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The Bottom Fauna of the Rapids of the Black Volta River in Ghana

by

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Introduction

The construction of the Akosombo dam in Ghana changed the environment over a large section of the Volta River from riverine to lacustrine. This resulted in a destruction of the original communities of the bottom fauna and its replacement by one typical of stagnant water (Petr, 1969). The fauna prevailing in rapids and other habitats exposed to permanent and strong water currents was presumably completely destroyed, while the fauna of the riverine flats, pools and backwaters served as a reservoir for colonization of the Volta Lake. The community of bottom invertebrates in rapids has been studied with the aim of obtaining any basic information on its composition, abundance and standing crop; this could be later used for a comparison with the data on bottom fauna of the man-made Volta Lake.

Description of the locality

A station was located at New Bator near Bui on the Black Volta river, some 100 km upstream from the northern end of the Volta Lake (see map). This area appeared to be topographically somewhat similar to the Akosombo gorge where the dam was built. The country at Bui is hilly and covered with savanna forest. Along the river banks there is a narrow belt of gallery forest. In the river the fast water of the rapids alternates with the slow flow of its deeper parts.

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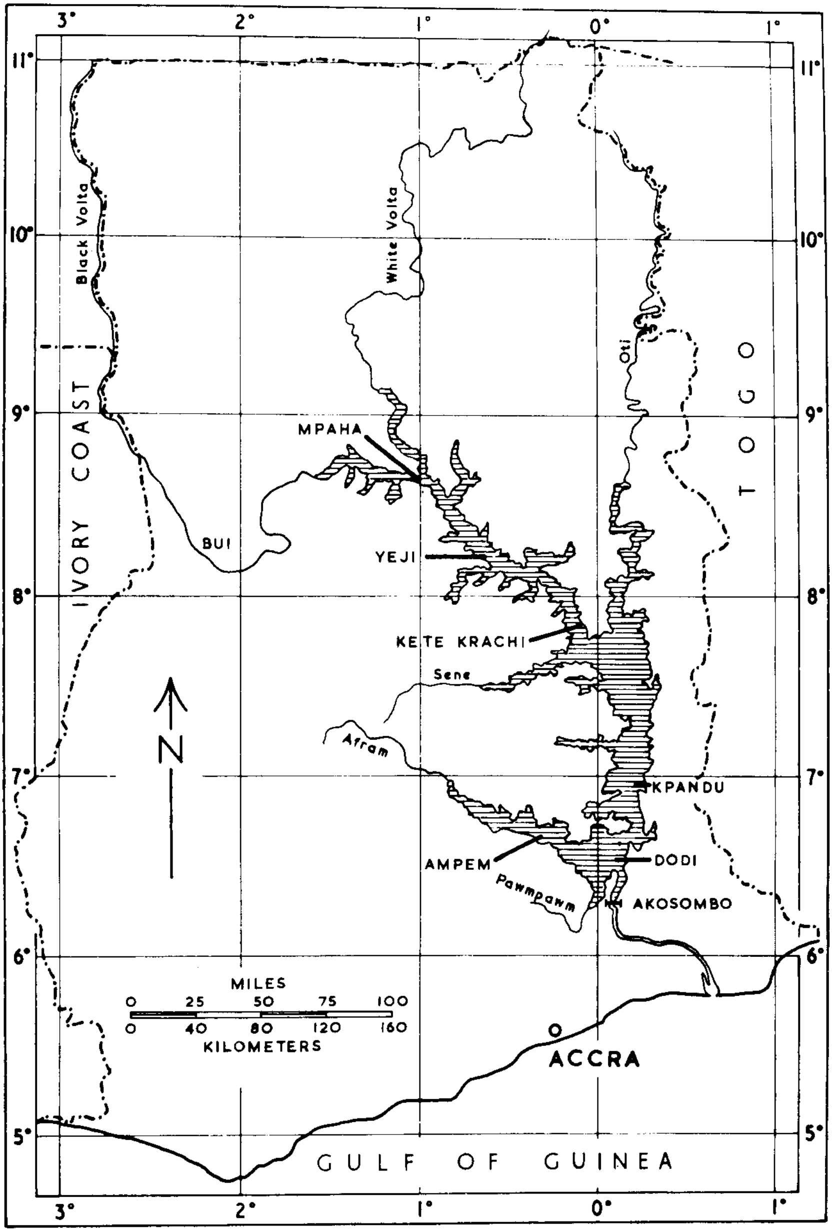

3°
2°
1°
0°
1°
11°
10°
9°
8°
7°
6°
5°
Black Volta
White Volta
Oti
IVORY COAST
TOGO
MPAHA
BUI
YEJI
KETE KRACHI
Sene
Afram
KPANDU
AMPEM
DODI
Pawmpawm
AKOSOMBO
N
MILES
0 25 50 75 100
0 40 80 120 160
KILOMETERS
ACCRA
GULF OF GUINEA

During the dry season the river at the rapids is about 25—50 m wide, and in slow flowing sections between 100 and 200 m wide. The following types of substrate are present: rocky bottom, stony bottom with gravel, and in deeper slowly moving sections coarse sand bordered by mud.

