Effect of programmed circadian temperature fluctuations on population dynamics of *Biomphalaria pfeifferi* (Krauss)

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Until now all life-table studies on freshwater snails involving temperature as the variable factor have been conducted at constant temperatures. This study evaluates the differences between carefully programmed, cyclic, daily temperature fluctuations, namely 18 to 28°C and 20,5 to 25,5°C and a constant temperature of 23°C on the population dynamics of *Biomphalaria pfeifferi* (Krauss), an intermediate host snail of *Schistosoma mansoni* Sambon. Life-tables were compiled for cohorts of 25 snails each at each of the above-mentioned temperature regimes and the customary population parameters calculated for each cohort. The best results were obtained at the highest daily temperature fluctuation to which the snails were subjected during this investigation.

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Tot dusver is alle lewenstabelondersoeke op varswaterslakke waar temperatuur as veranderlike faktor betrek is, uitgevoer by konstante temperature. Hierdie ondersoek evalueer die verskille tussen twee noukeurig geprogrammeerde, sikliese, daaglikse temperatuurskommelings, naamlik 18 tot 28°C en 20,5 tot 25,5°C en 'n konstante temperatuur van 23°C op die bevolkingsdinamika van *Biomphalaria pfeifferi* (Krauss), 'n tussengasheerslak van *Schistosoma mansoni* Sambon. Lewenstabelle met kohorte van 25 slakke elk is by elk van die bogenoemde temperatuurregimes saamgestel en die gebruiklike bevolkingsparameters is vir elke kohort bereken. Die beste resultate is verkry by die hoogste daaglikse temperatuurskommeling waaraan die slakke tydens hierdie ondersoek onderwerp is.

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Temperature is one of the important abiotic factors influencing conditions in the freshwater biotope. Various authors such as Shiff (1964), Shiff & Husting (1966), Shiff & Garnett (1967) and Prinsloo & Van Eeden (1969) undertook life-table studies to evaluate the influence of constant temperatures on the population dynamics of a number of freshwater snail species. In our own earlier investigations we elaborated on the experiments of the above-mentioned authors and compiled life-tables for five economically important freshwater snail species at a range of six different constant temperatures (De Kock 1973; De Kock & Van Eeden 1981b). Although the results of these experiments constituted a valuable contribution to our knowledge of the effects of temperature on the population dynamics of freshwater snails and its bearing on their geographical distribution, constant temperatures in excess of twelve consecutive hours rarely occur in nature. Furthermore, the results obtained with certain freshwater snail species in aquaria subjected to fluctuating room temperatures (serving as controls) during our earlier experiments at constant temperatures (De Kock 1973), seemed to indicate that temperatures fluctuating between certain limits might be beneficial to some freshwater snail species. The need was therefore felt to conduct life-table experiments at carefully controllable fluctuating circadian temperature regimes. The equipment to suit our needs was not commercially available. Consequently, a temperature simulator incorporating a minicomputer was developed which could control a sophisticated cooling and heating system. This device can be programmed to effect any given temperature fluctuation or prerecorded natural temperature regime in an aquarium accurately to within 0,1°C of the desired level. The simulator was developed and manufactured jointly by the staff of the Snail Research Unit of the Medical Research Council at Potchefstroom and the Electronics Department of the Potchefstroom University for Christian Higher Education.

The first experiment was designed to merely test our hypothesis that cyclic daily temperature fluctuations affect the population dynamics of some freshwater snail species beneficially. In this experiment, the effect was investigated of three different temperature regimes on various population statistics calculated from life-tables compiled from the egg production and mortality rates of three cohorts (groups of snails of exactly the same species, origin and age) of 25 snails each of *Biomphalaria pfeifferi* (Krauss). This snail is an intermediate host of the bilharzial parasite *Schistosoma mansoni* Sambon.

