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River Zonation in Southern Africa

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With 1 attached table

Introduction

In the first major hydrobiological survey of a South African river HARRISON and ELSWORTH (1958) make a serious attempt to divide the Great Berg River into a series of zones from source to mouth. These zones are based on physical features but it is shown that each has typical faunal associations. OLIFF (1960), in his study on the Tugela River, adopted a similar system but found it necessary to introduce certain modifications, showing how difficult it is to attempt to develop a zonation system to suit all rivers.

ILLIES (1961) outlines a system designed for rivers of all types in all latitudes. He bases this on a consideration of published studies on the Fulda-Weser, Germany, (lat. 50—51°N), the Huallaga-Maranon-Amazonas (lat. 0—10°S), the Chillón, Peru, (lat. 10°S) and the Great Berg River (lat. 33°S). He divides these rivers into two main zones, the mountain zone — Rhithron, and the lower foothill and plain zone — Potamon; these zones he divides into three subzones, Epi-, Meta- and Hypo-Rhithron and -Potamon.

ILLIES emphasises that the system in its present form is tentative and may have to be modified; nevertheless at a symposium on the influence of current on running-water organisms, organised by the International Association of Theoretical and Applied Limnology in Kastanienbaum, Switzerland, 1961, it was recommended that the practicability of classifying rivers in this way be examined.

ILLIES' system is based largely on physical conditions, mainly river profile, type of bottom and monthly mean temperatures; but he also outlines the nature of typical "rhithronic" and "potamonic" fauna. He correlates his system with the European Fish Zones, HUET (1946 and 1949), and the zonation used by HARRISON and ELSWORTH (1958) for the Great Berg River; the latter correlation is shown in Table 1. Using ILLIES' criteria the Tugela River (OLIFF, 1960), the Orange-Vaal System, the Sabie, Eastern Transvaal, and the Zambezi River have been fitted to the system (Table 1).

Physical Basis

Rhithron

ILLIES includes here that section of the stream arising from its source down to a level where the annual range of monthly mean temperature does not exceed 20°C. Water current velocity is high, the flow turbulent, and the oxygen saturation value of the water is high everywhere; the flow volume is small. The bottom consists of fixed rock, pebbles, gravel and fine sand. Mud formation and deposition occurs only in pools or corners sheltered from the current.

In Southern Africa these criteria would apply but it is considered that the range of monthly mean temperature is less important than the actual summer maxima. In the lower part of the rhithron the summer monthly mean would not be much higher than 20° C. An important point to consider is the turbidity and silt content of the water. This should be very low or negligible even during rain storms. Silt deposition should be negligible and surfaces of rocks, stones, pebbles, and trailing vegetation should be clean, even in backwaters. This lack of silt is essential for the preservation of typical montane or rhithronic fauna. Silt from mines in the Eastern Transvaal mountains appears to have done much damage in this regard.

Potamon

ILLIES includes here the section following the rhithron where the annual range of monthly mean temperatures exceeds 20°C or, in tropical latitudes, with a summer maximum of the monthly mean of more than 20°C. Current speed at the river bottom is low and the water flow is more or less "laminar" (unbroken). In deeper pools there is an oxygen deficit, partial to complete light extinction and mud formation. The flow volume fluctuates annually very considerably. River sediments are of sand, mud and can include gravel.

In Southern Africa this would all apply in the main. However, here again it is considered that the actual summer maximum temperature and, in some cases, winter minimum temperatures are important. The summer maximum of the monthly mean would rise well above 20° C, even in the Great Berg River. In the tropics it must be around 30° C, even in deep rivers, with daily maxima higher than 30° C. Winter minimum temperatures in the lower epipotamon of the Zambesi River appear to be over 20° C, though detailed figures are not available. In some parts of Southern Africa, specially in the Eastern Cape Province, Natal and parts of the Transvaal, water turbidity and silt loads are greatly increased by soil erosion. Conditions can be very bad during the rainy season (OLIFF, 1960) and even during the dry season the water may be markedly turbid.

