

THE EFFECTS OF TEMPERATURE ON SURVIVAL, GROWTH AND REPRODUCTION OF *BELLAMAYA BENGALENSIS* LAMARCK, IN THE LABORATORY

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Abstract : Population of *Bellamaya bengalensis* Lamarck, were exposed to various temperatures ranging from 0-45 °C with 5 °C interval to observe their survival, growth and reproduction. Juvenile (one week old) and adult snails (70, weeks old) were kept under observation for 24 and 32 weeks. It appeared that for both juvenile and adult snails optimum temperature for survival, growth and reproduction was 25.0 ± 1.0 °C. At this temperature snails also exhibited maximum specific growth rate for length and weight. However, condition factor was pointing to the fact that at this optimum temperature, weight increase was more pronounced than the length.

The snails could not tolerate the temperatures above 35.0 °C and below 15.0 °C beyond 96 hours (juvenile) and 7 days (adult).

Key Words : *Bellamaya bengalensis*, temperature, survival, growth, reproduction.

INTRODUCTION

The snails form an essential and easily vulnerable link in the transmission of trematode infections, which not only cause serious damage to the health and prosperity of human beings but also to his livestock and fish industry. The situation is even more damaging in developing countries, particularly those with agriculture based economies involving artificial irrigation systems. It was with these facts in mind that the present investigation was envisaged.

Different parameters of molluscan biology have been investigated under various temperature and environmental conditions. The details can be seen in recent reviews by Aldridge (1983), Burky (1983), Hoffman (1983), McMahon (1983), Riddle (1983) and Summers (1983).

Apart from these, some knowledge on the effect of temperature on growth and reproduction on various snail species is available (DeWitt, 1955; Michelson, 1961; Shiff, 1964; Shiff and Garnett, 1967; Krebs, 1972; Mousa and El-Hassan, 1972; Sturrock and Sturrock, 1972; Prinsloo and Van Eedan, 1973; Van der

Schalie and Berry, 1973; Hodasi, 1976; Aboul-Ela and Beddiny, 1980; a; McMahon and Payne, 1980; El-Emam and Madsen, 1982; Suliman *et al.*, 1987). They reported that optimum temperature for snails, lies between 24-30°C.

In addition, effect of temperature on physiological ecology of molluscs have been reported by many workers (Manzi, 1970; Konev, 1970; Demian and Ibrahim, 1970, 1972; Burky *et al.*, 1972; El-Hassan, 1974; Liang, 1974; Vaillancourt and Couture, 1975; McMahon, 1976; Harris and Charleston, 1977; Aboul-Ela and Beddiny, 1980b; DeKock and Van Eeden, 1985; Joubert and Pretorius, 1986; Joubert *et al.*, 1986; Tanveer, 1991).

Some preliminary work already done in this laboratory showed that *Bellamaya bengalensis*, a bottom dweller and completely refractory to trematode parasites, suppresses the population of other medically important snails. This may be due to the competition for common requirements i.e. their ecological niches are either similar or broadly overlapping. Before its implementation as a biological control agent its preference and tolerance range to the various ecological factors must be known. Among the various physioecological factors, temperature seems to be quite important, so it was decided to embark upon this study to evaluate the effects of temperature on the survival, growth and reproduction of laboratory populations of *B. bengalensis*. No detailed investigation, however, has been made earlier on such aspect of this snail species.

MATERIALS AND METHODS

Bellamaya bengalensis, used in these studies, were collected from the Ibrahimabad drain, Mustafabad (Kasur District). The snails were brought to the laboratory, washed thoroughly and checked for infection. Only healthy snails (actively crawling and voraciously feeding), were maintained for the establishment of colony. The details of keeping conditions of the breeding stock have been given by Tanveer *et al.* (1989). To achieve uniformity in the results, laboratory bred snails were used in all the experiments, unless otherwise stated. Prior to each experiment, snails were collected from the stock aquaria and the shell diameter were measured to the nearest 0.1 millimeter with a vernier caliper. The measured snails were grouped into populations (15 snails each, in three replicates) with similar means and extremes of shell diameter. For this evaluation two snail groups juvenile (one week old) and adult (70 weeks old) were tested separately at various

temperatures ranging from 0-45 °C with 5°C interval. Separate pots of area 624.92 cm² and 1146.43 cm² with water capacity of one and three litres, were used for the juvenile and adult snails, respectively.