Materials and Methods

The culture procedure was based on a system with circulating water which was described in detail by De Kock & Van Eeden (1980). The most significant modification was that each aquarium was enlarged to accommodate simultaneously eight cohorts of up to 40 snails each. The cohorts in a particular aquarium were kept separately in smaller containers suspended in the aquarium and consisted of perspex cylinders with perlon gauze bottoms of a specific mesh (De Kock & Van Eeden 1980). The improved system consisted of three separate stainless steel aquaria, each suspended in a waterbath and equipped with eight drip feed inlets through which culture water was supplied by gravitation from two large overhead reservoirs. The culture water flowed out of the aquaria through a sand and charcoal filter before being returned to the overhead reservoirs by means of a centrifugal pump.

The temperature in one of the three aquaria was kept constant at 23°C throughout the experiment. A second aquarium was subjected to a daily temperature fluctuation of 2,5°C below and 2,5°C above 23°C (20,5 to 25,5°C). In the third aquarium the temperature was set to fluctuate daily by 5°C above and 5°C below 23°C (18 to 28°C). In both the fluctuating temperature regimes equal time was spent at temperatures above and below 23°C (Figure 1). The average daily temperature was therefore the same in all three aquaria. Although the aquaria had a fairly large capacity (40 000 cm^3 each) no discernible horizontal or vertical temperature differences developed in them because the water in both the waterbaths and aquaria was continuously agitated. Additionally the ambient (room) temperature was controlled at a constant level of 22 ± 1,0°C which limited what would otherwise have been an unpredictable external influence on the accuracy of the experimental temperature regimes. The temperature in all three experimental aquaria was continuously monitored with mercury thermographs.

The culture water used in this experiment was taken from an ornamental fish pond and filtered through a sieve of perlon gauze of a very fine mesh (permeability 28% and mesh size 40 μm) to remove small organisms and debris before it was added to the system. The conductivity of this water was controlled at 360 ± 10 μS since our earlier experiments as well as many field observations suggested that this would fall within acceptable limits for most freshwater snail species.

The parental snails which laid the egg clutches needed to begin the experiment were collected from an earth dam on the farm Brushengo 220 in the Barberton district (grid reference: 25°35′S/31°20′E) and maintained in the laboratory at a constant temperature of 25°C until sufficient eggs were produced overnight to start the experiment at all three temperature regimes simultaneously. For each temperature regime, 25 juvenile snails were randomly selected as a cohort seven days after the first eggs started hatching. Surplus snails were discarded.

The experimental procedure, culture method and maintenance of the snails were the same as those detailed by De Kock & Van Eeden (1981b). Daily records were kept of mortality and egg production for the entire lifespan of every snail in each cohort. The total mass of each cohort of snails was determined fortnightly and the average mass per snail calculated. The population parameters, l_x (survivorship), m_x (age specific birth rate), $l_x m_x$ *(egg curve)*, r_m (innate capacity of increase), R_0 (net production rate), T (generation time) and λ (finite rate of increase), were calculated by using the equations given by Birch (1948), Andrewartha & Birch (1954), Southwood (1966) and Collier, Cox, Johnson & Miller (1973). These population parameters and their significance and interpretation are discussed in detail by De Kock & Van Eeden (1981b).

Results

The population statistics calculated from the data for the three experimental temperature regimes are given in Table 1. A perusal of Figure 2 shows that the three cohorts virtually did not differ in either the rate of mass increase per unit of time or in the final mean mass per snail eventually attained.

Although survival of the three cohorts was very similar (Figure 3) the onset of mortality came latest at the 18 to 28°C regime; and members of this cohort also lived longest. This regime was, furthermore, decidedly superior to the other two in respect of the m_x values (average number of fertile eggs per snail per fortnight) recorded (Figure 4). It is, however, also apparent from Figure 4 that up to the fourth fortnight no difference in fecundity was evident between the cohorts at the two fluctuating temperature regimes. This explains the small difference in r_m values of the two cohorts,

