THE INFLUENCE OF ABIOTIC FACTORS ON THE DISTRIBUTION OF BIOMPHALARIA PFEIFFERI (KRAUSS, 1848) (PLANORBIDAE : MOLLUSCA) AND ITS LIFE-CYCLE IN SOUTH-EASTERN AFRICA

by

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RESUMÉ

Previous studies on the influence of abiotic factors on the distribution of bilharzia intermediate host snails of the family Planorbidae are reviewed. Much of this work is basically descriptive and relatively few attempts have been made to examine the effects of these factors on snails in their natural habitats - to identify the factors precisely and to measure their critical levels.

An account is given of recent studies on *Biomphalaria pfeifferi* (Krauss) in two climatically different regions of south-eastern Africa, at 655m altitude on the eastern Transvaal escarpment and 19m on the coastal peneplain of northern Zululand. These have shown the species to undergo a similar annual life-cycle of three overlapping generations in both areas. Further, in these areas where the snail has a discontinuous distribution, two abiotic factors, stream geology and water temperature, were found to be important in limiting its distribution.

The longitudinal distribution of *B. pfeifferi* and another host snail *Bulinus* (*Physopsis*) *globosus* (Morelet), extended upstream in a perennial watercourse, the Gladdespruit, on the escarpment only as far as permanently lentic habitats were available. These habitats, usually detached from the channel, characterized the stream's lowest physical zone with its substratum of exposed granite, as opposed to the sandy-bottomed lotic zones upstream. The limit of the snails' occurrence lay close to the junction of these two substratum types. Granite is resistant to erosion but contains soft inclusions which erode more quickly than the hard matrix causing uneven weathering. This results in the formation of depressions in the stream bed (i.e. pools, potholes and backwaters) which provide the permanently lentic conditions necessary for the snails' survival. Temperature recordings made on this plain, upstream of the snails' limit, suggest that the water temperature here exceeded the critical lower levels required for a positive intrinsic rate of natural increase sufficiently often to permit the species to survive here, though not optimally. Above this point however, current velocities are continually in excess of the maximum tolerated (0.3 m/sec.) so that in this situation at least, current velocity is a dominant factor.

A contrasting situation exists on the coastal peneplain of northern Zululand where *B. pfeifferi* occurs in some lentic habitats and not in others. This discontinuous distribution is shown to be related to the prolonged duration of temperatures above the level for optimal increase. The apparently suitable habitats from which *B. pfeifferi* was absent were found to be both very shallow and to experience these prolonged high temperatures during spring and early summer. This corresponds to the maturation period of the *B. pfeifferi* 1st generation as defined by Appleton (1974) and causes reduced fecundity probably through impaired gonad development. The density of its filial (2nd) generation is correspondingly reduced. A statistically significant partial-correlation (at a 1% level) was found between the fecundity of the 1st generation and increasing periods of temperatures above the species' optimal limit in the habitats involved during its maturation period (spring). It is interesting to note here that *B. (Ph.) globosus*, which is known to be better adapted to high

temperatures than B. pfeifferi (Shiff & Husting, 1966) occurred in all the waterbodies concerned.

Both these factors therefore play important rôles in determining the country-wide distribution pattern of the host snails. This distribution is closely correlated with the availability of permanently lentic habitats. In river systems, which form the main environment for these snails, such stable habitats occur almost entirely in low-gradient reaches over hard bed-rock which is resistant to erosion. Current velocities above 0.3 m/sec. render steeper reaches and those over soft, non-resistant rock and sand (unstable substrata) unsuitable and therefore constitute a most important limiting factor. Temperature however becomes a dominant factor in permanently lentic waterbodies. Biomphalaria pfeifferi is adversely affected by high temperature régimes and where such régimes occur in waterbodies which are too shallow to permit temperature gradient to develop, the species cannot survive whereas B. (Ph.) globosus can do so. This intolerance of high temperature régimes on the part of B. pfeifferi accounts for the species' adoption of a discontinuous distribution over the coastal plain of south-eastern Africa. A comparable pattern has been reported for the species over this plain northwards to approximately 16°S latitude in Mozambique and is probably due to a similar high-temperature effect. Further northwards in equatorial latitudes B. pfeifferi is restricted to the more elevated and cooler areas above an altitude of 500 - 600 m, probably because the very high temperature régimes prevailing in the lowlands there exclude the species altogether.

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INTRODUCTION

Bilharzia or schistosomiasis, a parasitic disease caused by adult worms of the genus *Schistosoma* Weinland, 1858 (Platyhelminthes : Trematoda), today affects some two hundred million people in three continents, Africa, America and Asia (Vogel, 1973). Recent indications are that in some areas such as parts of South America actual geographic spread of the disease is in progress (Wright, 1973) while in Africa spread seems confined to irrigation schemes and other artificial environments. Further, in areas where the disease has long been established, it is now becoming more severe - worm loads are increasing. So important is it now among human parasitic diseases that bilharzia has been ranked second only to malaria by the World Health Organization.

Major extensions to its already wide distribution have been caused by human traffic from endemic to then non-endemic areas. It is generally believed for instance that *Schistosoma mansoni* Sambon, 1907 (human intestinal bilharzia) was carried to the New World from Africa by slaves during the 16th century. Here indigenous snails have proved most suitable intermediate hosts. These are now considered congeneric with *Biomphalaria* Preston, 1910, the African intermediate host of the parasite (Barbosa *et al*, 1961). The inclusion by Jaeckel (1969) of several African snails of the genera *Biomphalaria* and *Bulinus* in the exotic malacofauna of Brazil must be discounted since no mention of this potentially dangerous development has yet been made by Brazilian malacologists. Very recently however (1973) one of the South American host snails, *Biomphalaria* straminea (Dunker, 1848), was discovered in a stream in Hong Kong (Meier-Brook, 1975) posing a grave threat to much of Asia where at present S. mansoni does not occur.

An intimate knowledge therefore of the interactions between host snail dispersal and environmental factors is a pre-requisite not only to an understanding of the sometimes discontinuous distribution of both snail and parasite, but also to successful attempts at snail control. If snail control, which is widely held to be an important component of any anti-bilharzia programme, is to be effective it would have to be applied on a very extensive scale indeed and its rationale should be based upon knowledge gained over a correspondingly wide area.

Although a good deal has been written on the effects of abiotic environmental factors on host snail distribution, much is repetitive and anecdotal. Only four of these factors have received more than passing attention. The literature also contains a coherent picture of the life-cycles of host snails in different types of habitat. These population fluctuations are generally thought to be related to rainfall and temperature.

Little quantitative field research has been done to complement the laboratory studies (mostly by Harrison, Shiff and their co-workers in Rhodesia) of the effects on snails of abiotic factors, especially the calcium and bicarbonate ion concentrations and temperature. These authors have used the sensitive intrinsic rate of natural increase (r) to characterize the snails' performance in terms of fecundity and survival under experimental conditions. They have demonstrated that over the range of both Ca^{++} and HCO_3^-

concentrations and temperatures normally found in the field, snail fecundity was affected more than survival. Further, B. pfeifferi exhibited a narrower tolerance range to these factors than Bulinus (Physopsis) globosus (Morelet, 1866), the intermediate host of Schistosoma haematobium (Bilharz, 1852) (human urinary bilharzia).

It is known from field observations however that both host snail species have a particularly narrow tolerance range to current velocity. No detailed studies had been made on the influences of this factor until recently when Appleton (1975) investigated the connection between current velocity and stream geology with respect to host snail ecology. This study showed that in two perennial eastern Transvaal watercourses where B. pfeifferi and B. (Physopsis) are sympatric, persistent populations of these species occurred only on the stable substrata formed by the erosion of rocks with hardnesses of 5 and greater in Mohs' Scale of Hardness. The snails were either absent or present only as small, temporary populations on the unstable substrata formed by the erosion of rocks with hardnesses less than 5 in Mohs' Scale or on sand. The stability of the substratum and the influence this has on current velocity are thus most important factors determining the distribution of these snails in river systems. In lacustrine or lentic environments however, current velocity is obviously irrelevant and in such habitats temperature must become a dominant factor determining the occurrence of host snails.

In one of the watercourses referred to above - the Gladdespruit, near Nelspruit in the eastern Transvaal - Appleton (1974) followed the population fluctuations of both B. pfeifferi and B. (Ph.) globosus over 20 months and found that these two planorbids underwent similar annual life-cycles of three overlapping generations. Biomphalaria pfeifferi is however not as well adapted to high temperatures as B. (Ph.)globosus (Shiff & Husting, 1966) and it was therefore interesting to find that the 2nd of the three B. pfeifferi generations appeared during the hottest period of the year, late January and February.

It was thought that if a similar generation sequence was produced in a hotter area than Nelspruit, such as the coastal peneplain of south-eastern Africa, adverse temperature influences might cause this 2nd generation to vary relative to the others which spanned cooler months. The snail is in fact known to have a discontinuous distribution here (de Morais, 1956, 1959; de Azevedo et al, 1959, 1961; Brown, 1967) and the incidence of S. mansoni is very low (de Morais, 1959; Pitchford, unpubl. records; State Health Dept., unpubl. records). North of the Zambezia Province of Mozambique where temperatures rise still higher, B. pfeifferi is absent altogether below 500 to 600 metres above sea level (de Azevedo et al, 1961; Teesdale, 1962; Sturrock, 1965a & b). It is probable that the temperature régimes prevailing here exceed the species' tolerance range. By way of contrast, B. (Ph.) globosus is distributed throughout the lowlands of south-east and east Africa and S. haematobium infection is severe.

In order to investigate further the possible influence of temperature on this discontinuous distribution, a repeat sampling programme was carried out on B. pfeifferi over a year in and around Lake Sibaya on the coastal peneplain of northern Zululand, an area approximating to equatorial conditions as nearly as possible. Temperature has in fact been shown to exert a marked influence on the fecundity of B. pfeifferi and is widely regarded as being instrumental in determining its distribution pattern. Field temperature régimes are therefore likely to affect the fecundity of its natural populations but scant information exists as to how this might be achieved and none as to the levels of temperature at which it occurs. A possible modus operandi for a temperature influence on fecundity at the developmental level was provided by Michelson (1961) and van der Schalie & Berry (1973) but this has yet to be applied to African host snails. The present contribution attempts both to isolate component(s) of different temperature régimes which might affect fecundity and to establish their critical levels. In a wider context, temperature and a second factor, the influence of stream geology on substrate stability and current velocity, are shown to account in a large measure for the present distribution patterns of host snails, at least in South Africa. Prior to this however, a detailed review is necessary in order to assess what is known of the effects of abiotic factors on planorbid host snail distribution and whether they contribute towards an explanation of the problem outlined above.

PART 1

A REVIEW OF LITERATURE ON ABIOTIC FACTORS WHICH ARE THOUGHT TO INFLUENCE THE DISTRIBUTION OF INTERMEDIATE HOST SNAILS OF THE FAMILY PLANORBIDAE AND THEIR LIFE-CYCLES

The joint OIHP/WHO Study Group on Bilharziasis held in Cairo in 1949 recommended the collation of accurate records of the geographical distribution of bilharziasis and its intermediate host snails by WHO consultants. These consultants presented their findings at the WHO African Conference of Bilharziasis in Brazzaville (November 26th - December 8th, 1956). This contributed much to the knowledge of the world-wide endemicity of the disease and to the identification of the intermediate host snail species involved. At an earlier meeting in Paris however (3rd - 9th October of the same year) the WHO Study Group on the Ecology of Intermediate Snail Hosts of Bilharziasis had stressed that without a knowledge of the relationships between the ecology of host snail habitats, life-cycles and habits, practical control measures would have only limited success. Although isolated ecologically-orientated studies had been made earlier (Gordon _et al_, 1934; Barlow, 1935; Barlow & Muench, 1947; Mozley, 1939) the proceedings of this Paris conference, published in volume 18 (parts 5-6) of the Bulletin of the World Health Organization, laid the foundation for further research into the ecology of the disease.

Between 1950 and about 1964 then, medical malacologists were concerned primarily with field ecological survey-studies.

Abiotic factors which were thought likely to influence host snail distribution were examined in various countries in a generalized way, often incorporated into composite studies. These factors included analyses of water chemistry, observations on temperature, sunlight, turbidity, current velocity, dessication and substratum. Most attention has however been given to three of these, chemistry, temperature and dessication and their influences on the snails' life-cycles.

Where authors have referred in their texts to *Australorbis glabratus* and *A. centrimetralis*, these names are replaced by the currently accepted names of *Biomphalaria glabrata* and *B. straminea* respectively.

Water chemistry

General chemical analyses of water from snail habitats have been described by a variety of authors in many countries (Alves, 1958 in Rhodesia; de Azevedo *et al*, 1961 in Mozambique; de Meillon *et al*, 1958 and Schutte & Frank, 1964 in South Africa; El Gindy, 1957 and Gohar & El Gindy, 1960b in Egypt; De Andrade, 1954 and De Andrade *et al*, 1955 in Brazil; Harry *et al*, 1957 and Harry & Aldrich, 1958 in Puerto Rico; Lietar, 1956 in what is now Zaire; Marill, 1958 in Algeria; Mozley, 1939 and Webbe, 1962a in what is now Tanzania and Watson, 1958 in Iraq). These and other more generalized studies (Deschiens, 1957; Hubendick, 1958; WHO, 1957) demonstrated that host snails are tolerant of waters differing widely in chemical content so that their occurrence seems independent of the usual range of ionic composition found in field waters. Levels of salts lethal to snails are obviously seldom approached here.

Variation in population density may however be attributable to the chemical quality of water and subsequent work has centered around more specific aspects of the chemical régime.

The salt calcium bicarbonate was thought to have effects, though perhaps only subtle ones, on host snail physiology. This is really the only aspect of water chemistry where effects on host snail ecology have been investigated in depth, chiefly by Rhodesian and South African researchers. The concentration of the bicarbonate anion (alkalinity) is an indication of the buffering capacity of the water and since much of the snails' endemic waters in southern Africa flow over the insoluble Old Granite and Gneiss formations of the Archaean Complex, its effect on snails might provide information applicable over a large area. Macan (1949) had found that *Lymnaea peregrer* (Müll.) and *Planorbis albus* (Müll.) in the English Lake District had threshold calcium concentrations below which they could not survive, critical values of 3 and 5 mg/ℓ Ca^{++} respectively.

Harrison *et al*, (1960) showed that egg-production by *B. pfeifferi* kept in both natural stream water and artificial culture medium with high magnesium/calcium ratios (12.4 and 19.7 respectively) was significantly impaired and even prevented when compared with controls in which the metals were in equal proportions. Such magnesium-rich water flows off the soluble rocks of the Swaziland System which is associated with the Great Dyke in Rhodesia. Host snails are known to be absent from these rocks (Shiff, *in litt.*, 1975) which are largely serpentines (hydrous magnesium silicates). In the Republic of South Africa the Swaziland System is more widespread and similar magnesium-rich water is characteristic of parts of the Kaap and eastern Crocodile River systems in the south-eastern Transvaal. Though host snails are also rare on these rocks, Schutte & Frank (1964) did not find the water flowing off these formations, with mean Mg/Ca ratios of up to 17.4 (based on monthly analyses), to be unfavourable to their presence.

Frank (1963) and Schutte & Frank (1964) also pointed out that the sodium/calcium ratio may be important in affecting snail density and that *B.* (*Physopsis*) was more common than *B. pfeifferi* in waters where the ratio exceeded 2.4. They referred to observations by Malek (1958) that a low ratio was unfavourable for snails, only *B. pfeifferi* being found where the value was 0.2.

Frank (1963), Schutte & Frank (1964) and Williams (1970a) have shown that while *B.* (*Physopsis*) sp., *B.* (*Physopsis*) *globosus* and *B. pfeifferi* occur in waters with calcium bicarbonate concentrations ranging from 5 - 40 mg/ℓ Ca^{++} and 20 - 200 mg/ℓ HCO_3^- (very soft to very hard), they are most abundant in the hardest, above approximately 30 mg/ℓ Ca^{++} and 200 mg/ℓ HCO_3^-. In Rhodesia *B. pfeifferi* was absent from very soft waters (5 mg/ℓ Ca^{++} and 20 mg/ℓ HCO_3^-). In South Africa the frequency of host snail occurrence was found to be more-or-less proportional to hardness, hard and very hard waters being favoured. The hardness of these latter categories was frequently due not to calcium as Schutte & Frank (1964, Fig.5) might suggest, but to magnesium which is plentiful in the serpentines and magnesite ($MgCO_3$) of the Swaziland and Moodies Systems. A high magnesium content is as mentioned above typical of the watercourses draining these rocks. Calcium bearing rocks are rare in this area.

The findings of Williams (1970a & b) using the intrinsic rate of natural increase (r), also demonstrated that B. (Ph.) globosus is tolerant of a wider range of calcium and bicarbonate ion concentrations than B. pfeifferi. Williams found B. pfeifferi to exhibit greater variation in 'r' at different concentrations under experimental conditions than B. (Ph.) globosus, with peak values within the 'medium' category (5 - 40 mg/ℓ Ca^{++} and 20 - 200 mg/1 HCO_3^-). Further, the field abundance of B. pfeifferi was significantly correlated with r ($p<0.05>0.025$) whereas for B. (Ph.) globosus this was not so.

Harrison & Shiff (1966) and Harrison et al, (1970) criticized Williams' experiments on the grounds that his snails had done best in the water from which they had been collected (the only natural water used). They therefore repeated the experiments using snails from widely separated habitats and water of differing $CaCO_3$ content. Their results confirmed the attainment of the highest 'r' in 'medium' water as reported by Williams but showed as well that snails from geographically distinct populations differed both in their age at first oviposition and in egg-output. Harrison (1966) commented that because these populations had been separated at least since early Pleistocene times, genetically isolated populations or perhaps strains could now exist, each with its own physiological characteristics. He has in addition (Harrison, 1968) endorsed the finding that bicarbonate ion concentrations within the 'medium' range of Williams (1970a & b) are most suitable for host snails by demonstrating that oxygen consumption by B. pfeifferi varied significantly at different $^-HCO_3^-$ levels, from 15 - 300 mg/ℓ (as $CaCO_3$). He found that the highest oxygen uptake rate occurred at a bicarbonate concentration of 35 mg/ℓ, falling off rapidly above and below this level.

Jennings et al, (1973), employing electrical conductivity as a measure of total dissolved solids (TDS), have shown that for B. pfeifferi 'r' varied markedly under conditions of differing conductivity. Tested over a range of 50 - 1000 µS, the species attained highest 'r' values between 300 and 400 µS, the conductivity range associated with hard water by Schutte & Frank (1964). Jennings et al however changed the experimental temperature from 26° to 29°C once the snails had reached maturity and since, as will be mentioned later, 'r' varies with temperature, this might have affected the very high 'r' values recorded,up to 1.1489. Heeg (1975) has shown that the occurrence of Bulinus (Physopsis) africanus (Krauss, 1848) in waters with widely different dissolved solid content may be explained by its ability to acclimate to changes in TDS of the magnitude expected in natural waters. Biomphalaria pfeifferi which is known to be particularly sensitive to the ionic composition of water (Frank, 1963; Harrison, 1966, 1968; Williams, 1970a & b; Jennings et al, 1973) may not have this ability. This could account to some extent at least for its irregular and more restricted distribution pattern in South Africa.

These findings indicate that while the quality of water within the usual ranges found in natural waters may not affect the distribution pattern much, certain aspects may influence the snails' local abundance. They show further that B. (Physopsis) has a greater tolerance to changing chemical conditions both in the field and in the laboratory than does B. pfeifferi whose population density may be determined at least partly by factors such as the Ca^{++} and HCO_3^- concentrations.

Salinity

Although references to bilharzia transmission in lagoons and estuaries are to be found in the literature (Blair, 1956; Malek, 1958; Gilles et al (1965) little information is available on the effects of saline water on the host snails. Brumpt (1941) showed that Biomphalaria glabrata could survive for 35 days in sea water of 2°/oo and for only a few days at 2.5°/oo. Chernin & Bower (1971) found that the same species could survive in artificial sea water at or below a concentration of 1.25°/oo. Ezzat (1961) reported that Egyptian Lymnaea natalensis Krauss was intolerant of saline water and lived for only 48 hours in water of 3°/oo.

It seems therefore that even very low salinities are inimical to the snails but since claims are made from time to time that bilharzia transmission does occur in Natal estuaries, attention should be paid to the snails' tolerance of fluctuating salinities, i.e. tidal conditions. Bruton & Appleton (1975) did in fact find a fresh-water snail, Melanoides tuberculata (Müller) living under just such conditions in the Mgobezeleni estuary in northern Zululand.

Turbidity

Though host snails are frequently found in naturally turbid waters, those with high turbidities (due mainly to minerals in suspension) are considered unfavourable (Malek, 1958; Watson, 1958). Experiments by El Gindy (1957) revealed turbid Nile flood water to have no appreciable effects on either Bulinus truncatus or Biomphalaria alexandrina Ehrenberg. Recently Harrison & Farina (1965) have shown that while a turbidity of 360 mg/ℓ (due to suspended minerals from granite erosion) did not affect snails themselves, it prevented development and hatching of B. pfeifferi eggs. Neither B. (Ph.) globosus nor L. natalensis were similarly affected at this concentration and eggs of all three species hatched normally at a lower level of 190 mg/ℓ.

In the eastern Transvaal lowveld Schutte & Frank (1964) found that turbidity which is highest in summer, occasionally exceeded 150 mg/ℓ. It was due mostly to fine siliceous and clayish matter and was highest in soft waters where the snails were least common anyhow.

Temperature

Observations based largely on isolated recordings have shown that host snails of the family Planorbidae have broad tolerance ranges to field water temperatures (Ayad, 1956; Gordon et al, 1934; Malek, 1958; van Someren, 1946; Watson, 1958; WHO, 1957; Zakaria, 1955). These temperatures vary from as low as zero to around 40°C, though this seasonal range depends upon the climate of the region concerned. The favourable range lies between approximately 18° and 32°C with optimal conditions between 22° and 26°. Diurnal ranges of up to 20°C have been recorded from habitats containing B. pfeifferi on the Kenyan highlands (van Someren, 1946). These remarkably broad tolerances may however not be accurate since as Shiff (1966) has demonstrated both experimentally and in the field, B. (Ph.) globosus is sensitive to temperature gradients and will seek out parts of the habitat where temperatures are nearest the optimum (i.e. the surface layers during the cool Rhodesian highveld winter). It would be interesting to know whether B. pfeifferi exhibits a similar behaviour pattern.

Recent laboratory investigations have shown that although the temperatures at which host snails attained an optimal 'r' were similar, the range at which 'r' remained high varied for different species, just as tolerances to $CaCO_3$ concentrations were shown to do. Shiff (1964) worked on Rhodesian B. (Ph.) globosus; Sevilla (1965) on three species of Biomphalaria, Tanzanian pfeifferi, Egyptian alexandrina and Puerto Rican glabrata; Sturrock (1966) on Tanzanian B. pfeifferi; Shiff & Garnett (1967) on Rhodesian B. pfeifferi and Sturrock & Sturrock (1972) on St. Lucian B. glabrata. The highest 'r' value for each of these species was found to occur at 25°C. Values for B. (Ph.) globosus rose to a definite peak at 25°C (Shiff, 1964) whereas for B. pfeifferi Shiff & Garnett (1967) found a plateau of optimal though lower 'r' values between 20° and 27°C. Shiff & Husting (1966) consider this to indicate that B. (Ph.) globosus is profoundly influenced by temperature and that it can multiply rapidly under optimal conditions, even if these are of brief duration. Biomphalaria pfeifferi however showed little change in 'r' over a 7°C range of experimental temperatures, none producing a marked peak in 'r', which suggests an adaption to stable thermal conditions. The high values of 'r' attained by B. (Ph.) globosus at 25°C and 27°C (0.66 and 0.60 respectively) may therefore be considered a selective advantage to the species enabling it to capitalize on the harsh environmental conditions found in temporary waterbodies on for instance, the highveld plateau of central and southern Africa. In the absence of a clear peak 'r', B. pfeifferi may be expected to colonize more permanent habitats with cooler temperature régimes and this is precisely the type of habitat harbouring the species in South Africa.

Tanzanian B. pfeifferi, Egyptian B. alexandrina and Puerto Rican B. glabrata (Sevilla, 1965) and St. Lucian B. glabrata (Sturrock & Sturrock, 1972) showed no evidence of a plateau of 'r' values but rather peaks at 25°C similar to B. (Ph.) globosus (Shiff, 1964). Sturrock (1966) used only three experimental temperatures so that although there appears to be a peak at 25°C the existence of a plateau cannot be excluded. All these species are known to be inhabitants of temporary waterbodies. The genus Biomphalaria in the southern part of its range in Africa (south of the Zambezi River) thus appears to be adapted to permanent habitats whereas further north and in the New World its high intrinsic rate of natural increase enables it to survive satisfactorily in habitats which dry out regularly. High rates of increase involve high energy output which would be facilitated by natural selection in populations which are decimated periodically (Hairston, 1973).

Prinsloo & van Eeden (1969) have shown another South African planorbid (though not a vector of human bilharzia), Bulinus (B.) tropicus (Krauss) to have its highest 'r' at the highest temperature tested (27°C). This rate fell with decreasing temperature. A repeat of these experiments using temperatures above 27°C might have produced a more satisfactory result. They also found that L. natalensis had a peak 'r' at 18°C. The authors' contention was 'that a statistically significant correlation between the country-wide distribution patterns of L. natalensis and B. (Physopsis) sp. (van Eeden & Combrinck, 1966) might reflect common ecological requirements' and could therefore allow findings for the former to be applied to the latter. This reasoning must be doubted however because not only do the findings of Prinsloo & van Eeden (1969) militate against the occurrence of both species in Natal and the eastern Transvaal (where in fact they are abundant) but also because L. natalensis has been shown to undergo a fundamentally different life-cycle to that of B. (Ph.) globosus. The former breeds during the cooler months which may explain the low optimal temperature of 18°C whereas the latter does so during the warmer months (Appleton, 1974). Differences in their ecological requirements are further indicated by the much greater susceptibility of L. natalensis to dessication than B. (Ph.) globosus (Shiff, 1960; Cridland, 1967) and the evidence provided by Calow (1970, 1973, 1974) on Lymnaea peregrer (Müll.) and Planorbis contortus (Linn.) suggesting that Lymnaeidae are herbivores whereas Planorbidae are detritivores.

de Kock (1973) determined 'r' at different temperatures for five South African pulmonate species. He concluded that peak values for the three Bulininae investigated lay between 23° and 26°C for B. (Ph.) africanus, between 26° and 28°C for B. (Ph.) globosus and at 26°C for B. (B.) tropicus. Biomphalaria pfeifferi and L. natalensis had plateaux of near-optimal 'r' values from 26° to 29°C and 23° to 25°C respectively. These temperatures are noticeably higher, some by several degrees, than those calculated for B. (Ph.) globosus and B. pfeifferi by other authors (Shiff, 1964; Sevilla, 1965; Sturrock, 1966; Shiff & Garnett, 1967) and for L. natalensis by Prinsloo & van Eeden (1969) although their findings for B. (B.) tropicus are similar. The existence of a plateau of near-optimal 'r' values for B. pfeifferi does however agree with the results of Shiff & Garnett (1967). de Kock attributed his remarkably high optimal temperatures, especially for B. pfeifferi, to the parental generations of his experimental snails being native to hotter areas (his B. pfeifferi came from

Plaston near Nelspruit in the eastern Transvaal) than those used by other authors.

The difference found by de Kock between B. (Ph.) africanus and B. (Ph.) globosus is interesting and suggests that the former is adapted to cooler conditions than the latter. This is borne out by the findings of Brown (1966, 1967) who showed that in Natal and the south-eastern Transvaal, B. (Ph.) globosus is confined to the lowlands while B. (Ph.) africanus extended inland onto the Transvaal highveld and southwards into the Transkei. Schutte & Frank (1964) found the two species to be sympatric on the eastern Transvaal escarpment.

Populations of planorbid host snails expand optimally at constant temperatures around 25°C. Those species which have a distinct peak 'r' (usually 0.7 - 0.9) are capable of successful aestivation over prolonged periods of drought and thrive under naturally unstable or temporary conditions. Those with lower maximal 'r' values (0.4 - 0.5) spread over a range of temperatures however, inhabit more stable environments. These species do not aestivate readily. Host snail distribution patterns in southern Africa are thus determined more by the permanence of these stable habitats than by temperature differences between them.

Intrinsic rates of natural increase under field conditions have been calculated for a few snail species. Dazo et al (1966) reported values of 0.61 and 0.67 for Egyptian B. alexandrina and B. truncatus respectively. These values are lower than the maxima given by laboratory experiments but this is to be expected in view of the added environmental pressures, such as fluctuating temperatures which must affect 'r'. Sturrock (1973a) went further and demonstrated that in a variety of shallow habitats (of four different types) mean 'r' values for B. glabrata varied from 0.4456 during the stable phase of population growth, to -0.0788 during the stable phase, to -0.7463 during the decreasing phase. He unfortunately did not make it clear whether all or only some of these sites were temporary. Under permanent conditions one might expect the decline of the decreasing phase to be less drastic.

An important contribution to the modus operandi of the effect of temperature on 'r' is provided by van der Schalie & Berry (1973) who investigated temperature effects on growth and reproduction in members of three North American pulmonate and one prosobranch families. They found that although the optimum temperatures for three species of Helisoma, i.e. trivolvis (Say), anceps (Menke) and campanulatum (Say) (Pulmonata : Planorbidae) differed slightly, they fell within the 24^{o} - 26^{o}C range. At higher temperatures growth was better but offset by poor egg-production which dropped close to zero at 30^{o}C. Optima for two Lymnaeidae (Pulmonata), Lymnaea stagnalis Linn. and L. emarginata Say, lay at approximately 22^{o}C while Physa gyrina Say (Pulmonata : Physidae) had a wider tolerance range altogether (14^{o} to 24^{o}C). The only prosobranch tested, Amnicola limosa (Say) (Amnicolidae) was found to perform optimally in the 18^{o} to 24^{o}C range. Histological sections of gonads showed that at temperatures above and below the optimum range, tissue development was impaired. Little or no gonad activity was evident at sub-optimal temperatures although above the optimal range egg and sperm differentiation seemed in some cases to be normal. At these higher temperatures however fewer eggs were laid and their viability fell to about 50% of that within the optimal range. These results support those of Michelson (1961) who found an optimum temperature of 25°C for B. glabrata and that at 30°C, though growth was accelerated, repression of the female gonadial tissues occurred. Temperatures below the optimum retarded both growth and reproductive activity.

Temperature is clearly an important limiting factor to host snails, chiefly through its influence on their fecundity. Both the upper and lower critical limits lie at temperature levels commonly encountered in the field.

Population fluctuations

Numerous observations of fluctuations in the abundance of host snails have been reported. Reviewing the evidence, Webbe (1964) and Webbe & Jordan (1966) stressed the apparent dependence of reproductive and population cycles on the cyclic fluctuations of interrelated environmental factors. Generally the evidence shows a fall in snail densities during rainy periods with little or no breeding. During the ensuing drier and warmer months however, reproductive activity increases. Populations appear to follow an average growth curve, of which the maxima and minima were related to rainfall and temperature or environmental conditions due to them (Webbe, 1962; Sturrock, 1973a). In another review, Hairston (1973) noted that in sub-tropical and temperate regions population fluctuations were attributed largely to temperature influences while those in tropical areas were thought due to rainfall. An alternative approach is adopted here. Since fecundity and survival are influenced by drastic alterations of the habitat - periods of physical stress -

the permanence of habitats involved is taken into account and reduces the apparent lack of concensus among these reports.

Habitats in which host snail life-cycles have been investigated fall into two broad categories - temporary and perennial or permanent - the same criteria used by Mandahl-Barth (1954) and Cridland (1957a, b, 1958). Temporary habitats dry up for part of each year and include irrigation canals which may, like those in Egypt, be emptied annually for cleaning. As Mandahl-Barth (1954) has pointed out, these two habitat types place different demands on snails, particularly on their ability to withstand dessication. Only species capable of surviving through the dry season will survive in temporary habitats. This ability has since been demonstrated to be coupled with a peak 'r' value at high temperatures. It enables populations which survive periods of physical stress and heavy mortality to reproduce rapidly when conditions again permit, as recorded in the field by Pringle & Msangi (1961) and McCullough (1962). Phenomena which should be regarded as periods of stress are drying of the habitat and prolonged high and low temperatures, these latter affecting fecundity and possibly survival as well. In temporary habitats influences such as these must determine the snails' life-cycles. Floods may sometimes be important. Pimentel & White (1959) and Rowan (1959) found in Puerto Rico that only the most severe floods caused serious reductions in the densities of <u>B. glabrata</u> populations in streams there.