A carefully routinized schedule of feeding and water change every third day was followed throughout the experimental period. Snails were fed on semi-synthetic food (Proximate analysis = protein 48%, carbohydrate 24.0%, moisture 6.45%, ash 1.19%) provided in excess every third day. Before adding the new food, pots were cleaned thoroughly and filled with warm tap water of required temperature, at which the snails were already kept.

Snail group kept at 25.0±2.5 °C was considered as control group, since this is the temperature at which stock colony had been maintained. Experimental temperatures ranging from 0-45 °C with 5 °C intervals were maintained by means of thermostatically controlled immersible electric heaters. Photoperiod was also kept constant i.e., 12 hours day and 12 hours night.

For both juvenile and adult snails, parameters taken into consideration were survival (or mortality) and growth in terms of increase in shell length and weight. While reproduction (total number of juvenile produced per group) was noted for adult snails only. Juvenile and adult snails were kept under observation, for 24 and 32 weeks respectively.

All these observations were made daily, but for the sake of brevity, tabulated monthly. Cumulative survival, is the total number of snails left in the end of the experiment, as well as on monthly basis and is expressed as percentage of the initial number, at the start of the experiment. Specific growth rate (SGR) for weight and shell length data was calculated according to Odum (1971) and condition factor was computed as reported by Pekkeranin (1983). The data presented, has been analysed statistically by one way analysis of variance and 't' test (Sokal and Rohlf, 1969).

RESULTS

Effect of various temperatures on the survival, growth and reproduction on two age groups (i.e., juvenile and adult *B. bengalensis*) has been worked out, and following observations were made.

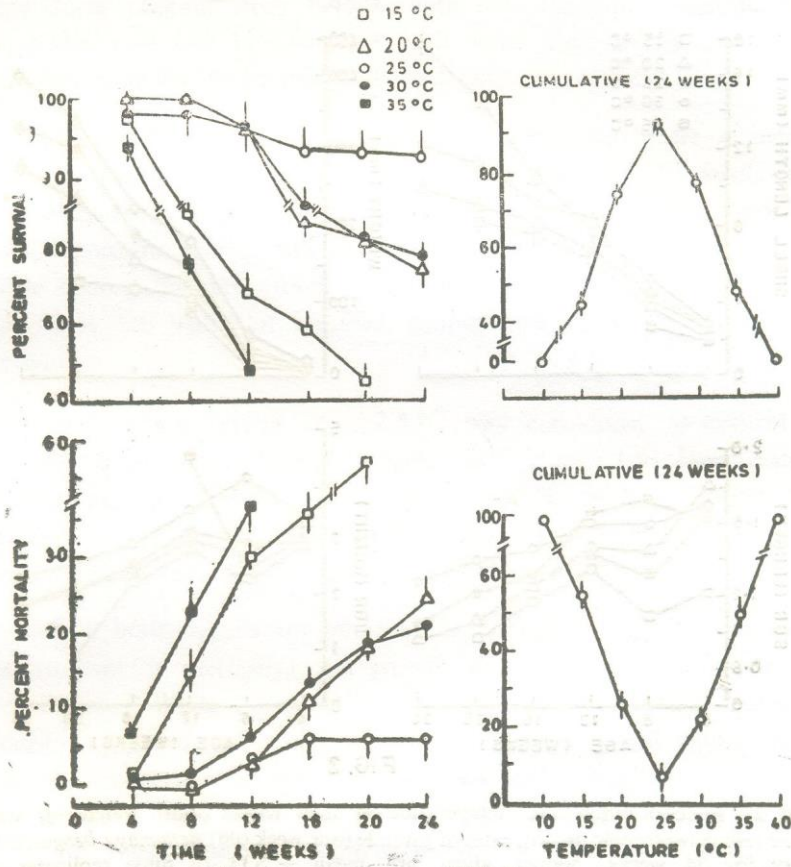


FIG. 1

Fig. 1. Percent survival and mortality of juvenile of (one week old) *Bellamaya bengalensis* kept at different test temperature for 24 weeks. Values given are mean \pm S.D. of three replicates of 15 snails each.