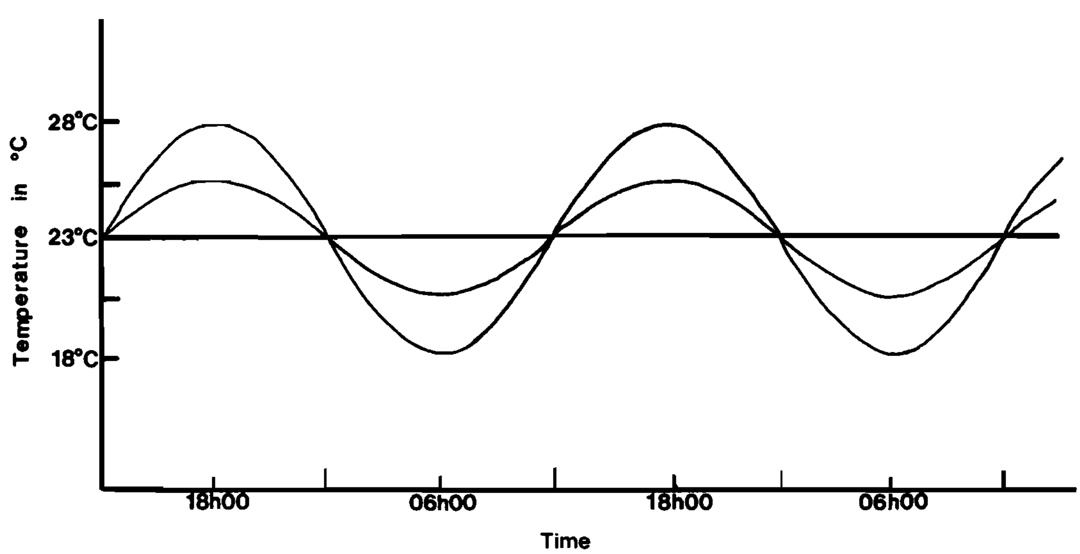

Figure 1 The constant fluctuating circadian temperature regimes at which the experiments were conducted.

Table 1 Population statistics recorded for the cohorts of *Biomphalaria pfeifferi*

	Population parameters						
Temperature regimes	Hatching time (days)	Hatching %	Days to onset of egg production	λ^a	$r_m{}^b$	$R_0{}^c$	$T_c{}^d$
18–28°C (10°C fluctuation)	9	98	32	3,8815	1,3562	986,96	5,0837
20,5–25,5°C (5°C fluctuation)	9	99	33	3,7004	1,3084	308,76	4,3812
23°C (constant)	10	99	36	2,8377	1,0430	322,16	5,5370

[a] λ = finite rate of increase per fortnight;
[b] r_m = innate capacity of increase per fortnight;
[c] R_0 = net reproduction rate;
[d] T_c = generation time in fortnights.

