biotopes preferred by pairs of species or preferred by one species and not by another.

The correlations were made using the Spearman Rank Correlation Test on the mean densities given in Table 1. In testing these correlations, densities of each kind of animal were ranked irrespective of month or sampling point, but data from Station 54 were not taken into account because the fauna there was unusual due to the intermittent flow. Significant correlations could therefore be due either to season or to sampling point.

The reasons for some of the significant correlations shown in Table 10 are readily apparent. *Caenodes* was significantly correlated with *Gomphocythere* and *Choroterpes* (*Euthraulus*) because these animals preferred the stones with cavities behind them (p. 542), and this preference was so strong that it masked density differences from sampling point to sampling point or from season to season. However, density differences due to both season and sampling point (Table 1) did result in there being no significant correlation between *Choroterpes* and *Gomphocythere*, although these were both cavity dwellers. *Catoxyethira* and Chironomini were significantly correlated because they preferred the stones with algae on top of them, but both these species were significantly correlated with Orthocladiinae, in spite of the fact that Orthocladiinae were not associated with stones having algae on top of them in single sample series (p. 553). Examination of Table 1 shows that these animals had the same sampling point preferences and that season was not important.

Table 10. *A trellis diagram of the significant correlations, based on arithmetic means from Table* 1, *between important species recorded from the stones-in-current biotopes of the lower Vaal River*

	Species	12	11	10	9	8	7	6	5	4	3	2	1
1	*Amphipsyche scottae*	–	–	–	0	0	0	0	0	–	+	+	
2	*Cheumatopsyche thomasseti*	–	–	0	0	0	0	+	0	0	0		
3	*Baetis glaucus*	0	0	0	0	0	0	–	0	–			
4	*Burnupia* sp.	0	0	0	0	0	0	0	0				
5	*Choroterpes* sp.	0	0	0	+	0	0	+					
6	?*Caenodes* sp.	0	0	0	0	0	+						
7	*Gomphocythere* sp.	0	0	0	0	0							
8	*Catoxyethira* sp.	0	0	+	+								
9	Chironomini	+	0	+									
10	Orthocladiinae	+	0										
11	*Hydropsyche* sp.	+											
12	All Simuliidae												
	Neurocaenis sp.	0	–	0	0	0	0	0	0	0	0	0	0

The species are numbered on the vertical axis and only the numbers are shown along the horizontal axis. Data from Station 54 were omitted when calculating correlations and only data for October, January and April were used for calculating the correlations between *Neurocaenis* sp. and the other species.

Key to sumbols: +, positive significant correlation; –, negative significant correlation; 0, correlation not significant.

The filter feeding component of the fauna clearly falls into two groups of animals whose densities were correlated with one another. The first group was Simuliidae and *Hydropsyche* which occurred together, and the second group was *Amphipsyche scottae* and *Cheumatopsyche thomasseti*. The members of each group were negatively correlated with the members of the other group, showing that the fauna either included large numbers of one group or of the other, but that large numbers of both groups were not found simultaneously at a sampling point. The original data given in Table 1 clearly illustrate these correlations and show that they were not due to season. When the faunas of Stations 52 and 54a were compared in relation to the fluctuations in water level (see above, p. 546) the same sort of difference between the filter-feeding component was found, but taking the data from all sampling points into account makes the contrast more marked as it brings in *C. thomasseti* too. Table 1 shows that *Simulium adersi*, *S. damnosum* and *S. mcmahoni* were found mainly at Stations 52 and 56, the sampling points where *Amphipsyche scottae* and *Cheumatopsyche thomasseti* were most abundant. It was *Simulium chutteri* which was positively correlated with *Hydropsyche* and negatively correlated with *Amphipsyche scottae* and *Cheumatopsyche thomasseti*. The data for Station 54, which were left out of consideration in calculating the correlations shown in Table 10, also showed that where *Simulium chutteri* densities were high other *Simulium* species were not abundant (Table 1). Here, due to the intermittent flow, the Hydropsychidae, which are evidently not as mobile as the Simuliidae, did not become established in large numbers.

The significant negative correlation between *Amphipsyche scottae* and Orthocladiinae (Table 10) was largely due to season, Orthocladiinae being most abundant in August when *A. scottae* were least abundant (Table 1). Season was also an important factor in the positive correlation between *Choroterpes* (*Euthraulus*) and Chironomini. However, leaving the August samples out of consideration, the negative correlation (Table 10) between *Neurocaenis* and *Hydropsyche* was due to different sampling point preferences. There was no obvious reason why these animals occurred in larger numbers at different sampling points, nor is it possible to account for the other significant correlations which have not been mentioned here but which are shown in Table 10. All that can be said about them is that they were not due to the animals showing preferences for the same or for different stones in single sample series.