In temporary habitats in tropical South America and the West Indies, <u>B. glabrata</u> in Brazil and St. Lucia and <u>B. straminea</u> have a single generation per year (Olivier, 1955; Olivier & Barbosa, 1955a

& b; Barbosa, 1962; De Andrade, 1962b and Sturrock, 1973b). At the close of the rainy season snails are numerous and most are large but when the habitats dry out many snails die and relatively few aestivate successfully. With the onset of the next rainy season these survivors, mostly smaller specimens, grow and reproduce rapidly. Within 50 - 60 days peak snail abundance has been restored. The snails seldom live beyond a year.

In an important, quantitative contribution, Shiff (1964a) examined the life-cycle of B. (Ph.) globosus in a temporary pond in Rhodesia. He found a cycle of one generation per year clearly related to both rainfall and temperature. By calculating seasonal rates of increase, he demonstrated that when temperatures were high (summer) fecundity was also high although longevity was reduced. The small proportion of snails attaining maturity were able to regenerate the population. When temperatures were low (winter), fecundity was reduced but offset by increased longevity. The species is therefore equipped to survive in both large waterbodies where moderate temperatures permit moderate fecundity with increased longevity and in small, temporary habitats where environmental conditions are severe, by responding to brief optimal spells with high egg-production. The resultant massive increase in numbers ensures the survival of the population during adverse conditions, despite poor longevity. This cycle was confirmed by Hira (1966) in a temporary habitat in Nigeria.

In the Middle East and North Africa where many habitats are temporary, the rainy season extends from December to April (winter). In Iraq Watson (1951, 1958) found however that B.

truncatus underwent two generations per year in the field. Numbers increased during early summer (May and June) after the emergence of individuals aestivating through the cold winter and/or winter closure of irrigation canals, reaching peak abundance in July with a smaller second peak in autumn (October) after the maximal summer heat. Temperatures here frequently approach 39° to 40°C (Pitchford, pers.comm., 1975). Pronounced reproductive activity in June and September accounted for the two peaks. This pattern was confirmed by Najarian (1961) also in Iraq, by Dazo et al, (1966) and Mousa & El Hassan (1970, 1972) in Egypt; by Marill (1956, 1958) in Algeria and by Gaud & Dupuy (1954) and Gaud (1958) in Morocco. Dazo et al also showed that B. alexandrina had a similar life-cycle. In these regions both the drying of the habitats and the extremely high summer and low winter temperatures may be considered to be periods of stress and were followed by intense egg-laying.

In tropical Africa many host snail habitats are also temporary, but there are two usually distinct rainy periods each year : the 'long' rains from April to May and the 'short' rains from November to December. These are due mainly to the south-east and north-east monsoon winds. A belt of 'rain in all seasons' lies along the equator, extending approximately 7 - 8° to the north and south.

Studies by Mozley (1939), Webbe & Msangi (1958), Webbe (1962a) and Sturrock (1965) in what is now Tanzania, Cridland (1957b, 1958) in Uganda and Lietar (1956) in what is now Zaire associated observed population fluctuations by a variety of snails of the genera Bulinus (Physopsis) and Biomphalaria with the change from dry to wet conditions. Two generations per year were usual. Increased egg-laying was apparent following the advent of each rainy period so that both appear to constitute periods of stress. The number of generations produced each year depends however on the permanence of the habitats during the period between the 'long' and 'short' rains (January - March).

In permanent habitats the effects of rainy periods are not as profound as in temporary ones and temperature régimes are more stable. Studies in such habitats have revealed that egg-production occurs throughout the year with a major breeding season in spring and summer and not in one or two isolated bursts as in temporary water-bodies. De Andrade (1962) and Ritchie et al, (1962) found that B. glabrata in permanent streams in Brazil and Puerto Rico respectively produced single density peaks at the start of each rainy season. Cridland (1957a) and Webbe (1960, 1962b) found only a single peak per year for Biomphalaria adowensis (Bourg.), sudanica (von Martens) and pfeifferi. Populations declined markedly following the 'long' rains but were unaffected by the 'short' rains. The stability of the two habitats in question, a permanent pond in Uganda and Lake Duluti in Tanzania, may account for the observed mild effects of the 'short' rains. Malek (1962) reported a similar cycle for B. truncatus in the Sudan as did Berrie (1964) for B. (Ph.) ugandae (Mandahl-Barth) and B. sudanica in a permanent habitat in Uganda, Baalawy & Moyo (1970) for B. (Ph.) nasutus (von Martens) in Tanzania and Onambiro (1972) for B. (Ph.)globosus in Sierra Leone.

Contributions by McCullough (1957) in permanent habitats in Ghana and Appleton (1974) in South Africa, regions with only one rainy period per year, revealed an annual cycle of three overlapping generations for B. (Ph.) globosus and B. pfeifferi. McCullough found that peaks occurred simultaneously in the four habitats he sampled, in December - January, March - June and September - October. Further studies on B. truncatus rohlfsi (McCullough, 1962) confirmed this. The pattern found by Appleton was similar and although the specific identity of the B. (Physopsis) was not given, Dr D.S. Brown has since examined examples from several localities on the stream (the Gladdespruit) and found only globosus (Brown, in litt., 18/9/75). The snails sampled by myself in the Gladdespruit therefore appear to be a homogeneous B. (Ph.) globosus population.

The Gladdespruit study revealed density peaks due to new generations in early and late summer (1st and 2nd generations respectively) and late autumn (3rd generation). These were sometimes small in size and probably not recognizeable as such when, as in many of the studies referred to above, snail sizes were not considered, densities were categorized (rare, common or abundant) and between-sample intervals were long (monthly or even six-weekly). When expressed as snail density (no. snails per sample) and not subdivided into size-classes, the Gladdespruit data present a pattern with one major peak from October to December (1st generation) and minor peaks in February (2nd generation) and May (3rd generation) (Fig.1). This presentation corresponds to those described by other authors and the three generation per year cycle is thought to be a more accurate picture of the sequence of events in permanent waterbodies.

Current velocity

Bilharzia host snails belonging to the family Planorbidae

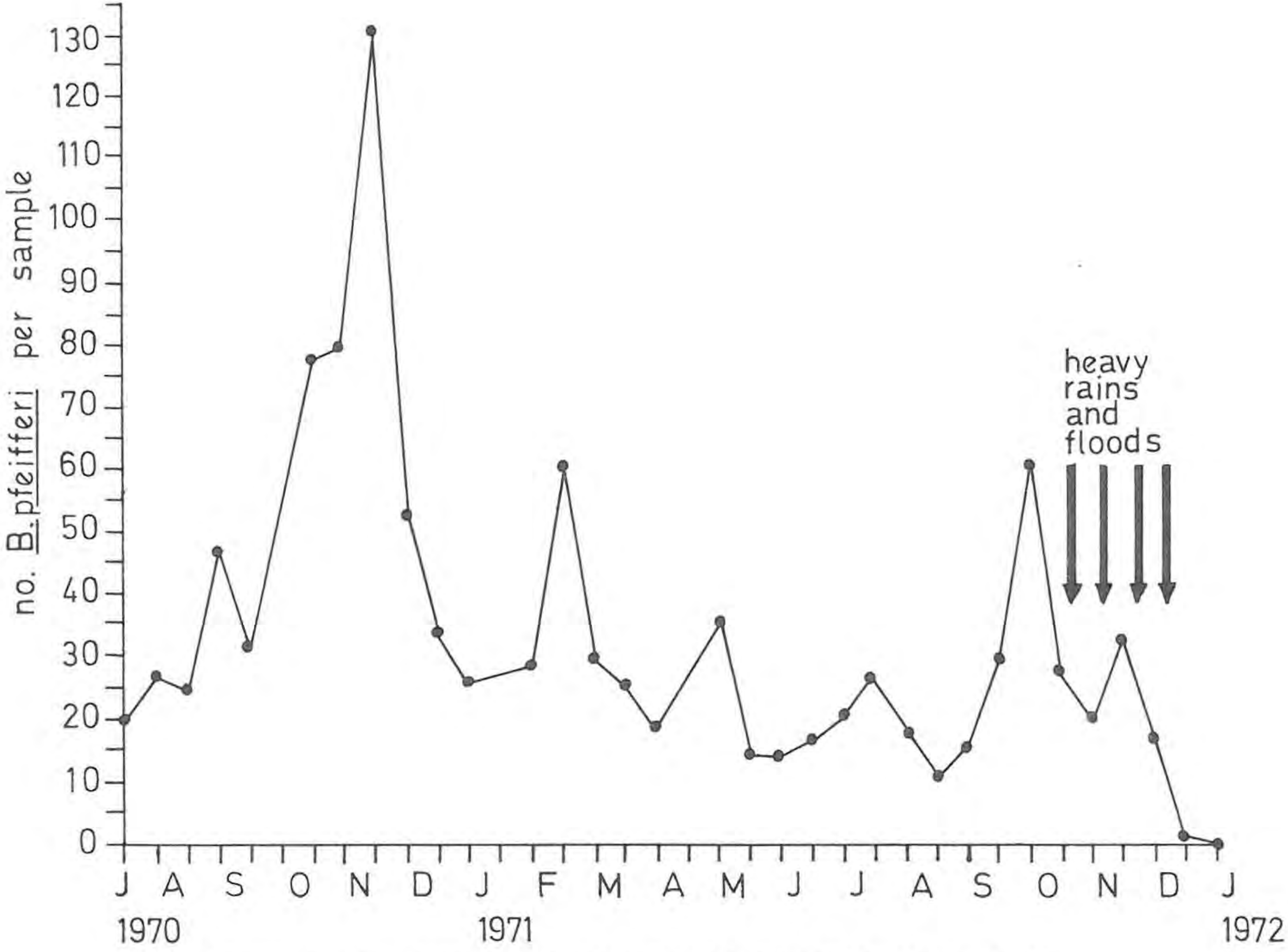

Figure 1 The Gladdespruit sampling data expressed simply as the number of B. pfeifferi taken per sample and not subdivided into size-classes as in Appleton (1974).

have been found to have a remarkably narrow tolerance range to current velocity. Most habitats in which they occur are lentic, but established, persistent populations occur also in very slowly flowing water, up to a limit of approximately 0.35 m/sec. (Luttermoser, 1944; Zakaria, 1955; Pimentel & White, 1957; Witenberg & Saliternik, 1957; WHO, 1957; Watson, 1957, 1958; de Meillon et al, 1958; Frank, 1964; Jobin & Ippen, 1964; Etges & Frick, 1966; Appleton, 1975). Scorza et al (1961) however provided a convincing illustration of this by showing a nearly linear negative correlation between the density of B. glabrata and current velocity, with a limit at 0.25 - 0.30 m/sec. in a stream in Venezuela. Only B. glabrata has so far been reported able to migrate upstream against weak currents. Radke & Ritchie (1961) described this as a common phenomenon in slowly flowing streams in Puerto Rico and Paulini (1963) found the same species capable of migrating against a velocity of 0.1 m/sec. in Brazil.

The reason for such a definite critical limit may be that the snails simply cannot remain clinging to a substratum exposed to velocities above 0.3 m/sec. for any length of time. Jobin & Ippen (1964) have shown that the hydrodynamic drag force created by velocities between 0.20 and 0.33 m/sec. at shell height caused B. glabrata to become immobilized on solid canal surfaces. At velocities greater than 0.33 m/sec. the snails became dislodged and swept away.

This dislodging of snails has been the modus operandi favoured by the authors referred to above but a limiting of the availability of preferred food may also be important. Recently

Calow (1973, 1974) has shown the European planorbid Planorbis contortus Linn. to be a detritus-feeder, particularly when the detritus is infected with live bacteria. This supports the contention of Boettger (1944) that the Planorbidae generally are detritivores, and casual observations by Oliff (1953), Malek (1958), Watson (1958) and Stiglingh & van Eeden (1970) that planorbids show a partiality for decaying matter, both animal and vegetable. Detritus will only be deposited however under lentic or very slowly flowing conditions, probably being carried away at velocities above 0.35 m/sec.

Water depth

Host snails are usually found in shallow water near the margins of their habitats and rarely below 1.5 - 2.0 m (WHO, 1957) though isolated records show them capable of living in deeper water, mostly in lakes. Veloso (1955) found B. glabrata down to 3m in muddy water in Brazil and Mandahl-Barth (1954) recorded Biomphalaria smithi Preston from 4.3m in Lake Edward and B. choanomphala (von Martens) from 12.2m in Lake Victoria. He considered this last species to be a predominantly lacustrine one.

Various bulinids of the subgenus Bulinus (Bulinus) are known from considerable depths in lakes. Bulinus trigonus (von Martens) is recorded by Mandahl-Barth from 7.3 - 9.2m in Lake Victoria; Gillet et al (1960) found Bulinus coulboisi (Bourg.) at 2.7m in Lake Kivu and Wright et al (1967) dredged Bulinus nyassanus (Smith) from 2 - 16m and collected Bulinus succinoides (Smith) from 3 - 4m, in Lake Malawi. Recently Boltt (1969) recorded Bulinus natalensis (Küster) down to 7m in Lake Sibaya.

No members of the subgenus B. (Physopsis) appear to have been found beyond about 2m depth.

Experiments by Deschiens & Jardin (1954) with B. adowensis and B. glabrata and by Gillet et al (1960) using B. pfeifferi showed these species capable of surviving at depths down to 10 - 15m for periods of up to six weeks. The small scale of these experiments (especially the former) and the lack of replication renders these findings inconclusive however. No comparable trials with bulinids appear to have been done.

Dessication

While host snail populations are able to persist in temporary habitats through the ability of a portion of their number to aestivate successfully during periods of drought, species and strains differ in their resistance to dessication (WHO, 1957). Barlow (1933, 1935) demonstrated that members of the genera Bulinus and Biomphalaria could survive the winter closure of Egyptian irrigation canals (a drying period of 40 - 50 days), and that they laid eggs immediately after re-filling. Cawston (1946) noted the resistance of B. (Ph.) africanus to environmental influences during droughts in South Africa and Annecke & Peacock (1951) found large numbers of B. tropicus aestivating amongst grass roots in temporary habitats in the Transvaal which had been dry for 18 months. They did not observe this for any Planorbinae (i.e. Biomphalaria). Successful aestivation has also been recorded for B. (B.) guernei in Senegal (Larivière, 1963), B. (B.) forskali in Kenya (McClelland, 1956), B. (B.) senegalensis in the Gambia (Smithers, 1956) and B. (B.) truncatus in Israel and Iraq by Witenberg & Saliternik (1957) and Zakaria (1955) respectively. Barbosa & Dobbin (1952) and Paraense et al (1955) reported aestivation by B. glabrata in Brazil but Pimentel & White (1959) could find no similar evidence for this species in Puerto Rico.

Watson (1958) found that B. truncatus in Iraq tolerated dessication for up to 9 - 10 months in habitats which dried gradually, permitting the snails to form protective epiphragms, whereas rapid drying was usually lethal. Olivier (1956a) found that survival of B. glabrata and B. straminea in the field was best in soil with a low moisture content and that prolonged dessication resulted in increased mortality. Barbosa & Dobbin (1952) observed successful aestivation by approximately 32% of a B. glabrata population in soil with a moisture content varying between 31.5 and 40.0%. Barbosa & Olivier (1958) reported that survival of B. glabrata was dependent on relative humidity. Decreasing relative humidity was accompanied by an increasing loss of body weight, culminating in death at very low R.H. levels (0.5%). Snails could survive until they had lost 47 - 50% of their original weight, but generally died when this approached 60%. The influence of relative humidity on drought survival by snails was further emphasized by Sturrock (1970). By simulating expected levels of four selected factors (relative humidity, temperature, exposure time and snail size) he showed their effects on St. Lucian B. glabrata to be interrelated. Using a multiple regression to interpret his data, he suggested that of the individual effects, that of the saturation vapour deficit (thereby excluding the effect of temperature on relative humidity) was the most important and temperature the least so. In the only study on the important question of whether snail eggs can resist dessication. Chernin & Adler (1967) found that B. glabrata eggs died after even short periods of dessication and under conditions of 90 - 100% relative humidity.

Shiff (1960) and Cridland (1967) investigated the survival of Rhodesian B. pfeifferi, B. (Ph.) africanus and globosus and L. natalensis under conditions of controlled temperature and relative humidity. The three former species survived fairly hot outdoor conditions for 30 - 50 days when protected from direct sunlight and particularly in conditions of high relative humidity. Lymnaea natalensis however was more susceptible to dessication, even at low temperatures and low relative humidity. This species nevertheless laid eggs on damp mud and these remained viable for 20 days. The hatchlings survived in microhabitats until the onset of the rains.

In another comparative study, Larivière et al (1962) showed that Bulinus guernei could survive for up to five weeks under experimental conditions of gradual dessication whereas with Biomphalaria pfeifferi only 50% survived for a month. Chu et al (1967b) and Hira (1968) indicate that medium-sized snails (young adults) survive aestivation best.

Evidence for active entry by the snails into drying substrata is scant. Chu et al (1967c & d), Hira (1968) and Larivière et al (1962) have reported apparently purposeful penetration into mud under conditions of gradual dessication by several Bulininae, both experimentally and in the field. Hira recorded penetration to a depth of 8mm. Olivier (1956a) and Larivière et al (1962) did not however find this ability with either Biomphalaria glabrata or B. pfeifferi.

Bulinid snails, Bulinus (Bulinus) and Bulinus (Physopsis), thus appear better able to withstand periods of prolonged dessication (up to a year) and to bury themselves beneath the substratum than members of the Planorbinae (i.e. Biomphalaria) or Lymnaea.

Olivier (1956b) and Olivier & Barbosa (1956) concluded that the ability of B. glabrata and B. straminea to withstand dessication was a characteristic of their habitats rather than of the snails themselves. Those from permanent habitats such as lakes where they could have had little opportunity to develop resistance to dessication did not survive as well as those from temporary pools where drying is a seasonal phenomenon possibly enabling resistant strains to develop. This important finding was confirmed by Colombo (1958), Barbosa & Barbosa (1959) and Kloetzel (1959). Barbosa & Barbosa in fact suggested that the ability of B. glabrata to aestivate was genetically controlled.

Richards (1967) considered that genetic factors did influence the morphological (i.e. apertural lamellae) and physiological changes (i.e. a change in the colour of the hepatopancreas) that are associated with successful diapause and prolonged aestivation. This author differentiated between these two terms, the former referring to the snails actually leaving the water and entering a state of diapause and the latter to the prolonged survival in a dormant state. There are, according to Richards (1968), no true breeding lamellar strains which points to the possession of this characteristic (associated with the ability to aestivate successfully) by some snails as a genetic mechanism ensuring that part of a population in a temporary habitat will survive the dry seasons.

It is interesting to note that no lamellar B. glabrata have been found on St. Lucia (Sturrock, 1970), a strain which Sturrock considered poorly adapted to withstanding dessication. Likewise, no lamella-bearing B. pfeifferi have been reported among southern African populations so far though this character may not have been looked for.

While many species of the genera Bulinus and Biomphalaria are known to be able to aestivate, some for considerable periods, neither Rhodesian nor South African B. pfeifferi have been recorded doing so under natural conditions although this has been demonstrated in the laboratory (Shiff, 1960; Cridland, 1967).

Light intensity

Practically all observations on the influence of light intensity on host snails are descriptive. Biomphalaria glabrata occurs in both shaded habitats and those exposed to direct sunlight whereas African vector snails appear to avoid the latter. Most vector species have nevertheless been recorded as being able to live for several consecutive generations in almost total darkness (Deschiens, 1957a; Deschiens & Bijan, 1956; WHO, 1957; Watson, 1961). The effect of sunlight is probably an indirect one, related to photosynthesis and the availability of food (Boycott, 1936; Zakaria, 1955; Malek, 1958; Watson, 1958).

Sodeman (1972) found no obvious influence of light and dark conditions on B. glabrata activity although there was some evidence of a fall in activity with subsequent recovery following a change from light to dark. Several authors (Gordon et al, 1934; Deschiens, 1956; Stiglingh & van Eeden, 1970 and Pitchford, pers.comm., 1975) have remarked on the congregation of planorbid host snails on the water surface during the hours between sunset and sunrise. I also noticed this phenomenon in outdoor aquaria at Lake Sibaya Research Station (northern Zululand) in 1973. Preliminary experiments on B. (Ph.) globosus there showed that the snail exhibited a regular nocturnal activity pattern, and further that most eggs were laid at night. The snails emerged from behind shelters between 14h00 and17h00 after temperatures had begun to fall and daylight was fading and returned at about 06h00 (first light) when temperatures started to rise. No difference was recorded in this behaviour pattern between days with plentiful cloud cover (only 3.5 hrs direct sunshine) and those without (8.6 hrs direct sunshine and the maximum for the season) as measured by a 'Campbell-Stokes' sunshine recorder. The fact that the snails moved to and from shaded areas at first and last light respectively, suggests that their activity might be associated with the intensity of diffuse rather than direct sunlight. Observations under controlled conditions should help ellucidate this behaviour pattern. It is possible that, like many molluscs, the bilharzia host snails may be nocturnal in habit. The likelihood of this does not seem to have ever been taken into account and could be an important aspect of its ecology.

Stream geology

The WHO Study Group (1957) pointed out that the physiography of a region influenced the diversity, abundance and size of fresh-water habitats and therefore the occurrence of snails as well. The concept of geomorphology affecting the distribution of fluviatile organisms in this way is not new (Allee *et al*, 1950; Hack, 1969).

However, apart from a series of valuable papers on the physiographic aspects of B. glabrata ecology in Puerto Rico (Harry & Cumbie, 1956a & b); Harry & Aldrich, 1958; Pimentel & White, 1957, 1959) no serious attempt seems to have been made to relate the distribution of planorbid host snails to the distribution and properties of the bedrock making up their habitats.

Recently Appleton (1975) postulated the existence of a relationship between the occurrence of the snails B. pfeifferi and B. (Ph.) globosus and low gradient stretches of watercourses over rocks with hardnesses of 5 or greater in Mohs' Scale of Hardness, especially granite, in the south-eastern Transvaal. These rocks are resistant to erosion and weather unevenly resulting in the formation of lentic habitats detached from the channel. I have included a copy of my 1975 paper which deals specifically with this point. Substrata of these resistant rocks are more stable than those of non-resistant rocks or sand and are less porous. These qualities both contribute to an important factor determining host snail distribution - habitat permanence.

The nature of the substratum itself as a factor has not been emphasized as being of much importance. Firm mud, usually rich in decaying organic matter, is the type of substratum generally associated with host snail habitats (van Someren, 1946; Malek, 1958; Watson, 1958; Gohar & El Gindy, 1960) though whether there is any substratum-controlled distribution of snails within a particular waterbody is not known. de Meillon et al (1958) suggested that the degree of compactness of the substratum might be more important to the snails than its organic content. van Eeden & Combrinck (1969) could however find no active selection of substratum types by *B. tropicus* and *L. natalensis* under experimental conditions. They concluded that the capacity for increase of these snails was correlated with the availability of food (microflora) rather than the type of substratum.

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The influence of stream geology on the distribution of the bilharzia host snails, *Biomphalaria pfeifferi* and *Bulinus (Physopsis)* sp.

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Considering the practical value accruing from an understanding of abiotic factors influencing the irregular distribution of bilharzia intermediate hosts in southern Africa, surprisingly few contributions have been made towards this goal during the past decade. Those available deal with the effects on snail fecundity of temperature (Shiff, 1964; Shiff and Garnett, 1967); turbidity (Harrison and Farina, 1965); general water chemistry (Schutte and Frank, 1964), and more specifically, the calcium and bicarbonate concentration (Williams, 1970*a*, *b*). Harrison and Shiff (1966) amply reviewed the publications mentioned. Harrison *et al.* (1966) have since produced evidence suggesting that a high magnesium/calcium ratio hinders egg production by *Biomphalaria pfeifferi* (Krauss). The tolerance of host snails to current speed was mentioned by Frank (1964).

In the following discussion geology emerges to be of the utmost importance in influencing certain physical characteristics of aquatic environments in the Gladdespruit and the Komati River, two perennial south-eastern Transvaal watercourses. Reference is also made to the North Kaap River.

Links between geology, host snail distribution, and bilharzia endemicity were suggested by the initial survey of the Gladdespruit, and then applied to the Komati River to ascertain whether it would yield information on the curious prevalence pattern of urinary bilharzia along this river (Eastman-Nagle, 1956; Pitchford and Schutte, 1967).

THE GLADDESPRUIT

A survey of this stream, from October 1969 to June 1971, was done in order to view the longitudinal distribution of the host snails *B. pfeifferi* and *Bulinus* (*Physopsis*) sp. against the physical zonation of the stream, especially in the light of the altitudinal limit of approximately 920 m for their occurrence in streams up the Drakensberg escarpment. (Schutte and Frank, 1964).

The Gladdespruit, a perennial stream rising near the hamlet of Kaapsche Hoop, 1620 m above sea level on the edge of the Transvaal highveld plateau, flows to its confluence with the Crocodile River at 655 m, 2 km northwest of Nelspruit (Fig. 1). It was selected for the study because of its relatively short length of 40 km, its proximity to Nelspruit and the fact that, like other streams descending the escarpment, it flows from a non-endemic bilharzia area to one of high endemicity.

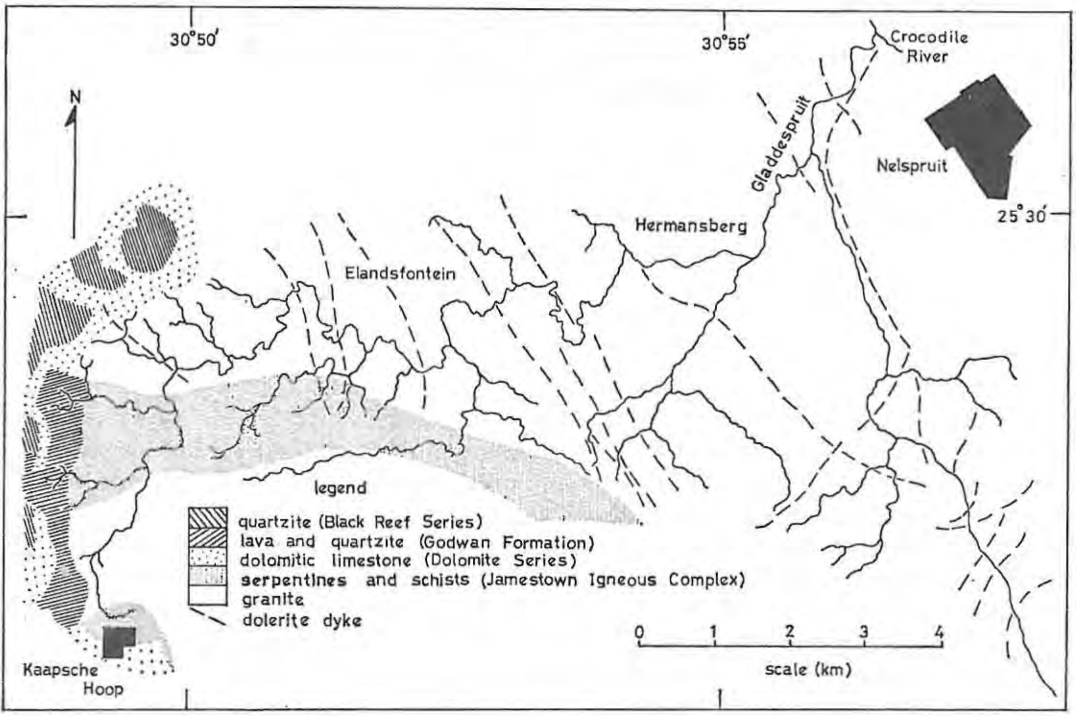

FIG. 1. Geological map of the Gladdespruit catchment (adapted from Visser, 1956). The built-up areas of Nelspruit and Kaapsche Hoop and the farms Elandsfontein and Hermansberg are also shown.

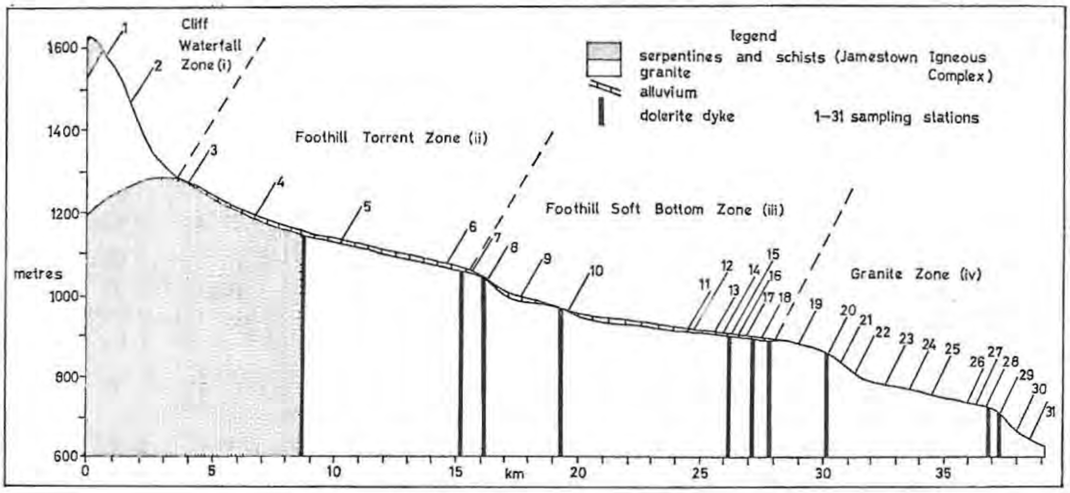

FIG. 2. Schematic profile of the Gladdespruit showing the sequence of geological formations, zonation and sampling stations.

Geology

The stream flows over several geological formations (Fig. 1). It has created a deep valley which descends towards the lowveld plain of the south-eastern Transvaal. Weathering has resulted in deposition of a layer of Recent alluvial clay 1–3 m thick over the granite valley floor from an altitude of approximately 1130 m to 900 m (Fig. 2). This clay was derived from the fine-grained serpentines of the Jamestown Igneous Complex and has been constrained by seven dolerite dykes situated between 1 190 m and 900 m above sea level (Fig. 2). These dykes strike northwest-southeast so that the consequent damming-up of alluvial sediments is accentuated in the Gladdespruit valley, which runs in a north-easterly direction. The stream therefore crosses them more or less at right angles, resulting in the formation of an alluvial plain traversed by a canal-like stream with a bed of coarse sand derived from the weathering on the edge of the highveld plateau of quartzitic rocks of the Godwan formation which overlies the clay. From the 900 m contour downwards, stream action has exposed the granite which becomes the bed of the Gladdespruit for the remainder of its course to the Crocodile River.

Zonation

Four distinct physical zones are discernible (Fig. 2), each with a characteristic stream type*:

zone (i) *Cliff Waterfall Zone* from 1 620 m to 1 300 m above sea level, with intermittent waterfalls, 8–10 m high over steep, sunlit faces of granite, and fed in a stepwise fashion from pools densely shaded by riverine trees.

zone (ii) *Foothill Torrent Zone* from 1 300 m to 1 060 m, with stickles whose flow is broken by cobbles on coarse sand, lined with low grasses (Fig. 3). (A stickle is a shallow stream flowing over stones in the current.)

zone (iii) *Foothill Soft Bottom Zone* from 1 060 m to 900 m; a fast-flowing, canal-like, sandy run bordered by trailing grasses, reeds and sedges (Fig. 4).

zone (iv) *Granite Zone* from 900 m to 655 m; unevenly eroded granite containing depressions such as pools, backwaters and potholes at the sides of the main channel (Fig. 5). Emergent and aquatic plants are common, especially in the calmer habitats. A canopy of riverine trees shades the stream intermittently throughout this zone.

Distribution of Mollusca

Records of Mollusca collected at 31 sampling-sites along the stream (Fig. 2) are shown relative to the zones in Table I.

The distribution of the bilharzia intermediate host snails was as follows: *B. pfeifferi* occurred in detached and semi-detached pools and backwaters from an altitude of 823 m to 655 m, a distance of 8 km, but was absent within this 8 km from heavily shaded stretches and those with currents faster than about 0·3 m/s; *B. (Physopsis)* sp. was found in similar biotopes but its distribution extended slightly higher to 838 m; both species were therefore confined to zone iv.

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*Terminology (Zones i–iii) taken from Harrison and Elsworth (1958) and Bland *et al.* (1967). No equivalent for zone (iv).