Methods

Physical and chemical methods

Water temperature was measured using a mercury thermometer with an accuracy of 0.1°C. For measuring the hydrogen-ion concentration (pH) a colorimeter B.D.H. indicator kit was used which proved accurate to 0.1 of a unit when compared with a portable electrode apparatus. Total alkalinity was estimated by titration with N/50 sulphuric acid using methylene-orange cyanol as indicator. Dissolved oxygen was measured by the Winkler method.

Sampling of bottom fauna

A Surber sampler as described by Welch (1948) was used. The frame of this sampler was pressed against the bottom, where it enclosed an area of 913 cm^2. The larger stones from inside the frame were removed and placed in a white dish. Gravel and sand were thrown by hand into a bag made of plastic netting of approximately 0.6 mm mesh. The bag was fixed at right angles to the frame, and downstream from it.

Animals were separated from the substrate immediately after sampling and preserved in 4% formaldehyde solution for later examination. Only those organisms visible to the naked eye were collected. In the laboratory the higher taxons and in some instances also the species, were counted. Each taxon was weighted separately on a torsion balance, after being dried for approximately five minutes on blotting paper.

Results

Samples of bottom fauna were collected in April 1965 and in April 1967 at the end of the dry season when the water level in the river was low and the Surber net could be used. Attempts to obtain samples from deeper sections of the river failed owing to the unsuitability of such bottom samplers as the Ekman-Birge and the Rigosha, for the collection of samples from coarse sandy and gravely bottoms.

Physical and chemical data

TABLE I

Physical and chemical data for the Black Volta River.

day	depth	current speed cm/sec	time	temp. °C	pH	alk. mg $CaCO_3$/l	Oxygen mg/l	%/sat.
11/IV/65	20 cm	20—40	09.00	29.8	8.5	80	8.1	109
13/IV/65	1 m	—	12.00	30.5	8.5	83	7.6	103
	2 m	—	12.00	30.5	8.5	90	7.9	107
	4 m	—	10.00	30.5	8.6	83	7.8	105
	7 m	—	10.00	30.4	8.5	83	7.0	95
	10 m	—	10.15	30.4	8.6	83	6.8	92
	14 m	—	10.15	30.3	8.5	90	6.4	86
21/IV/67	25 cm	5	13.30	31.7	7.7	76	6.6	90
	25 cm	75	13.30	31.7	7.7	76	7.0	96
	25 cm	140	13.40	31.7	7.7	76	7.6	104

The temperature was measured in a cross section of the river, about 500 m below the rapids on the 13/IV/1965. The range, of only 0.2°C, indicates that water in the river was well mixed. The pH did not show any significant differences. Alkalinity generally increased with depth. Oxygen gradually decreased with depth, but its concentration at the maximum depth of 14 m was still considerable.

Data obtained in 1967 for rapids of different current speeds suggest that water in the faster currents is better oxygenated.

Bottom fauna

Samples of bottom fauna were collected along a transect across the rapids to obtain data for different current velocities. The type of substrate varied. The river bottom in the fastest sections with current speeds between 75 and 140 cm per sec. was composed of stones of a diameter up to 30 cm and of stones and coarse gravel up to 10 cm in diameter in slower currents of 20—40 cm per sec and 5 cm per sec. In the slowest current there was a small addition of sand and silt which was evidently deposited in this locality after the river level felt and the current was reduced.

The surface area of sampled stones was not measured. The surface area sampled will have been smaller in areas with a higher current speed, where larger stones predominated.

The rapids could be classified according to the current speed as cascades, runs and stickles as a large range of rates flow was recorded. The most constant characteristic of the locality during the dry season corresponds to ALLEN's (1951) definition of a stickle as 'shallow water with a rapid current and usually broken flow'. HARRISON & ELSWORTH (1958) have refined this definition for South African streams, and have given as characteristic a range of current velocity between 18 and 88 cm per sec during the dry season. This leaves the 140 cm per sec section of Black Volta to be close to a cascade section which has in South Africa a velocity of 90—135 cm per sec. Also the depth between 10 and 75 cm in this classification corresponds with that of the Black Volta.

The lack of taxonomic knowledge made identification of most of the organisms possible only to the genus level. Ephemeroptera, one of the most frequent groups by number of specimens consisted almost entirely of new species (PETERS, personal communication) and new genera, which have yet to be described. Even recently published descriptions of trichopteran and coleopteran larvae (MARLIER 1962, BERTRAND 1962) do not make possible the identification of the material in many instances further than to genera.

The quantitative data are summarized in Table II. The table is arranged according to current velocities. Sampling in April 1965 was limited to current velocities in the range between 20 and 40 cm/sec. In April 1967 5 cm, 75 and 140 cm/sec speeds were sampled.