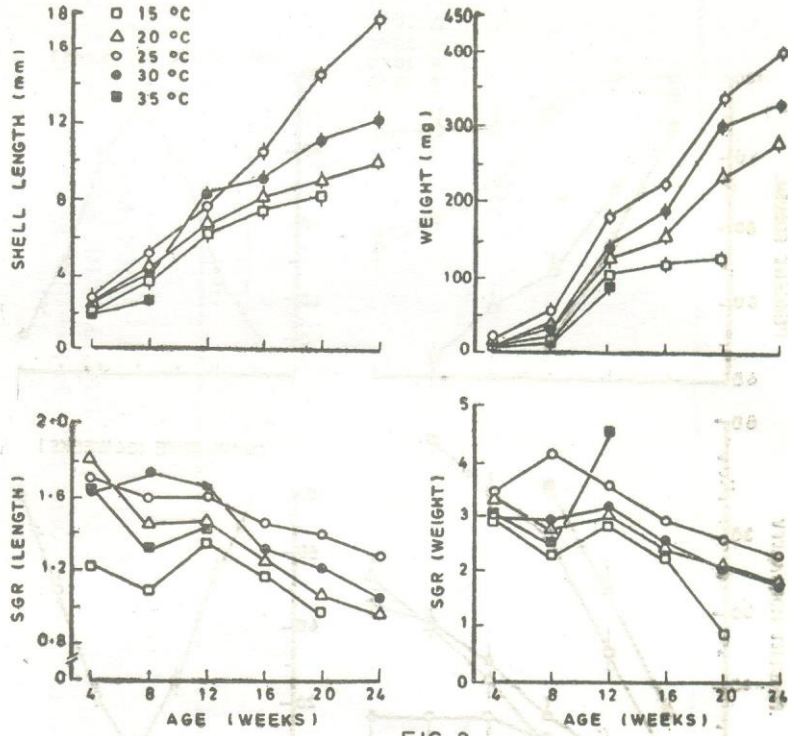


FIG. 2

Fig. 2. Effect of different test temperature on shell length (mm), weight (g) and their respective specific growth rates of juvenile (one week old) *Bellamya bengalensis*, kept for 24 weeks. Values given are mean \pm S.D. of three replicates of 15 snails each.

*Studies on juvenile B. bengalensis.**Survival*

Effect of various temperatures on the survival and mortality of juvenile snails is presented in Fig. I. It is clear from this figure that there was no long term survival above 35 and below 15 °C. Although at these temperatures the survival was zero, nevertheless, time taken for the whole population to die, was different. At 0 °C, there was 100 percent mortality after 6 hours. While this occurred after 24 and 96 hours at 5 and 10 °C respectively. At 45 °C all snails died within two hours (Table I). The percent cumulative survival at optimum temperature (25 °C) was 93.33 ± 2.87 while at 20 and 30 °C (the two temperatures on both side of optimum temperature) the cumulative survival was 75.0 ± 2.86 and 78.33 ± 1.84 after 6 months. The mortality of the snails kept at the same temperature for 6 months increased slowly and the monthly record of this parameter showed that there was a significant increase in mortality in the successive months, as compared to the first month ($P < 0.01$, see Fig. I). It may be mentioned here that at the optimum temperature, there was a constant survival after 4 months (93.33%) which remained at this level till 6 months, the end of the experimental period i.e., no further mortality was observed in this group. This probably was due to the successive increase in size of the snails which may have developed more resistance to temperature than the smaller (younger) snails.