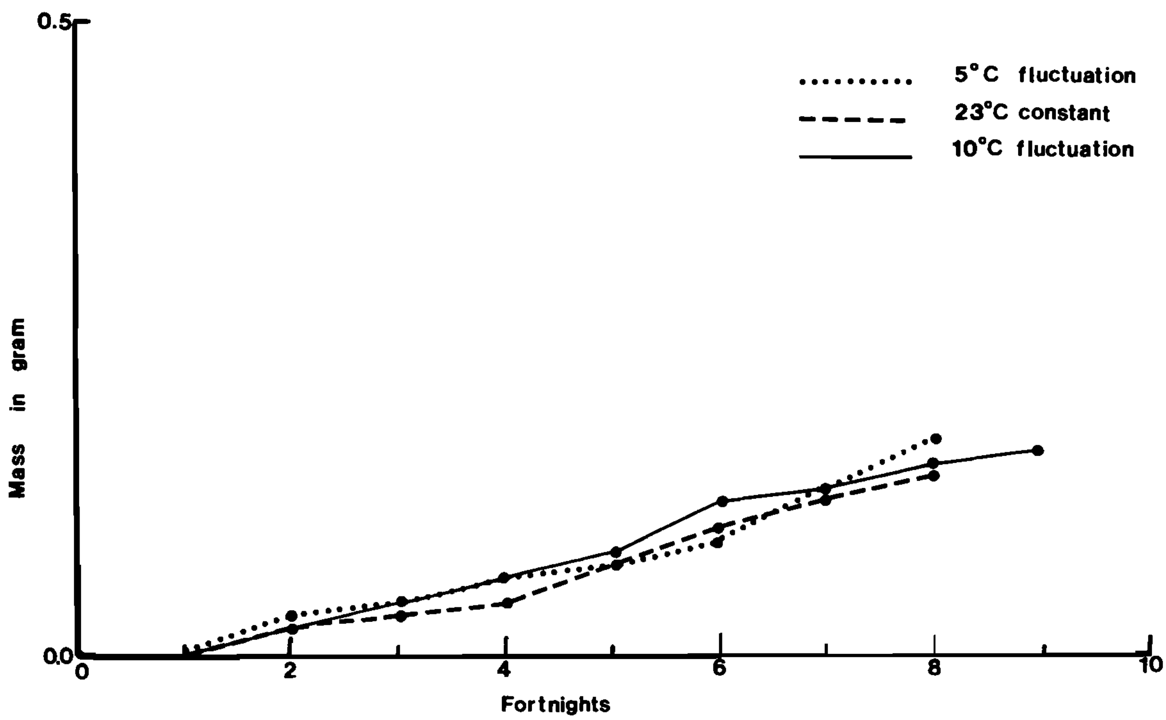

Figure 2 Mean fortnightly mass per snail of the cohorts of *Biomphalaria pfeifferi*.

despite the much higher total egg production at the 18 to 28°C regime as reflected by the net reproduction rate recorded in Table 1. It was demonstrated by De Kock & Van Eeden (1981a) that the first two fortnights of egg production of any cohort of freshwater snails may contribute as much as 98% towards the final value of r_m. Although the cohort at the constant temperature regime yielded higher m_x values and a higher R_0 value than did the one at 20,5 to 25,5°C, the onset of egg production of the former occurred three days later; and the number of eggs laid was smaller at that early stage. This lower egg production at a critical stage accounted for a decidedly lower innate capacity of increase of the cohort at the constant temperature regime as compared to that of the cohort at 20,5 to 25,5°C.

Discussion and Conclusion

The results of experiments conducted at various constant temperatures in the laboratory with cohorts of *B. pfeifferi* by authors such as Harrison & Shiff (1966), Shiff & Husting (1966), Sturrock (1966), Shiff & Garnett (1967) and De Kock & Van Eeden (1981b) indicated that this species seemed best adapted to populate warm, stable habitats. This conclusion was based on the snail's relatively low innate capacity for increase and relatively long generation time even at optimal constant temperatures. Our present findings, however, reveal that it is not essential for the temperature regime to be exceptionally stable. In fact, the best overall results as regards the population parameters in the present evaluation were obtained at the regime which fluctuated daily between 18 and 28°C.

In discussing the influence of temperature on the life-cycle and distribution of *B. pfeifferi*, Appleton (1977) concluded that the two most important components of the thermal regime which adversely affect the fecundity of *B. pfeifferi* in south-eastern Africa are mean maximum temperature and degree hours above 27°C per week (27°C is generally considered as near optimal for this species). The results of an experimental investigation by Appleton & Eriksson (1984)