Variations in individual taxa, in number of organisms and in the standing crop can be correlated with the different rates of flow. The ephemeropteran nymphs *Tricorythus* and *Caenis*, caddisfly larvae *Protomacronema* and *Cheumatopsyche sp. 1*, and also the coleopteran larvae *Pachyelmis* are more abundant on substrates exposed to fast currents. Oligochaeta, the Leptophlebiidae and *Choroterpes*, and the coleopteran larvae *Potamodytes* and *Potamocares* prefer substrates in slow current. Other species, mostly far less abundant than those mentioned above, do not seem to show a well marked preference for any particular current velocity. Nevertheless, some of them, such as Heptageniidae (Ephemeroptera) were absent from 140 cm/sec. current, and *Baetis*, *Chimarra*, *Macronema*, *Aethaloptera*, and *Cheumatopsyche* were not found in the 5 cm/sec the slowest current sampled for organisms.

On basis of the abundance data, the tolerance and preference of some Black Volta River species for different current velocities are shown in Fig. 1. Larvae of *Tricorythus* and *Cheumatopsyche* prefer substrates exposed to the fastest current. Leptophlebiidae sp. 1 and *Choroterpes* on the other hand favour the substrates exposed to the slowest current. Both groups gradually decrease or increase in number with decrease in the rate of current flow (Fig. 2).

Total number and total standing crop for individual families are given in Fig. 3. Oligochaetes, apart from molluscs the only group of permanent fauna, are the least important both by number and by

TABLE II

Bottom fauna of the Black Volta River rapids.

Current velocity in cm/sec	Number per square metre 5	20—40*	75	140	Standing crop in mg per square metre 5	20—40*	75	140
Organism								
Oligochaeta	66				10.9			
Plecoptera	11	201		22	181.8	1138.8		278.1
Neoperla spio	11	201		22	181.8	1138.8		278.1
Ephemeroptera	1041	4703	1995	2740	1931.6	3928.4	3625.6	4453.4
Baetidae								
Baetis sp. 1	33	296	121	88	19.7	212.4	87.6	111.7
Pseudocloeon sp. 1		40	99	121		16.8	82.1	173.0
Acentrella				77				40.5
Baetidae sp. 1	22	18		88	19.7	27.7		60.2
Heptageniidae								
Afronurus sp. 1	11		55		87.6		154.4	
Afronurus sp. 2		139				343.1		
Leptophlebiidae								
Choroterpes (Euthraulus)	723	66	307	77	1300.1	41.6	240.9	39.5
Thraulus	22		11		76.7		16.4	
Leptophlebiidae sp. 1	33	26			24.1	14.6		
Tricorythidae								
Tricorythus	22	621	1095	1654	190.5	1315.8	2923.7	3590.5
Caenidae								
Caenidae sp. 1	164	3493	307	635	87.6	1954.6	120.5	438.0
Prosopistomatidae								
Prosopistoma	11	4			8.8	1.8		
Odonata	44	44	33	22	1179.3	3465.7	8501.5	5438.8
Zygoptera	33		11		856.3		317.5	
Anisoptera sp. 1, 2, 3	11	44	22	22	323.0	3465.7	8184.0	5438.8
Trichoptera	343	1332	2170	7206	655.9	5215.1	6507.6	30835.2
Philopotamidae								
Chimarra		15		11		18.3		18.6
Ecnomidae								
Ecnomus sp. 1	321				652.6			
sp. 2			77				186.2	
sp. 3				33				49.3

Hydropsychidae								
Aethaloptera dispar l. + p.		131	187			787.9	3087.9	
Macronema sp. 1				219				14116.7
Cheumatopsyche digitata			22				34.2	
Cheumatopsyche sp. 1		854	1686	6625		2630.2	2769.0	14039.1
Cheumatopsyche sp. 2		11				35.4		
Protomacronema		197	33	197		1690.0	304.4	2534.9
Leptoceridae								
Pseudoleptocerus sp. 1	22	124	154	121	3.3	53.3	117.5	76.6
Pseudoleptocerus sp. 2			11				8.4	
Coleoptera	198	242	274	482	244.3	94.2	359.2	1702.8
Dryopidae								
Potamocares	22				62.4			
Potamodytes	11				70.1			
Stenelmis	55	88	33	252	27.4	29.2	21.9	124.9
Stenelmis im.				11				16.4
Pachyelmis	99	106	219	186	35.1	41.3	82.1	59.1
Pachyelmis im.			11	11			3.3	4.4
Microdinotes		4				2.2		
Gyrinidae			11	11			251.9	1478.3
Dytiscidae				11				19.7
Dytiscidae im.	11	44			49.3	21.5		
Lepidoptera			11	11			26.3	59.1
Pyralididae			11	11			26.3	59.1
Diptera	372	205	449	395	156.6	273.5	153.3	190.5
Tipulidae l. + p.	11		22	66	13.1		8.8	96.5
Leptidae		18				213.2		
Simuliidae		4				1.5		
Chironomidae	361	157	427	285	143.5	35.4	144.5	59.1
Chironomidae p.		11		44		9.5		32.9
Diptera l. not identified		15				13.9		
Pelecypoda			11				11878.6	
Etheria eliptica			11				11878.6	
TOTAL	2075	6727	4932	10878	4459.0	14115.7	19173.5	42957.9

* area sampled: 2739 cm^2; for other current velocities the area sampled was 913 cm^2 in each.
The weight (standing crop) of Leptoceridae is given without cases; Pelecypoda are not included into TOTAL.
All organisms are larvae, unless otherwise indicated; p. = pupa, im. = imago, l. = larva.