Growth

Growth in terms of increase in weight (mg) and shell length (mm) was noted at those temperatures where the snails showed survival for more than one month. The snails kept at 15, 20, 25, 30 and 35 °C showed different patterns of growth. However, the maximum growth was observed at 25 °C (Fig. 2), which is also the optimum temperature for survival. The difference in growth as a function of temperature was statistically significant according to analysis of variance and 't' test ($P < 0.01$)

Specific growth rate for weight (SGRW)

Snails acclimated at 25 °C showed considerable increase in specific growth rate for weight during the first two months (Fig. 2), while in all other groups a downward trend was observed. After this time the growth rate gradually decreased till the end of the experiment (6 months). The snails

kept at 35 °C showed an extraordinary increase in SGRW after three months. Immediately after this time, all snails kept at this temperature died, due to some unknown reason.

Specific growth rate for length (SGRL)

As far as specific growth rate for length is concerned, there was a gradual decrease in all the groups with the increase in age.

Condition factor

Condition factor in all the groups was highest after first month as compared to the subsequent months (see Figure 3). Furthermore, the snails kept at 15 °C gave maximum values after 12 weeks which indicates that during the first three months, the increase in length in this group was relatively slow than the increase in weight. After this time the condition factor gradually declined and this decline was characteristic of the groups kept at the specific temperature (Fig. 3).

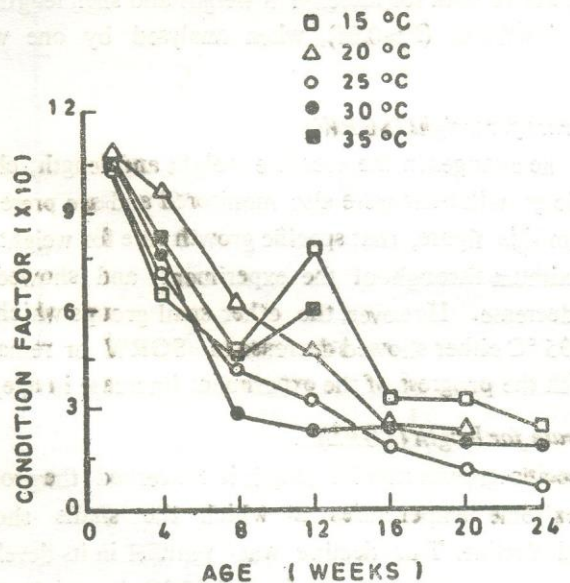


FIG. 3

Fig. 3. Effect of different test temperature on the condition factor ($\times 10$) of juvenile (one week old) *Bellamaya bengalensis*, kept 24 weeks.

Studies on adult B. bengalensis

Survival

The data regarding the survival and mortality of adult *B. bengalensis* has been presented in Fig. 4 and 6. Although the data was recorded every day, the presentation is made on monthly basis. The cumulative percent survival has been presented in Fig. 6. The result clearly showed that 25 °C is the optimum temperature because of maximum survival (93.33 ± 1.66). Below 15 °C and above 35 °C, *B. bengalensis* exhibited 100 percent mortality, but the time taken for this mortality (total population death) was less than 24 hours at 0 °C, 4 days at 5 °C, 7 days at 10 °C, 4 days at 40 °C (Table II). This data therefore, has not been included in the figures.

Growth

In addition to survival and mortality, the growth of adult *B. bengalensis* was also studied at various temperatures ranging from 15-35 °C. The results presented in Fig. 5 showed that optimum temperature for growth was 25 °C. The monthly tabulated data for increase in weight and shell length was found to be statistically significant ($P > 0.01$), when analysed by one way analysis of variance.

Specific growth rate for weight (SGRW)

Apart from the changes in the absolute weight and length, changes in their respective specific growth rates were also monitored and are presented in Fig. 5. It is obvious from this figure, that specific growth rate for weight of snails kept at 25 °C was maximum throughout the experiment and showed an increase after an initial decrease. However, the other snail groups which were kept at 15, 20, 30 and 35 °C either showed decrease in SGRW or remained more or less constant with the progress of the experiment (increase in age).