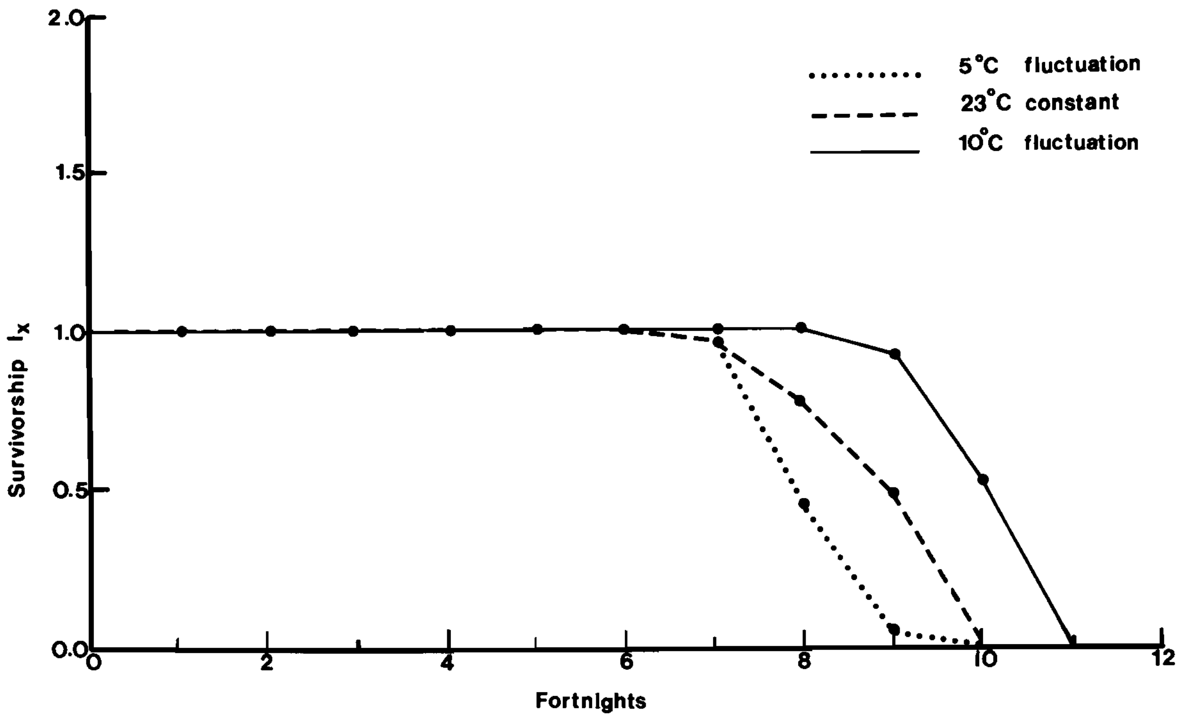

Figure 3 Age-specific survival of the cohorts of *Biomphalaria pfeifferi*.