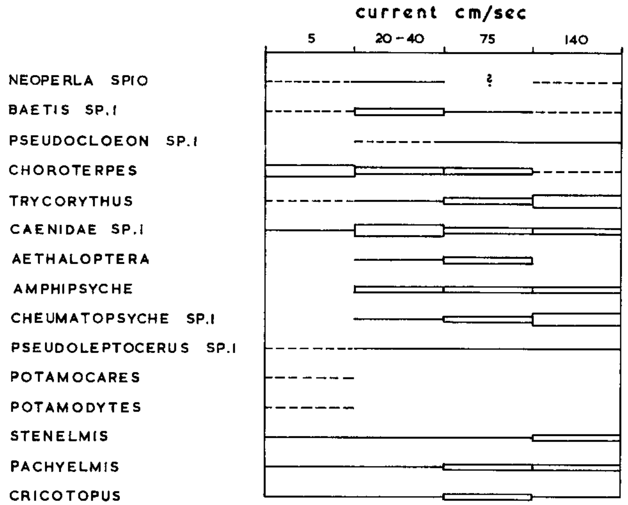

Fig. 1. Tolerance and preference for different current velocities of some bottom living organisms from the Black Volta River.

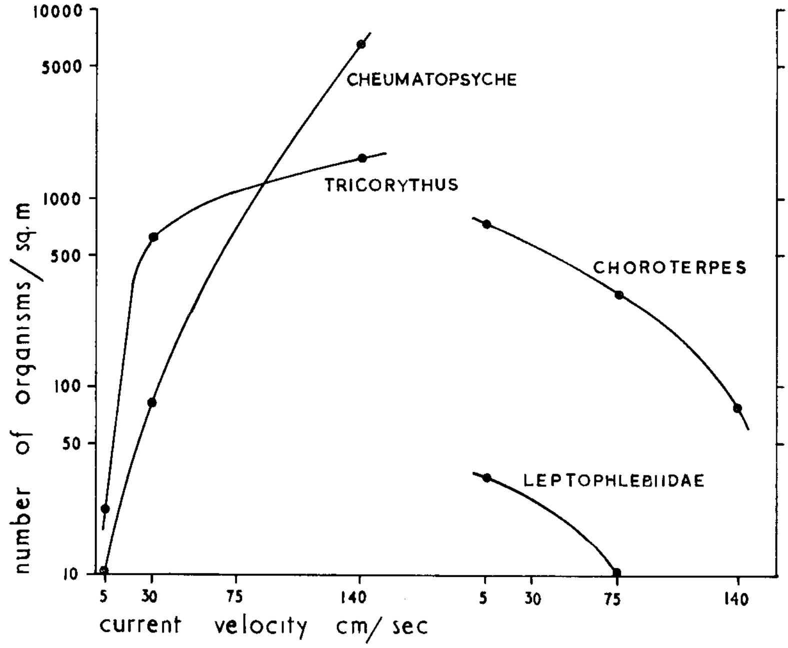

Fig. 2. Correlation between the current velocity and abundance of some bottom living organisms of the Black Volta River rapids.