Table I

Longitudinal distribution of Mollusca in the Gladdespruit

Mollusc species	Granite Zone (iv)													Foothill Soft Bottom Zone (iii)												Foothill Torrent Zone (ii)				Cliff Water-fall Zone (i)	
Station no.	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
Biomphalaria pfeiffer	×	×	×	×	×	×	×	×	×	×																					
Bulinus (Physopsis) sp.	×	×	×	×	×	×	×	×	×	×	×																				
Bulinus (B.) forskali	×			×	×			×		×																					
Gyraulus connollyi											×	×		×	×		×	×			×	×		×	×						
Gyraulus costulatus	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×				×	×		×	×						
Lymnaea columella	×	×	×	×	×			×	×		×	×	×	×			×														
Lymnaea natalensis	×	×	×	×	×	×		×	×	×	×	×	×				×	×		×		×									
Succinea patentissima	×																														
Succinea striata	×			×	×			×																							
Burnupia brunnea	×	×		×			×	×					×									×		×		×	×	×	×	×	×
Burnupia caffra		×									×						×							×	×						
Burnupia capensis																						×									
Burnupia transvaalensis									×	×	×	×																	×		
Ferrissia cawstoni	×		×	×	×	×					×	×	×		×					×											
Melanoides tuberculata	×		×	×		×																									
Melanoides victoriae	×			×	×																										
Unio caffer	×		×	×	×	×																									
Aspatharia wahlbergi	×																														
Pisidium langleyanum																								×	×				×		
Pisidium ovampicum					×			×		×	×	×											×						×	×	×
Pisidium viridarium				×		×					×	×								×		×							×	×	×

FIG. 3. A stickle on serpentine in Zone (ii). The instrument on the right bank is a thermograph.

FIG. 4. A sandy run lined with trailing grass and reeds in Zone (iii).

FIG. 5. A detached pool partially blocked with reeds and sedges in the exposed granite of Zone (iv).

FIG. 10. Unstable substrate formed by erosion of soft rocks of the Onverwacht Series.

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The upper limit of zone (iv) lies close to the 920 m (3 000 ft) contour, which corresponds with the greatest altitude at which host snails were recorded in streams on the escarpment between latitudes 24°S and 26°S (Schutte and Frank, 1964; Official records – State Health Department). Both species reappear on the Transvaal highveld plateau (van Eeden and Combrinck, 1966) so that there is a discontinuity in their distribution corresponding to the fast-flowing reaches of perennial watercourses descending the escarpment, exemplified by Gladdespruit zones (i–iii).

Weirs built across the stream in zones (ii) and (iii) created artificial lentic (standing or calm) habitats which served to extend the longitudinal distribution of many animals beyond the limit of their naturally occurring calm environments in zone (iv). Host snails were not found in any weirs upstream of zone (iv).

Water Temperature and Chemistry

Continuous water temperature recordings were made over a year in zones (ii), (iii) and (iv). Seasonal chemical analyses were made on water from these zones during 1970. Neither of these variables will be considered further because (a) temperature ranges fall within those at which Shiff (1964), Shiff and Garnett (1967) and Pitchford and Visser (1969) have shown host snails to be capable of maintaining themselves, (b) the two species occur on the Transvaal highveld where temperatures colder than those of the Gladdespruit prevail and (c) the seasonal ranges of ionic concentrations found fall well within those recorded from snail habitats by Schutte and Frank (1964) and Williams (1970*a*, *b*).

Current Speed and Gradient

Current speeds were measured using a simple Pitot tube in midstream at several localities in each zone. The ranges obtained are tabulated in Table II. The lentic environments afforded by zone (iv) were the only habitats, except pools atop waterfalls in zone (i), which did not flow continually faster than about 1·7 m/sec.

TABLE II

Current speed ranges (measured in m/s) in zones (i–iv), during the dry and rainy seasons

	Zones					
	(i)		(ii)	(iii)	(iv)	
	pools	waterfalls	stickles	runs	backwaters	runnels
Dry season (March–Oct.)	not measured		1·3–2·4	0·6–1·6	0·0–1·0	0·0–3·1
Rainy season (Nov.–Feb.)	0·0–1·7	1·5–5·0	1·8–4·8	1·4–4·7	0·0–1·7	1·3–4·5

By measuring the current speed next to live snails, ranges of tolerance were drawn up for nine species (Table III). A comparison with Table I shows that those species tolerant of wide ranges of current speeds were distributed furthest upstream. Both host snail species were found to have a very narrow range agreeing with stream velocities of 0·3 m/s for *B. pfeifferi* and *B.* (*Physopsis*) sp. (Frank, 1964) and 0·25–0·30 m/s for *B. glabratus* (Scorza *et al.*, 1961). Field observations by Paulini (1963) demonstrated that *B. glabratus* is capable of migrating upstream against a flow of the order of 0·1 m/s. It is thus not surprising to find the longitudinal distribution of the host snails arrested close to the point on the stream above which current speeds seldom fall below 0·3 m/s. Temperature and water analysis data show that this distribution might otherwise be expected to extend above 920 m altitude.

TABLE III

Current speed tolerance ranges of nine gastropod species in the Gladdespruit

Species	Current speed tolerance range (m/s)
Biomphalaria pfeifferi	0-0–0·3
Bulinus (Physopsis) sp.	0-0–0·3
Gyraulus connollyi	0-0–1·4
Lymnaea columella	0-0–1·7
Lymnaea natalensis	0-0–1·9
Burnupia brunnea	0-0–3·2
Ferrissia cawstoni	0-0–1·4
Melanoides tuberculata	0-0–0·3
Melanoides victoriae	0-0–1·9

Zone (iii) lies on the alluvial plain which has a fairly steep gradient (0·019) and the stream has cut a uniform, deepish channel through the alluvium which it once deposited. Rainfall causes a vertical rise in water level and pools or backwaters do not form as the water subsides. On a plain with a flatter gradient however, such as that of the North Kaap River (gradient 0·0065) flowing about 15 km south of Nelspruit, the channel is wide and rainfall causes the water to spread out laterally. Consequently with subsidence, pools and backwaters become separated from the main channel and may retain host snails during the ensuing dry season.

Stream action in zone (iv) has exposed granite bedrock and flow is increased occasionally by short steep gradients resulting in a change in the potential habitats of host snails. In the lower reaches of zone (iv) these snails have colonized the generally calm main channel

TABLE IV

Prevalence of bilharzia in the Gladdespruit catchment

Area	No. children examined	No. positive	% positive	
Kaapsche Hoop*	74	4	5·4	*S. haematobium*
(zones i and ii)	70	3	4·3	*S. mansoni*
Elandsfontein†	47	3	6·4	*S. haematobium*
(zone iii)	43	2	4·6	*S. mansoni*
Hermansberg‡	43	25	58·1	*S. haematobium*
(zone iv)	42	13	39·5	*S. mansoni*

* From Pitchford and Schutte (1967).
† From Pitchford (unpublished data, March 1969).
‡ Examination done in May 1971.

as well as pools and backwaters. In the middle the gradient changes abruptly from 0·015 to 0·120 over a distance of about 250 m. Towards the top of zone (iv) small cascades form in the main channel and local velocities increase well above those of the lower reaches. Being intolerant of these faster speeds, host snails maintain themselves in habitats separate from the channel, which are rarely affected by fast flow, even during floods.

The Prevalence of Bilharzia in the Gladdespruit Catchment

The prevalence of *Schistosoma haematobium* and *S. mansoni* infection was determined by an examination of urine and stool samples from children under the age of 11 years. Three areas, corresponding broadly to the different zones, were investigated and included most of the stream's catchment. High infection rates followed closely the distribution of the host snails (Table IV, Fig. 2).

THE KOMATI RIVER

Geology

The geological formations of the area, adapted from Kynaston (1906), Hall (1918) and Visser (1956) are shown in Fig. 6. The important formations correspond to (1) the Pre-Cambrian age of European geology; (2) the Karroo System which dates from the Carboniferous age, and (3) the granites and other igneous rocks.

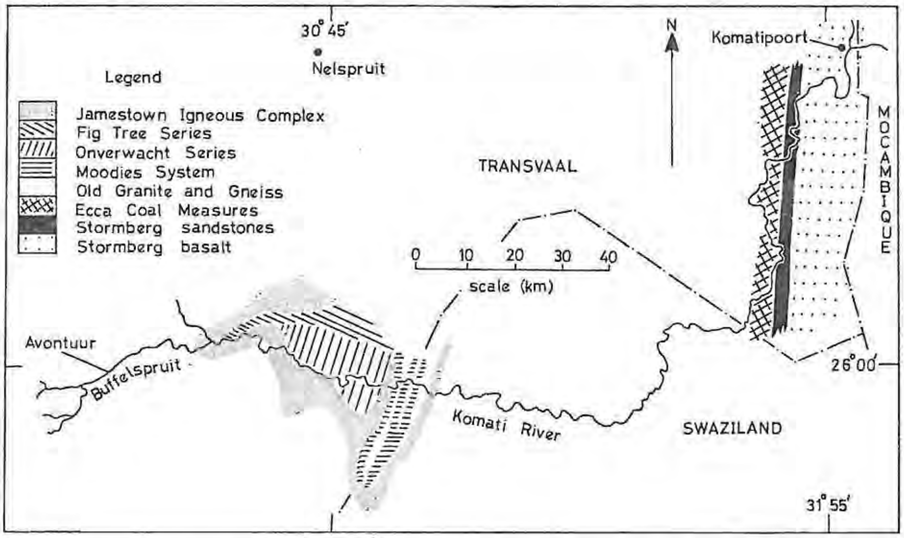

FIG. 6. Simplified geological map of the Buffelspruit and Komati River (adapted from Kynaston, 1906; Hall, 1918 and Visser, 1956).

(1) The Pre-Cambrian rocks comprise the Moodies System which consists of conglomerates, calcareous quartzite, limestones and shales and the Swaziland System comprising (a) the Fig Tree Series principally of shales with greywracke and some bands of chert and (b) the Onverwacht Series consisting of basic lavas largely altered to carbonate and talc schists and serpentinite.

TABLE V

Occurrence of Mollusca on the geological formations of Buffelspruit and the Komati River from Avontuur (alt. 1097) to Komatipoort (alt. 146 m)

	Formation or deposit forming substrate (see Figs. 6 and 7)	Altitude (m)	Distance (km)	Mollusca present in main channel	Mollusca present in lentic habitats (where present)	Host snail populations
Buffelspruit	alluvial sand over granite	1097–1067	1·5	*Burnupia brunnea*		absent
	exposed granite	1067–945	15·0	*Gyraulus connollyi* *Gyraulus costulatus* *Lymnaea columella* *Lymnaea natalensis* *Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Lymnaea columella* *Lymnaea natalensis*	persistent
	Jamestown Igneous Complex	945–915	1·5	*Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Lymnaea columella* *Lymnaea natalensis* *Burnupia brunnea*	temporary
Komati River	Fig Tree Series	915–884	1·5	*Lymnaea columella* *Lymnaea natalensis* *Burnupia brunnea*		absent
	Jamestown Igneous Complex	884–870	4·5	*Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Lymnaea columella* *Lymnaea natalensis* *Burnupia brunnea*	temporary
	exposed granite	870–853	2·0	*Lymnaea columella* *Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Gyraulus connollyi* *Gyraulus costulatus* *Lymnaea columella* *Lymnaea natalensis* *Ferrissia* sp.	persistent
	Jamestown Igneous Complex	853–841	4·5	*Burnupia brunnea*		absent
	Jamestown Igneous Complex and Onverwacht Series	841–759	39·0	*Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Lymnaea columella* *Lymnaea natalensis*	temporary
	Jamestown Igneous Complex, Moodies System, granite	759–671	10·0	an inaccessible region, no localities visited		

TABLE V–Cont.

	Formation or deposit forming substrate (see Figs. 6 and 7)	Altitude (m)	Distance (km)	Mollusca present in main channel	Mollusca present in lentic habitats (where present)	Host snail populations
Komati River	alluvial sand over granite	671–604	7·5	*Gyraulus costulatus* *Lymnaea columella* *Lymnaea natalensis* *Ferrissia* sp.	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Gyraulus costulatus* *Lymnaea columella* *Lymnaea natalensis* *Pisidium langleyanum*	temporary
	exposed granite	604–587	2·0	*Lymnaea columella* *Burnupia brunnea*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Gyraulus costulatus* *Lymnaea columella* *Lymnaea natalensis* *Pisidium langleyanum*	persistent
	alluvial sand over granite	587–243	91·0	*Gyraulus costulatus* *Lymnaea columella* *Ferrissia* sp. *Melanoides tuberculata*		absent
	alluvial sand over Ecca Coal Measures	243–198	40·0	*Gyraulus costulatus* *Ferrissia* sp. *Pisidium langleyanum*		absent
	alluvial sand over Stormberg sandstones and basalt	198–149	45·0	*Gyraulus costulatus* *Ferrissia* sp.	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Lymnaea natalensis* *Melanoides tuberculata* *Unio framesi* *Corbicula africana*	temporary
	exposed Stormberg basalt	149–146	3·5	*Gyraulus costulatus*	*Biomphalaria pfeifferi* *Bulinus* (*Physopsis*) sp. *Gyraulus costulatus* *Anisus natalensis* *Segmentorbis angustus* *Lymnaea natalensis* *Succinea patentissima* *Ferrissia cf cawstoni* *Melanoides tuberculata* *Unio framesi* *Corbicula africana* *Eupera parasitica* *Pisidium pirothi*	persistent

(2) The Karroo System in the area comprises the Ecca Series as the shales of the Komatipoort Coal Measures and the Stormberg Series of sandstones and basalts.

(3) The Igneous rocks of the area comprise the Jamestown Igneous complex consisting of green and blue serpentinite, amphiboles and talc schists, and the granite and gneiss.

North of Swaziland the river flows in a northerly direction but in the vicinity of Coopersdal it turns eastwards exposing part of the Stormberg basalt, much as granite is exposed in the Gladdespruit.

Distribution of Mollusca

In the interpretation of the results from the Komati River, two types of host snail population have been recognized: persistent populations which maintain themselves in their habitats despite the ravages of the annual floods, and temporary populations which become greatly reduced with the onset of floods due to the inconstancy of their habitats. Temporary populations were found to be evidence of a persistent population either further upstream or in a tributary. The average annual increase in velocity of 100 m^3/sec. (calculated from Jordaan, 1968) in the Komati River each summer from 1949 to 1959 would be sufficient to transform all the temporary lentic habitats seen during the survey into torrent-washed banks.

Either no host snails or only temporary populations were found where the river flows over the Jamestown Igneous Complex, the Fig Tree Series, the Onverwacht Series, and where alluvial sand covered granite, the Ecca Measures and Stormberg basalt. Persistent populations were found where granite and basalt were exposed and not overlain by alluvial sediments (Fig. 7). This snail distribution pattern was related to the occurrence of per-

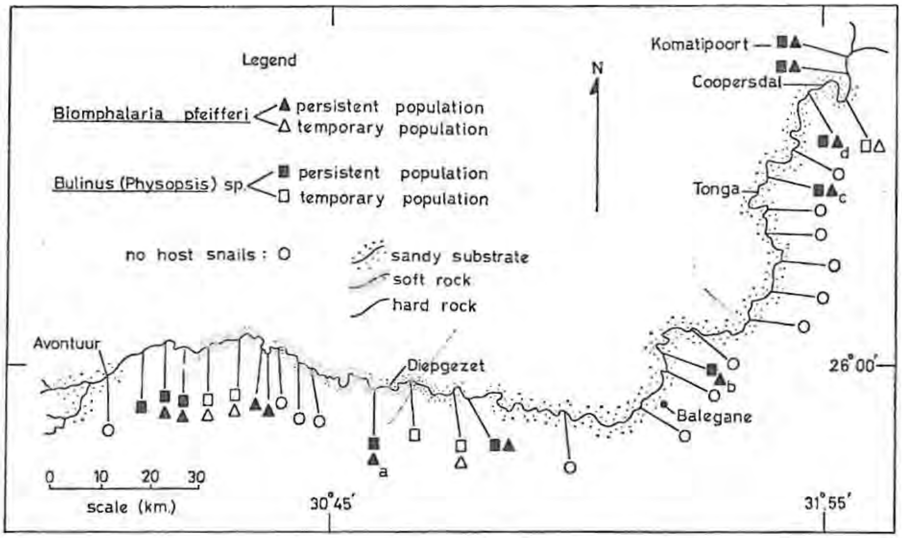

FIG. 7. Map of the Buffelspruit and Komati River showing the distribution of bilharzia host snail populations and substrate types as revealed by the survey. Persistent populations in weirs built on substrata of sand or soft rock are marked: a (west of Diepgezet); b (north of Balegane); c (Tonga); d (Coopersdal).

manent, lentic habitats which formed in substrata of exposed granite and basalt, but not in those of the Jamestown Complex, the Swaziland System or alluvial deposits. The formation of these lentic habitats was dependent on the resistance offered by the particular rock to weathering by flowing water. Weirs situated (a) west of Diepgezet, (b) north of Balegane, (c) at Tonga and (d) at Coopersdal (Fig. 7) favoured the establishment of persistent host snail populations regardless of the stability of the river bed.

Prevalance of Bilharzia

S. haematobium surveys of the area (Eastman-Nagle, 1956; the Swaziland Department of Health, 1959, 1961, and 1962; Pitchford and Schutte, 1967 and Pitchford, unpublished data) are shown in Fig. 8. The low prevalence of *S. haematobium* in Africans living along the river between longitudes 30° 45′E and 31° 55′E, corresponds to the occurrence of temporary host snail populations. The comparatively high prevalence at Tjakastad was probably due to permanent snail populations in water unconnected with the Komati River. Temporary habitats were therefore of little importance in the epidemiology of bilharzia in an area where bilharzia transmission is negligible during the dry winter.

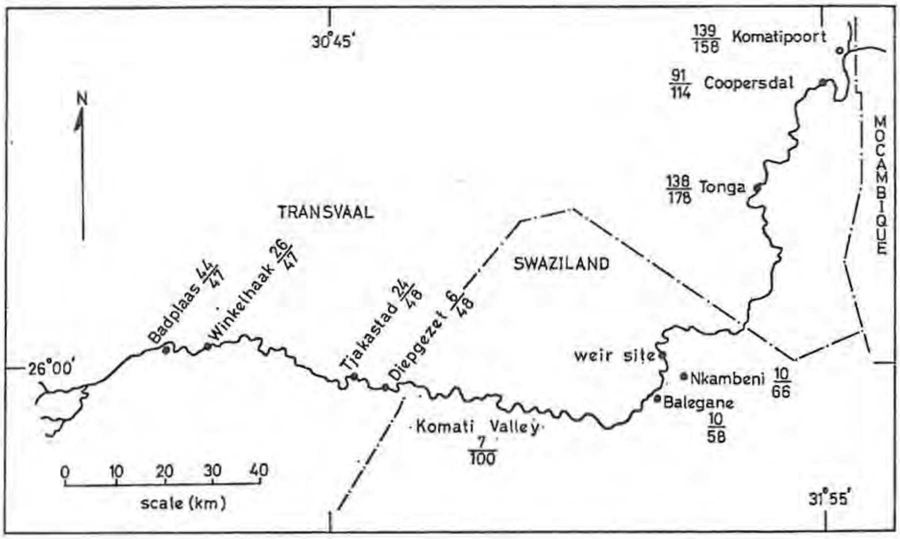

FIG. 8. Map showing the prevalence of *S. haematobium* in Bantu children along the Buffelspruit and Komati River. Numerators denote the number infected and denominators the number examined.

ANALYSIS

Geological formations functioned as fundamental determinants of current speed in the two watercourses and so were responsible for the striking differences between those reaches harbouring bilharzia intermediate hosts and those not. The observations possibly apply in natural streams and rivers over many bilharzia endemic areas.

Weathering by stream action takes place through mechanical erosion and involves the loosening and subsequent removal of material by flowing water. Local velocities and turbulence contribute to this through various hydraulic processes involving the disintegration of bedrock by cavitation, abrasion of the channel's sides and floor by solid debris in transport, and the breaking up of this transported material by friction and impact. Chemical erosion augments the weathering process by a general weakening of coherence between minerals which renders them more susceptible to physical forces, and by exfoliation as the result of the alteration of outer layers or rock.

The resistance offered by a rock to weathering can be gauged by its hardness, and where particular rocks are sufficiently extensive, distinctive stream types develop on them. Mohs' Scale of Hardness reflects this hardness of minerals in values from 1 (the softest) to 10 (the hardest). Table VI shows approximate values for the dominant constituent minerals of the rocks encountered and the type of substrate produced by their erosion. Soft rocks such as serpentines, schists and shales are subject to more rapid weathering than the harder, more resistant granites, quartzites and basalt. Flowing water penetrates soft rocks readily, breaking them down to silt, clay and sand whereas the erosion of hard rocks is slower though it may be affected by the presence of softer inclusions.

TABLE VI

Hardness of the exposed bed-rocks of the Komati River

Formation	Principal rock types	Dominant constituent mineral(s)	Approx. hardness on Mohs' scale	Stability of substrate produced
Old granite	granite	quartz, felspar	7 6	stable
Jamestown Igneous Complex	serpentines, talc and hornblende schists	peridotite	3–4	unstable
Fig Tree Series	shales	various sediments	4	unstable
Onverwacht Series	serpentines	olivine	3–4	unstable
Stormberg Series	basalt	pyroxenes, felspar	5–6 6	stable

Unstable substrata resulted from the erosion of soft rocks with hardness values below 5 in Mohs' scale, forming an evenly contoured (Fig. 9A) stream bed which was often littered with 'stones-in-the-current', products of the weathering of harder rocks further upstream (Figs. 3 and 10), and water flowing over alluvial sand creating a uniform channel, frequently with steep banks (Figs. 4 and 11). In both these stream types the channel floor and sides are continually exposed to current speeds beyond the tolerance range of the host snails, creating permanently lotic (running or flowing) conditions. During the dry season, some sites on the Komati River such as the mouths of seasonal tributaries, or pools on small islands, or calm water sheltered by sandbanks, harboured temporary host snail populations.

Similar calm conditions occurred behind beds of the reed *Phragmites australis* near the concave banks at sharp bends in the river where turbulence during the rainy season caused deep erosion: no host snails were found, but it seemed possible that they could survive temporarily in these situations. Bands of chert (hardness 7) in the otherwise soft rocks of

FIG. 11. Unstable substrate formed by alluvial sand overlying the Stormberg basalt.

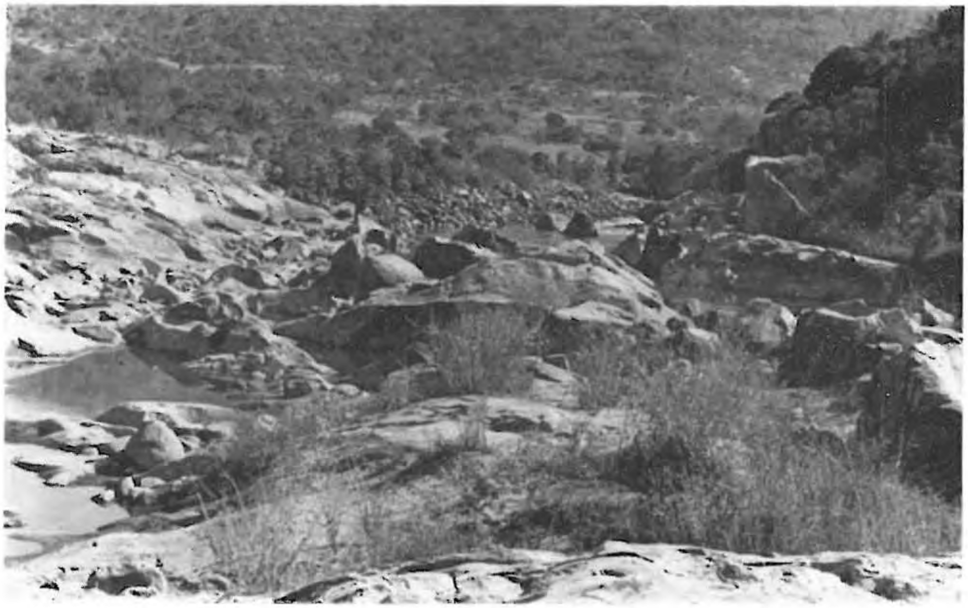

FIG. 12. Stable substrate formed by erosion of granite.

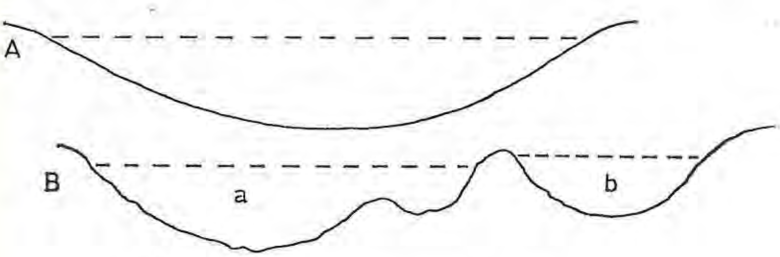

FIG. 9. Diagrammatic cross sections of hard and soft rock-bed eroded by stream action.

the Fig Tree Series appeared to create these bends. Host snails were thus only found in a few temporarily lentic habitats during the dry season when the water level was low and its velocity reduced.

Stable substrata resulted from erosion of granite and basalt not overlain by alluvium. These crystalline rocks have hardnesses greater than 5 in Mohs' scale: disintegration is slow though they may break up along planes of weakness due to inclusion of varying amounts of softer minerals like mica (hardness 2·5) causing uneven weathering. The subsequent formation of isolated depressions such as potholes, backwaters and pools at the sides of the channel (Figs. 5, 9B and 12) provides lentic habitats which harbour persistent host snail populations. Similar suitable conditions are also afforded by weirs built across the river.

My findings agree in several respects with reports by Harry and Cumbie (1956*a*, *b*) on *B. glabratus* in streams in Puerto Rico, in that they found no established snail populations in low gradient sandy channels, and the few individuals that were collected were considered to have come from smaller tributaries in higher reaches where the species was abundant. Snails did however occur in detached pools and seepage areas. They also found that streams flowing over wide serpentine belts had high gradients with a substrate of exposed rock, and did not contain *B. glabratus*. Though the gradient here would depend on the hardness of the rocks above and below the serpentine, analogous situations exist in zone (ii) of the Gladdespruit and parts of the Komati River. They found the snail often occurred in detached pools beyond the upstream limit of its establishment in the stream's main channel; a similar situation was noted for host snails in zone iv of the Gladdespruit.

Hughes (1966) surveyed the upper reaches of four rivers which flow down the Drakensberg escarpment between Nelspruit district and Swaziland (Fig. 6). He found no host snails although the altitude range, 1 097 m to 793 m corresponded to zone iii and part of zone (iv) of the Gladdespruit. However about two-thirds of his collecting stations were lotic habitats on soft rocks of the Jamestown Igneous Complex and Moodies System. He stated that 'the biotopes examined in this survey are the function of the variation of a single factor, namely current velocity'.

In Kenya, Kinoti (1971) reported an association between the occurrence of the host snails *B.* (*Physopsis*) *africanus* and *B.* (*Physopsis*) *nasutus* and soil type in deltaic conditions on the Kano plain bordering Lake Victoria. The snails were absent from the waterways and pools of the plain which had a poorly drained, clay soil but were present on the better drained, coarser soil on slightly higher ground. This last was of granite, grandodiorite and phonolites which are hard rocks. Unfortunately he did not investigate the association further. It is felt however, that as soil type is related to local geology, the association may be similar to that outlined for the Gladdespruit and Komati River.

As the relationship between host snail occurrence and the distribution of hard rock became apparent it was possible to predict fairly accurately what would be found at any particular locality. It should therefore be feasible with the aid of 1:250 000 geological and 1:250 000 trigonometrical survey maps, to assess from the hardness of the bedrock the type of substrate in a stretch of river and, allowing for the presence of deposits of alluvial sediments, the likelihood of finding persistent host snail populations. 1:30~~0~~ 000 aerial photographs and 1:50 000 trigonometrical survey maps were useful for locating weirs and other artificial waterbodies which could harbour host snails. The 1:50 000 trigonometrical survey maps of Swaziland which incorporated symbols representing the physical characters of the river bed and which marked exposed granite outcrops, were particularly helpful. Persistent host snail populations should be sought in long streches of sandy bed at these granite outcrops.

SUMMARY

The Gladdespruit and Komati River surveys have shown that similar environmental conditions have developed where the watercourses flowed over particular rock types. In these watercourses a potentially useful association was found between the occurrence of permanent, lentic habitats produced by the weathering of bedrock with a hardness above 5 in Mohs' Scale of Hardness and the longitudinal distribution of persistent populations of the bilharzia intermediate host snails *Biomphalaria pfeifferi* and *Bulinus* (*Physopsis*) sp. Bilharzia transmission follows this pattern in these waterways.

Weathering of bedrock with hardness below 5 in Mohs' scale, and/or flow over beds of alluvial sand, produced perpetually lotic (flowing) environments without persistent host snail populations because of the snail's inability to tolerate high current speeds. However a few temporary populations survived in temporarily lentic habitats during the dry winter season.

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REFERENCES

Annual Medical and Sanitary Report for the Year 1959. Department of Health, Swaziland.

Annual Medical and Sanitary Report for the Year 1961. Department of Health, Swaziland.

Annual Medical and Sanitary Report for the Year 1962. Department of Health, Swaziland.

Brand, P. A. J., Kemp, P. H., Oliff, W. D. & Pretorius, S. J. (1967).The Tugela River and its tributaries. In *Water Quality and Abatement of Pollution in Natal Rivers*, **111**, 1–12.

Eastman-Nagle, E. R. D. (1956). Schistosomiasis mansoni in Swaziland. *South African Medical Journal*, **30**, 890–895.

Frank, G. H. (1964). The ecology of the intermediate hosts of bilharzia. In *Ecological Studies in Southern Africa*, ed. Davis, D. H. S., pp. 353–362. The Hague: W. Junk.

Hall, A. L. (1918). The geology of the Barberton gold mining district. *South African Geological Survey*, **9**, 13–230.

Harrison, A. D. & Elsworth, J. F. (1958). Hydrobiological studies on the Great Berg River, Western Cape Province. *Transactions of the Royal Society of South Africa*, **35**, 125–226.

Harrison, A. D. & Farina, T. D. W. (1965). A naturally turbid water with deleterious effects on egg capsules of planorbid snails. *Annals of Tropical Medicine and Parasitology*, **59**, 327–330.

Harrison, A. D., Nduku, W. & Hooper, A. S. C. (1966). The effects of a high magnesium-to-calcium ratio on the egg-laying rate of an aquatic planorbid snail, *Biomphalaria pfeifferi*. *Annals of Tropical Medicine and Parasitology*, **60**, 212–214.

Harrison, A. D. & Shiff, C. J. (1966). Factors influencing the distribution some species of aquatic snails. *South African Journal of Science*, **62**, 253–258.

Harry, H. W. & Cumbie, B. G. (1956*a*). The relation of physiography to the types of freshwater environment and the presence of *Australorbis glabratus* in Puerto Rico. *American Journal of Tropical Medicine and Hygiene*, **5**, 742–756.

Harry, H. W. & Cumbie, B. G. (1956*b*). Stream gradient as a criterion of lotic habitats suitable for *Australorbis glabratus* in Puerto Rico. *American Journal of Tropical Medicine and Hygiene*, **5**, 921–928.

Hughes, D. A. (1966). Mountain streams of the Barberton area, eastern Transvaal. I: A survey of the fauna. *Hydrobiologia*, **27**, 401–438.

Jordaan, J. M. (1968). Monthly flow records of gauging stations up to September 1960. *Hydrographic Survey Publications*, **8**, 481–485.

Kinoti, G. K. (1971). The epidemiology of *Schistosoma haematobium* infection on the Kano plain of Kenya. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **65**, 637–645.

Kynaston, H. (1906). The geology of the Komatipoort coal field. *Geological Survey Memoir*, **2**.

Paulini, E. (1963). Field observations on the upstream migration of *Australorbis glabratus*. *Bulletin of the World Health Organization*, **29**, 838–841.

Pitchford, R. J. & Schutte, C. H. J. (1967). Schistosomiasis in non-endemic areas in relation to migration. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **61**, 217–220.

Pitchford, R. J. & Visser, P. S. (1969). The use of larval schistosomes in assessing the bilharzia potential of non-endemic areas. *South African Medical Journal*, **43**, 983–995.

Schutte, C. H. J. & Frank, G. H. (1964). Observations on the distribution of freshwater Mollusca and chemistry of the natural waters in the south-eastern Transvaal and adjacent northern Swaziland. *Bulletin of the World Health Organization*, **30**, 389–400.

Scorza, J. V., Silva, J., Gonzalez, L. & Machado, R. (1961). Stream velocity as a gradient in *Australorbis glabratus* (Say, 1818). *Zeitschrift für Tropenmedizin und Parasitologie*, **12**, 191–196.

Shiff, C. J. (1964). Studies on *Bulinus* (*Physopsis*) *globosus* in Rhodesia. I: The influence of temperature on the intrinsic rate of natural increase. *Annals of Tropical Medicine and Parasitology*, **58**, 94–105.

Shiff, C. J. & Garnett, B. (1967). The influence of temperature on the intrinsic rate of natural increase of the freshwater snail *Biomphalaria pfeifferi* (Krauss) (Pulmonata: Planorbidae). *Archiv für Hydrobiologie*, **62**, 429–438.