Most of Southern Africa is greatly elevated and rivers are geologically young and so few, except for those on the east coast, have a flood plain (meta- and hypo-potamon). In fact the major part of all rivers falls into the

epipotamon. Arising also from the elevation of the subcontinent is the phenomenon of "rejuvenation" which occurs usually in the epipotamon. This results from rivers cutting through consecutive geological strata with differing resistance to erosion. Thus the profile of the epipotamon might begin to flatten out, approaching hypopotamon, only to steepen again when the river meets some less erodable rock formation. This can be repeated more than once down the course of a river and is shown clearly by the profile of the Tugela River (OLIFF, 1960) where, in the rejuvenated section hyporhithron-like stony runs appear, with sand-bed epipotamon above and below. More striking examples are the Augrabies Falls section of the Orange River and the Victoria Falls and related rapids on the Zambezi River (Table 1).

The Fauna

Rhithron

ILLIES describes the fauna as being cold stenothermal, rheobiotic, polyoxybionic and typically derived from glacial border species. Some have strong morphological adaptations for life in flowing water. He gives a list of typical families.

In Southern Africa the typical fauna appears to be largely of cold stenothermal, rheobiotic forms, although mixed with these in varying proportions are more widespread eurythermal forms, notably certain Baetidae, Simuliidae, and Chironomidae, specially in the hyporhithron. Typical forms would include so-called "palaeogenic forms", STUCKENBERG (1962), comprising Corydalidae (Megaloptera), Nemouridae (Plecoptera), Ephemerellidae (Ephemeroptera), and Blepharoceridae (Diptera). Cold stenothermal forms belonging to families well represented in the Potamon are Planariidae, Baetidae (*Baetis* spp., *Acentrella* spp. and *Pseudocloeon* spp.), Leptophlebiidae (*Adenophlebia* spp., *Aprionyx* spp. and *Castanophlebia* spp.), Ecdyonuridae (*Afronurus* spp.), Leptoceridae and other caddis, Elmidae, Helodidae and Hydraenidae.

Unfortunately there is no glaciation in Southern African mountains and so glacial border relict species cannot be defined. However in Central Africa at least one member of a glacial relict group occurs below the glaciers on the Ruwenzori Mountains and Mount Kenya: *Diamesa ruwenzoriensis* FREEMAN (Chironomidae — Diamesinae).

Not all the rhithronic species are rheobiotic, some are pool dwellers but are cold stenothermal and demand clean water and substrata free from silt. Others may be rheobiotic but more eurythermal, nevertheless demanding silt-free conditions.

As predicted in ILLIES' paper the cold stenothermal forms are driven to higher and higher altitudes at lower and lower latitudes. In the Southern

Table 1. ILLIES' RIVER ZONES AND SOUTHERN AFRICAN RIVERS

	GREAT BERG Harrison & Elsworth 1958	TUGELA Oliff, 1960	VAAL	ORANGE	SABIE Eastern Transvaal	ZAMBEZI
ILLIES' ZONES MOUNTAIN SOURCE	Zone I Mountain Source Zone 2. Waterfalls	Zone 1. Source	(Elands River)	Sunqu or Upper Orange		Absent
Altitude, metres	1525-1220	3050-2290	3335-3050	3353-3050	2150	
EPIRHITHRON	Zone II Mountain Torrent	Zone 3 Mountain Torrent	(Elands River)	Sunqu or Upper Orange		Absent
Altitude, metres	1220-305	2290-1525	(Similar to Tugela)	3050-2740	2130-1525	
Length, km.	9.7	6.9		16?	?	
METARHITHRON	Zone III A Upper Foothill Hard Bottom Zone	Zone 4 Foothill Torrent Zone	(Elands)			Absent
Altitude, metres	305-152			2740-2130		
Length, km.	6.4			25?		
HYPORHITHRON	Zone III B Lower Foothill Hard Bottom Zone	Ditto	(Source of Klein Vaal)			Absent
Altitude, metres	152-90	1524-1230	down to 1525	2130-1830	2130-1525	
Length, km.	40	17		40?	16	
EPIPOTAMON	Lower end of Zone III and Zone IV Foothill Soft Bottom Zone	Zone 5 Valley Sand Bed Zone including rejuvenation zone 910-550 m in 114 km	Source of Vaal at 1680 m 960 km to Orange confluence confluence at 1070 m Rejuvenation at Augrabies Falls, 120 m drop in 26 km.			Source at 1525 m Rejuvenation at Suapuma cataracts and other places, specially Victoria Falls, 64 km of rapids.
Altitude, metres	91 to almost sea level	1230 to almost sea level	1830 to 91		1524- c. 91	1524 to 240
Length, km.	193	488	2010		322	2898
METAPOTAMON					Joins Incomati	Below Kebrabasa Rapids to Lupuata Gorge 244-122
Altitude, metres						320
Length, km.						
	Zone V	Absent	Very short, if present, and se- verely scoured out seasonally (Brown, 1959)			
HYPOPOTAMON	Flood Plain					Lupuata Gorge to sea. 122 to almost sea level
Altitude, metres	Almost sea level		90 to sea level		90 to almost sea level	
Length, km.	16		45		320	320