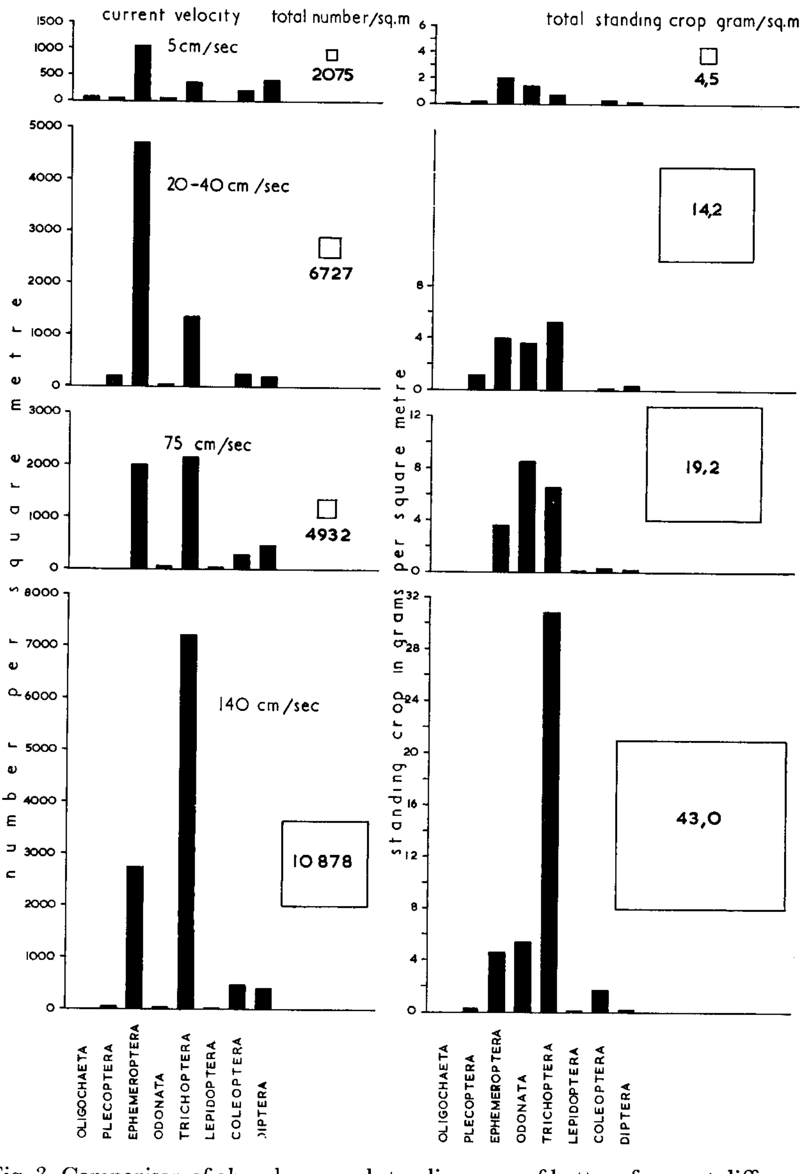

Fig. 3. Comparison of abundance and standing crop of bottom fauna at different rates of current flow in the Black Volta River rapids.

standing crop. Plecoptera, with only the one species *Neoperla spio* (NEWMAN), were most common in 20—40 cm /sec, but they were collected also from other current speeds. The highest number of Ephemeroptera was found in the 20—40 cm/sec flow, with Caenidae the most important among them. *Tricorythus* contributed greatly to the standing crop in the two habitats with fast currents. Only a few odonatan nymphs were found and they were more important in terms of total standing crop than of abundance. Lepidopteran larvae are also very scarce. Trichoptera contribute greatly to the total number and standing crop in substrates exposed to the fastest current. Their high standing crop in currents of 140 cm/sec was mainly due to the abundance of *Cheumatopsyche.* Other genera such as *Macronema, Ecnomus, Aethaloptera, Pseudoleptocerus* were much less abundant. Coleoptera, both larvae and adults, and dipteran larvae, had low frequency in all samples. *Stenelmis* and *Pachyelmis* were the most abundant genera. Both of them seemed to avoid the substrates with the slowest current.

Among the dipteran larvae chironomids were most frequent. The distribution of individual larval types at different rates of current flow is given in the Table III. Of the commoner types, the Orthocladiinae (*Cricotopus*?), Chironomini sp. 1 and Chironomini sp. 2 seem to prefer fast currents. *Polypedilum sp.* 1 and *Stictochironomus* occur predominantly in substrates exposed to slow currents. Types marked by an asterisk were commonly found in the bottom fauna of the

TABLE III

Chironomid larvae of the Black Volta River rapids (absolute numbers)

current velocity Organism	5 cm/sec	20—40 cm/sec	75 cm/sec	140 cm/sec
*Tanypodinae	21	5	4	4
Orthocladiinae (Cricotopus?)	2	3	9	4
Chironominae	24	16	24	11
Chironomini	21	16	22	10
*Cryptochironomus		1		
*Polypedilum sp. 1	20	3	1	
*Polypedilum sp. 2		1		
Stictochironomus	1	10	1	
Chironomini sp. 1			15	6
Chironomini sp. 2		1	5	4
Tanytarsini	3		2	1
*Tanytarsus sp. 1			2	1
*Tanytarsus sp. 2	3			
TOTAL	47	24	37	19

Volta Lake. In the Black Volta River all of these prefer slow current, except the *Tanytarsus sp. 1* in the Volta Lake.

Total abundance and standing crop of bottom fauna (Fig. 2, Table II) were highest on the substrates associated with 140 cm/sec current. Standing crop gradually decreased with decreasing current speed. The number of organisms per m^2 was lowest in the slowest current, but at 20—40 cm/sec it was higher than that of 75 cm/sec. This is due to the mass occurrence of Caenidae nymphs, as mentioned above. The net spinning caddisfly larvae of *Cheumatopsyche* and the Trichoptera in general can be considered as the most important item of the Black Volta rapids bottom fauna, and they determine the magnitude of the standing crop in individual samples collected at different current speeds.