Shiff, C. J. & Husting, E. L. (1966). An application of the concept of intrinsic rate of natural increase to studies on the ecology of freshwater snails of the genera *Biomphalaria* and *Bulinus* (*Physopsis*) in Southern Africa. *Proceedings and Transactions of the Rhodesian Scientific Association*, **51**, 1–8.

van Eeden, J. A. & Combrinck, C. (1966). Distributional trends of four species of freshwater snails in South Africa with special reference to the intermediate hosts of bilharzia. *Zoologica Africana*, **2**, 95–109.

Visser, D. J. L. (1956). The geology of the Barberton area. *Geological Survey Special Publication*, **15**, 1–242.

Williams, N. V. (1970*a*). Studies on aquatic pulmonate snails in Central Africa, I. Field distribution in relation to water chemistry. *Malacologia*, **10**, 153–164.

Williams, N. V. (1970*b*). Studies on aquatic pulmonate snails in Central Africa, II. Experimental investigations of field distribution patterns. *Malacologia*, **10**, 165–180.

PART 2

THE INFLUENCE OF TEMPERATURE ON THE LIFE-CYCLE OF BIOMPHALARIA PFEIFFERI IN SOUTH-EASTERN AFRICA

The reasons prompting a re-investigation of the life-cycle of *B. pfeifferi* in an area hotter than Nelspruit (where the sampling programme described by Appleton (1974) was carried out) have already been given in the foregoing introduction. They may usefully be outlined again here. The discontinuous distribution of *B. pfeifferi* (and *S. mansoni*) over the coastal peneplain of Natal and Mozambique (to approximately altitude 16°S) is fairly well documented. Also established is the fact that north of this latitude the species is absent altogether from the plain, occurring only above altitudes of 500 - 600m. This restricted distribution of both snail and parasite has been generally regarded as due to the very high temperatures prevailing on the plain, especially in equatorial latitudes, but has never been satisfactorily explained or even investigated. The fact that *B.* (*Ph.*) *globosus* (and *S. haematobium*) are both common here suggests that, because *B.* (*Ph.*) *globosus* is better adapted to high temperature régimes than *B. pfeifferi* (Shiff & Husting, 1966), it is reasonable to view temperature as a probable limiting factor.

The life-cycle of *B. pfeifferi* as found by Appleton (1974) near Nelspruit (altitude 655m) was thought to contain a possible 'weak link' vulnerable to high temperatures. If, in hotter areas, the species could be shown to undergo a similar generation sequence, the 2nd generation (which at Nelspruit appeared during the hottest

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The Population Fluctuations of Five Fresh-water Snail Species in the Eastern Transvaal Lowveld, and their Relationship to Known Bilharzia Transmission Patterns

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The author describes a study of the breeding patterns of five bilharzia host snails and discusses some of the factors which affects their populations.

Little is known about the population fluctuations of *Biomphalaria pfeifferi* and *Bulinus (Physopsis)* sp., the respective intermediate hosts of intestinal and urinary bilharzia in South Africa. The programme reported here was carried out at two sites chosen for their convenience and because they lie on a perennial stream, the Gladdespruit, which has been the subject of previous study.

Over the period of 20 months from July 1970 to February 1972, samples of five gastropod species were taken at intervals of approximately two weeks, from two sites within 100 m of each other on the stream at an altitude of 655 m above sea-level, 2 km west of Nelspruit. The five species were *Biomphalaria pfeifferi* (Krauss), *Bulinus (Physopsis)* sp.*, *Lymnaea columella* Say, and *Lymnaea natalensis* Krauss. Another species, *Gyraulus costulatus* (Krauss) was usually present but too few were taken to provide adequate population fluctuation data. *Melanoides tuberculata* (Müller) was abundant and always taken in samples, whereas *M. victoriae* (Dhrn.) seemed rare.

Both sampling sites were small lentic bodies of water in depressions in the granite stream bed. They differed in that one (site A) was a backwater normally attached to the stream (Fig. 1) and with marginal vegetation, chiefly *Phragmites australis* (Cav.) Trin. ex Streud, *Mariscus congestus* C.B.Cl., *Commelina diffusa* Burm.f. and *Leersia hexandra* Sw. The other (site B) was a detached pool partially blocked with the same plant species and was joined to the stream only rarely after exceptionally heavy rains during which both sites experienced measurable current speeds.

Experimental Procedure

Sampling

The sampling technique employed at both sites on each occasion was careful, systematic, manual collecting with shallow nets of 6 mesh cm^{-1} and a surface area of approximately 570 cm^2 by the same two people for 20 min. Evaluations of this technique[3,4] have shown it to give a reasonably reliable estimate of the probable snail density in the habitats sampled. At site A two biotopes were sampled separately; 10 ℓm of marginal vegetation to a depth of 40 cm and approximately 20 m^2 of smooth granite covered with a thin layer of fine mud extending from the water's edge, also to a depth of 40 cm. At site B both biotopes were present but owing to the small size of the pool (*ca.* 9 m^2) no differentiation was made. All sampling was done between about 11h00 and 11h30.

Snails were identified, counted, measured to nearest 0.5 mm and returned to the stream immediately afterwards. Egg capsules taken in the nets were collected, identified and clutch-sizes recorded using a dissecting microscope, before being returned to the stream. Floods on December 10, 1971 destroyed the marginal vegetation which was sampled at site A, so that subsequent samples were from site B only.

A criticism of the technique is that changes in the water-level at the sampling sites could have created false population peaks due to an increased density of snails in a decreasing volume of water, and *vice versa*. However, the water-level of the Gladdespruit about 4 km upstream of the sampling sites during the period June 1970 to December 10, 1971 was consistently low compared with the more normal summers of 1969-70 and 1971–72 (Fig. 2). Site B remained at a constant level due to the entrance of seepage water from a nearby

Fig. 1 Gladdespruit, sampling site A. The marginal vegetation on the backwater's far side was sampled until 10/12/71 when it was washed away by floods. The granite substrate sampled was that on the right hand side of the picture.

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*Though only *B. (Physopsis) globosus* (Morelet) has been recorded from the Gladdespruit, this species and *B. (Physopsis) africanus* (Krauss) appear to be sympatric in the lowveld of the south-eastern Transvaal[1] and because they are virtually indistinguishable using conchological characters[2], both species may have occurred in the present samples.

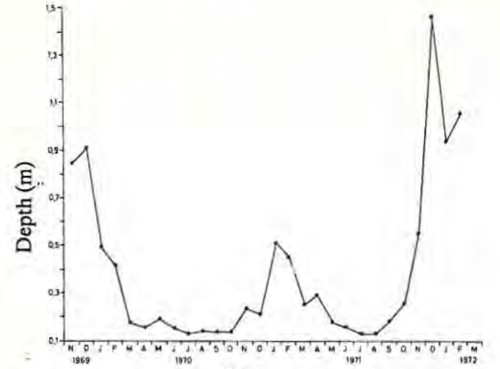

Fig. 2 Average monthly water depth in the Gladdespruit, measured at a point 4 km upstream of the sampling sites.

irrigation canal. There were therefore no marked fluctuations in water-level which might have affected the interpretation of the results prior to December 10, 1971.

Measurement of temperature

Continuous water temperature at site A was recorded using a thermograph with the probe at about 25 cm depth, from July 1970 to December 10, 1971 (Fig. 3), when the floods damaged the instrument.

Identification of egg capsules

Egg capsules collected from the Gladdespruit samples were separated simply into lymnaeid and planorbid as no entirely satisfactory method was found for distinguishing those laid by either *L. columella* or *L. natalensis* on the one hand, and *B. pfeifferi* or *B. (Physopsis)* sp. on the other. The possibility of the egg counts being upset by the inclusion of eggs laid by *G. costulatus* was excluded due to the small numbers taken; no more than 16 specimens were found on any occasion. No egg production counts were made after December 10, 1971 because of floods.

Colonies of *B. pfeifferi*, *B. (Physopsis)* sp., *L. columella* and *L. natalensis* from a dam near Nelspruit were kept in outdoor aquaria at the Nelspruit laboratory from October 1971 to February 1972. Here snails of sizes within successive integer values were kept in separate aquaria in order to ascertain the shell sizes of mature snails, that is, the size at which the first oviposition occurred, and whether old snails stop laying. Table I indicates the shell sizes at which maturity was attained. A size of 5.0 mm for *B. pfeifferi* is close to the sizes of about 4.3, 4.6 and 5.8 mm for snails kept at constant temperatures of 30°, 25° and 19°C, respectively[5]. *B. pfeifferi* with a shell diameter of 11.9 mm were fertile, and likewise *B. (Physopsis)* sp. with a shell height of 13.9 mm. Because no specimens as large as these were found in the Gladdespruit samples, none was considered infertile through age and consequently only separation into mature and immature individuals was necessary.

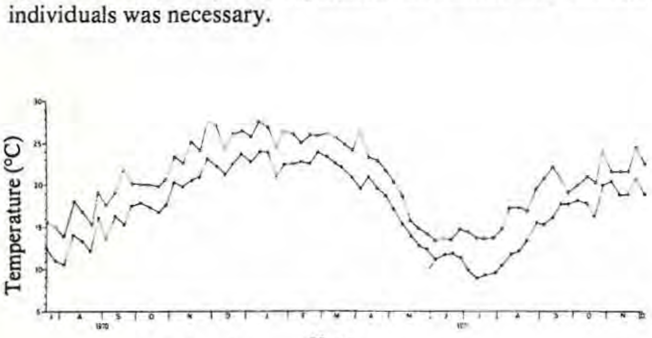

Fig. 3 Mean ~~fortnightly~~ weekly water temperature maxima and minima at site A; the probe of the thermograph was at 25 cm depth.

Results

The sample data from both sites are combined as kite diagrams incorporating all the snails taken on each occasion. This enabled the courses of the different generations to be traced using as criteria, the appearance of juveniles, the disappearance of adults and egg production. In many instances it was possible to follow the passage of a generation through the increasing sizes of its members in consecutive samples.

The fluctuation pattern for mature and immature individuals and eggs for each species was similar at both sites, except that periods of peak reproductive activity at site B appeared to be 2 to 3 weeks later than at site A but were nevertheless always in the same sequence. The combined results are shown in Fig. 4. Egg production is shown in Fig. 5.

The two series of samples from site A revealed that *B. pfeifferi* and *B. (Physopsis)* sp. occurred mostly on marginal vegetation but *B. pfeifferi* with a shell diameter greater than about 4.5 mm, and *B. (Physopsis)* sp. with a shell height greater than about 5.0 mm, were occasionally found on mud. *L. columella* was most abundant on rock at the water's edge, especially during spring, while *L. natalensis* was common on vegetation. *M. tuberculata* was found almost exclusively on mud.

B. pfeifferi

B. pfeifferi had three generations per year (Fig. 4).

First generation: the eggs starting this generation were laid by over-wintering adults during September and October 1970, and resulted in a peak of juveniles from late October to December. These matured from November to early January, laid eggs mostly in December and disappeared by the end of February.

Second generation: Snails from the December eggs hatched during January and early February, were mature by late February and disappeared during April and May. Eggs were laid from late February to April.

Third generation: Juveniles appeared from April to June and over-wintered as small adults. From June to July as well as September to early October, they laid eggs and had disappeared by November. Most of the eggs hatched during October producing individuals of the first generation.

During the sampling period the three generations had approximate durations (from oviposition to death) as follows: the first from early September to early February (6 months), the second from early December until early June ($7\frac{1}{2}$ months) and third from late February to late October ($8\frac{1}{2}$ months). The over-wintering adults of the third generation grew largest with shell diameters of 9.0–10.0 mm, whereas those of the other generations did not exceed 8.0 mm.

B. (Physopsis) sp.

This species, like *B. pfeifferi*, was found to have three overlapping generations per year (Fig. 4). The first generation was short and for practical purposes, merged with the second.

First generation: eggs laid by over-wintering adults from September to early November commenced this generation. They hatched from late October to mid-November, had matured by late December and disappeared in January.

Second generation: juveniles from eggs laid in December

Table I Shell sizes when the first oviposition in aquaria occurred.

Species	Shell diameter (mm)
B. pfeifferi	5.0
	Shell height (mm)
B.(Physopsis) sp.	6.0
L. columella	6.5
L. natalensis	7.0

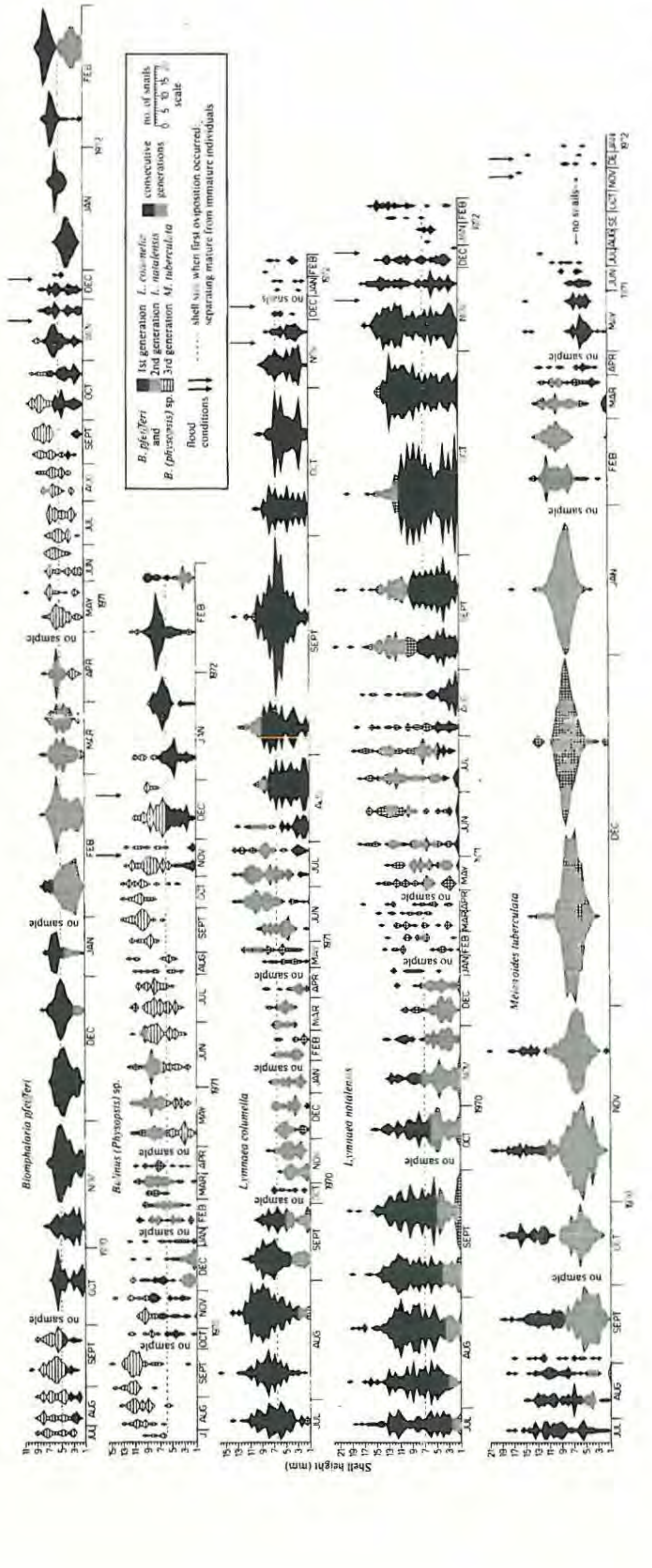

Fig. 4 Results of sampling programme, expressed as kite diagrams, for *Biomphalaria pfeifferi*, *Bulinus (Physopsis)* sp., *Lymnaea columella*, *L. natalensis* and *Melanoides tuberculata*. Consecutive generations are indicated by different designs.

appeared during December and early January, matured during February and March and disappeared during June and July. Their eggs were laid in late March and April.

Third generation: the eggs hatched from late April to late June, and the snails matured by July. These adults over-wintered and disappeared in late November. Eggs were laid during late June and early July and again during September and October. By late October these eggs had all hatched to begin the first generation.

During the sampling period the approximate durations of the three generations (from oviposition to death) were as follows: the first lasted from late September to late January (4½ months), the second from early December to late July (8 months), and the third from mid-March to late October (7½ months). Over-wintering adults of the third generation were, like *B. pfeifferi*, the largest specimens found, with shell heights of 12.0–15.0 mm, whereas those of the other generations did not exceed 12.0 mm.

Lymnaea columella

Adults of this species reached peak abundance during August/September (Fig. 4). Juveniles were found mainly from late August to early December. These became adult by late June and produced their juveniles from August to October. The longevity of each generation was therefore approximately 15 months. A correlation between Fig. 4 and the lymnaeid egg production in Fig. 5, suggests that *L. columella* bred earlier (June-July) than *L. natalensis* (September-October). The June-July 1971 peak is therefore ascribed chiefly to *L. columella*.

L. natalensis

The population of this species (Fig. 4) had an annual fluctuation very similar to that of *L. columella*. *L. natalensis* laid most of its eggs during August-September in 1970 and during September-October in 1971 (Fig. 5).

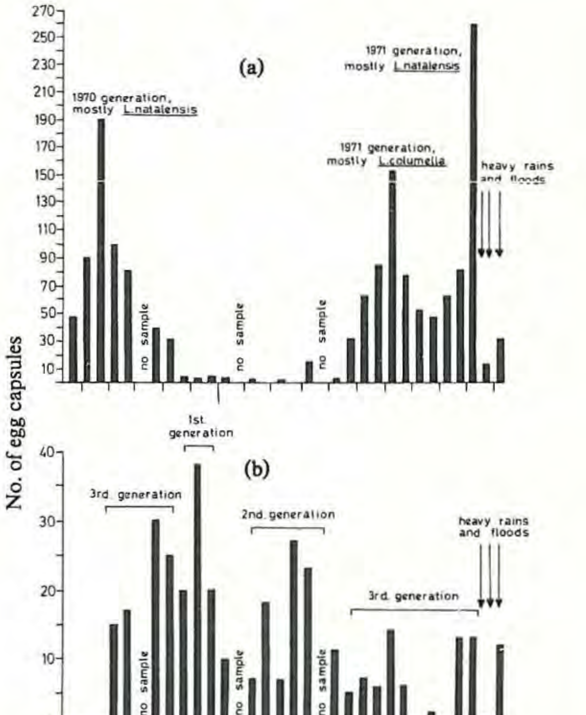

Fig. 5 Egg production as revealed by the samples, (a) shows production by the Lymnaeidae (*Lymnaea columella* and *L. natalensis*) with peaks identified by correlation with Fig. 4. (b) indicates production by the Planorbidae (*Biomphalaria pfeifferi* and *Bulinus (Physopsis)* sp.) with peak egg-laying by the successive generations of both species according to Fig. 4.

Melanoides tuberculata

From the available data *M. tuberculata* appeared to have a single generation per year (Fig. 4). Breeding took place during autumn with peak abundance being reached during the summer months. Sampling should however be continued for a longer period in order to establish the population fluctuations of this species.

The effects of floods

Flood conditions prevailed in the Gladdespruit after very heavy rains in its catchment during late November and late December 1971, with marked effects on the snail population (Fig. 4). Unfortunately very few eggs were found after the floods as dead and floating vegetation, which was an important site for oviposition, had been carried away and consequently was no longer taken in samples. The low snail counts made in late November and late December were ascribed to the high water-level of both habitats after the floods (Fig. 2).

The main effect of the floods on *B. pfeifferi* and *B. (Physopsis)* sp. appears to have been the removal of the remaining over-wintering adults of the third generation and many of the recently matured members of the first generation. Within a month of the water beginning to subside, there was a rapid increase in the numbers of juveniles of both species, presumably due to egg-laying by the surviving mature individuals as a response to the catastrophic flood conditions. The sudden reduction in numbers of *B. (Physopsis)* sp. in late February 1972 may have been due to overcrowding and competition with the expanding second generation of *B. pfeifferi*. By late February, however, (2½ months after the floods) the *status quo* of both populations was comparable with that during February 1971. The populations of *L. columella* and *L. natalensis*, which did not breed during the warm months, were severely reduced but would probably have recovered by spring. Summer floods of this nature usually occur annually but not necessarily at the same time of year. It is thought that their effect on snail populations would be similar irrespective of when they occurred.

Discussion

A review of available information on the population fluctuations of bilharzia intermediate host snails in tropical East Africa[6] provides evidence for breeding by *B. pfeifferi*, *B. (Physopsis) africanus*, *B (Physopsis) globosus* and *Bulinus (Physopsis) nasutus* (Martens) after the two main rainy periods (March to April and September to November). Two population peaks of *B. (Physopsis) nasutus* during the year were found at Mwanza (Tanzania)[7]; one during October to November, and the other from February to March. The first and last peaks corresponded to periods of high rainfall though the author's diagrams indicate that there might be another during May, as the dry season was approaching.

The two periods of rainfall so characteristic of these tropical areas, and with which the seasonal fluctuations of East African snail populations have been associated, are absent from the Eastern Transvaal lowveld where there is a single rainy period from October to March. The population fluctuations revealed by the present investigation cannot therefore be related to rainfall. This is the more so since rainfall during the sampling period was abnormally low, yet definite population fluctuations occurred. In temporary habitats, however, rainfall is presumably of utmost importance. A close relationship between the population fluctuations of *B. (physopsis) globosus* and the rains was noted in a temporary habitat in Rhodesia[8].

The results shown in Fig. 4 indicate that the first generation (the shortest) of *B. (Physopsis)* sp. and *B. pfeifferi* appeared during the late spring and summer when temperatures were higher than those prevailing during the lives of the longer lived second and third generations. This lends support, in the form of field observations, to laboratory studies on *B. (Physopsis) globosus*[9], *B. pfeifferi*[5,10] and *B. glabrata*[11] which showed that the snails' mean generation times shorten with increasing temperature.

Relation to schistosome transmission patterns

Incubation periods of *Schistosoma mansoni* Sambon, *S. haematobium* (Bilharz) and *S. mattheei* Veglia & le Roux in snails infected at different times throughout the year were recorded at the Nelspruit laboratory[12]. These data were gained from routine observations over a number of years and at varying temperatures.

Schistosoma mansoni and *Biomphalaria pfeifferi*

Two peaks of *S. mansoni* transmission from snails, based on rodent immersions have been demonstrated[13,14] in the Eastern Transvaal lowveld. The first occurred mainly from July to December and the second from January to April. The cyclical relationships between these cercarial transmission peaks and the generation sequence of *B. pfeifferi* (given in Fig. 4) are shown in Fig. 6.

Schistosoma haematobium, *S. mattheei* and *Bulinus (Physopsis)* sp.

S. haematobium and *S. mattheei* were shown to have broadly similar shedding patterns over what seems to be a single, prolonged peak period from early October to early March, though *S. mattheei* shows only a slight decrease during the winter months[13,14]. The relationships between the generation sequence of *B. (Physopsis)* sp. (Fig. 4) and *S. haematobium* and *S. mattheei* are shown in Fig. 7a and 7b respectively.

The following is a possible explanation for *S. haematobium* and *S. mattheei* not undergoing the fall in transmission during January shown by *S. mansoni*[14]. Evidence shows that the first generation of *B. (Physopsis)* sp. was short, with the result that the juveniles and young adults of the first and then the second generations provided a more or less constant quantity of snails less than 10 weeks old in the population from October to March. The incubation periods of the schistosomes in the snail for this

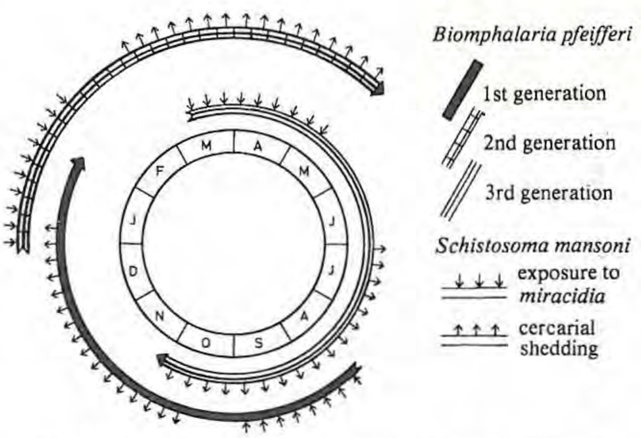

Fig. 6 Diagram illustrating the cyclical relationship between the generation sequence of *Biomphalaria pfeifferi* as revealed by the present study (Fig. 4) and the transmission pattern of *Schistosoma mansoni*[13,14]. Schistosome development in each snail generation is indicated from exposure to miracidia until cercarial shedding, separated by appropriate incubation periods[12]. The diagram takes into account only those miracidia likely to infect young snails, and not those present in the water at other times.

period range from 73–35 days for *S. haematobium* and 69–34 days for *S. mattheei*[12]. These would be of sufficient length to bring about continual shedding by members of the first and second generations of *B. (Physopsis)* sp. from late November to March.

Further, the cercarial output by *B. (Physopsis)* sp. started to drop about 8–10 weeks after shedding had begun[12]. Accepting that juveniles and young adult snails are more susceptible to infection than the older adults, and, as has been demonstrated, young snails were always plentiful in the population from October to March, sustained *S. haematobium* and *S. mattheei* shedding throughout this period would be expected. These relationships might be limited to regions of sub-tropical climate (such as the eastern Transvaal lowveld) where the seasonal differences are more marked than in tropical areas, but less so than in temperate ones.

Summary and conclusions

The present findings indicate that during the study period the bilharzia host snails were predominantly warm-month breeders, though the breeding season of *B. pfeifferi* extended from September to July, and that of *B. (Physopsis)* sp. from September to May. Both species had three overlapping generations per year. The population fluctuations of these species correlate well in a cyclical fashion with the known seasonal transmission periods of the larval bilharzia parasites *Schistosoma mansoni*, *S. haematobium* and *S. mattheei* for which they are the intermediate hosts. It is significant that these fluctuations in schistosome transmission observed at Malelane in the Transvaal lowveld eight years ago[14] can be correlated closely with the population fluctuations of the host snails in a locality 59 km to the west and 351 m higher in altitude as revealed by the present study. The present findings also corroborate those relating to snail longevity, shedding patterns and schistosome incubation periods as observed in aquaria at the Nelspruit laboratory[12].

The two *Lymnaea* species were predominantly cold-month breeders. *L. columella* bred mostly from June to August and *L. natalensis* from September to October. They had only one generation per year.

The data for *M. tuberculata* are incomplete, but suggest that this species bred in autumn and has a single generation per year.

The severity of floods in the two sampling habitats from November and December 1971 was clearly worse at site A than at site B because of the destruction of marginal vegetation which provided shelter and a substrate for oviposition. The populations of all the species sampled except *M. tuberculata* (the data being insufficient) were affected through the loss of many of their numbers. This was most marked in *B. pfeifferi* and *B. (Physopsis)* sp. since they were actively breeding at the time and had many juveniles in their populations. Egg-laying by the remaining mature individuals was apparent in all four species immediately following the floods, and had restored the *status quo* of the populations by late February, some two months later.

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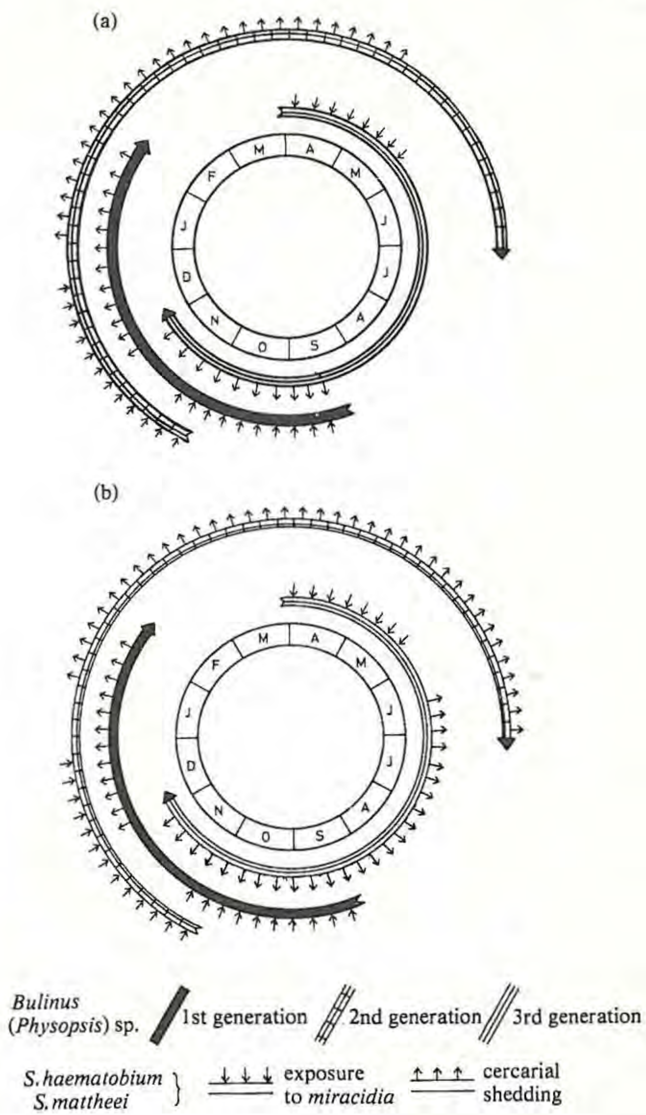

Fig. 7 Diagrams illustrating the cyclical relationships between the generation sequence of *Bulinus (Physopsis)* sp. as revealed by the present study (Fig. 4) and the transmission patterns of (a) *Schistosoma haematobium* and (b) *S. mattheei*[13,14]. Schistosome development in each generation is indicated from exposure to miracidia until cercarial shedding, separated by appropriate incubation periods[12]. The diagrams take into account only those miracidia likely to infect young snails, and not those present in the water at other times.

[1] Schutte, C. H. J. and Frank, G. H. (1964). Observations on the distribution of freshwater Mollusca and chemistry of the natural waters in the South-eastern Transvaal and adjacent Northern Swaziland. *Bull. Wld Hlth Org.*, **32**, 389-400.

[2] Brown, D. S. (1966). On certain morphological features of *Bulinus africanus* and *B. globosus* (Mollusca: Pulmonata) and distribution of these species in south-eastern Africa. *Ann. Natal Mus.*, **18**, 401-405.

[3] Hairston, N. G., Hubendick, B., Watson, J. M. and Olivier, L. J. (1958). An evaluation of techniques used in estimating snail populations. *Bull. Wld Hlth Org.*, **19**, 661-672.

[4] Olivier, L. J. and Schneiderman, M. (1956). A method for estimating the density of aquatic snail populations. *Exptl. Parasit.*, **5**, 109-117.

[5] Sturrock, R. F. (1966). The influence of temperature on the biology of *Biomphalaria pfeifferi* (Krauss), an intermediate host of *Schistosoma mansoni*. *Ann. trop. Med. Parasit.*, **60**, 100-105.

[6] Webbe, G. and Jordan, P. (1966). Recent advances in knowledge of schistosomiasis in East Africa. *Trans. roy. Soc. trop. Med. Hyg.*, **60**, 279-306.

[7] Baalawy, S. S. and Moyo, H. G. (1970). Studies on the population dynamics of *B. (P.) nasutus* and natural *S. haematobium* infection rates in relation to rainfall at Misungwi and Usagara, Mwanza. *E. Afr. med. J.*, **47**, 472-478.

[8] Shiff, C. J. (1964). Studies on *Bulinus (Physopsis) globosus* in Rhodesia. III. Bionomics of a natural population existing in a temporary habitat. *Ann. trop. Med. Parasit.*, **58**, 240-255.

[9] Shiff, C. J. (1964). Studies on *Bulinus Physopsis) globosus* in Rhodesia, I. The influence of temperature on the intrinsic rate of natural increase. *Ann. trop. Med. Parasit.*, 58, 94-105.

[10] Shiff, C. J. and Garnett, B. (1967). The influence of temperature on the intrinsic rate of natural increase of the freshwater snail *Biomphalaria pfeifferi* (Krauss) (Pulmonata: Planorbidae). *Arch. Hydrobiol.*, 62, 429-438.

[11] Sturrock, R. F. and Sturrock, B. M. (1972). The influence of temperature on the biology of *Biomphalaria glabrata* (Say), the intermediate host of *Schistosoma mansoni* on St. Lucia, West Indies. *Ann. trop. Med. Parasit.*, 66, 385-390.

[12] Pitchford, R. J. and Visser, P. S. (1969). Cercarial shedding patterns of various schistosome species under outdoor conditions in the Transvaal. *Ann. trop. Med. Parasit.*, 63, 359-371.

[13] Pitchford, R. J. and Visser, P. S. (1962). Results of exposing mice to schistosomiasis by immersion in natural water. *Trans. roy. Soc. trop. Med. Hyg.*, 56, 294-301.

[14] Pitchford, R. J. and Visser, P. S. (1965). Some further observations on schistosome transmission in the Eastern Transvaal. *Bull. Wld Hlth Org.*, 32, 83-104.

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months of the year, late January and February) might be adversely affected. A reasonable extension of this hypothesis was that any such adverse effects may offer explanations not only for the species' discontinuous distribution over the coastal plain in Natal and much of Mozambique but also its absence further north.