Cape (lat. 34° S), where mountain streams drop straight into the sea, these forms reach the estuaries; in Southern Rhodesia there are not many left at 1980 metres (lat. 17—18° S). See also Table 1.

Potamon

ILLIES describes the fauna as being eurythermal or warm stenothermal and rheotolerant, coming mostly from family groups whose main development is in standing water. His remarks certainly apply to Southern African rivers; many of the species come from groups more typical of standing water and many species are actually found in both standing and running water, e. g., Cladocera and Copepoda, *Cloeon* spp. (Baetidae) and many species of Notonectidae, Corixidae, Dytiscidae, Hydrophilidae and Chironomidae.

However, many species are truly riverine, some belonging to typically riverine families such as Oligoneuridae, Leptophlebiidae, Ecdyonuridae (Ephemeroptera), Hydropsychidae (Trichoptera), Simuliidae and Orthocla-diinae (Chironomidae); these are mainly found in the epipotamon but some, notably marginal vegetation dwellers, penetrate the meta- and hypopotamon, e. g., *Notonurus cooperi* CRASS in the lower Pongola River (lat. 27° S) and coastal rivers in Moçambique.

Many potamonic species are found throughout Southern Africa but, at lower latitudes, warm stenothermal or tropical species appear in the lower epipotamon and meta- and hypopotamon. Here temperatures are high, specially minima, but other physical features may be the same as upstream. Four main categories may be distinguished:

1. Species found throughout the whole of the potamon over the whole of Southern Africa: e. g., *Baetis bellus* BARNARD; this is rheobiotic but temperature and silt tolerant, in the Great Berg River it is found from the hyporhithron to the estuary. It occurs in the hyporhithron and epipotamon all over Southern Africa but is also found in the metapotamon of the Pongola River during the wet season (lat. 27° S), the lower epipotamon of the Sabi (Save) River (lat. 21°30' S) and the lower epipotamon of the Zambezi (lat. 15°35' S). This species lives mainly in the marginal vegetation and requires a current speed of 0.3 m/sec. or so.

2. Species found in the lower epipotamon to meta-hypopotamon all over the Southern African region. For example *Simulium bovis* DE MEILLON which is found in this region in the Great Berg River, Tugela River, Lundi-Sabi (Save) rivers into Moçambique, Zambezi River and undoubtedly many more. It seems to prefer larger rivers and its distribution could be due to adult behaviour to some extent. Species in this and the former category show a wide temperature tolerance.

3. Species which are less temperature tolerant, some are limited to the cooler and upper, and others to the warmer, lower parts of the potamon. A single genus may show a zonation of species, for instance *Cheumatopsyche afra* (MOSELEY) (Trichoptera-Hydropsychidae), wrongly identified in some papers cited here as *Ch. maculata* (MOSELEY), is found in the rhithron but also extends into the upper epipotamon. Here it overlaps *Ch. thomasseti* (ULMER), wrongly identified in some papers cited here as *Ch. zuluensis* (BARNARD), and *Ch. falcifera* (ULMER) and possibly other species, with *Ch. triangularis* (ULMER) appearing somewhat lower downstream. At higher latitudes these species extend to the coast or coastal plain but at lower latitudes (possibly north of 25° S) they are replaced in the lower epipotamon by *Ch. lesnei* (MOSELEY) probably accompanied by other warm stenothermal, tropical species.