Stones which are the chief substratum of the rapids in all parts sampled, are often separated from each other by deep crevices (10—25 cms). In these the current speed is greatly reduced and species which prefer a slow current may there find hiding-places. However, the total number of organisms is determined by the predominance of the most abundant species, which are the true inhabitants of the rapids.

Discussion

Current velocity seems to be one of the most important physical factors responsible for quantitative and qualitative differences in the bottom fauna of the River Volta rapids. In nature current distribution is extremely heterogeneous and a full scale of variations may exist within a small area. Measuring current at different levels from the bottom has shown that this varies considerably even within very short distances from the bottom (Ambühl, 1959). As no suitable equipment was available, the rate of flow given in the present study is for measurements at the water surface; this may be expected to show higher values than those which would be obtained at the bottom. In fast currents of the rapids of very shallow rivers such as the Black Volta the depth during the dry season is, however, less than 30 cm and thus the difference between the surface and the bottom is not as large as in deeper sections or in deeper rivers in general.

In the rapids of the Black Volta the substrate at the margins differs only slightly from that of the middle part of the river, though during the dry season the differences in the current speed in different parts of the rapids are substantial. The characteristics of the river bottom in the rapids are largely determined by events during the flood season. At that time the current greatly increases; this results in a complete washing out, especially at the margins, of all small particles, such as mud, sand and small gravel, deposited during the dry season. The substrate of the Black Volta rapids after the floods becomes practically homogeneous, and consists predominantly of large stones. NIELSEN (1950) compiled from various authorities the relation of current speed to substratum and gives the diameter of objects moved by different rates of current flow. Stones up to 45 mm diameter are moved by current speeds of 150 cm/sec, up to 80 mm by 200 cm/sec and up to 180 mm by 300 cm/sec. This last is a current speed which may be expected during floods in rapids of the Black Volta, as one can judge from the type of substrate deposited in rapids.

Comparison of the fauna of the Black Volta with other African rivers of some interest.

In the Volta the dominant species in 75 cm/sec and 140 cm/sec current is *Cheumatopsyche* (Hydropsychidae), a net spinning caddisfly larva. A great predominance of Hydropsychidae, i.e. trichopteran larvae spinning webs, over the larvae building cases, is mentioned as characteristic of tropical rivers in the Congo by MARLIER (1954). He explains their great abundance as being due to the availability of large quantities of food in suspension which is swept by the current into the nets of these omnivorous creatures.

CHUTTER (1963) found the highest density of *Cheumatopsyche thomasseti* to be immediately below the Vaal Barrage in South Africa, where large amounts of zooplankton provided this species with an abundance of food. The number of individuals of *Cheumatopsyche thomasseti* there was 5508 per one m^2 compared with 334 to 377 further downstream. The zooplankton was rapidly removed from the river and 8 km below the dam no longer had any effect on the stony run fauna. A similar effect of abundance of food has been noted by MÜLLER (1956) and ILLIES (1957) who found netspinning caddisfly larvae in considerable quantities in some outlets of lakes on the River Lulealv and in Lapland forest streams in Sweden. The figure given by CHUTTER for *Cheumatopsyche thomasseti* is lower than that found for the 140 cm/sec section of the Black Volta River rapids, where 6625 larvae of *Cheumatopsyche sp. 1* were counted per m^2. As on the Volta River, there is no plankton rich lake or pond situated immediately above the rapids, it would appear that the nutritive value of the water in the river is directly related to the rate of flow. In faster reaches more organic particles are carried in suspension than in the slower sections. Stones in faster currents therefore harbour a larger population of web spinning trichopteran larvae, than those in the slower flowing waters.

PHILLIPSON (1954) using Trichoptera in a trough, investigated the effect of different current speeds upon them. Larvae of different netspinning species were found to have different requirement of current velocity. While the nets of some species were destroyed by a fast current, other species started spinning only when exposed to a high current speed. This later condition may apply for the Black Volta River *Cheumatopsyche sp. 1*, as this is most abundant in the fastest current, but is absent in areas where the water current is 5 cm/sec.

The second most abundant organism in 75 cm/sec current is *Tricorythus* whose flattened nymphs are adapted for clinging to the substrate in rapidly flowing water. They can easily withstand the strongest current of the rapids where they feed on periphytic algae.

In water currents at 20 to 40 cm/sec most abundant organisms by number are nymphs of Caenidae, followed by *Cheumatopsyche sp. 1*, *Tricorythus*, *Baetis sp. 1* and *Neoperla*. In terms of standing crop the Trichoptera are the most important item, followed by Ephemeroptera and Odonata.

It is noticeable that Caenidae were much more abundant in water flowing at 20—40 cm/sec in 1965 than in 1967. There may be several reasons for this. If the time of sampling and the water level are assumed to have been identical in both years, there are several factors which might have been responsible for the low occurrence of Caenidae in 1967. Thus, for example, a heavy rain preceding the sampling might have swelled the river for a short period, washing out the Caenidae, since they have no special adaptation for resisting a strong current. Heavy predation by fish may be another reason. Some authors are of the opinion that changes in the fish and invertebrate fauna of streams not only coincide but are directly correlated. According to STRAŠKRABA (1966) fish predation is a factor which may cause the complete disappearance of animals from a biotope. Lunar dependent emergence is most probably not involved, as samples were collected in 1965 two days before full moon, and in 1967 one day before full moon.