A repeat sampling programme was therefore carried out in the vicinity of Lake Sibaya on the coastal plain of northern Zululand (Natal) - a considerably hotter area than Nelspruit. A copy of my Nelspruit (Gladdespruit) sampling results (Appleton, 1974) is included here. Throughout the following text, the generation nomenclature used in this paper is retained, i.e. 1st generation in spring, 2nd generation in summer and the 3rd generation during autumn and winter.

GEOGRAPHICAL FEATURES AND GEOLOGY OF THE SAMPLING LOCALITIES

The locality sampled by Appleton (1974) lies at an altitude of 655m (25°28'S; 30°57'E) in a permanent stream - the Gladdespruit - on the eastern Transvaal escarpment, part of the Drakensberg mountain range (Fig.2). Schulze (1947) considered the escarpment to be a separate climatic region, distinguished from the eastern Transvaal highveld by its warmer summer temperatures. He placed the escarpment in the category 'temperate (warm) with mean temperatures of the warmest month above 22.6°C, and with summer rainfall' according to the Köppen (1931) classification. The mean annual rainfall over the decade 1964 to 1973 was 761mm, falling mostly between October and March with November to January the wettest months (120 - 129mm/month) (records of the Citrus and Subtropical

Figure 2 Map of south-eastern Africa showing the localities of the two sampling sites. The 914m (=3,000 ft) contour is shown as a dotted line and marks the position on the Drakensberg escarpment.

G—Gladdespruit E—Empayeni pond

Fruits Research Institute, Nelspruit). The sampling site itself was a shallow backwater with a mean depth of approximately 0.5m and an area of approximately 140m^2, formed by a depression in the granite stream bed. A thin layer of fine mud covered the granite. The Gladdespruit is a tributary of the Crocodile River which in turn forms part of the Incomati River system.

The repeat programme was carried out in a completely different environment. This was a large, permanent pond - Empayeni (27°23'S; 32°43'E) - adjacent to the eastern shore of Lake Sibaya at an altitude of 19m on the coastal peneplain of northern Zululand (Figs 2 and 3). This is one of the 'lesser lakes' of Tinley (1958) and though named Empayeni by him, the pond is known as 'Shali' to the local Thonga tribesmen.

The extreme northerly part of this northern Zululand plain (also known as Tongaland), which includes Empayeni pond, experiences according to Schulze (1947) a 'tropical rain climate (savannah) with the coldest month having a mean temperature above 18°C, and with summer rainfall'. The mean annual rainfall at Lake Sibaya Research Station (0.8km north of Empayeni) for the six years from 1968 to 1973 was 1130mm. The rainy season extends from September to March, during which each month has at least 80mm precipitation. The peneplain itself is of Pliocene age and is covered by unconsolidated Plio/Pleistocene marine deposits over-lying Cretaceous beds (King, 1972). Empayeni pond has a mean depth of approximately 2.3m and an area of approximately 2732m^2. The pond (Fig.4) was open with a marginal fringe of emergent monocotyledons, mainly Scirpus litoralis Schrad., Typha latifolia L. ssp. capensis Rohrb., Cyperus isocladus

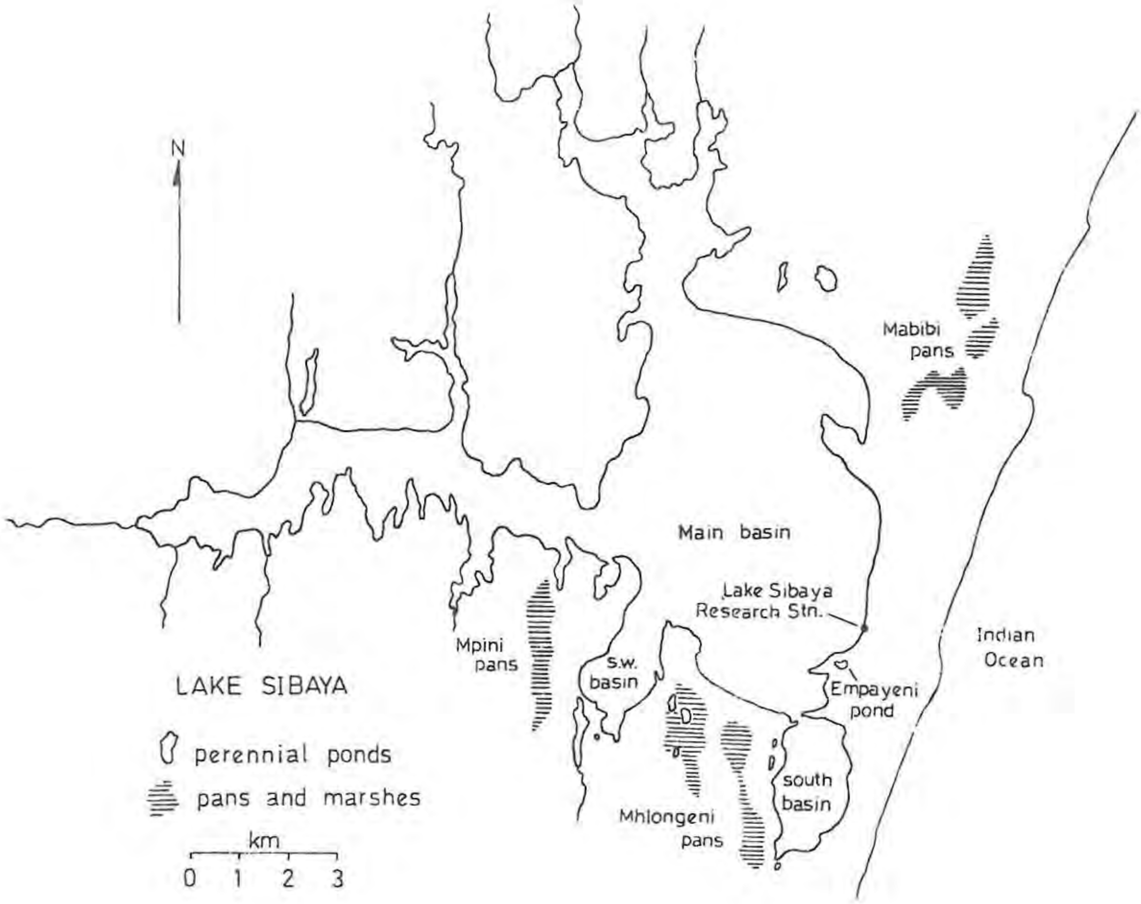

Figure 3 Map of Lake Sibaya on the coastal plain of northern Zululand, showing the localities referred to in the text. Names have been taken where possible, from Tinley (1958) but in some cases local names have been used.

Figure 4 Photograph of Empayeni from its eastern bank. The open character of the waterbody and the marginal fringe of reeds are illustrated. The sampling area was in the immediate vicinity of the thermograph (I). The white buoy (2) was moored at 2m depth marking the depthwise limit of both rooted vegetation and <u>B. pfeifferi</u> distribution.

Kunth. and the angiosperm Hydrocotyle bonariensis Lam. The substratum to a depth of approximately 2.0m was sandy mud while below that it changed to fine, black mud.

Following the discovery of unusually dense B. pfeifferi populations in submerged weed beds in the sheltered bays of Lake Sibaya itself, it was decided to extend the sampling programme to one of these - a small bay at the southern end of the lake's south-west basin (27°24'S; 32°40'E) (Figs 3 and 5). The sampling site here was a dense, submerged bed of Myriophyllum spicatum L., Ceratophyllum demersum L. and Potamogeton schweinfurthii A.Benn. growing in fine, black mud to a depth of about 2m.

A third habitat in the vicinity of Lake Sibaya - Sitatisi pan (27°18'S; 32°44'E) in the Mabibi area (Fig.3) - was selected as an example of a type of perennial waterbody in which B. pfeifferi did not occur but B. (Ph.) globosus did. The pan (Fig.6) had an area of approximately $580m^2$ and a maximum depth of only 1.3m. Emergent monocotyledons, especially S. litoralis, filled the pan except for a small central area in which Nymphaea capensis Thunb. and Utricularia sp. were common. The substratum throughout was fine, black mud.

METHODS

The sampling technique described by Appleton (1974) was used again in both Empayeni pond and the south-west basin. Each sample involved simple manual collecting along the same 10m of shoreline with uniform, shallow, long-handled nets by the same two people for 20 minutes. Samples were taken at fortnightly intervals over a year (December 1972 to November 1973) in Empayeni and for

Figure 5 Photograph showing a part of the sheltered bay at the southern end of the south-west basin of Lake Sibaya. The reed fringe is mostly of *Typha latifolia*. In the foreground is the thermograph mounted on a raft and moored over the submerged weed bed (mostly *Myriophyllum spicatum*) in approximately 1.4m depth. This bay was connected to the south-west basin by a narrow entrance.

Figure 6 Photograph of Sitatisi pan from its western bank. The reeds filling the pan (mostly <u>Scirpus litoralis</u>) and the position of the thermograph are clearly shown. Notice the steep banks which suggest that it was at one time deeper.

$4^1/_2$ months (November 1973 to March 1974) in the south-west basin. In the south-west basin though, sampling had to be done from a small boat which was always anchored in the same place, near a moored thermograph. Snails were counted and measured immediately after collection and then returned to the habitat.

Continuous temperature recordings were made using mercury-in-steel thermographs mounted on poles close to the water's edge. A Negretti & Zambra 'Mersteel' portable temperature recorder was set up in Empayeni on 11/12/72 and operated until 28/4/74 ($16^1/_2$ months) and another in Sitatisi from 29/1/73 to 28/4/74 (15 months). The probes of both instruments were suspended at a depth of 15cm from floats and were within some 2m of the bank. Their recordings therefore relate to marginal water only. In addition a Lambrecht T 256 thermograph was mounted, also in Empayeni, so that its probe was at a depth of 70cm, about 3m offshore from the 15cm instrument. This operated from 9/3/73 to 9/7/73 (5 months), when it was removed, mounted on a raft and moored in 1.4m of water in the south-west basin over the weed bed which was later sampled for B. pfeifferi. It remained in operation from 23/7/73 to 7/5/74 ($9^1/_2$ months). The charts of all thermographs were changed weekly.

RELATIONSHIP BETWEEN THE LIFE-CYCLE OF B. PFEIFFERI AND TEMPERATURE IN THE HABITATS EXAMINED

In this study the sampling programme reported by Appleton (1974) is compared with the repeat programme conducted in the Lake Sibaya area.

Appleton (1974) described the population fluctuations of B. pfeifferi in terms of generation cycles over a 20 month period in a permanent eastern Transvaal stream - the Gladdespruit. The snail was found, in common with another planorbid B. (Ph.) globosus, to undergo a sequence of three over-lapping generations per year. The 2nd of these three generations is a stage in the life-cycle which is potentially vulnerable to high thermal régimes and if this could be demonstrated in a hotter habitat than the Gladdespruit, an explanation might be found, as noted earlier, for the species' restricted distribution over the lowlands of south-east and east Africa.

With this as the basic problem in view, the repeat programme was begun in December 1972 at Sibaya. The aims of a comparison between this and the Gladdespruit data were however fourfold. These were :

i) to discover whether differences existed in the generation sequence of B. pfeifferi in a hotter area than Nelspruit and in particular whether there were any differences in the 2nd generations;

ii) to ascertain whether any such observed differences could be attributed to the influence of high temperatures and if so, what were the critical levels;

iii) to discover whether other generations in the same habitats were similarly affected;

iv) to provide an explanation for the discontinuous distribution of B. pfeifferi over the coastal peneplain of south-east and east Africa.

In addition to B. pfeifferi the Sibaya sampling sites harboured a variety of Pulmonata : four other Planorbidae, B. (Ph.) globosus, B. (B.) natalensis, Gyraulus costulatus (Krauss) and Ceratophallus sp.; as well as Lymnaea natalensis, Burnupia sp. and the Prosobranchia, Melanoides tuberculata and Bellamya capillata (Frauenfeld).

The generation sequence found here for B. pfeifferi corresponded closely with that recorded at Nelspruit. Life-spans of generations from both localities were shortest during the warmest months (2nd generation) and longest during the coolest months (3rd generation). Approximate generation times are given in Table 1. The mean generation time of 188 days compares well with the 200 days reported by Jobin (1970) from field data for B. glabrata in Puerto Rico.

Biomphalaria pfeifferi therefore undergoes a similar annual life-cycle of three over-lapping generations in different types of permanent waterbody, widely separated from each other. The cycle is as follows :

1st generation: eggs laid by over-wintering adults during late winter and early spring start this generation. By early summer (December) the bulk of the snails have reached maturity and lay eggs. They have died by mid-summer.

2nd generation: juveniles hatch during early summer (December and January) from eggs laid by the 1st generation, are mature by late summer (February), lay their eggs during early autumn and have disappeared by late-autumn.

3rd generation: eggs laid by the previous generation produce juveniles in mid-autumn, these over-winter, have matured by late winter and lay their eggs in early spring to start the next 1st generation. The 3rd generation has disappeared by mid-spring.

Routine observations on egg-production by a colony of snails from Empayeni, but kept in outdoor aquaria at Lake Sibaya

Table 1 Approximate generation times of B. pfeifferi in the Gladdespruit and Empayeni sampling sites, recorded during 1970 - 1972 and 1973 respectively.

APPROXIMATE GENERATION LIFE-SPANS AND TIMES (DAYS)

Generation	Gladdespruit		Empayeni Pond	
	life-span	days	life-span	days
1st	early August to late February	202	late August to early March	180
2nd	mid December to late May	158	mid January to late June	153
3rd	early March to mid November	250	late April to late October	186

Research Station showed, as found by Appleton (1974), that while egg-production never actually ceased, there were three periods of increased egg-laying during a year. These peaks coincided with the appearance of the three generations in the field samples.

An interesting discrepancy was found between the annual life-cycle of B. pfeifferi at Nelspruit and Empayeni. Although the generation sequences were similar, the densities of the 2nd and 3rd generations (especially the 2nd) were much reduced at Empayeni (Fig.7). It was the 2nd generation which the Nelspruit study suggested was a part of the cycle which might be vulnerable in hotter areas. Since temperature is known to exert a profound influence on the fecundity and growth of B. pfeifferi (Sturrock, 1966; Sevilla, 1965; Shiff & Garnett, 1967; de Kock, 1973) it was thought that high thermal régimes or component(s) of them could account not only for the reduced snail densities in the two Empayeni generations, but also for the species' erratic distribution over the northern Zululand peneplain. If however, impaired fecundity is to reduce the density of a particular generation, it is the parent generation which must become suspect, especially its maturation period. This period, from hatching to the attainment of maximal reproductive activity, takes about 24 weeks (Shiff & Garnett, 1967). In the case of the 2nd generation reduction in Empayeni being due to temperature effects therefore, it is the thermal conditions during the maturation period of its parent (1st) generation (late August to early January) which are likely to be important.

Thermal régimes

The Lake Sibaya area is a marginal one in the distribution

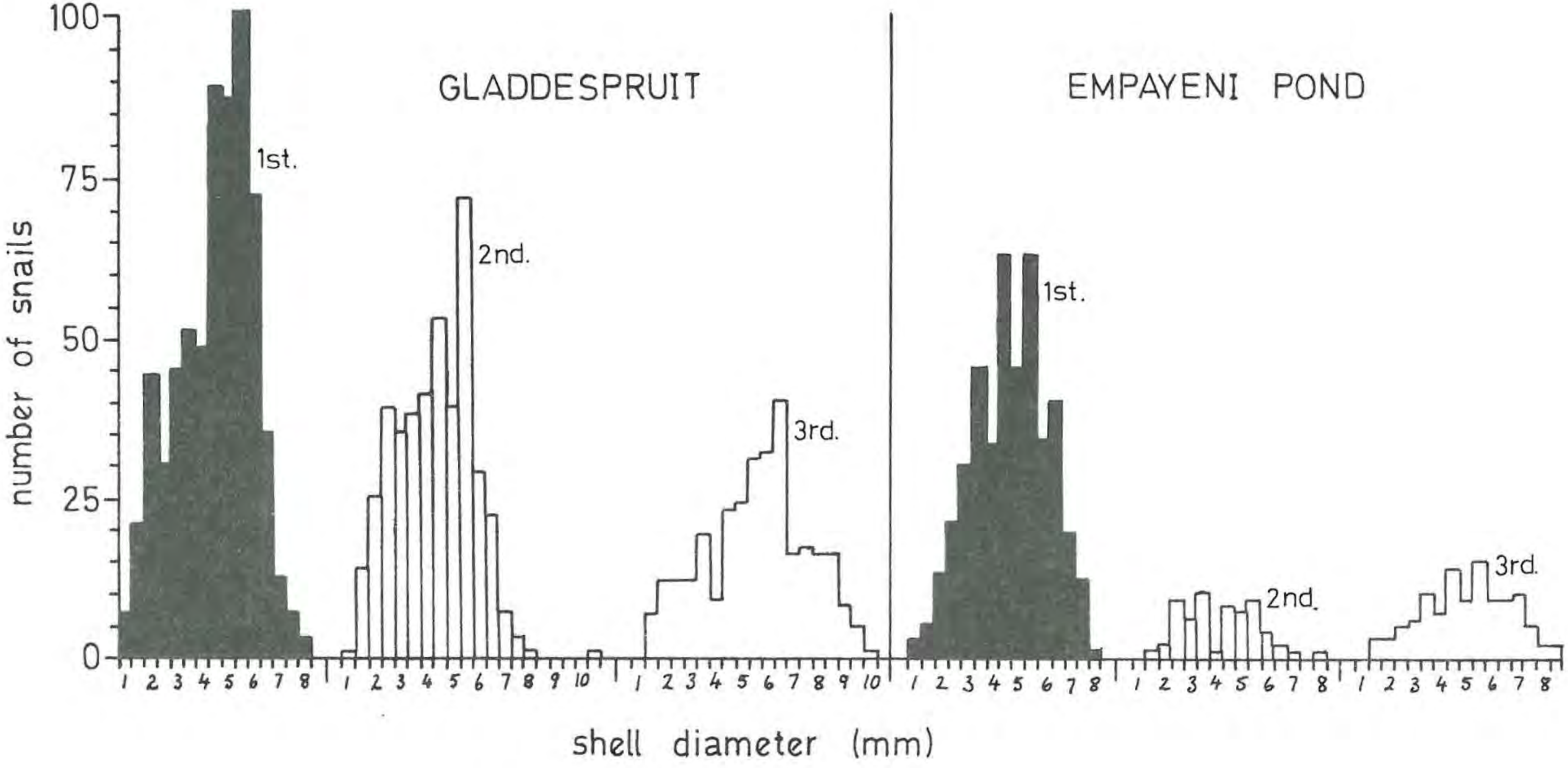

Figure 7 Diagram comparing the size distribution of snails in the three generations from the Gladdespruit and Empayeni pond. The total number of snails belonging to each generation are shown within 0.5mm size-classes.

pattern of B. pfeifferi and the snail does not occur in all apparently suitable habitats associated with the lake. A survey revealed it to be absent from pans (shallow though usually perennial waterbodies filled with emergent vegetation) and also from the many shallow streams in the area. Bulinus (Ph.) globosus was found to be widespread here. A study was thus made of the thermal régimes not only in the habitats sampled for B. pfeifferi, but also for comparative purposes in a typical pan - Sitatisi.

The régimes in three of the waterbodies, Empayeni pond, Sitatisi pan and the Gladdespruit (sampled by Appleton, 1974) were found to be very variable not only seasonally but also daily. These thermal régimes are usefully described in degree hours per week, an expression combining both the average level of temperature reached and the time for which it was maintained. Unless a specific baseline is given, the parameter °hrs/wk integrates the whole temperature curve above the minimum weekly temperature recorded at the particular site. At both Empayeni and Sitatisi the minimum weekly temperature was 16.4°C, in the Gladdespruit 11.3°C and in the south-west basin, 16.8°C.

In Empayeni (Fig.8) the water temperature ranged from 2805 °hrs/wk in July 1973 to 5896 °hrs/wk in March 1974, compared to 2755 °hrs/wk and 4939 °hrs/wk during July and December 1973 respectively in Sitatisi (Fig.8). The fact that temperatures in Empayeni were frequently higher than in Sitatisi was offset by broader daily ranges and more rapid rates of warming and cooling in the shallow Sitatisi, resulting in this latter experiencing more extreme thermal conditions, particularly during the biologically

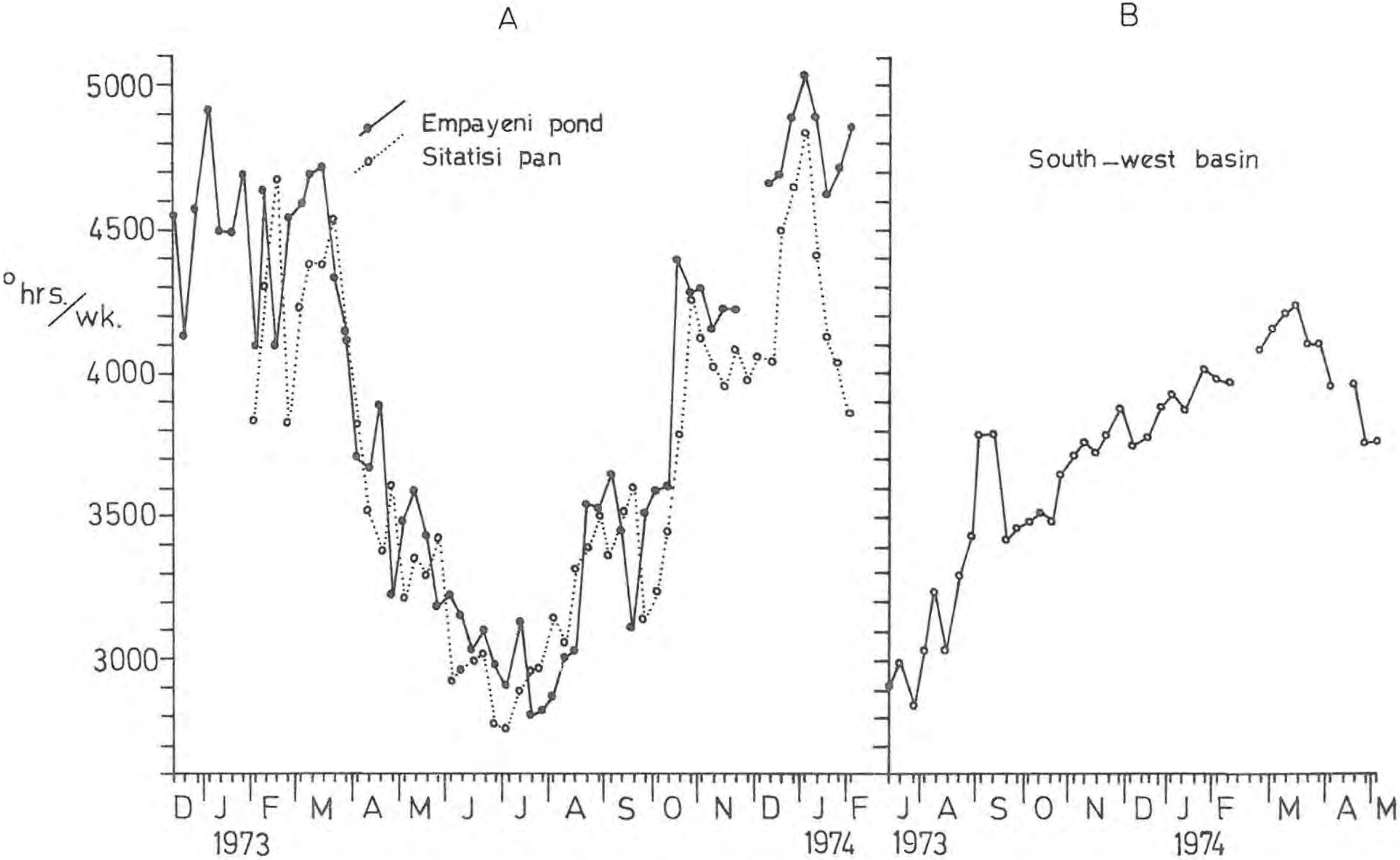

Figure 8 The thermal régimes at the three Sibaya habitats, expressed as degree hours per week. (A) Empayeni pond at 15cm from December 1972 to February 1974 and Sitatisi pan at 15cm from February 1973 to February 1974. (B) The south-west basin at 1.4m from July 1973 to May 1974.

important spring and early summer - the development period of the 1st B. pfeifferi generation.

The thermal conditions in the Gladdespruit sampling site (Fig.9) were variable like Empayeni and Sitatisi, though cooler than either. Temperatures in this backwater ranged between 1881 and 4351 °hrs/wk.

The fourth régime examined, in the small bay in the south-west basin of Lake Sibaya (Fig.8), was found to be remarkably stable. This stability may reasonably be attributed to the buffering influence of the thermal capacity of the lake's vast water mass. Temperatures here varied from 2822 °hrs/wk in August 1973 to 4234 °hrs/wk the following March.

Analysis of the temperature interactions

Two aspects of the possible influence of temperature on the fecundity of B. pfeifferi are exposed by the available data. These are (1) whether as suggested earlier, the observed reduction in density of the Empayeni 2nd generation might be attributable to one or more components of the thermal régime affecting the fecundity of the parent (1st) generation and (2) whether any thermal component which might be incriminated in this way affected the density of subsequent generations and their survival within individual habitats. Inspection of the relevant data showed no likely relationship between fecundity and other abiotic factors such as habitat depth, substratum, duration of direct sunshine or rainfall. The sample and temperature data were subjected to a statistical analysis in order to interpret these important points.

No direct observations were made on egg-production in the

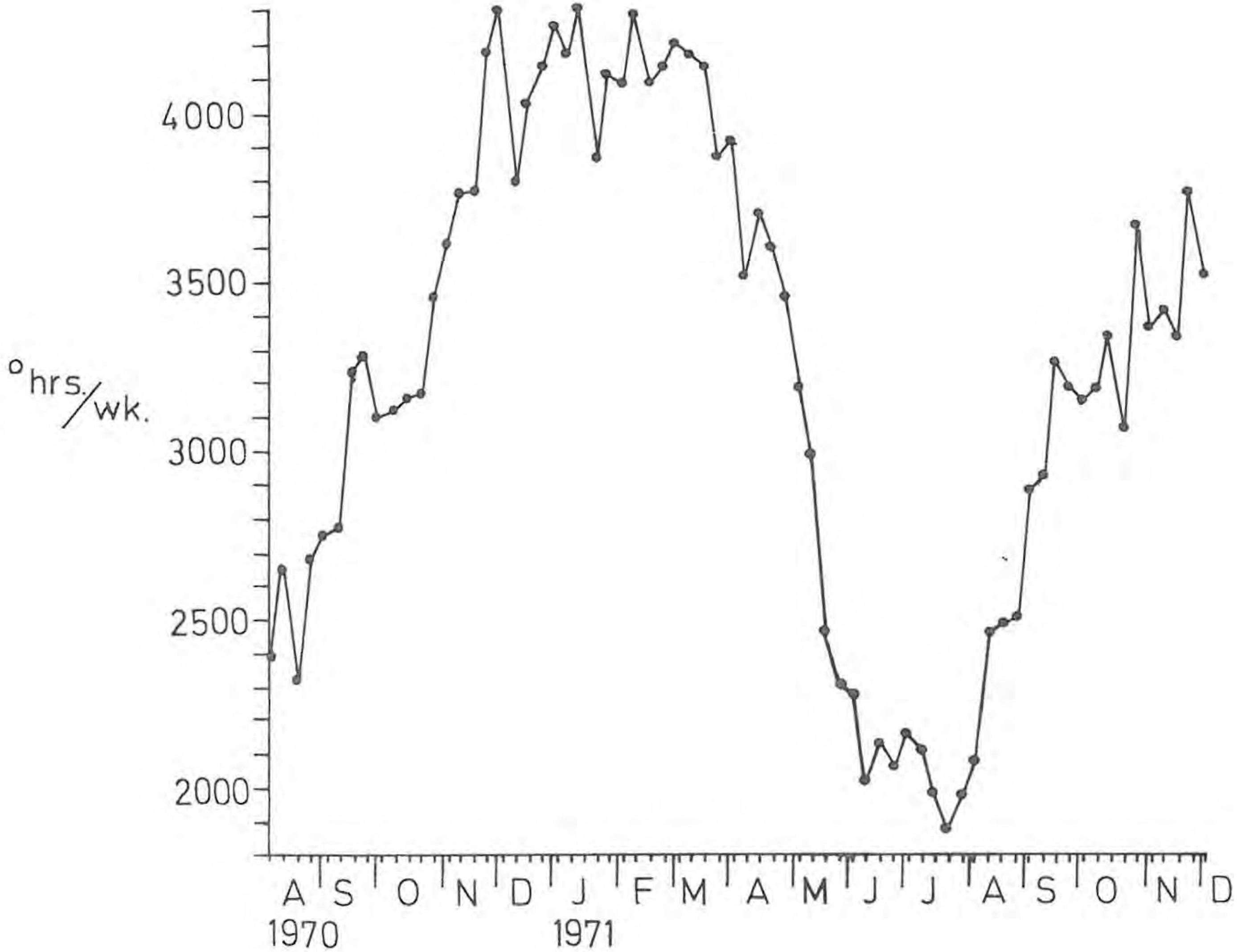

Figure 9 The thermal régime at 25cm depth in the Gladdespruit sampling site from August 1970 to December 1971, expressed as degree hours per week.

Sibaya habitats because, unlike the Gladdespruit site where eggs were frequently laid on dead and floating vegetation, little such material was present at Empayeni and none in the south-west basin so that oviposition occurred mostly on submerged, attached vegetation. Regular removal of this might have seriously altered the sampling sites. Instead the mean number of 2nd generation snails per sample was used as an index of the fecundity of its parent (1st) generation and a lag correlation was anticipated. The validity of employing a reproductive index as an estimate of the birth rate in conjunction with fortnightly sampling has been discussed by Webbe (1962) and Sturrock (1973a). These authors, who used an index on a daily basis rather than on a generation basis as in the present context but for the same reasons, have pointed out that since it did not take into account mortality of eggs, and hatchlings less than two weeks old, it probably under-estimated the true birth rate. This limitation does not appear to be serious however since available estimates of mortality rates in permanent habitats (Webbe, 1962; Dazo et al, 1966) indicate little variation which might affect this index.

Correlation coefficients were calculated between the natural logarithm of the fecundity index and the means of ten selected components of the thermal régime during the maturation period of the respective parent (1st) generations, and also the density of this parent generation (both as untransformed data and its natural logarithm) (Table 2). Snail densities are expressed as logarithms simply to shorten the scale and not for any statistical purposes.

Table 2 Correlation coefficients between the natural logarithm of the fecundity index of the 1st generation (= mean no. 2nd generation snails/sample) and the means of ten selected thermal variables and the density of the 1st generation itself (untransformed and as natural logarithm) in the four waterbodies examined.

	Index of 1st generation fecundity (No. 2nd generation snails/sample) ln(x+1)	Mean temperature (°C)	Minimum (°C)	Maximum (°C)	°hrs/week	°hrs 26°C/week	°hrs 27°C/week	Daily range (°C)	Warming rate (°/hr)	Cooling rate (°/hr)	Heat budget gm.cals/cm^2	1st generation density (No. 1st generation snails/sample	1st generation density (No. 1st generation snails/sample) ln(x+1)
S.W. Basin	4.14	21.4	21.0	21.7	3613	0	0	0.7	0.16	0.06	310	72.0	4.29
Gladdespruit	3.75	20.2	18.5	21.9	3427	58	31	3.5	0.54	0.30	365	53.7	4.00
Empayeni	1.89	22.9	21.3	24.4	3845	180	120	3.1	0.47	0.23	1403	29.5	3.40
Sitatisi	0	22.7	19.5	25.8	3803	256	179	6.4	0.96	0.45	416	0	0
Correlation coefficient		-0.777	0.032	-0.991*	-0.763	-0.983*	-0.991*	-0.871	-0.868	-0.802	-0.267	0.987*	0.937**

* This correlation coefficient is greater than that given at the 1% level of significance for 3 degrees of freedom by Snedecor & Cochran (1967, Table A11).

** This correlation coefficient is greater than that given at the 5% level of significance for 3 degrees of freedom by Snedecor & Cochran (1967, Table A11).

The ten thermal variables were selected so as to cover dissimilar aspects of the thermal environment. In addition to degree hours per week (integrating the whole temperature range) baselines of 26° and 27°C were used because this temperature level was shown experimentally by Shiff & Garnett (1967) to be critical for B. pfeifferi. The highest constant temperature at which the species maintained an optimal intrinsic rate of natural increase ($r = 0.4376$) was 27°C.

Table 2 shows significant negative correlations between the natural logarithm of the fecundity index and three of the ten thermal variables, mean maximum temperature and degree hours above 26° and 27°C per week, at a 1% level. There were also significant positive correlations between the index and the density of the parent (1st) generation at a 1% level and the natural logarithm of this density at a 5% level. Although many of the coefficients themselves were high, 'n' the number of correlative pairs was small (4) so that $p<0.878$ is likely to be insignificant (Snedecor & Cochran, 1967).