Specific growth rate for length (SGRL)

As far as specific growth rate for length is concerned the groups kept at 15 and 35 °C (two extreme temperatures at which the snails showed survival) showed a gradual decline. This decline was parallel in its development in the two groups. The groups kept between 20 and 30 °C showed fluctuations in the beginning but had similar values till 82 weeks of age. After this time, however, the groups kept at 25 °C started separating themselves from the other two groups by showing increase in SGRL.

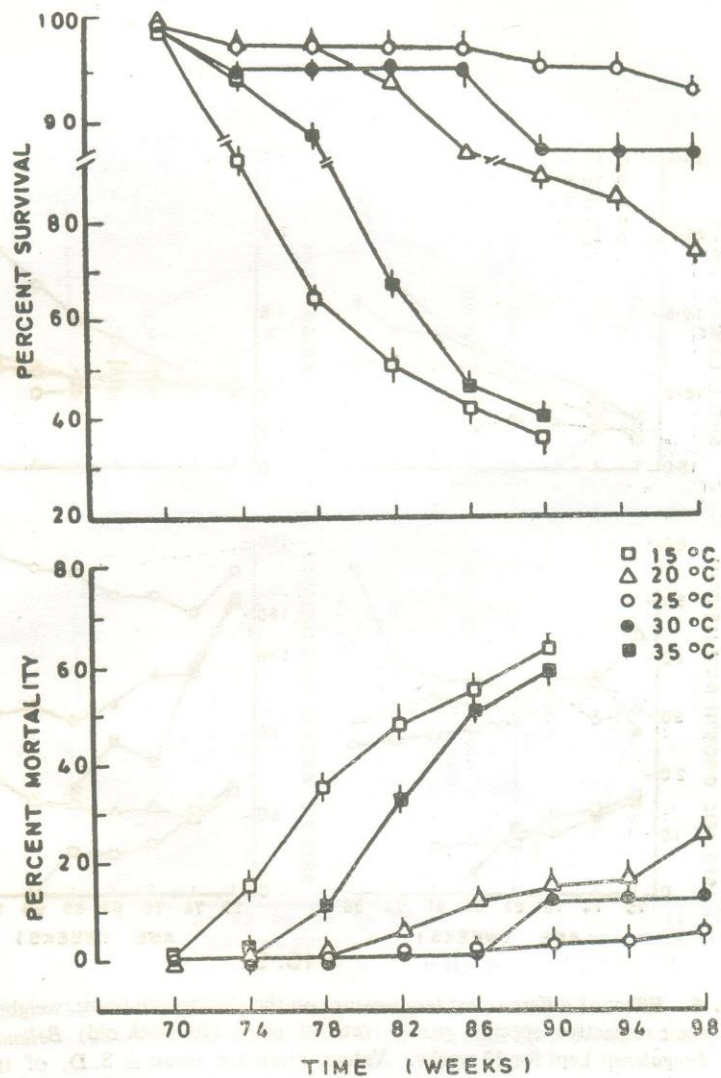


FIG. 4

Fig. 4. Effect of different test temperature on the percent survival and mortality of adult (70 week old) *Bellamaya bengalensis* kept for 32 weeks. Values given are mean \pm S.D. of three replicates of 15 snails each.