DISCUSSION

(a) *The Simuliidae*

The first reason why the Simuliidae should occur in such large numbers in the Warrenton area and not in other parts of the Vaal River is that there the river falls rapidly (Fig. 2). Places where the current speed is suitable for *Simulium* larvae are frequent. Secondly, there is obviously sufficient food for the large larval populations. However, during the study period, there was no large and regular enrichment of the water below the Diversion Weir, to which the large amounts of food material for the *Simulium* larvae might be ascribed, in the way in which Harrison (1958b) was able to ascribe the *Simulium* outbreak in the Great Berg River at Wellington to microplankton increases due to organic enrichment further upstream. The most likely explanation is that a lot of microplankton developed in the waters held back by the Weir.

The biotope most successfully exploited by *S. chutteri* larvae was a temporary stony run (Station 54). The alteration of the natural river bed during alluvial diamond mining has probably resulted in an increase in the number of such biotopes. Moreover, associated with the gradual increase in flow from August to November (Fig. 4), there is a gradual and continuous covering of previously dry parts of the river bed. This gradual increase in flow before the coming of the summer rains is unnatural in the South African summer rainfall area and is due to the release of additional water from Vaal Dam, nearer the source of the Vaal River than Warrenton. It results in the presence over 3 months of most highly favourable *S. chutteri* larval habitats, which the species rapidly invades.

S. chutteri was found in large numbers in biotopes where fluctuations in water level, due to the weekly cycle of daily flows, were greatest. However, the numbers of several hydropsychid Trichoptera were low in these places. The large larvae of these animals would eat *Simulium* larvae if they drifted into their nets. From what is known of the feeding habits of the very small larvae it seems that they would be in competition with the large *Simulium* larvae for food. The lower numbers of Hydropsychidae where the water level fluctuation were greatest was unlikely to be due to a shortage of suitable food, stone size or current speed, but might be due to the weekly fluctuation in water level. It is likely that where the water level frequently fluctuates the area within a stones-in-current biotope that can be utilized by animals such as Hydropsychidae, which build a fixed refuge and a fixed net, is restricted. However, this did not apply to all Hydropsychidae for *Hydropsyche* was found where *Simulium chutteri* was abundant. The Simuliidae would be at an advantage in such places because they are free to move up and down with the water level.

One possible reason for the large numbers of *S. chutteri* where the fluctuation in water level was greatest is therefore that they were freed from competition for food and from predation when drifting by the majority of Hydropsychidae. This might also explain why such large numbers of *S. chutteri* occurred in the temporary stones-in-current biotopes for Hydropsychidae were rare in them. Other animals which did not occur in large numbers where the fluctuation in water level was greatest, or in the temporary biotopes, were the other *Simulium* species. In such places *S. chutteri* either competed highly successfully with these species or else did not have to compete with them at all. Insofar as *S. damnosum* is concerned it is interesting that its distribution in October, April and August and its complete absence in January is in accord with Crisp's (1956) and Wanson & Henrard's (1945) observations that fluctuating flows and water levels are unfavourable for this species.

There are clearly important differences between the larval biology of *S. chutteri* on the one hand and of the other *Simulium* species on the other. *S. chutteri* would appear to be a species whose larva readily changes its site of attachment. There is evidence that the other species, *S. adersi*, *S. damnosum* and *S. mcmahoni*, do not move about as freely as *S. chutteri*. They were rare at Station 54 and not particularly abundant at Station 54a (Table 1) which were both sampling points where conditions would favour *Simulium* larvae readily changing their sites of attachment. They were most abundant at Stations 52 and 56 in spite of the large numbers of Hydropsychidae at these stations. The effects of hydropsychid predation on *Simulium* larvae would be influenced by the amount of site changing undertaken by the *Simulium*. Data from these stations therefore also suggest that *S. adersi*, *S. damnosum* and *S. mcmahoni* change their sites of larval attachment less frequently than does *S. chutteri*. Below the Vaal Barrage (Chutter 1963) there were large numbers of *S. adersi*, *S. damnosum* and *S. mcmahoni* together with large numbers of Hydropsychidae, particularly *Cheumatopsyche thomasseti* and *Amphipsyche scottae*. *Simulium chutteri* was not recorded here, although there was a plentiful supply of plankton food and the current speed was of the order of that in the stones-in-current biotopes in the Warrenton area. *S. chutteri* has been recorded further upstream than the Vaal Barrage (Lewis 1965). Its absence below the Barrage would be readily understandable if its habits led to its being particularly heavily preyed upon by the Hydropsychidae.