4. Strictly rheobiotic species which disappear in the meta- and hypopotamon, specially when the flow is low during the dry season. Many of these are stony run dwellers; marginal vegetation dwellers have a better opportunity to penetrate flood plain regions. Species in this category may also fall into 2. and 3.

Very little is known about the fauna of the meta- and hypopotamon of the rivers on the east coast; it is quite likely that species will be found which are largely limited to these lower zones.

As latitudes become lower the montane end of the epipotamon extends to higher and higher altitudes. Here the true cold stenothermal, rhithronic fauna is replaced by more widespread eurythermal species. Some of these are found throughout the whole of the epipotamon at more temperate latitudes but are pushed into the montane epipotamon in the tropics. Others extend from this zone into the lower parts of the tropical epipotamon to varying degrees. Prominent among the rhithronic fauna replacements are Baetidae, Leptophlebiidae (mainly *Euthraulius* spp.), Ecdyonuridae, Tricothyridae, Caenidae (Ephemeroptera), Perlidae (*Neoperla spio* NEWMAN), Aeschnidae, Coenagriidae, Hydropsychidae, Leptoceridae, Hydraenidae, Elmidae, Psephinidae (*Eubrianax* spp.), Simuliidae and Orthocladiinae (Chironomidae). Many of these extend well up into the rhithron, e. g., *Baetis harrisoni* BARNARD.

Rejuvenation in the potamon.

When this occurs the river profile steepens, rock is exposed and soft bottoms give way to stony rapids and runs. In the Tugela River (OLIFF 1960) these are colonised by widespread rheobiotic, eurythermal species. In the lower Lundi River (lat. 21°15' S), in the Chipinda Pools rapids (alt. approximately 260 m.) this is also the case but warm stenothermal, rheobiotic forms appear.

It is apparent from this short revue of Southern African conditions that ILLIES' river zones are useful. His insistence that rising temperature is the main factor limiting the downstream distribution of typical mountain fauna certainly applies, although rising silt content must be taken into account. It is more important to take these two factors into account when defining the rhithron, than such factors as changing profile and slower current speeds.

The epipotamon stands out by far as the longest and most important zone in an elevated sub-continent such as Southern Africa; its lower limit is fixed by flattening river profile and resulting slower current speeds, however higher temperatures downstream do influence the faunal composition, specially in the tropics and subtropics. In spite of its great length it would be difficult usefully to divide the epipotamon.

ILLIES has doubts about the usefulness of his division of the flood plain zone, or navigable reaches of rivers, into two, the meta- and hypopotamon. With the Great Berg, Pongola and Sabie-Incomati this division seems unnecessary, but, from what little is known of the biology of the lower Zambezi, it might be useful there.

Summary

It is difficult to devise a system for zonation of rivers which is universally applicable. HARRISON and ELSWORTH, in their study on the Great Berg River, divided the river into 5 zones along its length; these were based on physical features but also had characteristic faunal associations. OLIFF used a similar system for the Tugela River. J. ILLIES has devised a system for wider use (epi-, meta-, and hyporhithron and epi-, meta-, and hypopotamon) and an attempt is made to fit Southern African rivers into this. It is concluded that the physical basis he uses corresponds with faunal conditions and that his zonation system is a useful one.

Zusammenfassung

Es ist schwierig, ein allgemeingültiges System für die Flußzonierung zu entwerfen. Bei ihren Untersuchungen des Great Berg-Flusses, Südafrika, haben HARRISON und ELSWORTH (1958) den ganzen Flußlauf in fünf Zonen eingeteilt; diese wurden auf physikalischen Faktoren begründet, hatten jedoch auch kennzeichnende Faunenverbindungen. OLIFF (1960) benutzte ein ähnliches System für den Tugela-Fluß. J. ILLIES (1961) hat ein System für alle Klimazonen aufgestellt, und es ist erfolgreich versucht worden, die Flüsse des südlichen Afrikas darin einzuordnen.

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