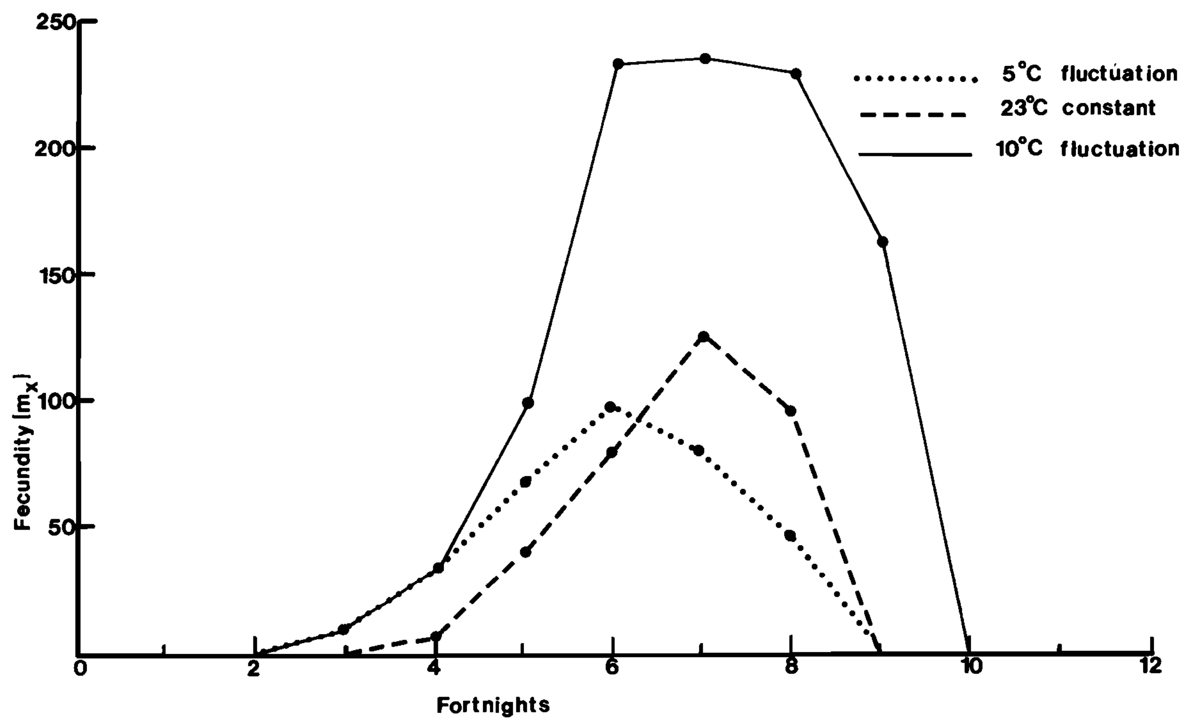

Figure 4 Age-specific fecundity of the cohorts of *Biomphalaria pfeifferi*.

of the influence of fluctuating above-optimal temperature regimes on the fecundity of *B. pfeifferi* showed that fecundity falls off rapidly following exposure to temperature regimes incorporating more than 46 degree hours above 27°C per day. From this they concluded that the end point of the plateau of nearly optimal r_m values for *B. pfeifferi* as reported by Shiff & Garnett (1967) should lie around a constant 29°C, as was indeed found by De Kock & Van Eeden (1981b); or, alternatively, a fluctuating 45 to 50 degree hours above 27°C per day. The highest daily cyclic fluctuation temperature regime to which the snails were subjected during our present investigation (18 to 28°C) incorporated only three degree hours above 27°C per day and therefore still fell within the range of the above-mentioned optimal plateau.

Although the r_m value calculated for the cohort at the 18 to 28°C temperature regime was only 0,048 higher in absolute value than that of the cohort at the 20,5 to 25,5°C temperature regime, this could, in the light of the findings reported by De Kock & Van Eeden (1976), be considered an important difference. The difference between the r_m values of the cohort at the 20,5 to 25,5°C temperature regime and that of the cohort kept at the constant temperature is even more significant. Although the total amount of available heat was 3 864 degree hours per week for each cohort throughout the present investigation, the population statistics calculated for each, differed. Therefore it is apparent that not only degree hours per week but also daily temperature ranges and daily maxima and minima in a given temperature regime should be taken into consideration when assessing the likelihood of *B. pfeifferi* colonizing a specific body of water.

Judging from the results of the present investigation and the findings of Appleton & Eriksson (1984), it seems possible that a population of *B. pfeifferi* could benefit from a temperature regime with a daily fluctuation of more than the 10°C range reported on here. Our study clearly indicates that better overall results can be expected by rearing populations of *B. pfeifferi* in the laboratory at carefully selected daily fluctuating temperatures instead of at optimal constant temperatures. This finding was not entirely unexpected because the results of our constant-temperature experiments with this species (De Kock & Van Eeden 1981b) revealed that the highest values for different population parameters such as natality, survival and growth rates were generally attained at different constant temperatures. As a rule, the lower constant temperatures favoured longevity while the higher constant temperatures favoured growth rate and fecundity. Thus, with circadian temperature fluctuations exceeding a certain minimum amplitude, there are bound to be periods in every 24 hours during which the temperature should be optimal for either one or the other of a series of physiological activities. On the other hand, a temperature kept constant throughout might favour only a single physiological activity. The circadian temperature rhythm must, therefore, on the whole be more beneficial to the snail than any constant temperature.

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