(b) *General*

This study of the Vaal River at Warrenton has begun to reveal the role of biotic relationships among the many other factors contributing to the composition of a river fauna. Reduction in the size of *S. chutteri* populations is certainly assisted by parasitism of the larvae by mermithid nematodes. The competition for a food source between Simuliidae and juvenile Hydropsychidae is highly probable and the outcome of this competition appears to be dependent on changes in the physical environment. The predation effects of large hydropsychid larvae have been suggested above. The algae-browser relationship has only been glanced at, but it is clear that the close correlation between *Catoxyethira* and Chironomini is due to both of them utilizing the epiphytic habitat. *Catoxyethira* makes its case from algae and probably eats them too (Nielsen 1948) and the Chironomini are effective browsers of this rich 'Aufwuchs'. In winter when the epiphytic growth is most luxurious other groups, particularly *Nais*, *Chaetogaster* and Orthocladiinae, take advantage of the increased food supply and microhabitats now available. These conclusions have been drawn from a field study not primarily designed to investigate these relationships, but they do nevertheless indicate the very great advances that will be made in our understanding of river ecology when a detailed approach is adopted. It is this detailed approach which has so far been neglected in many of the published studies of South African river faunas.

The sampling method employed in the stones in current at Warrenton was unusual and yielded highly variable estimates of the faunal density. Some reasons for this variability must lie in the very great variability of conditions within stony runs. They form a multiplicity of habitats, some, such as the cavities occupied by *Gomphocythere*, *Caenodes* and *Choroterpes* (*Euthraulus*) or the algal 'Aufwuchs', readily recognized by the human observer. Others, dependent perhaps on factors such as the thickness of the boundary layer (Ambuhl 1959), are impossible to recognize in the turbid waters so frequently encountered in the field. Even where it was possible to recognize habitats such as the cavities, the size of these habitats was not closely related to the surface area of the stones as the range of stone sizes was restricted. These physical factors contribute to the very great variability of the fauna from stone to stone and doubtless biotic relationships do so too. However, in spite of this variability of densities from stone to stone, and the consequence that it was not possible to compare data from different sample series by means of the precise methods available in parametric statistics, the sampling method has been justified by the considerable contribution the data it yielded have made to our understanding of the ways in which the fauna in South African rivers is related to environmental and biotic factors.

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SUMMARY

Simulium chutteri Lewis is a blackfly whose female feeds freely on the blood of cattle and horses. Large numbers of *S. chutteri* larvae were found in some, but not all, stones-in-current biotopes in the Vaal River below the Vaal Hartz Diversion Weir, where water is diverted to a large irrigation area. The size of populations of these larvae and also of the other invertebrates occupying these biotopes were assessed at several sampling stations. An unusual sampling method, which involved the collection of the fauna of individual

stones, was used. The important variables in the aquatic environment were measured. Stone size, current speed and temperature varied little between the sampled biotopes and could not be shown to account for the station to station differences in the fauna.

The largest populations of *S. chutteri* larvae were found in a semi-permanent biotope and in a biotope where the water level fluctuation was greater than elsewhere. At these two places numbers of larvae of hydropsychid Trichoptera and of other *Simulium* species were low. Conversely, permanent biotopes in places where there was little water level fluctuation had larger populations of Hydropsychidae and of other *Simulium* species and few *S. chutteri*. From this it was concluded that *S. chutteri* larvae readily move about in the river and rapidly invade newly covered parts of the river bed, whereas their main predators, the hydropsychid larvae, and their main competitors, the other Simuliidae and the very young Hydropsychidae, are less mobile.

There were several reasons for the appearance of the large *S. chutteri* population below the Weir and not elsewhere. In this part of the river there were many places where the current speed of the water was suitable for *Simulium* larvae. It seemed likely that there was a build up of microplankton, which would provide food for the larvae, in the large body of still water held back by the Weir. The flow characteristics of the river were artificial in two respects which evidently favoured *S. chutteri*. Water was not diverted for irrigation at week-ends, so that there was a sharp weekly change of flow and consequently of water levels in the stones-in-current biotopes. At the end of winter and in spring there was an artificial and gradual increase in the flow of the river as water was released from storage reservoirs. The river then spread gradually into previously dry parts of its bed. The number of temporary stones-in-current biotopes has probably been increased by the alluvial diamond mining which has taken place in the river bed.

Fewer *S. chutteri* pupae were present when there were many larvae parasitized by mermithid nematodes, suggesting that the parasite prevents the successful pupation of the larvae. Other than the Hydropsychidae, the principle invertebrate predators of *Simulium* larvae were probably a leech and a plecopteran nymph. Dense growths of diatoms and algae may have reduced the area of the river bed suitable for Simuliidae in the late spring. *Catoxyethira* (Hydroptilidae, Trichoptera) and Chironomini were found mainly on stones with a permanent growth of algal tufts. Two mayflies and an ostracod were found to be inhabitants of cavities beneath stones.

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