ULFSTRAND (1968) found during his four years of observations on Lapland streams considerable fluctuations from year to year. Thus, for example, values for the standing crop in July ranged between 27.9 and 128.0 g/m^2. He considered the different timing of the life cycles as one of the reasons of these fluctuations. In his study of the microdistribution of benthic species with regard to depth, current and substrate conditions ULFSTRAND (1967) expressed the opinion that the interplay of environmental factors is more important than that of the factors considered individually and that this was second in importance after the availability of food in termining detailed distribution of the fauna. The Black Volta data seem to be in keeping with this. The existence of a particular type of substrate is determined by the water current, and the water current is also the major source of food for those organisms, which in the Volta River rapids are the dominant forms. Until, however, more is known about the life cycle of aquatic insects of tropical rivers, it will be not possible to assess the effect of emergence on the standing crop and abundance of bottom fauna.

Data on the abundance of bottom fauna in rapids in streams and rivers of South Africa have been compiled for comparison with those from the Black Volta River (Table IV). Only those localities have been selected which were not under influence of pollution. The most striking difference is the far greater abundance in numbers reported by ALLANSON (1961) and OLIFF (1960). By using a smaller mesh-size net in their Surber sampler, greater number of organisms were taken. ALLANSON (1961) for example records a very great abundance of Oligochaeta, Copepoda and Platyhelminthes together with that of *Cheumatopsyche*, *Austrocaenis*, *Baetis*, *Simulium*, *Euthraulus* and *Pseudocloen*. In OLIFF's (1960) samples the same groups are common together with a large number of minute Chironomidae such as Orthocladiinae and *Tanytarsus*. In these rivers the permanent fauna contributed greatly to the abundance of the total benthic fauna. In the Black Volta the permanent fauna, i.e. the Oligochaeta, Crustacea, Platyhelminthes, Mollusca is practically absent from the samples, which consisted exclusively of insect larvae and adults; that is a temporary fauna.

The fauna of the stony-run zone of the Great Berg River (HARRISON & ELSWORTH, 1958) has some common features with that of the Black Volta, especially in the abundance of Ephemeroptera, in the presence of a variety of Trichoptera and of clinging beetles. Many organisms found by these authors for the lower foot stony-run zone, were also found in the Black Volta, such as Tricorythidae, Caenidae is similar to that of the Black Volta. OLIFF (1960) found *Baetis*, *Euthraulus*, *Simulium*, Orthocladiinae, *Tanytarsus* and Naididae to be the most abundant groups in the Tugela, while in the Mooi River (OLIFF, 1964) the greatest densities of Ephemeroptera were recorded in the dry season, when they formed 50% of the total population.

From these comparisons it may be concluded that if the same sampling method is used, the differences between the total number of organisms per unit area for rapids in South African streams and rivers and in the Black Volta rapids are small. A smaller mesh size will obviously sample many more small organisms and young stages, giving a much higher abundance by number. How far these small organisms contribute in the total standing crop or the production of bottom fauna of this biotope has yet to be discovered. None of the authors quoted above analysed the individual samples collected

TABLE IV

Data on the abundance of bottom fauna in unpolluted localities with stony substrates in streams and rivers of South Africa, compared with data for the Black Volta River.

Author	River System	No. org./m²	Current speed cm/sec	Season	Denomination of habitat	Mesh size used
HARRISON & ELSWORTH (1968)	Great Berg River River	872— 1030 671— 2478	90—112 18—135	dry	cascades, runs and stickles	about 1 mm across
ALLANSON (1961)	Jukskei – Crocodile Rivers	15953—18094		dry	stone runs	about 0.3 mm
OLIFF (1960)	Tugela River system	3500—19000	48— 91	dry	stones in rapids	about 0.3 mm
HUGHES (1966)	Mountain streams of Barberton area Eastern Transvaal	1787—11532 average 5278		dry	stickles	?
PETR	Black Volta	2075 6727 4932 10878	5 20— 40 75 150	dry	rapids	about 0.6 mm

from the same transect separately. Yet it seems likely that different samples from the same transect were taken from areas of different current speeds. This is attributable to the fact that their immediate interest lay in the distribution of organisms along the lengths of the rivers and not in the detailed distribution within short reaches. Furthermore there are considerable difficulties in obtaining reliable samples from closely defined habitats. This is well shown in the work of NEEDHAM & USINGER (1956). Using a square foot Surber sampler, they found that to obtain an estimate of the total number of organisms in a single riffle significant at the 95% level of cofidence, no less than 63 samples of the benthic fauna were required. Two or three samples were nevertheless sufficient to ensure that at least one representative of each of the commonest genera was present.