In other words then, the highest correlation exists between the fecundity of the 1st generation (as the fecundity index) and the mean maximum temperature and degree hours above 26° and 27°C per week during its own maturation period (spring). This is however obscured by the existence of an almost equally strong correlation between 1st generation fecundity and its own density. In order therefore to exclude this influence of 1st (parent) generation density upon that of its filial (2nd) generation (used here as the fecundity index of the 1st generation), partial correlations coefficients were calculated between the latter and the three thermal variables with which it was most strongly correlated. A partial correlation coefficient ($p_{12.3}$) is described by Snedecor & Cochran (1967) as the correlation between variables 1 (2nd generation density = index of the fecundity of the 1st generation) and 2 (the thermal components) where both bear the same relation to variable 3 (density of 1st generation and its log.). Variable 3 is held constant so that only 1 and 2 are involved in the correlation.

Prior to these calculations however, the simple correlation coefficients between 1st generation density and the ten thermal variables during its own maturation period were obtained (Table 3). Significant negative correlations existed at a 1% level between 1st generation density and mean maximum temperature and degree hours above 26° and 27°C per week and at a 5% level with daily range and warming rate. 1st generation density is therefore as strongly correlated with degree hours above 26° and 27°C per week and almost as strongly with mean maximum temperature as its fecundity. The partial correlation coefficients are given in Table 4.

Significant negative partial correlations, significant at a 1% level, were found between 1st generation fecundity (= fecundity index) and mean maximum temperature and degree hours above 27°C per week during its own maturation period.

The isolation of these two from a wide range of variables, points to the <u>level</u> and <u>duration</u> of high temperatures (above 27°C) as the components of thermal régimes responsible for adverse effects on 1st generation fecundity. This impaired fecundity is considered to account not only for the marked variation of 2nd generation

Table 3 Correlation coefficients between absolute 1st generation density (mean no. 1st generation snails/sample) and the means of ten selected thermal variables during its maturation period in the four waterbodies examined.

	No. snails 1st gen./ sample	Mean temperature (°C)	Minimum (°C)	Maximum (°C)	°hrs/week	°hrs 26°C/week	°hrs 27°C/week	Daily range (°C)	Warming rate (°/hr)	Cooling rate (°hr)	Heat budget gmcals/ cm^2
S.W. Basin	72.0	21.4	21.0	21.7	3613	0	0	0.7	0.16	0.06	310
Gladdespruit	53.7	20.2	18.5	21.9	3427	58	31	3.5	0.54	0.30	365
Empayeni	29.5	22.9	21.3	24.4	3845	180	120	3.1	0.47	0.23	1403
Sitatisi	0	22.7	19.5	25.8	3803	256	179	6.4	0.96	0.46	416
Correlation coefficient		-0.700	0.148	-0.973**	-0.685	-0.991*	-0.991*	-0.923**	-0.917**	-0.872	-0.276

* This correlation coefficient is greater than that given at the 1% level of significance for 3 degrees of freedom by Snedecor & Cochran (1967, Table A11).

** This correlation coefficient is greater than that given at the 5% level of significance for 3 degrees of freedom by Snedecor & Cochran (1967, Table A11).

Table 4 Partial correlation coefficients between 1st generation fecundity and mean maximum temperature and degree hours above 26° and 27°C per week during its own maturation period in the four waterbodies.

Partial correlation coefficients

Thermal variable	to exclude the effect of 1st generation density (untransformed)	to exclude the effect of the natural log. of 1st generation density
maximum temperature	-0.8262	-0.9945*
°hrs 26°C/week	-0.2270	-0.9743
°hrs 27°C/week	-0.5992	-0.9928*

* this partial correlation coefficient is greater than that given at the 1% level of significance for (n-2) = 2 degrees of freedom by Snedecor & Cochran (1967, Table A11).

density but also for the absence of B. pfeifferi from pans in the vicinity of Lake Sibaya. In the investigated area the critical duration of these high temperatures above which a B. pfeifferi population cannot survive, lies between 120 and 179 ^{o}hrs>27^{o}C/wk - the levels in Empayeni and Sitatisi respectively during the maturation period of the 1st generation (spring).

Similar temperature correlated density-variations were thought likely to occur among different generations within the same habitat. By comparing generation density per sample with the mean maximum temperature during (a) its parent generation's life-span and (b) its own life-span, it was hoped to provide a measure of the effect that this variable has on fecundity and survival respectively in each generation. The evidence for this was examined by applying a 'one way analysis of covariance with unequal subclass numbers' (Snedecor & Cochran, 1967).

This analysis unfortunately did not produce a significant result due to maxima in the south-west basin of Lake Sibaya being relatively low, probably well below the critical level. It was therefore repeated by defining a temperature baseline and using degree hours above 27^{o}C per week for which a significant correlation was found above. This proved of no significance either, and the data are simply plotted in Figs 10 and 11.

Figure 10 shows the density (i.e. the mean no. of snails/sample/generation) of each of 14 generations followed in the three habitats. These densities are plotted against the mean maximum temperature and degree hours above 27^{o}C per week during the lifetime of their respective parent generations. Here the density of each

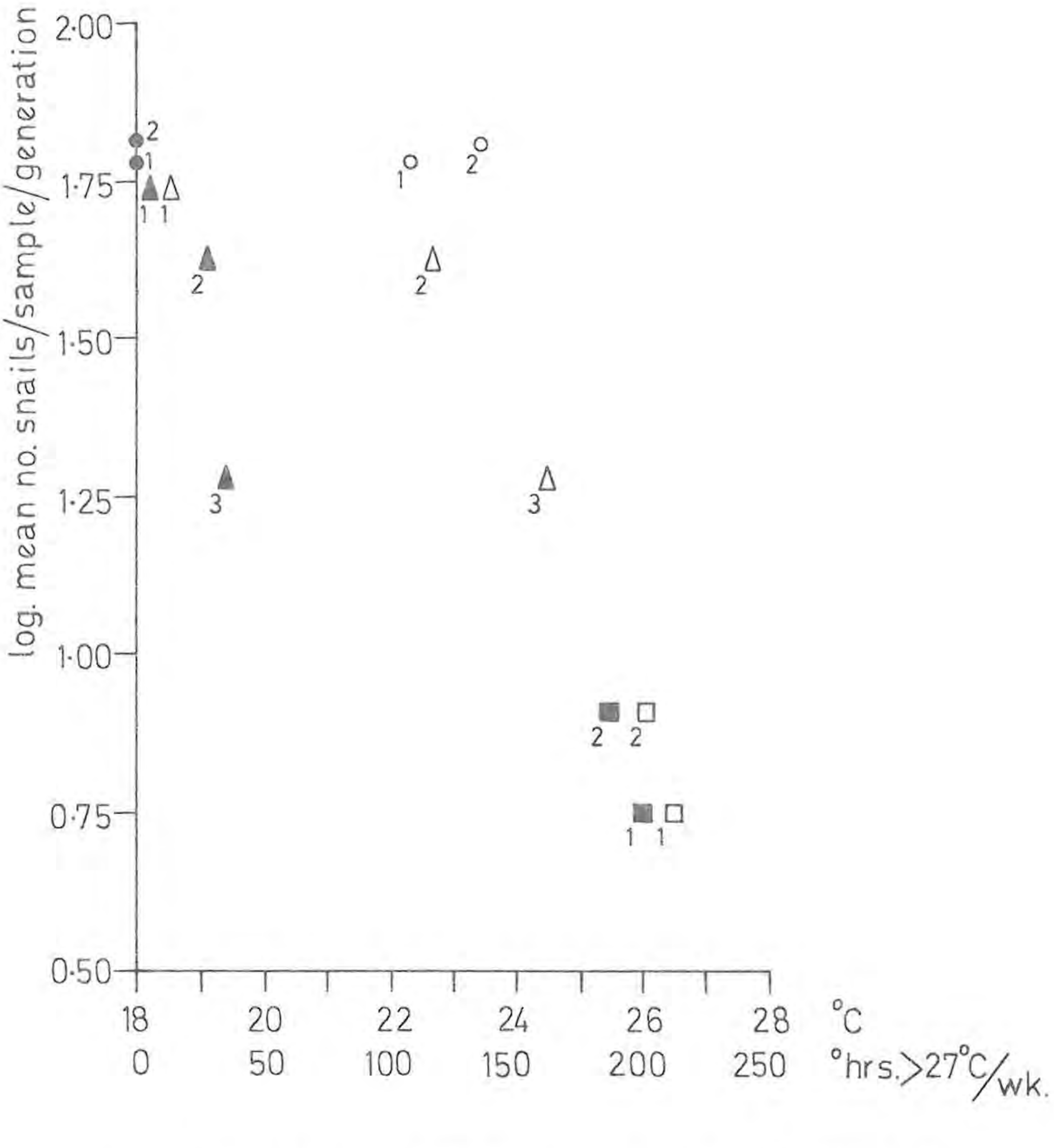

Figure 10 This relates the fecundity of each of 14 generations followed in the field (expressed as mean no. snails/sample/filial generation) to two thermal components during its own lifetime. Symbols used are : circles = south-west basin, triangles = Gladdespruit and squares = Empayeni pond. Empty symbols refer to mean maximum temperature and solid ones to degree hours above 27°C per week. Generation 'names' (1st, 2nd and 3rd) are given beside the relevant symbols.

generation is used as an index of the fecundity of its parent generation, and is examined in relation to the dimensions of the two thermal components during the parents' lifetime.

A definite trend exists which associates reduced fecundity with high temperature on the one hand and with increasing periods of temperatures above 27°C on the other. In Empayeni pond, which has a high thermal régime, both components are almost equally important whereas in the Gladdespruit and south-west basin which experience more moderate régimes, degree hours above 27°C per week is the more critical. This association might well have proved a significant one if more replicates had been available.

In a similar way Figure 11 relates the density (mean no. snails/sample/generation) of each of the 16 generations followed in the three habitats to the mean maximum temperature and degree hours above 27°C per week <u>during their own lifetimes</u>. Here the absolute density of each generation is related to the two thermal components during its own lifetime as a measure of their effect on snail survival within that generation.

Although in the south-west basin and Empayeni pond there is no marked difference between the effects of the two components, there is a difference in the Gladdespruit. Reductions in generation density here are associated more with increased periods above 27°C than with high maxima. The magnitude of changes in the densities of consecutive generations in the three sites was greatest in Empayeni pond which had the highest thermal régime while those recorded in the south-west basin remained virtually unchanged. In this latter habitat daily temperature ranges seldom exceeded 2°C

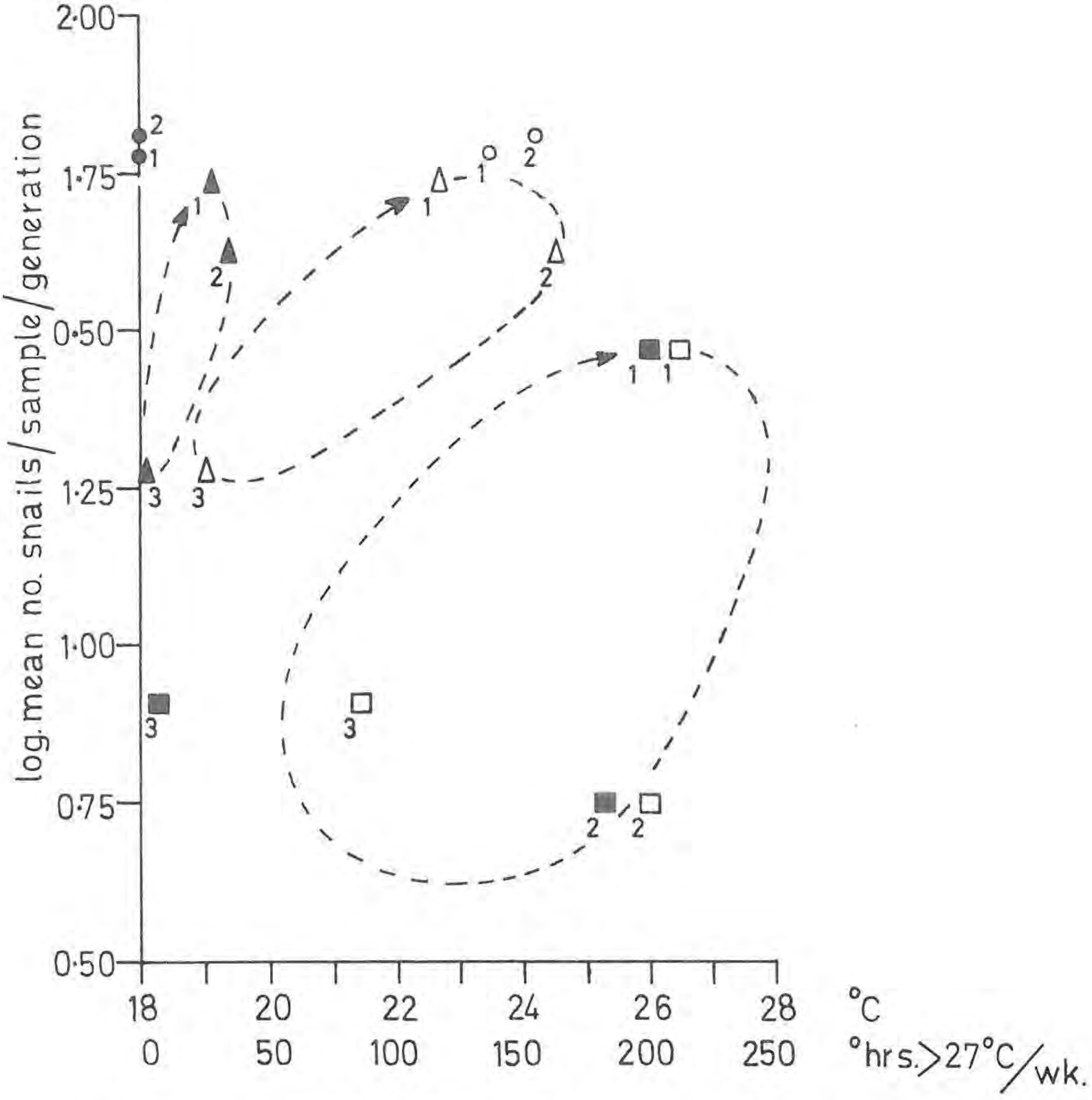

Figure 11 The relationship between snail survival and two thermal components. The density of each of 16 generations is used here as a measure of snail survival within that generation and plotted against mean maximum temperature and degree hours above 27°C per week during its own lifetime. Symbols used are: circles = south-west basin, triangles = Gladdespruit and squares = Empayeni pond. Empty symbols refer to mean maximum temperature and solid ones to degree hours above 27°C per week. Generation 'names' (1st, 2nd, 3rd) are given beside the relevant symbols. Dotted lines link the densities of different generations in individual sites.

and the temperature rose above 27°C only once during the period of observation (14/3/74) for about four hours.

It is useful to link the generation densities within the same habitat to illustrate the cyclic relationship between density increases and decreases. Densities were highest during spring (1st generation) but fell during summer (2nd generation), especially in Empayeni. During autumn and winter (3rd generation) the density in the Gladdespruit fell still further probably due to the cool winter whereas in Empayeni with its warmer régime the density of the 3rd generation rose a little. Rising temperatures during spring are presumably responsible for the increased 1st generation densities at both sites. Densities in the south-west basin hardly varied at all.

The results of the analysis therefore offer the following explanations of the two questions (1 and 2) outlined earlier.

(1) Certain components of the thermal régime (mean maximum temperature and degree hours above 27°C per week) appear to exert an adverse influence on the fecundity of the 1st generations. A partial correlation, significant at a 1% level, exists between 1st generation fecundity and these two thermal components during its own maturation period at the four sites examined.

(2) It was not possible to demonstrate a similar temperature influence on the fecundity of successive generations within individual habitats. It could be shown however that in individual habitats a clear trend exists suggesting that in Empayeni with its high thermal régime generation fecundity decreased as the level and duration of high temperatures increased. In the other two sites where moderate temperatures prevail, degree hours above 27°C per week appear to

exert a more profound effect on fecundity than maximum temperature. High maxima doubtless do affect fecundity, but only above a certain level. Two of the sites used, the Gladdespruit and south-west basin of Lake Sibaya, scarcely ever reached high maxima. Neither had a clear influence on survival but again, where high régimes prevail little difference between the effects of the two thermal components is likely while in more moderate ones, degree hours above 27°C per week seem more important.

Temperatures during the maturation period of the 1st generation exceeded 27°C for longer in Sitatisi (where B. pfeifferi is absent) than in Empayeni (where it does occur) by between 52 and 454 °hrs 27°C/wk (Fig.12). It is reasonable therefore to accept that in Sitatisi the effects of these high temperatures during this period (spring) are responsible for reducing the species' fecundity to a level where it is insufficient for the continued survival of a B. pfeifferi population there. A similar temperature limitation probably prevents the colonization of the other pans around Lake Sibaya (at Mabibi, Mhlongeni and Mpini) by B. pfeifferi. In this area B. pfeifferi is also absent from the numerous shallow, sluggish streams flowing into the lake, but unfortunately no temperature data are available for them.

In the Lake Sibaya area therefore, the length of time that temperatures exceed 27°C emerges as the component of the thermal régime which is most likely to impair the fecundity of B. pfeifferi. The critical duration lies, according to the available data, between 120 and 179 °hrs 27°C/wk. Maxima doubtless also affect fecundity, but will only be relevant above a certain level. Degree hours above

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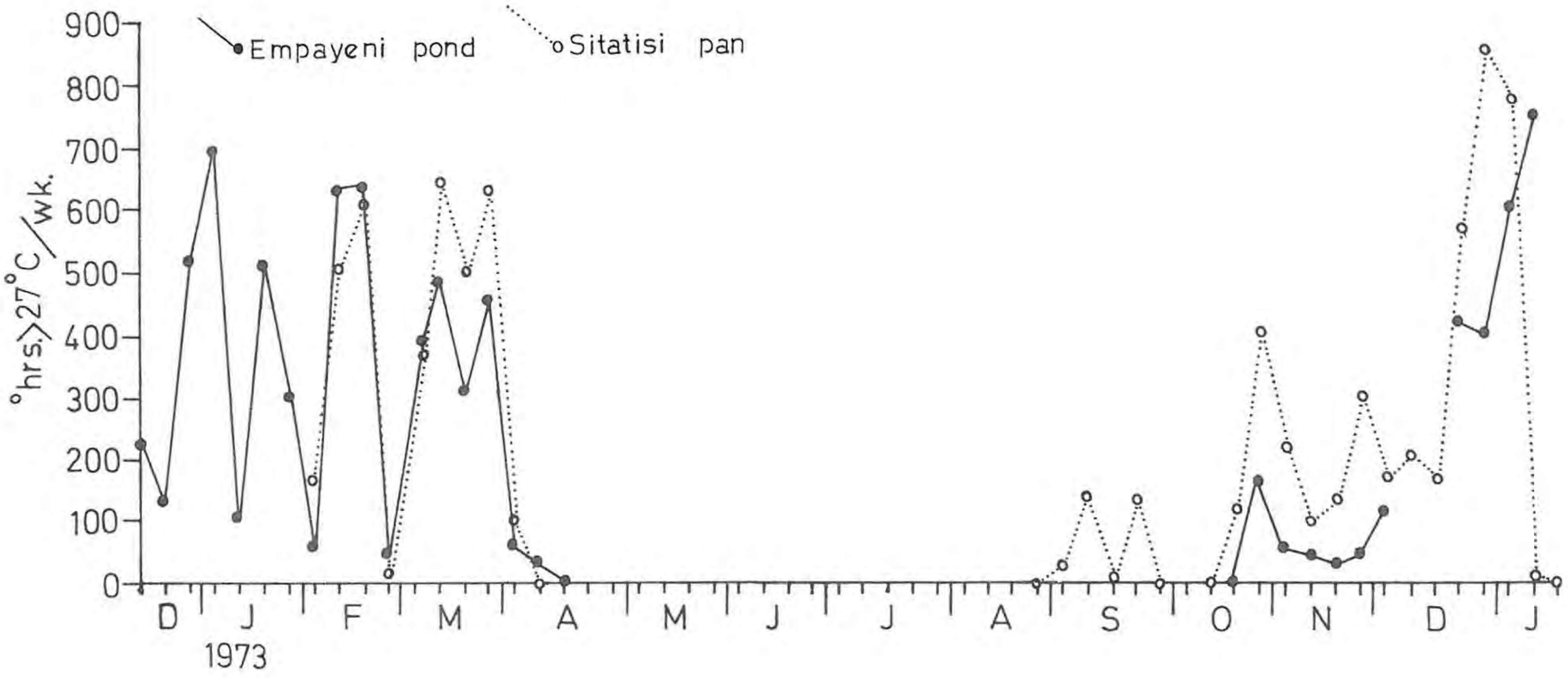


Figure 12 Degree hours above 27°C per week at 15cm in Empayeni pond from December 1972 to January 1974 and at 15cm in Sitatisi pan from February 1973 to January 1974.

27°C per week defines this level and as such is a more meaningful parameter in this context.

The thermal régime in pans, a type of perennial waterbody fairly common around the lake, exceeds the critical duration of high temperatures during spring, a time when the fecundity of a B. pfeifferi population is vulnerable to adverse temperature influences. This provides as explanation for the species' absence from habitats of this type and for its discontinuous distribution over the coastal peneplain of south-east Africa. It may reasonably be assumed too, that in equatorial regions where B. pfeifferi is absent altogether, temperatures exceed the critical duration above 27°C in most if not all potential habitats.

Ecological succession amongst habitats associated with Lake Sibaya

The inverse relationship between the severity of the thermal régimes in the Sibaya habitats investigated and the abundance of B. pfeifferi is explicable by a consideration of the recent history of these waterbodies. These habitats, probably once part of a larger Lake Sibaya, appear to be phases in an ecological succession brought about by a lowering of the water level of the lake. Empayeni pond was once connected to the lake's main basin via a still traceable channel. By surveying the floor of this channel with a theodolite, it was found that a previous lake level 2m higher than at present (1973) such as Hill (1969) has shown to have existed, would have joined the pond to the lake (Fig.13), probably as a sheltered bay similar to that in the south-west basin today. The other ponds around the lake could well have been similarly connected.

Separation of Empayeni from the lake took place according

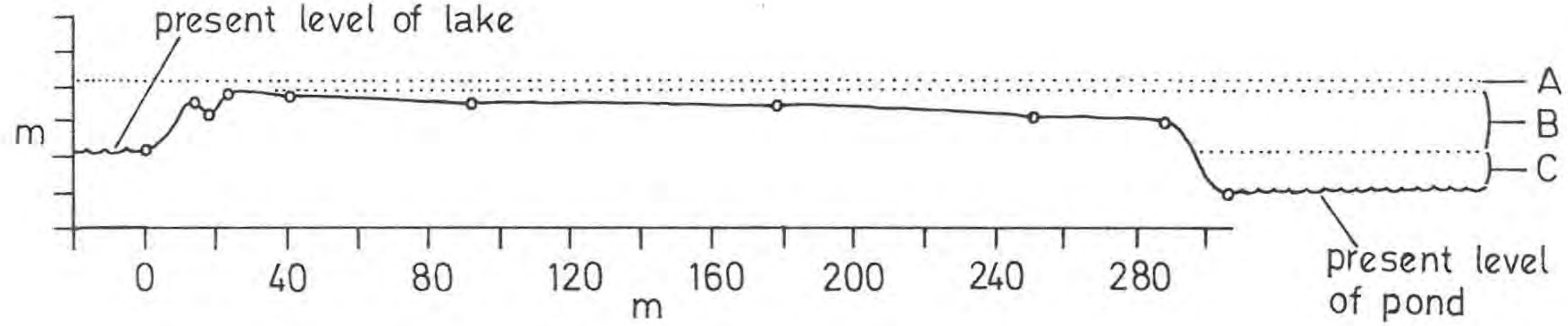


Figure 13 Section along the floor of the channel which joined Empayeni pond to the main basin of Lake Sibaya (surveyed on 18/10/73). Dotted line 'A' represents the lake level 2m higher than at present, joining pond to lake; 'B', the maximum height of channel floor above present lake level = 1.48mm; 'C', the difference between present lake and pond levels = 1.95m.

to local tradition, 20 to 30 years ago. Since this time there has been a further 2m drop in the water level of Empayeni. This may have facilitated pioneering by emergent monocotyledons, since a bed of Typha latifolia which today almost divides the pond does not appear in aerial photographs taken in 1942. At the time that Empayeni was cut off from the lake, the Mabibi pans (including Sitatisi) were apparently much more extensive, again according to local knowledge. It seems reasonable then to believe that just as ponds were cut off within the last three decades, the pans were similarly cut off earlier. Not only are they farther from the lake than ponds, but as a comparison between Figs 4 and 6 will show, they lie in deep land bowls which give the appearance of having once been inundated.

The succession from bay to pond to pan and the gradual lowering of their water levels after separation from the lake, accompanied by a spread of vegetation, has resulted in profound environmental changes. Present thermal régimes show a sequence from the stability of a sheltered bay within the lake (i.e. that in the south-west basin) to the greater variability of a shallow though open pond (i.e. Empayeni) to the extreme conditions prevailing in a very shallow pan (i.e. Sitatisi). Temperatures did not exceed 27°C in the bay, but did so for a considerable time in both Empayeni and Sitatisi (Fig.12). In the latter however it was more severe than in Empayeni from late August to early January - the maturation period of the 1st generation of B. pfeifferi. It is probable that this coupled with the shallowness of the pan has created an unfavourable thermal environment in which the species is unable to survive. Although temperatures in Empayeni rose almost as high in the shallows

(15cm) as in Sitatisi, the presence of cooler water at depths down to the vegetation limit at 2m probably enables the snail to survive here. Mean weekly temperatures at 70cm depth were up to 1.5°C cooler than at 15cm during the summer, and would be cooler still at 2m. The snails may survive either through (i) surface dwellers migrating to cooler depths or (ii) surface dwellers dying off and those individuals living at the cooler depths ensuring the survival of the population.

The diversity of fresh-water Mollusca occurring in these three types of lentic waterbody associated with Lake Sibaya fell from 12 in sheltered bays within the lake to 11 in ponds to 4 in pans (Table 5).

Distribution of Mollusca in submerged weed beds in Lake Sibaya

Submerged weed beds in sheltered, eutrophic bays (along all except the lake's eastern shore) harbour a rich malacofauna. Twelve species of aquatic Mollusca (omitting the Succineidae which are semi-aquatic in habit) were recorded by Allanson *et al* (1974) from these beds, though Boltt (1969) had found only five in similar beds in exposed situations in the main basin of the lake. In order to compare the depthwise distribution of molluscs in a sheltered bed with that in an exposed situation, series of samples were taken in May and July 1973 over two beds, one protected and the other exposed.

The sheltered bed was that in Guguswana Bay at the southern end of the south basin. A dense fringe of *S. litoralis*, *T. latifolia* and the herb *Polygonum tomentosum* dominate the marginal vegetation. *Nymphaea capensis* occurs in open water beyond this fringe and extensive submerged beds of *C. demersum*, *M. spicatum* and *P. schweinfurthii* grow

Table 5 The occurrence of twelve species of fresh-water Mollusca in sheltered bays within Lake Sibaya and the ponds and pans adjacent to it.

	Sheltered bays within Lake Sibaya	Perennial water-bodies adjacent to Lake Sibaya	
		Ponds	Pans
Gastropoda			
Bellamya capillata	x	x	
Melanoides tuberculata	x	x	
Lymnaea natalensis	x	x	x
Biomphalaria pfeifferi	x	x	
Gyraulus costulatus	x	x	
Ceratophallus sp.	x	x	x
Bulinus (*B.*) *natalensis*	x	x	
Bulinus (*Physopsis*) *globosus*	x	x	x
Burnupia sp.	x	x	x
Lamellibranchiata			
Corbicula africana	x	x	
Sphaerium capense	x	x	
Eupera ferruginea	x		

in fine, black mud beneath. The other bed investigated was off the exposed southern shore of the south basin and consisted of *S. litoralis*, *C. demersum* and *M. spicatum*. Qualitative weed samples were taken at approximately 5m intervals along transect lines over the beds. The results are presented in Fig.14. The Guguswana Bay samples are expressed quantitatively as snail density (no. snails/kg weed wet weight, mostly *M. spicatum*) are given in Table 6.

It is evident from Fig.14 that in sheltered weed beds pulmonates (except *B. natalensis* and *Burnupia* sp.) penetrate deeper than in the exposed bed which experiences considerable wave action due to northerly winds sweeping the length of the lake.

The presence in the Guguswana Bay samples, of several lymnaeid egg capsules attached to weed at various depths from 1.0 to 4.7m indicates that *L. natalensis* (the only lymnaeid present) breeds well below the surface. Likewise the finding of juvenile (maximum shell dimension 1.0 - 1.5mm) *B. pfeifferi*, *B. natalensis* and *Burnupia* sp. at 4.5, 5.0 and 4.5m respectively suggests that they might do so as well. Table 6 shows that the six Pulmonata sampled here were most abundant between 1.4 and 2.8m at the time of the investigation (July 1973).

It is clear that these snails, particularly *B. pfeifferi*, hitherto regarded as inhabitants of marginal waters less than about 2m deep, can successfully colonize habitats to several times this depth. In the micro-climate of these protected weed beds temperatures were remarkably stable, seldom rising above 25°C or varying by more than 2°C each day. Further, since weed fronds do not reach the surface these snails must obtain their oxygen directly from the

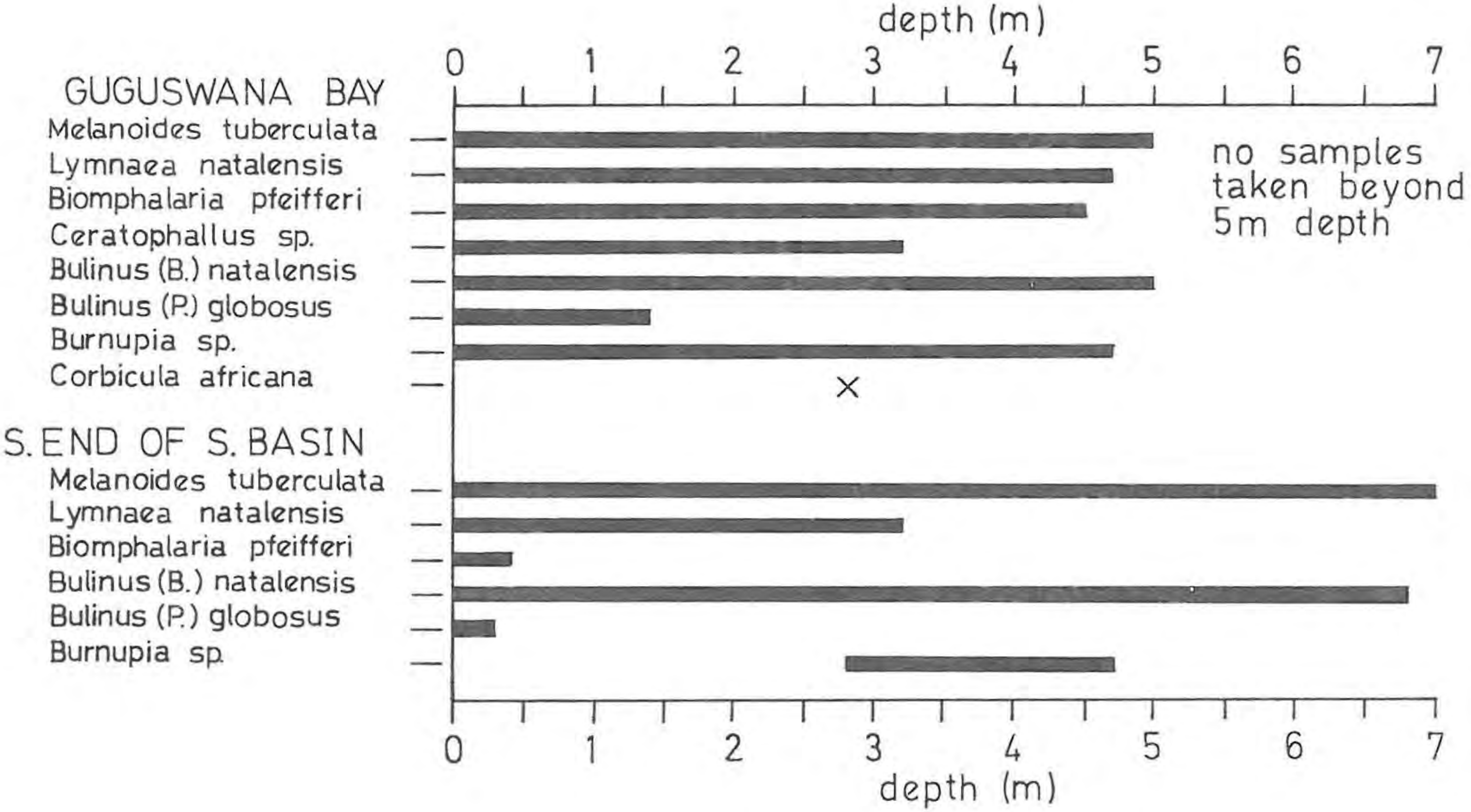


Figure 14 Diagrammatic representation of the depthwise distribution of Mollusca in the sheltered weed bed in Guguswana Bay and the exposed bed at the southern end of the south basin.