It is almost impossible to follow the seasonal changes in benthic fauna of tropical rivers by direct methods of sampling the substrate. The river is so swollen during floods that its level greatly exceeds that of the dry season for several months. As the life cycle of the majority of aquatic insects and other invertebrates takes one to four months (CORBET 1956, WHYTE, pers. communication), several generations may theoretically emerge before the river bottom can be sampled again. In practice this does not occur as is explained below.

An increased water level with a permanently fast current is probably a great obstacle to recolonization of the bottom after the emergence of the last generation hatched from eggs laid at the end of the dry season. Adults cannot lay their eggs directly on the substrate during floods, and the only way open for colonization is by migration of larvae from the river banks. The mechanical destruction of larvae when the bed is greatly disturbed and stones and rocks are being rolled and carried about must be immense and probably eliminates the majority of organisms for a considerable period of time. Recolonization probably starts only when the river level drops sufficiently for the substrate to be again accessible to the adult insects. At that time migration of species from the littoral of the river banks is probably also much more effective.

Emergence of many species in the tropics is bound to lunar periodicity but continuous emergence is also common (CORBET, 1964). Larvae of some species hatch continuously, so that in samples several instars are usually present at once. This is true both for the Volta Lake and for the Black Volta River species (PETR, unpublished data). Data collected for a tropical river on standing crop and abundance of bottom fauna during the dry season may therefore be considered as valid only for the dry season, but even then there may be a trend of increasing abundance and biomass during the course of the dry season as the water level drops.

Until more is known about the life histories of the bottom organisms of tropical rivers, the standing crop cannot be used as an index of the rate of productivity. Organisms with shorter life cycles may be expected to be more productive than those with longer life cycles. LINDEMAN (1941) employed this principle to estimate the annual production rate of aquatic organisms by multiplying the standing crop by the number of generations per year. WATERS (1961) similarly points out that standing crop will be directly related to production rate, only when groups of similar longevity are compared, or at least when the large long-lived forms are excluded from the estimation of the standing crop.

In the Black Volta a high production rate can be expected whereever several instars of the same species are present at the same time. Under tropical conditions this guarantees a practically continuous emergence, modified at some species by the lunar cycle into periodic emergence, and a continuous laying of eggs and hatching of new generations.

Some factors, such as flood waters, can, however, drastically reduce the productivity of some sections of a river for a certain period by destroying the habitat. Thus a detailed knowledge of the life cycles of the major species and of the changes occurring in the habitat during a year under the influence of climatic conditions are essential for any estimation of the production rate of bottom fauna.

In the case of a permanent flooding of rapids, as has happened for example after the damming of the Volta River, the bottom fauna of the rapids will be almost completely destroyed. Some genera, however seem to adapt themselves to the life in habitats exposed to waves and well saturated with oxygen. *Ecnomus* has been found to be abundant in the bark of flooded trees exposed to wave action in the Volta Lake, (PETR, 1970). Larvae of Orthocladiinae (Chironomidae) were found in the same habitat and these require water of high oxygen content (BRUNDIN, 1951). Larvae of Orthocladiinae (*Cricotopus*?) show the preference for the current speed of 75 cm/sec, where they formed 24% of chironomid larvae present. This genus formed 14% in the total number of chironomids collected from rapids. This figure is comparable with the 12% occurrence of *Cricotopus* larvae found in the bark of tress exposed to wave action in the Volta Lake at Kpandu discussed elsewhere (PETR, 1970). But it is the bottom fauna of the riverine pools, flats and backwaters which can be considered as the real source of aquatic invertebrates in the new water impoundments such as the Volta Lake, since many of the species found in slow water currents or in stagnant water are pre-adapted for life in the new environment.

Summary

The increase in abundance and biomass of the bottom fauna in the Black Volta River rapids seems to be closely related to increasing rate of water flow. These differences are due mainly to the increasing numbers of *Cheumatopsyche* larvae, a web spinning caddisfly. At higher current speeds more food is provided for this omnivorous species, and this seems to determine its density on the substratum. In a very slow current which prevents the use of webs for food catching, this genus is absent.

The abundance and standing crop of bottom fauna at the end of dry season can be considered as the highest for the whole year. The presence of several instars of the commonest species guarantees almost continuous emergence and recolonization of the substratum during the dry season. With the onset of heavy rains and floods the communities found in the rapids are disturbed, and eventually completely destroyed. This is because the substrate is carried away by the swift flow of the river. Recolonization can be expected after the rains when the water level is low and the substratum again stabilized.

The fauna of rapids is a community which can be expected to be almost completely destroyed when it becomes permanently flooded in any man-made lake. Some organisms, however, such as the larvae of *Ecnomus* and *Cricotopus* may establish themselves again in a habitat physically and chemically akin to that of rapids; such a habitat is for example the bark of flooded trees exposed to wave action and surrounded by water well saturated with oxygen.

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