Table 6 Transect through a submerged weed bed (mostly *M. spicatum*) from 0.5 to 5.0m in Guguswana Bay at the southerly end of the south basin in Lake Sibaya. Results are expressed here as the number of snails per kilogram weed (wet weight) at different depths.

Depth (m)	*B. pfeifferi*	*B. (P.) globosus*	*B. natalensis*	*Ceratophallus sp.*	*L. natalensis*	*Burnupia sp.*	*M. tuberculata*
0.5	5.0	1.8	3.6	0	1.1	0	1.4
1.0	4.0	1.6	7.3	0.3	0.7	0.3	3.0
1.4	7.7	2.3	21.0	0.5	6.4	0	4.9
2.8	3.3	0	43.9	0.7	1.8	2.3	7.9
3.2	1.2	0	29.6	0.7	0	1.1	13.2
3.4	1.1	0	10.7	0	0	0	3.6
3.7	1.0	0	16.0	0	0.5	0.5	4.0
4.5	2.8	0	26.7	0	0.3	0.7	3.9
4.7	0	0	17.5	0	0	0.7	1.4
5.0	0	0	6.0	0	0	0	6.7

water, utilizing cutaneous respiration alone. In the small bay in the south-west basin not only was *B. pfeifferi* noticeably abundant but it attained an unusually large size. Specimens with a shell diameter of 13.0mm were not uncommon whereas the largest recorded from the Gladdespruit was 10.5mm and from Empayeni pond, 8.5mm.

DISCUSSION

The previous sections of this study have drawn attention firstly to the abundance of 'anecdotal' writing on a variety of abiotic factors which were thought to influence the distribution of the bilharzia intermediate host snails, and secondly to the lack of quantitative evidence on this important aspect of the ecology of bilharziasis. The quantitative evidence that is available however, reveals a number of important findings which contribute to an understanding of the snails' distribution patterns, particularly in South Africa where some major discontinuities occur. Investigations in these marginal areas provide valuable opportunities for measuring changes in abiotic factors in habitats harbouring the organism in question and those which do not.

Fundamental differences have been found in the tolerances of *B. pfeifferi* and *B.* (*Physopsis*) spp. to various abiotic factors. *Bulinus* (*Ph.*) *globosus* is for instance tolerant of a wider range of calcium and bicarbonate ion concentrations and also temperature (Shiff & Husting, 1966; Williams, 1970a & b). de Kock (1973) has suggested from experimental evidence that *B.* (*Ph.*) *africanus* is better adapted to cooler conditions than *B.* (*Ph.*) *globosus*. These findings are reflected respectively in the rather restricted distribution pattern of *B. pfeifferi* compared with that of *B.* (*Physopsis*) (van Eeden & Combrinck, 1966) and the allopatric distributions of *B.* (*Ph.*) *africanus* and *globosus* in Natal (Brown, 1966, 1967). Experiments reported by Heeg (1975) indicate moreover that *B.* (*Ph.*) *africanus* can live in natural waters differing widely in chemical quality by being able to acclimate to conditions within the range of fluctuations expected in the field. Such an ability is probably possessed by the other planorbid host snails to a greater or lesser degree. It also explains the observations of many researchers in many countries that water quality, within the range of ionic composition normally found in field waters, seldom approaches the lethal limit for snails and therefore cannot be regarded as constituting an important limiting factor to them. They do however influence the snails' local abundance.

Snails have also been collected in waters ranging widely in water temperature. Quantitative studies have shown not only that snails can survive, albeit with varying measures of success, over a wide range of temperatures, but that both the upper and lower critical limits for population survival lie at levels commonly recorded in natural waterbodies. It is this important aspect of the snails' temperature tolerance range that was investigated in the present study and which is shown to play a rôle in determining the distribution pattern of B. pfeifferi. Whether it does so for the two B. (Physopsis) species is not yet known.

Another abiotic factor which stands out as being instrumental in determining distribution is current velocity. Planorbid host snails from both Africa and South America have been observed to occur mostly in lentic habitats, but populations have been reported in waters flowing at velocities of up to 0.3 m/sec. The critical velocity has been determined experimentally for B. glabrata to lie at 0.33 m/sec. (Jobin & Ippen, 1964). This narrow tolerance range of 0 - 0.3 m/sec. must restrict the longitudinal distribution of these snails in river systems and render large parts of these watercourses uninhabitable despite the chemical composition and temperatures of the water being suitable.

Current velocity as a limiting factor was examined by Appleton (1975). I found that in the Gladdespruit, a perennial stream on the eastern Transvaal escarpment, the upstream distribution limits of the host snails B. (Ph.) globosus and B. pfeifferi lay at altitudes of 838 and 823m respectively. These altitudes coincided not only with a change in the stream's physical zonation from a stable granite substratum to an unstable sandy one but also from reaches where lentic habitats occur both detached and semi-detached from the channel to perpetually lotic zones. These limits also lie close to the 914m contour which Schutte & Frank (1964) had noted to be the farthest up the escarpment that host snails occurred in the south-east Transvaal. Temperature recordings made in the lotic reaches of the Gladdespruit, above the limits of host snail occurrence, indicate that the thermal régime there was still favourable for at least a low rate of increase since it exceeded the critical level of approximately 3000 °hrs/wk intermittently from October to April. This is considered to be the level (constant 17° - 18°C = 2856 - 3024 °hrs/wk) below which, according to Shiff & Garnett (1964) and de Kock (1973), host snails are unlikely to achieve positive 'r' values and would therefore be unable to maintain expanding populations. The snails' absence from these lotic reaches may be attributed to the perennial flow here in excess of the critical velocity. This indicates an important rôle for current velocity as a limiting factor in natural watercourses and that in lotic environments, temperature has a subordinate influence.

The factors determining water velocity are largely geomorphic ones, in particular the resistance offered to erosion by the rock formations which constitute the river or stream bed. This is not by any means a new concept, but it has only recently been applied to host snail ecology (Appleton, 1975). During this study I found it necessary to distinguish between those host snail populations living in lentic habitats secure from flushing or destruction by annual floods - persistent populations, and those in habitats which became lotic or even torrential each rainy season - temporary populations. Persistent populations were found to occur in low gradient reaches of watercourses (up to approximately 1.5%) over resistant rock formations with hardness values of 5 and above in Mohs' Scale of Hardness. In the Gladdespruit these snails also occurred in detached and semi-detached pools in steeper reaches, as far upstream in fact as lentic habitats were available.

The nature of the bedrock however affects not only current velocity and the stability of the substratum but also the permanence of the habitat. Hard rocks (≥5 in Mohs' Scale) not only form discrete, lentic habitats often detached from the channel as described by Appleton (1975), but their impermeability prevents their rapid drying during the dry season.

Appleton (1975) used Mohs' Scale of Hardness to categorize rock types as either resistant or susceptible to erosion and related this to host snail distribution in two eastern Transvaal watercourses - the Gladdespruit and Komati River. Although Mohs' Scale is neither accurate nor completely linear (Burridge, 1973), it can provide a further classification of rock formations on the same basis. It is possible thus to classify rocks as being (i) hard (ii) intermediate and (iii) soft, categories which are reasonably consistent over the entire country. Categories (i) and (ii) are considered resistant to erosion and (iii) non-resistant. The rocks of category (ii) are in fact mixed and the physical nature of the substratum produced depends very much on local composition. The point of demarcation between (i) and (ii) lies close to 5 in Mohs' Scale. When this criterion is applied to the rock formations of South Africa, Lesotho and Swaziland, they fall into the pattern shown in Fig.15. When the distributions of the host snails *B. pfeifferi* and *B.* (*Physopsis*) are superimposed on those of the three rock hardness categories, a remarkably close fit emerges between snail distribution and hard and intermediate formations (Fig.16).

The endemic area of *B. pfeifferi* is almost entirely over hard rocks (mostly granites), while that of *B.* (*Physopsis*) is wider though predominantly over the same formations and includes some anomalies. These are marked a - g in Fig.16. In addition to hard and intermediate formations, *B.* (*Physopsis*) occurs on the soft shales and sandstones of (a) north-western Natal and (b) the coastal areas of the Transkei, while both *B.* (*Physopsis*) and *B.pfeifferi* occur on (c) the unconsolidated sands of the northern Zululand coastal peneplain and (d) part of the Natal coastal strip. These positive anomalies occur where certain geomorphic features permit the development of natural impoundments in unstable and sometimes porous substrata. They are discussed individually below.

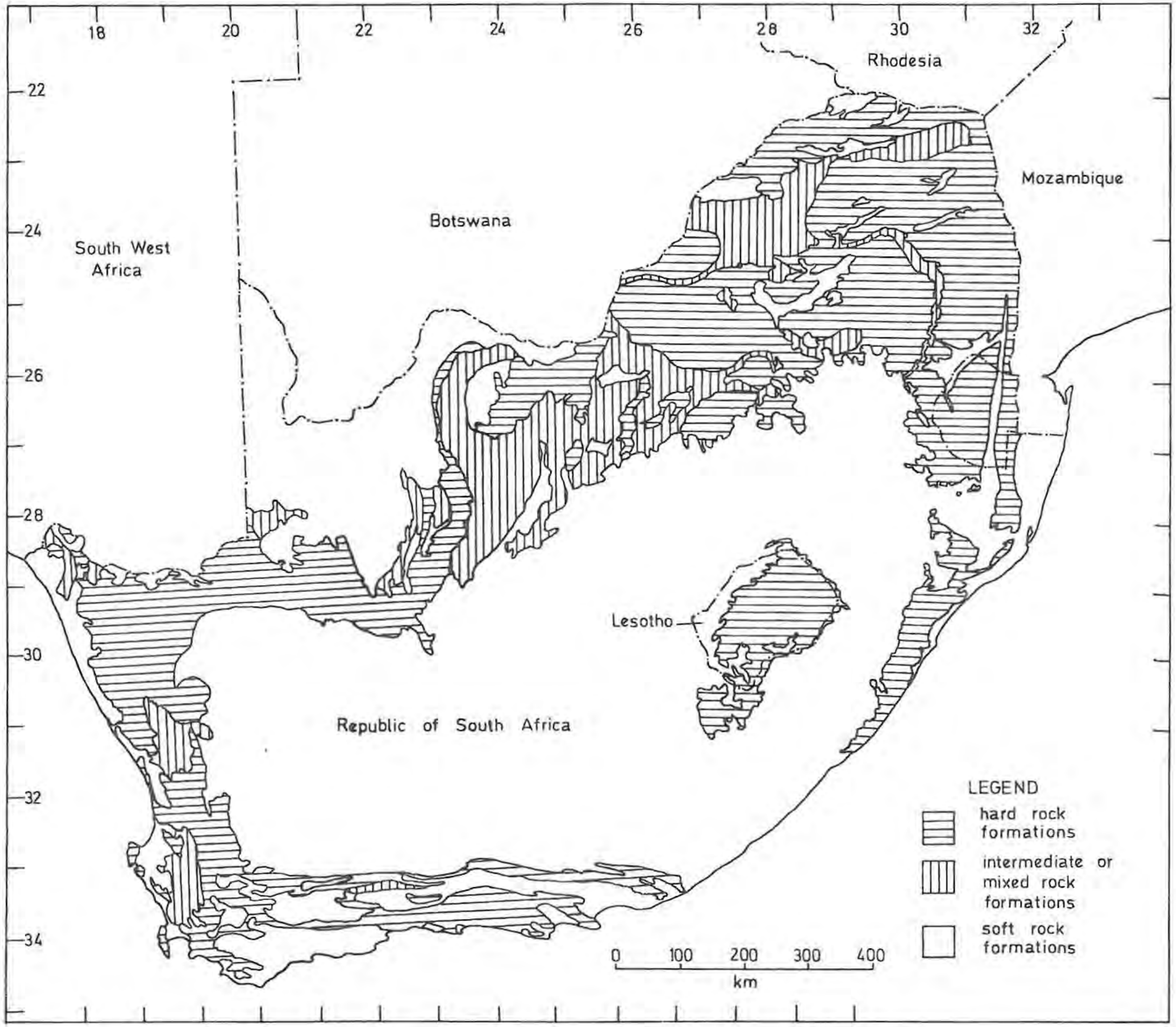
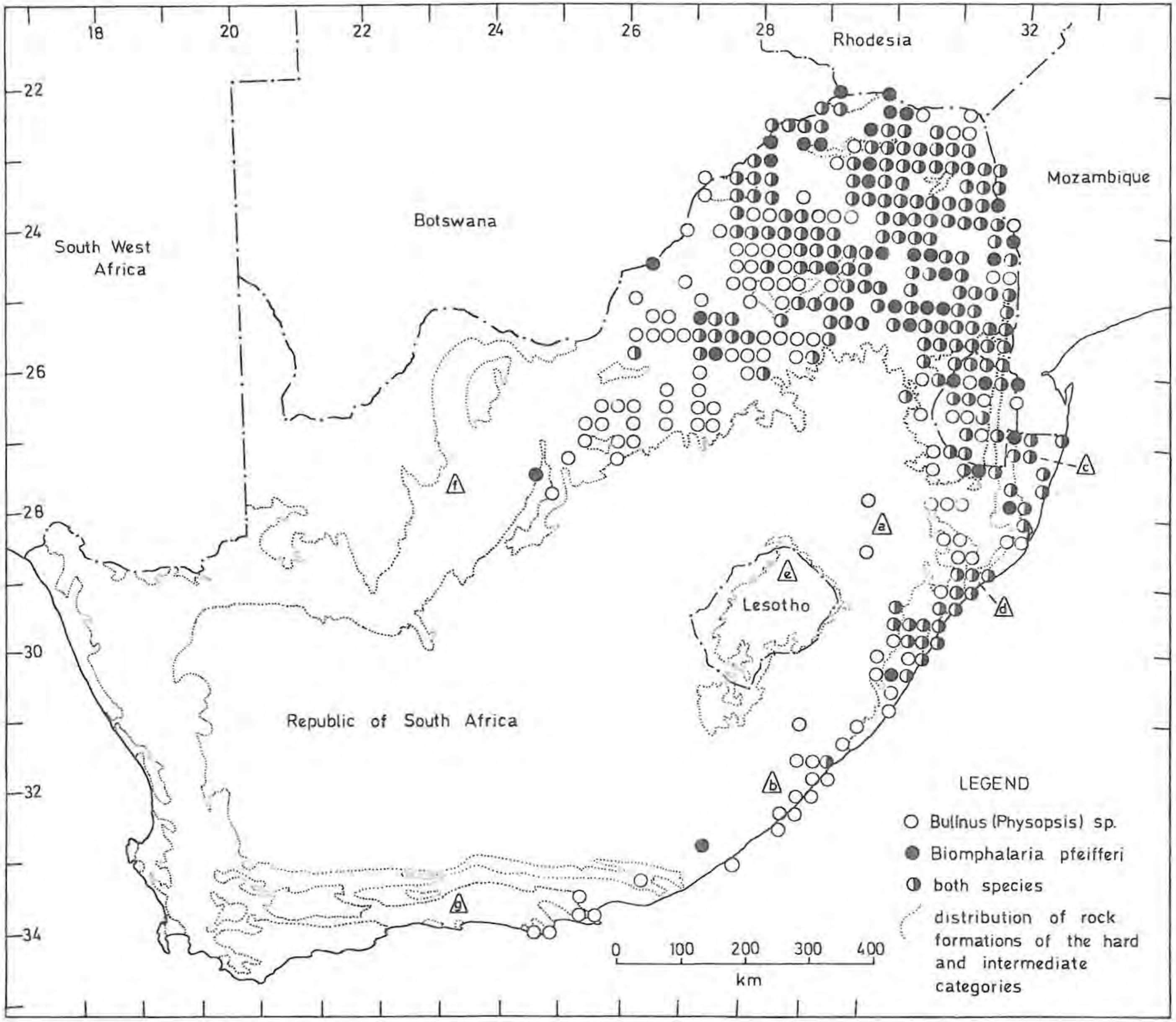


Figure 15 Map showing the distribution of hard, intermediate and soft rock formations in the Republic of South Africa and the Kingdoms of Lesotho and Swaziland.

Figure 16 Map showing the distribution of the bilharzia host snails B. pfeifferi and B. (Physopsis) (taken from van Eeden & Combrinck, 1966) superimposed on the distribution of rock formations which are resistant to erosion (hard and intermediate categories).



(a) These records lie around the towns of Newcastle, Ladysmith and Colenso in the Tugela River basin while those west of Pietermaritzburg in the Natal midlands are in the basin of the Umgeni River. All these localities lie on the beds of the soft sedimentary Beaufort and Ecca Series of the extensive Karroo System which, in this area are well known to contain many intrusive dolerite dykes and sills (Blignault & Furter, 1940; du Toit, 1954; King, 1951). Due to the hardness of dolerite, these intrusions form barriers causing rapids or cascades to develop and where a river crosses a number of these barriers sections of rapids alternate with sections of impounded, graded channel. Each barrier acts as a local base level preventing deeper erosion (and therefore grading) on its upstream side, regardless of the presence of soft rocks. The permanence of these impoundments may be augmented by underground water which often rises to the surface as springs where sediments and dolerite intrusions are in contact (King, 1951). These together with the potholes and plunge-pools associated with the rapids, may harbour host snails.

Many of these anomalies lie in the rejuvenation zones of the two rivers (Oliff, 1960, 1963; Brand et al, 1967). These are stretches where uplift of the coastal plain during the Tertiary Period has caused the rivers to regrade through their own alluvial deposits (King, 1951). This downward erosion has uncovered the bed-rock strata resulting in the development of extensive rapids in low meandering reaches. These create lentic habitats in a manner similar to that described for dykes and sills.

(b) The discontinuous distribution of B. (Physopsis) through the Transkei may be due to relict populations surviving the extended droughts characteristic of the area on soft Karroo beds in habitats created as described above for north-western Natal. These populations may originally have been part of a wider distribution pattern during Pleistocene pluvial conditions when rainfall was greater by up to approximately 40% of the present day figure (Cooke, 1964). The southerly limit of Karroo dolerite intrusions crosses the Transkei coastal region at about latitude 33°10'S (near Kidd's Beach), immediately south of the southernmost anomalous record. South of this limit the species is known to be absent from the Great Fish River catchment, probably due to the sandy river beds there being unstable since there are no hard intrusions to form impoundments. It is interesting to note that when the river beds again cut through hard rocks, i.e. the Table Mountain Sandstone in the vicinity of Port Elizabeth and Humansdorp, the snail reappears. The record for King William's Town (32°52'S; 33°24'E) is an old one and Pitchford (pers.comm., 1975) believes the species to be extinct there now.

(c) The anomaly presented by the northern Zululand coastal peneplain may be explained by the existence there of numerous natural, permanently lentic waterbodies (lakes, ponds and pans) and by pooling of the plain's many sluggish streams. Due to the virtual absence of any gradient on the plain, these streams exist simply as series of interconnected pools. Although in sand which in riverine habitats is too unstable a substratum for persistent snail populations to withstand, these pools provide pond-like conditions in which snails, inhabitants of the calmest parts of river systems, can survive. Except for the narrow range of longshore dunes on its eastern margin, the topography of this plain rarely exceeds an altitude of 107m while the surface of Lake Sibaya, a major drainage basin of the plain, is 21m above sea level (Hill, 1969). Though the mean annual rainfall is high (between 757 and 1130mm), flushing of streams is never severe due to the very low gradients involved (between 0.12 and 0.62%) and the snail populations, chiefly B. (Ph.) globosus, are minimally disturbed.

(d) Records of both host snail species along the narrow strip of sand and shale on the Natal coast are probably due to individuals washed down to the estuarine zones of the many eastwards-flowing rivers there. These flow off hard granite and Table Mountain Sandstone further inland where snail populations are plentiful. Weirs and dams have been built across many of these rivers close to the sea and provide artificial, permanently lentic conditions.

Considerable expanses of hard and intermediate rock exist outside the present endemic area of B. (Physopsis). These important negative anomalies are (e) the highlands of Lesotho, (f) large parts of the north-eastern and northern Cape Province and (g) the coastal belt of the southern and south-western Cape.

(e) This is a montane area lying above an altitude of 1829m. It should probably be disregarded as containing even potential host snail habitats since torrential water velocities can be expected over most of this rugged terrain and temperatures will undoubtedly be too low for much of the year, especially since winter snow falls throughout the area. A single undated and unsubstantiated record of B. (Ph.) africanus by A. Porter from Morija south-east of Maseru was quoted by Connolly (1939). Prinsloo & van Eeden (1973) did not find the species in Lesotho at all.

(f) Increasing aridity westwards across the western Transvaal, north-eastern and northern Cape will obviously hamper colonization by host snails and the distribution of B. (Physopsis) does in fact become patchy in the extreme western Transvaal. Records of B. pfeifferi from Vryburg (27°10'S; 24°43'E) and Postmasburg (28°20'S; 23°04'E) in the northern Cape (Connolly, 1939) have not been substantiated by van Eeden & Combrinck (1966). Isolated populations of B. pfeifferi are however known near Buxton in the north-eastern Cape and Lichtenburg in the western Transvaal (de Kock, 1973).

(g) The distribution of B. (Physopsis) in the south-eastern Cape Province stops at the Kromme River (24°17'E), and is probably due to the acidity of many of the streams flowing off the Table Mountain Sandstone formations in the southern Cape. Bond (1946) found pH values between 4.5 and 5.5 in most streams he examined here and concluded that this localized acidity was due largely to organic acids (humic) derived from vegetation through which the water percolated and to a lesser degree to free CO_2 in solution. The limit of the westward distribution of B. (Physopsis) also coincides with the most easterly occurrences of the 'acidobiontic' faunal association found by Harrison & Agnew (1962) to be endemic to these streams and in particular to areas which also enjoy a high rainfall. They recorded pH values between 5.0 and 6.7 here. This fauna did not contain any Gastropoda, presumably due to a lack of the calcium necessary for shell construction in these unbuffered waters. Harrison & Agnew found this faunal association in streams eastwards as far as the Kruis River (24°08'E) which flows only a few kilometres to the west of the Kromme River, the most southerly occurrence known for B. (Physopsis). Sioli (1956) attributed the absence of B. straminea from many streams in Amazonia (Brazil) to their water being unbuffered and therefore acid, with pH values between 4.1 and 5.2.

In lotic environments then, current velocity is a most important abiotic factor and is believed to be the limiting one in river systems and determines much of the distribution of B. pfeifferi and B. (Physopsis) in South Africa. It has a greater influence than either water temperature or its chemical quality when distribution per se is considered. In permanently lentic environments such as those on the northern Zululand coastal plain however, current velocity is obviously irrelevant and temperature assumes greatest importance.

This attempt at explaining the present distribution pattern of bilharzia host snails in South Africa is a logical application, and extension, of the hypothesis advanced by Appleton (1975). Snail populations are shown not to be confined entirely to areas of resistant rock formations so that their distribution patterns are not due to any one factor alone, although their extremely narrow tolerance to flowing water is perhaps of greatest individual importance. There is instead a superimposition of abiotic factors which may be interpreted as (1) the availability of habitats which are either permanently lentic or experience only moderate flood disturbance and (2) a temperature régime under which the species can survive as an expanding population.

Other abiotic factors, such as low calcium and bicarbonate ion concentrations and high magnesium to calcium ratios in water may also limit distribution, especially of B. pfeifferi, but these situations are generally rather localized. It is interesting however to recall the observations of Harrison *et al* (1970) that *B. pfeifferi* was rare or even absent in streams running over poorly mineralized granite and quartzite formations where waters were soft, whereas *B.* (*Ph.*) *africanus*, *globosus* and *L. natalensis* were common. This suggests that *B. pfeifferi* which is known to require both calcium and bicarbonate ions at a moderate level for optimal increase and whose endemic area in southern Africa lies largely over granites, might be surviving at below optimal rates of increase throughout much of its range here.

The present study relating fecundity of *B. pfeifferi* to temperature has revealed that as the duration of above-optimum temperatures (>27°C) increase and the higher the temperature levels that are reached, the less suitable the habitat becomes for the survival of the species. This is due largely to a reduction in fecundity which in turn is probably the result of a retardation of gonad development. This last aspect has however yet to be investigated with respect to *B. pfeifferi*.

Bulinus (*Ph.*) *globosus* is clearly able to survive where *B. pfeifferi* cannot, both in the laboratory and in the field. *Biomphalaria pfeifferi*, because of its intolerance of high temperatures, has a discontinuous distribution from Natal northwards. In Natal it is most abundant near the coast (Brown, 1967) but although south of the Umgeni River (approx. lat.30°S) it is found within a few kilometres of the sea, there are wide discontinuities in its distribution as it approaches its southern limit, the Mngazi River just south of Port St. Johns (van Eeden *et al*, 1965). In north-eastern Zululand (Tongaland) the species is confined to deeper, perennial waterbodies such as Lakes Sibaya (Allanson et al, 1974), Mgobezeleni (Bruton & Appleton, 1975), the large, perennial pans of the Pongola River floodplain (Pretorius et al, 1975) and the ponds associated with Lake Sibaya (personal observations). In Mozambique, surveys by de Morais (1956, 1959) and de Azevedo et al (1956, 1961) show the species to be sporadically distributed over the coastal plain (below the 500m contour) to the vicinity of Antonio Enes (approx. lat.16°S). It is absent from the northernmost province of Cabo Delgado. Both McClelland (1956) and Sturrock (1966) have referred to the natural absence of B. pfeifferi from the coastal strip of East Africa northwards to the Red Sea and southwards to Madagascar, while Teesdale (1962) noted that it did not occur below an altitude of 600m in the coastal region of Kenya.

Water temperatures on this plain become very high indeed, particularly in its equatorial regions. In northern Zululand mean monthly temperatures in the habitats examined in the present study reached 27° to 29°C consistently for four consecutive months. On the coastal plain of Tanzania and Kenya respectively Sturrock (1966) and Webbe & Msangi (1958) recorded mean values between 28° and 30°C and 27° and 34°C for several consecutive months.

In the Lake Sibaya area the duration of high temperatures in spring which today prevents B. pfeifferi from colonizing pans (although it probably occurred in these habitats in the past when they were deeper) must lie between the levels in Statisi and Empayeni, i.e. between 120 and 179 °hrs>27°C/wk. Further field work will be necessary to establish the critical duration more precisely, particularly in different climatic regions where local physiological strains of *B. pfeifferi* may exist.

The expression of temperature as degree hours per week (above a certain baseline) provides a valuable method for applying laboratory findings to field situations. It also offers a tool for assessing the likelihood of the species colonizing new areas. This last facet is important today when impressive irrigation schemes are being built in developing countries, sometimes in areas where *B. pfeifferi* (and therefore *S. mansoni* as well) do at present not occur, without much regard to their impact on amongst other things, the epidemiology of vector-borne diseases.

REFERENCES

Allanson, B.R., Bruton, M.N., Hart, R.C. (1974) The plants and animals of Lake Sibaya, Kwazulu, South Africa : a checklist. Rev.Zool.afr., 88 : 507-532.

Allee, W.C., Emerson, A.E., Park, O., Park, T., Schmidt, K.P. (1950) Principles of animal ecology. W.B. Saunders Co., Philadelphia. 837 pp.

Alves, W. (1958) Chemical constituents of surface water in Southern Rhodesia, with special reference to the molluscan vectors of bilharziasis. Bull.Wld Hlth Org., 18 : 1071.

Annecke, S. and Peacock, P.N.B. (1951) Bilharziasis in the Transvaal. S.Afr.Med.J., 25 : 676-679.

Appleton, C.C. (1974) The population fluctuations of five freshwater snail species in the eastern Transvaal lowveld, and their relationship to known bilharzia transmission patterns. S.Afr.J.Sci., 70 : 145-150.

Appleton, C.C. (1975) The influence of stream geology on the distribution of the bilharzia host snails, *Biomphalaria pfeifferi* and *Bulinus* (*Physopsis*) sp. Ann.trop.Med. Parasit., 69 : 241-255.

Ayad, N. (1956) Bilharziasis survey in British Somaliland, Eritrea, Ethiopia, Somalia, the Sudan and Yemen. Bull. Wld Hlth Org., 14 : 1-117.

Baalawy, S.S. and Moyo, H.G. (1970) Studies on the population dynamics of *B.* (*P.*) *nasutus* and natural *S. haematobium* infection rates in relation to rainfall at Misungwi and Usagara, Mwanza. E.Afr.Med.J., 47 : 472-478.

Barbosa, F.S. (1962) Aspects of the ecology of the intermediate hosts of Schistosoma mansoni interfering with the transmission of bilharziasis in north-eastern Brazil. in Bilharziasis, eds : Wolstenholme, G.E.W. and O'Connor, M., pp. 23 - 35. Churchill, London.

Barbosa, F.S. and Barbosa, I. (1959) Observations on the ability of the snail Australorbis nigricans to survive out of water in the laboratory. J.Parasit., 45 : 627-630.

Barbosa, F.S. and Dobbin, J.E. (1952) Effects of the dry season on Australorbis grabratus (Mollusca: Planorbidae). Publ. Avuls.Inst.Aggeu Magalhaes. 1 : 145-148.

Barbosa, F.S., Hubendick, B., Malek, E.T.A. and Wright, C.A. (1961) The generic names of Australorbis, Biomphalaria, Platytaphius, Taphius and Tropicorbis (Mollusca, Planorbidae). Ann.Mag.nat.Hist., 13 : 371-375.

Barbosa, F.S. and Olivier, L. (1958) Studies of the snail vectors of bilharziasis mansoni in north-eastern Brazil. Bull.Wld Hlth Org., 18 : 895-908.

Barlow, C.H. (1933) The effect of the winter rotation of water upon snails involved in the spread of schistosomiasis in Egypt, 1930 - 1931 and 1931 - 1932. Amer.J.Hyg., 17 : 724-742.

Barlow, C.H. (1935) Further studies of the revival, after drying, of the snail hosts of the human schistosomes of Egypt. Amer.J.Hyg., 24 : 587-599.

Barlow, C.H. and Muench, H. (1947) Life span and monthly mortality rate of Bulinus truncatus and Planorbis boissyi, the intermediate hosts of schistosomiasis in Egypt. J.Parasit., 37 : 165-173.

Berrie, A.D. (1964) Observations on the life-cycle of Bulinus (Physopsis) ugandae Mandahl-Barth, and its ecological relation to Biomphalaria sudanica tanganyicensis (Smith), and its role as an intermediate host of Schistosoma. Ann.trop.Med.Parasit., 58 : 457-466.

Blair, D.M. (1956) Bilharziasis survey in British West and East Africa, Nyasaland and the Rhodesias. Bull.Wld Hlth Org., 15 : 203-273.

Blignault, J.J.G. and Furter, F.J.J. (1940) The northern Natal coalfield (Area no. 1). The Vryheid - Paulpietersburg area. Coal Survey : Memoir no. 1. 13-336, Dept. of Mines, Govt. printer, Pretoria.

Boettger, C.R. (1944) Basommatophora. in: G. Grimpe & G. Wagler, ed. Die Tierwelt der Nord-und Ostsee. 35 : 241-478. Leipzig, Akademische Verlagsgesellschaft.

Boltt, R.E. (1969) The benthos of some southern African lakes. Part II: The epifauna and infauna of the benthos of Lake Sibayi. Trans.roy.Soc.S.Afr., 38 : 249-269.

Bond, G.W. (1946) A geochemical survey of the underground water supplies of the Union of South Africa. Union of S.A. Dept. of Mines, Geological Survey, Memoir no. 41. Govt. printer, Pretoria.

Boycott, A.E. (1936) The habitats of freshwater Mollusca in Britain. J.Anim.Ecol., 5 : 116-186.

Brand, P.A.J., Kemp, P.H., Pretorius, S.J. and Schoonbee, H.J. (1967) Survey of the three rivers region. in:Water quality and abatement of pollution in Natal rivers. pt.II. Natal Town and Regional Planning Report, 13 : 1-224.

Brown, D.S. (1966) On certain morphological features of Bulinus africanus and B. globosus (Mollusca: Pulmonata) and the distribution of these species in south-eastern Africa. Ann.Natal Mus., 18 : 401-415.

Brown, D.S. (1967) A review of the freshwater Mollusca of Natal and their distribution. Ann.Natal Mus., 18 : 477-494.

Brumpt, E. (1941) Observations biologiques diverses concernant Planorbis (Australorbis) glabratus, hôte intermédiare de de Schistosoma mansoni. Ann.Parasit.hum.comp., 18 : 9-45.

Bruton, M.N. and Appleton, C.C. (1975) Survey of Mgobezeleni lake-system in Zululand, with a note on the effect of a bridge on the mangrove swamp. Trans.roy.Soc.S.Afr., 41 : 283-294.

Burridge, A.D. (1973) Diamond is hardest by any standard. Optima, 23 : 199-202.

Calow, P. (1970) Studies on the natural diet of Lymnaea peregrer obtusa (Kobelt) and its possible ecological implications. Proc.malac.Soc.Lond., 39 : 203-215.

Calow, P. (1973) Field observations and laboratory experiments on the general food requirements of two species of freshwater snail, Planorbis contortus (Linn.) and Ancylus fluviatalis Müll. Proc.malac.Soc.Lond., 40 : 483-489.

Calow, P. (1974) Evidence for bacterial feeding in Planorbis contortus Linn. (Gastropoda: Pulmonata). Proc.malac. Soc.Lond. 41 : 145-156.

Cawston, F.G. (1946) Influence of a decreasing rainfall on Physopsis africanus Krauss. Nature : 413.

Chernin, E. and Adler, V.L. (1967) Effects of dessication on eggs of Australorbis glabratus. Ann.trop.Med.Parasit., 61 : 11-14.

Chernin, E. and Bower, C. (1971) Experimental transmission of Schistosoma mansoni in brackish waters. Parasitology, 63 : 31-36.

Chu, K.Y., Bijan, H. and Massoud, J. (1967) The ability of Bulinus truncatus, Biomphalaria alexandrina and Lymanea gedrosiana to survive out of water in the laboratory. Ann.trop.Med.Parasit., 61 : 1-5.

Chu, K.Y., Arfaa, F. and Massoud, J. (1967) The survival of Bulinus truncatus buried in mud under experimental outdoor conditions. Ann.trop.Med.Parasit., 61 : 6-10.

Chu, K.Y., Massoud, J. and Bijan, H. (1967) The location of Bulinus truncatus in dry habitats in Iran. Ann.trop.Med. Parasit., 61 : 134-138.

Chu, K.Y., Massoud, J. and Arfaa, F. (1967) The survival time and fecundity of Bulinus truncatus after dessication in mud. Ann.trop.Med.Parasit., 61 : 139-143.

Colombo, B.A. (1958) Natural and experimental dessication of Australorbis glabratus (Mollusca, Planorbidae) of the city of Salvador, Bahia, Brazil. Bol.Fundacao Goncalo Moniz., 13 : 13-24.

Connolly, M. (1939) A monographic survey of South African non-marine Mollusca. Ann.S.Afr.Mus., 33 : 1-660.

Cooke, H.B.S. (1964) The Pleistocene environment in southern Africa. in Ecological studies in Southern Africa, ed. D.H.S. Davis, pp. 1 - 23. The Hague, W. Junk.

Cridland, C.C. (1957a) Ecological factors affecting the numbers of snails in permanent bodies of water. *J.trop.Med.& Hyg.*, 60 : 250-256.

Cridland, C.C. (1957b) Ecological factors affecting the numbers of snails in temporary bodies of water. *J.trop.Med.& Hyg.*, 60 : 287-293.

Cridland, C.C. (1958) Ecological factors affecting the numbers of snails in a permanent stream. *J.trop.Med.& Hyg.*, 61 : 16-20.

Cridland, C.C. (1967) Resistance of *Bulinus* (*Physopsis*) *globosus*, *Bulinus* (*Ph.*) *africanus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* to experimental dessication. *Bull.Wld Hlth Org.*, 36 : 507-513.

Dazo, B.C., Hairston, N.G. and Dawood, I.K. (1966) The ecology of *Bulinus truncatus* and *Biomphalaria alexandrina* and its implications for the control of bilharziasis in the Egypt -49 project area. *Bull.Wld Hlth Org.*, 35 : 339-356.

De Andrade, R.M. (1954) Alguns dados hidroquimicos de criadouros para o conhecimento de planorbideos no Distrito Federal. *Rev.Brasileira Malariologia*, 6 : 473-475.

De Andrade, R.M. (1962a) Ecology of *Australorbis glabratus* in Belo Horizonte, Brazil. I. Annual fluctuation in population density and in infection indices by *Schistosoma mansoni* (Pulmonata: Planorbidae). *Rev.Brasileira Malariologia*, 14 : 261-289.

De Andrade, R.M. (1962b) Ecologia de *Australorbis glabratus* em Belo Horizonte, Brasil. II. Variacoes anuais e trimestrais do diâmetro dos caramujos (Pulmonata, Planorbidae). *Rev. Inst.Med.Trop.Sao Paulo*, 4 : 366-374.

De Andrade, R.M., Santos, I.N. and Oliveira, R. (1955) Contribuicao para o conhecimento dos criadouros de planorbineos, na área do Distrito Federal : I. Variacao de diferentes factôres quimicos de suas águas. Rev.Brasileira Malariologia, 7 : 103-130.

de Azevedo, J.F. (1956) Present status of the bilharziasis problem in the Portuguese territories in Africa (Guinea, Angola and Mozambique). WHO/Bil.Conf./60, 20 pp.

de Azevedo, J.F., de Medeiros, L. do C.M., Faro, M.M. da C., Xavier, M. de L., Gândara, A.F. e de Morais, T. (1961) Os moloscos de agua doce do ultramar Português III - Moloscos de Mozambique. Junta de Investigacoes do Ultramar, no.88. Lisboa, 394 pp.

de Kock, K.N. (1973) Die bevolkingsdinamika van vyf medies en veeartsenykundig belangrike varswaterslakspesies onder toestande van beheerde temperatuur. Unpubl. D.Sc. thesis, Potchefstroom University. 388 pp.

de Meillon, B., Frank, G.H. and Allanson, B.R. (1958) Some aspects of snail ecology in South Africa : a preliminary report. Bull.Wld Hlth Org., 18 : 771-783.

de Morais, T. (1956) Subsidios para estudo dos moluscos hospedeiros intermediarios das bilharzioses nos distritos de Mozambique, Niassa e Cabo Delgado (Provincia de Mozambique). Anais Inst.Med.Trop., 16 : 187-198.

De Morais, T. (1959) A bilharziose em Mozambique. Anais Inst. Med.Trop. Lisbon, 16 : 179-186.

Deschiens, R. (1957a) Sur la perpétuation des élevages des mollusques vecteurs des bilharzioses a l'obscurité. Bull.Soc. Path.Exot., 50 : 229-233.

Deschiens, R. (1957b) Les facteurs conditionnant l'habitat des mollusques vecteurs des bilharzioses leurs incidences épidémiologiques. Ann.Inst.Pasteur, 92 : 576, 711; 93 : 1, 153.

Deschiens, R. and Bijan, H. (1956) Comportement d'élevages de mollusques vecteurs des bilharzioses à l'obscurité. Bull.Soc.Path.Exot., 49 : 658-661.

Deschiens, R. and Jardin, J. (1954) Viabilité des mollusques vecteurs des bilharzioses dans les eaux profondes. Bull.Soc.Path.Exot. 47 : 668-671.

du Toit, A.L. (1954) The Geology of South Africa. Oliver & Boyd, Edinburgh, 611 pp.

El Gindy, M.S. (1957) Distribution and ecology of the snail vectors of schistosomiasis in Egypt. J.Egyptian Med.Ass., 40 : 192-204.

Etges, F.J. and Frick, L.P. (1966) An experimental field study of chemoreception and response in Australorbis glabratus (Say) under rheotactic conditions. Amer.J.trop.Med.Hyg., 15 : 434-438.

Ezzat, M.A.E. (1961) The salinity of water and its effect on the vitality of Lymnaea cailliaudi, the snail intermediate host of Fasciola gigantica in Egypt. J.Arab Vet.Med.Ass. 21 : 177-183.

Frank, G.H. (1963) Some factors affecting the fecundity of Biomphalaria pfeifferi (Krauss) in glass aquaria. Bull. Wld Hlth Org., 29 : 531-537.

Frank, G.H. (1964) The ecology of the intermediate hosts of bilharzia. In Ecological Studies in Southern Africa, ed. Davis, D.H.S., pp. 353-362. The Hague : W. Junk.

Gaud, J. (1958) Rythmes biologiques des mollusques vecteurs des bilharzioses : facteurs saisonniers et climatiques influencant le cycle reproduction de Bulinus truncatus et de Planorbarius metidjensis en Afrique du Nord. Bull.Wld Hlth Org., 18 : 751-769.

Gaud, J. and Dupuy, R. (1954) Rythmes saisonniers de développement de Bulinus truncatus en élevages au laboratoire. Bull.Inst. Hyg.Maroc, 14 : 111-116.

Gilles, H.M., Lucas, A., Linder, R., Cockshott, W.P., Anand, S.V., Ikeme, A. and Cowper, S.G. (1965) Schistosoma haematobium infection in Nigeria. III : Infection of boatyard workers at Epe. Ann.trop.Med.Parasit., 59 : 451-456.

Gillet, J., Bruaux, P. and Wolfs, J. (1960) Résultats de prospections malacogiques en profondeur au lac Kivu et recherches sur la survie de Biomphalaria en eau profonde. Ann.Soc. Belge. de Méd.Trop., 40 : 643-649.

Gohar, H.A.F. and El Gindy, H.I. (1960a) The ecology of Egyptian snail vectors of bilharziasis and fascioliasis. I. Physical factors. Proc.Egyptian Acad.Sci., 15 : 70-78.

Gohar, H.A.F. and El Gindy, H.I. (1960b) The ecology of Egyptian snail vectors of bilharziasis and fascioliasis. II. Chemical factors. Proc.Egyptian Acad.Sci., 15 : 79-86.

Gordon, R.M., Davey, T.H. and Peaston, H. (1934) The transmission of human bilharziasis in Sierra Leone, with an account of the life-cycle of the schistosomes concerned, S. mansoni and S. haematobium. Ann.trop.Med.Parasit., 28 : 323-418.

Hack, J. (1969) The area, its geology : Cenozoic development of the southern Appalachians. In The distributional history of the southern Appalachians, ed. Holt, P.C., pp. 1-17. Research Division Monograph no.1. Virginia Polytechnic Inst., Blacksburg, Va.

Hairston, N.G. (1973) The dynamics of transmission. In Epidemiology and control of schistosomiasis (Bilharziasis). ed. Ansari, N., pp. 250-336. Karger, Basle.

Harrison, A.D. (1962) Hydrobiological studies on the alkaline and acid still waters in the western Cape Province. Trans.roy. Soc.S.Afr., 36 : 213-244.

Harrison, A.D. (1966) The study of the biology of schistosome host snails, C.Afr.J.Med., 12 : 124-127.

Harrison, A.D. (1968) The effects of calcium bicarbonate concentration on the oxygen consumption of the freshwater snail Biomphalaria pfeifferi (Pulmonata : Planorbidae). Arch. Hydrobiol., 65 : 63-73.

Harrison, A.D. and Agnew, J.D. (1962) The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. Ann.Cape Prov.Mus., 11 : 273-291.

Harrison, A.D. and Elsworth, J.F. (1958) Hydrobiological studies on the Great Berg River, Western Cape Province. I: General description, chemical studies and main features of the flora and fauna. Trans.roy.Soc.S.Afr., 35 : 125-226.

Harrison, A.D. and Farina, T.D.W. (1965) A naturally turbid water with deleterious effects on egg capsules of planorbid snails. Ann.trop.Med.Parasit., 59 : 327-330.

Harrison, A.D., Nduku, W. and Hooper, A.S.C. (1966) The effects of a high magnesium-to-calcium ratio on the egg-laying rate of the aquatic planorbid snail, Biomphalaria pfeifferi. Ann.trop.Med.Parasit., 60 : 212-214.

Harrison, A.D. and Shiff, C.J. (1966) Factors influencing the distribution of some species of aquatic snails. S.Afr.J. Sci., 62 : 253-258.

Harrison, A.D., Williams, N.V. and Greig, G. (1970) Studies on the effects of calcium bicarbonate concentrations on the biology of Biomphalaria pfeifferi (Krauss) (Gastropoda : Pulmonata). Hydrobiologia, 36 : 317-327.

Harry, H.W., Cumbie, B.G. and de Jesus, J.M. (1957) Studies on the quality of fresh waters of Puerto Rico relative to the occurrence of Australorbis glabratus (Say). Amer.J.trop. Med.Hyg., 6 : 313-322.

Harry, H.W. and Aldrich, D.V. (1958) The ecology of Australorbis glabratus in Puerto Rico. Bull.Wld Hlth Org., 18 : 819-832.

Harry, H.W. and Cumbie, B.G. (1956a) The relation of physiography to the types of freshwater environments and the presence of Australorbis glabratus in Puerto Rico. Amer.J.trop.Med.Hyg., 5 : 742-756.

Harry, H.W. and Cumbie, B.G. (1956b) Stream gradient as a criterion of lotic habitats suitable for Australorbis glabratus in Puerto Rico. Am.J.trop.Med.Hyg., 5 : 921-928.

Heeg, J. (1975) A note on the effects of drastic changes in total dissolved solids on the aquatic pulmonate snail Bulinus (Physopsis) africanus (Krauss). J.Limnol.Soc.S.Afr., 1 : 29-32.

Hill, B.J. (1969) The bathymetry and possible origin of Lakes Sibayi, Nhlange and Sifungwe in Zululand (Natal). Trans. roy.Soc.S.Afr., 38 : 205-216.

Hira, P.R. (1968) Studies on the capability of the snail transmitting urinary schistosomiasis in western Nigeria to survive dry conditions. W.Afr.Med.J., 17 : 153-160.

Hira, P.R. and Muller, R. (1966) Studies on the ecology of snails transmitting urinary schistosomiasis in western Nigeria. Ann.trop.Med.Parasit., 60 : 198-211.

Hubendick, B. (1958) Factors conditioning the habitat of freshwater snails. Bull.Wld Hlth Org., 18 : 1072-1080.

Jaeckel, S.G.A. (1969) Die mollusken Südamerikas. in Biogeography and Ecology in South America, eds. Fittau, E.J., Illies, J., Klinge, H., Schwabe, G.H. and Sioli, H. 2: 794-827. The Hague, W. Junk.

Jennings, A.C., de Kock, K.N. and van Eeden, J.A. (1973) The effect of the total dissolved salts in water on the biology of the freshwater snail Biomphalaria pfeifferi. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B : Natuurwetenskappe, nr. 50, 26 pp.

Jobin, W.R. (1970) Population dynamics of aquatic snails in three farm ponds of Puerto Rico. Am.J.trop.Med.Hyg., 19 : 1038-1048.

Jobin, W.R. and Ippen, A.T. (1964) Ecological design of irrigation canals for snail control. Science, 145 : 1324-1326.

King, L.C. (1951) South African Scenery. Oliver & Boyd, Edinburg, 379 pp.

King, L.C. (1972) The coastal plain of south-east Africa : its form, deposits and development. Z.Geomorph.N.F., 16 : 239-251.

Kloetzel, K. (1959) Resisténcia á dessecacao de Australorbis glabratus. Comparacao entre os caramujos de Olinda (Pernambuco) e um dos focos de Salvador (Bahia). Rev. Inst.Med.Trop.Sao Paulo, 1 : 279-288.

Larivière, M., Hocquet, P. and Ranque, P. (1962) Étude de la résistance à l'anhydrobiose des gastropodes d'eau douce Bulinus guernei Dautzenberg et Biomphalaria pfeifferi gaudi Ranson. C.R.Soc.Biol., 156 : 725-726.

Larivière, M., Camerlynck, P. and Hocquet, P. (1963) Résistance expérimentale de Bulinus guernei Dautzenberg à une anhydrobiose de six mois. C.R.Soc.Biol., 157 : 602-604.

Lietar, J. (1956) Biologie et écologie des mollusques vectors de bilharziose a'Jadotville. Ann.Soc.Belge Méd.Trop., 36 : 919-1036.

Luttermoser, G.W. (1944) The possibility of eliminating the schistosome snail Australorbis glabratus, from canals by control of water flow. J.Parasitol., 30 (Suppl.) : 15.

Macan, T.T. (1949) The ecology of fresh-water mollusca in a soft-water district. Verh.int.Ver.Limnol., 10 : 277-279.

Macan, T.T. (1958) The temperature of a small stony stream. Hydrobiologia, 12 : 89-106.

Macan, T.T. (1961) Factors that limit the range of freshwater animals. Biol.Rev., 36 : 151-198.

Malek, E.A. (1958) Factors conditioning the habitat of bilharziasis intermediate hosts of the family Planorbidae. Bull.Wld Hlth Org., 18 : 785-818.

Malek, E.A. (1962) Bilharziasis control in pump schemes near Khartoum, Sudan, and an evaluation of the efficacy of chemical and mechanical barriers. Bull.Wld Hlth Org., 27 : 41-58.

Mandahl-Barth, G. (1954) The Freshwater mollusks of Uganda and adjacent territories. Ann.Mus.roy.Congo belge, Série in 8°, Sc.Zool., 32, 206 pp.

McClelland, W.F.J. (1956) Studies on snail vectors of schistosomiasis in Kenya. J.trop.Med.Hyg., 59 : 229-242.

McCullough, F.S. (1957) The seasonal density of populations of Bulinus (P.) globosus and B. forskali in natural habitats in Ghana. Ann.trop.Med.Parasit., 51 : 235-248.

McCullough, F.S. (1962) Further observations on Bulinus (B.) truncatus rohlsfi (Clessin) in Ghana : seasonal population fluctuations and biology. Bull.Wld Hlth Org., 27 : 161-170.

Marill, F.-G. (1956) Seasonal variations in the reproductive cycle of certain freshwater snails and particularly Bulinus contortus Michaud. WHO/Bil/Ecol./28., 67 pp.

Marill, F.-G. (1958) Sur les variations de la composition chimique de l'eau et les variations d'abondance de Bulinus truncatus Audoin. Bull.Wld Hlth Org., 18 : 1064-1070.

Meier-Brook, C. (1975) A snail intermediate host of Schistosoma mansoni introduced to Hong Kong. WHO/Schisto/75.37.

Michelson, E.H. (1961) The effects of temperature on growth and reproduction of *Australorbis glabratus* in the laboratory. *Am.J.Hyg.*, 73 : 66-74.

Mousa, A.H. and El Hassan, A.A.A. (1970) The effects of water temperature and movements on the snail intermediate hosts of schistosomiasis. *J.Parasitology*, 56 : 450-451.

Mousa, A.H. and El Hassan, A.A.A. (1972) The effect of water temperature on the snail intermediate hosts of schistosomiasis in Egypt. *J.Egyptian med.Ass.*, 55 : 148-165.

Mozley, A. (1939) The freshwater Mollusca of the Tanganyika territory and Zanzibar Protectorate and their relation to human schistosomiasis. *Trans.roy.Soc.Edin.*, 59 : 687-744.

Najarian, H.H. (1961) Biological studies on the snail *Bulinus truncatus* in central Iraq. *Bull.Wld Hlth Org.*, 25 : 435-446.

Onambiro, S.D. (1972) Studies in schistosomiasis in Sierra Leone. II. Seasonal fluctuations in the population density of *Bulinus* (*P.*) *globosus* and *Bulinus forskali* in a schistosomiasis endemic town in Sierra Leone. *Ann.trop.Med.Parasit.*, 66 : 375-383.

Oliff, W.D. (1953) *Report on snail ecological investigations during the year 1952.* C.S.I.R., unpublished, 12 pp.

Oliff, W.D. (1960) Hydrobiological studies on the Tugela River system. Part 1. The main Tugela River. *Hydrobiologia*, 14: 281 - 385.

Oliff, W.D. (1963) Hydrobiological studies on the Tugela River system. Part 111. The Buffalo River. *Hydrobiologia*, 21: 355 - 379.

Australorbis glabratus and *Tropicorbis centrimetralis*, on and in the soil of dry natural habitats. *J.Parasitology*, 42 : 81-85.

Olivier, L. (1956b) Observations on vectors of _Schistosomiasis mansoni_ kept out of water in the laboratory. I. _J.Parasitology_, 42 : 137-146.

Olivier, L. and Barbosa, F.S. (1955a) Seasonal studies on _Australorbis glabratus_ Say from two localities in eastern Pernambuco, Brazil. _Publicacoes Avuls.Inst.Aggeu Magalhaes_, 4 : 79-103.

Olivier, L. and Barbosa, F.S. (1955b) Seasonal studies on _Tropicorbis centimetralis_ in north-eastern Brazil. _Publicacoes Avuls.Inst.Aggeu Magalhaes_. 4 : 105-115.

Olivier, L. and Barbosa, F.S. (1956) Observations on vectors of _Schistosomiasis mansoni_ kept out of water in the laboratory. II. _J.Parasitology_ 42 : 277-286.

Paraense, W.L., Pereira, O. and Pinto, D.B. (1955) Um aspecto da ecologia do _Australorbis glabratus_ que favorece a reinfestacao dos criadouros. _Rev.Servico Especial de Saúde Pública_. 7 : 573-581.

Paulini, E. (1963) Field observations on the upstream migration of _Australorbis glabratus_. _Bull.Wld Hlth Org._, 29 : 838-841.

Pimentel, D. and White, P.C. (1957) Geographic distribution of _Australorbis glabratus_, the snail intermediate host of _Schistosoma mansoni_ in Puerto Rico. _Amer.J.trop.Med.Hyg._, 6 : 1087-1096.

Pimentel, D. and White, P.C. (1959) Physiochemical environment of _Australorbis glabratus_, the snail intermediate host of _Schistosoma mansoni_ in Puerto Rico. _Ecology_, 40 : 533-541.

Pretorius, S.J., Jennings, A.C., Coertze, D.J.R. and van Eeden, J.A. (1975) Aspects of the freshwater mollusca of the Pongola River flood plain pans. S.Afr.J.Sci., 71 : 208-212.

Pringle, G. and Msangi, A.S. (1961) The experimental study of water snails in a fish pond in Tanganyika. I. Preliminary trial of the method. East African Med.J., 38 : 275-293.

Prinsloo, J.F. and van Eeden, J.A. (1969) Temperature and its bearing on the distribution and chemical control of freshwater snails. S.Afr.Med.J., 43 : 1363-1365.

Prinsloo, J.F. and van Eeden, J.A. (1974) Habitat varieties and habitat preferences of Lymnaea truncatula, the intermediate host of Fasciola hepatica, in Lesotho. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B : Natuurwetenskappe, nr 60, 28 pp.

Radke, M.G. and Ritchie, L.S. (1961) Field observations on the migration of marked Australorbis glabratus snails. J.Parasitology, 47 : 712.

Richards, C.S. (1967) Estivation of Biomphalaria glabrata (Basommatophora: Planorbidae). Associated characteristics and relation to infection with Schistosoma mansoni. Amer.J.trop.Med.Hyg., 16 : 797-802.

Richards, C.S. (1968) Aestivation of Biomphalaria glabrata (Bassommatophora: Planorbidae) genetic studies. Malacologia, 7 : 109-116.

Ritchie, L.S., Radke, M.G. and Ferguson, F.F. (1962) Population dynamics of Australorbis glabratus in Puerto Rico. Bull. Wld Hlth Org., 27 : 171-181.

Rowan, W.B. (1959) Seasonal effect of heavy rains on the population density of Australorbis glabratus in a Puerto Rican watershed. Amer.J.trop.Med.Hyg., 8 : 570-574.

Schulze, B.R. (1947) The climates of South Africa according to the classifications of Köppen and Thornthwaite. S.Afr. geogr.J., 29 : 32-42.

Schutte, C.H.J. and Frank, G.H. (1964) Observations on the distribution of freshwater Mollusca and chemistry of the natural waters in the south-eastern Transvaal and adjacent northern Swaziland. Bull.Wld Hlth Org., 30 : 389-400.

Sevilla, J.Z. (1965) The effects of temperature on the intrinsic rate of increase of three species of pulmonate snails. Unpublished Ph.D. thesis, University of Michigan, Ann Arbor, Michigan.

Scorza, J.V., Silva, J., Gonzalez, L. and Machado, R. (1961) Stream velocity as a gradient in Australorbis glabrata (Say, 1818). Ztschr.Tropenmed.u.Parasit., 12 : 191-196.

Shiff, C.J. (1960) Observations on the capability of freshwater vector snails to survive dry conditions. J.trop.Med.Hyg., 63 : 89-93.

Shiff, C.J. (1964a) Studies on Bulinus (Physopsis) globosus in Rhodesia. I. The influence of temperature on the intrinsic rate of natural increase. Ann.trop.Med.Parasit., 58 : 94-105.

Shiff, C.J. (1964b) Studies on Bulinus (Physopsis) globosus in Rhodesia. III Bionomics of a natural population existing in a temporary habitat. Ann.trop.Med.Parasit., 58 : 240-255.

Shiff, C.J. (1966) The influence of temperature on the vertical movement of *Bulinus* (*Physopsis*) *globosus* in the laboratory and in the field. *S.Afr.J.Sci.*, 62 : 210-214.

Shiff, C.J. and Garnett, B. (1967) The influence of temperature on the intrinsic rate of natural increase of the freshwater snail *Biomphalaria pfeifferi* (Krauss) (Pulmonata: Planorbidae). *Arch.Hydrobiol.*, 62 : 429-438.

Shiff, C.J. and Husting, E.L. (1966) An application of the concept of intrinsic rate of natural increase to studies on the ecology of freshwater snails of the genera *Biomphalaria* and *Bulinus* (*Physopsis*) in southern Africa. *Proc.trans. Rhod.sci.Ass.*, 51 : 1-8.

Sioli, H. (1956) The only focus of endemic bilharziasis (*S. mansoni*) in the Amazon region. Observations on the ecology of the vector *Tropicorbis paparyensis* F. Baker and their practical importance. *WHO/Bil/Ecol./1*. 15 pp.

Smith, F.E. (1954) Quantitative aspects of population growth. In: Boell, E. ed. *The dynamics of growth processes*: 277-294. Princetown University Press.

Smithers, S.R. (1956) On the ecology of schistosome vectors in the Gambia, with evidence of their rôle in transmission. *Trans. R.Soc.trop.Med.Hyg.*, 50 : 354-365.

Snedecor, C.W. and Cochran, W.C. (1967) *Statistical Methods*. 6th ed. Iowa State University Press : Ames, Iowa, U.S.A. 593 pp.

Sodeman, W.A. (1972) Influence of light on activity of *Biomphalaria glabrata*. Abstract No. 152, *47th Annual Meeting of the American Society of Parasitologists*. p. 60. Abstract only.

Stiglingh, I. and van Eeden, J.A. (1970) Notes on the feeding behaviour of Bulinus (Bulinus) tropicus (Krauss) Basommatophora : Planorbidae. Wetenskaplike Bydraes van die P.U. vir C.H.O. Reeks B : Natuurwetenskappe, nr 22, 14 pp.

Sturrock, R.F. (1965a) Studies on the biology of Biomphalaria angulosa Mandahl-Barth and on its ability to act as an intermediate host of Schistosoma mansoni. Ann.trop.Med. Parasit., 59 : 1-9.

Sturrock, R.F. (1965b) The development of irrigation and its influence on the transmission of bilharziasis in Tanganyika. Bull.Wld Hlth Org., 32 : 225-236.

Sturrock, R.F. (1966) The influence of temperature on the biology of Biomphalaria pfeifferi, an intermediate host of Schistosoma mansoni. Ann.trop.Med.Parasit., 60 : 100-105.

Sturrock, R.F. (1970) An investigation of some factors influencing the survival of St. Lucian Biomphalaria glabrata deprived of water. Ann.trop.Med.Parasit., 64 : 365-371.

Sturrock, R.F. (1973a) Field studies on the population dynamics of Biomphalaria glabrata, intermediate host of Schistosoma mansoni on the west Indian island of St. Lucia. Int.J. Parasit., 3 : 165-174.

Sturrock, R.F. (1973b) Field studies on the transmission of Schistosoma mansoni and on the bionomics of its intermediate host Biomphalaria glabrata, on St. Lucia, West Indies. Int.J.Parasit., 3 : 175-194.

Sturrock, R.F. and Sturrock, B.M. (1972) The influence of temperature on the biology of Biomphalaria glabrata (Say), intermediate host of Schistosoma mansoni on St. Lucia, West Indies. Ann.trop.Med.Parasit., 66 : 385-390.

Teesdale, C. (1962) Ecological observations on the molluscs of significance in the transmission of bilharziasis in Kenya. Bull.Wld Hlth Org., 27 : 759-782.

Tinley, K.L. (1958) A preliminary report on the ecology of Lake Sibayi, Tongaland. Natal Parks Board records, unpublished.

van der Schalie, H. and Berry, E.G. (1973) The effects of temperature on growth and reproduction of aquatic snails. Sterkiana, 50 : 1-92.

van Eeden, J.A., Brown, D.S. and Oberholzer, G. (1965) The distribution of freshwater molluscs of medical and veterinary importance in south-eastern Africa. Ann.trop.Med.Parasit., 59 : 413-424.

van Eeden, J.A. and Combrinck, C. (1966) Distributional trends of four species of freshwater snails in South Africa with special reference to the intermediate hosts of bilharzia. Zool.Afr., 2 : 95-109.

van Eeden, J.A. and Combrinck, C. (1969) The influence of the substratum on population increase and habitat selection by Lymnaea natalensis Krs. and Bulinus (B.) tropicus Krs. (Mollusca: Basommatophora). Malacologia, 9 : 39.

van Someren, V.D. (1946) The habits and tolerance ranges of Lymnaea (Radix) caillaudi, the intermediate snail host of liver fluke in Eastern Africa. J.Anim.Ecol., 15 : 170-197.

Veloso, H.P. (1955) A preliminary note on a new method of application of molluscicides for control of schistosomiasis, quoted by: Gillet, J. et al. (1960).

Vogel, H. (1973) Foreword, in Epidemiology and control of schistosomiasis (Bilharziasis). ed.: Ansari, N. pp. xvii - xviii. Basle, Karger.

Watson, J.M. (1951) Studies on bilharziasis in Iraq. Part VI. Seasonal variation of the vector snail Bulinus truncatus. J.Faculty Med.Baghdad., 15 : 33-68.

Watson, J.M. (1957) The effect of water movement on populations of Bulinus truncatus. J.Egyptian Med.Ass., 40 : 308-324.

Watson, J.M. (1958) Ecology and distribution of Bulinus truncatus in the Middle East : with comments on the effect of some human activities in their relationship to the snail host on the incidence of bilharziasis haematobia in the Middle East and Africa. Bull.Wld Hlth Org., 18 : 833-894.

Watson, J.M. and Ali-Ali, A.S. (1961) The breeding of Bulinus truncatus in total darkness. J.Helminthology, Suppl., 199-204.

Webbe, G. (1960) Observations on the seasonal fluctuation of snail population densities in the northern province of Tanganyika. Ann.trop.Med.Parasit., 54 : 54-59.

Webbe, G. (1962a) The transmission of Schistosoma haematobium in an area of Lake Province, Tanganyika. Bull.Wld Hlth Org., 27 : 59-85.

Webbe, G. (1962b) Population studies of intermediate hosts in relation to transmission of bilharziasis in East Africa. in Bilharziasis, eds.: Wolstenholme, G.E.W. and O'Connor, M. pp. 7-22. London, Churchill.

Webbe, G. (1964) Biology of the intermediate hosts of schistosomiasis with particular reference to control of transmission. Ann.trop.Med.Parasit., 58 : 228-233.

Webbe, G. and Jordan, P. (1966) Recent advances in knowledge of schistosomiasis in East Africa. Trans.R.Soc.trop.Med.Hyg., 60 : 279-306.

Webbe, G. and Msangi, A.S. (1958) Observations on three species of Bulinus on the east coast of Africa. Ann.trop.Med. Parasit., 52 : 302-314.

Williams, N.V. (1970a) Studies on aquatic pulmonate snails in Central Africa. I. Field distribution in relation to water chemistry. Malacologia, 10 : 153-162.

Williams, N.V. (1970b) Studies on aquatic pulmonate snails in Central Africa. II. Experimental investigation of field distribution patterns. Malacologia, 10 : 165-178.

Witenberg, G. and Saliternik, Z. (1957) Studies on vectors of Schistosoma in Israel. Bull.Res.Counc.of Israel, 6B : 107-141.

W.H.O. (1957) Study Group on the Ecology of intermediate snail hosts of bilharziasis. Wld Hlth Org.'techn.Rep.Ser., 120 : 38 pp.

Wright, C.A., Klein, J. and Eccles, D.H. (1967) Endemic species of Bulinus (Mollusca: Planorbidae) in Lake Malawi (=Lake Nyasa). J.Zool., Lond., 151 : 199-209.

Wright, W.H. (1973) Geographical distribution of schistosomes and their intermediate hosts. in Epidemiology and control of Schistosomiasis (Bilharziasis). ed.: Ansari, N. pp.32 - 249. Basle, Karger.

Zakaria, H. (1955) Further study on the ecology of the intermediate host of Schistosoma haematobium, Bulinus truncatus Baylis. Bull.Endem.Dis. 1 : 123-155.