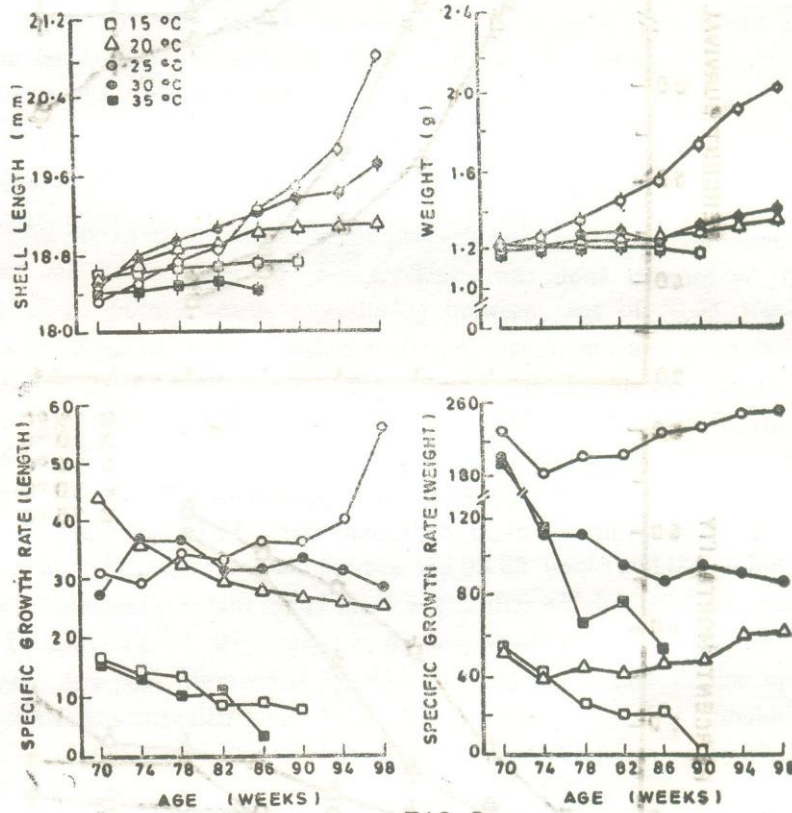


FIG. 5

Fig. 5. Effect of different test temperature on the shell length (mm), weight (g) and their respective specific growth rate of adult (70 week old) *Bellamya bengalensis* kept for 32 weeks. Values given are mean \pm S. D. of three replicates of 15 snails each.

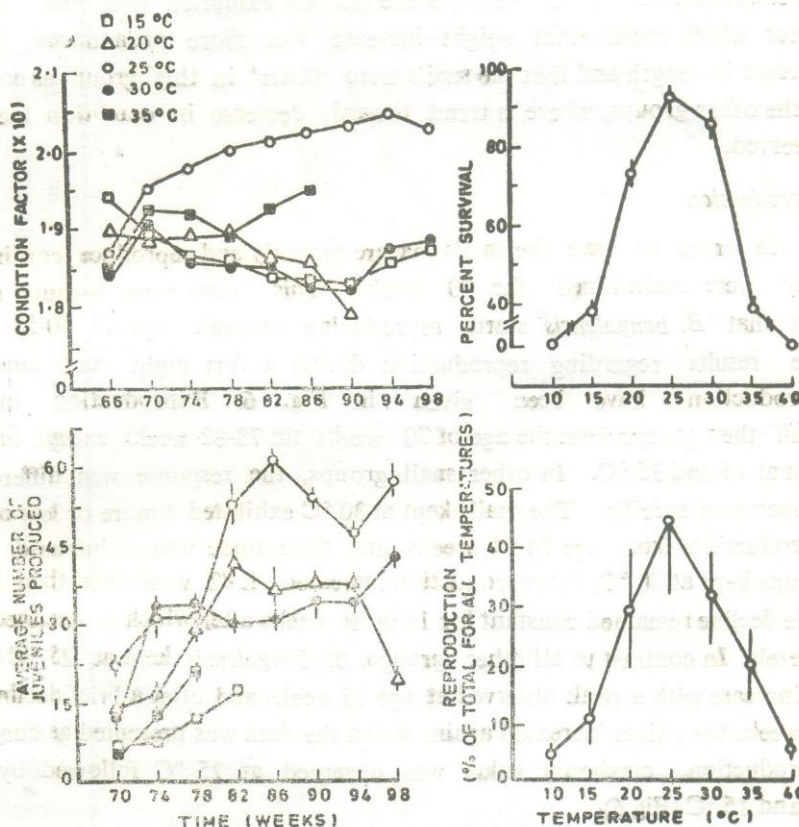


FIG. 6

Fig. 6. Effect of different test temperature on the condition factor, percent survival (cumulative) and reproduction of adult (70 week old) *Bellamoya bengalensis*, kept for 32 weeks.

Condition Factor

The change in the condition factor of adult *B. bengalensis*, kept at various temperatures have been presented in Fig. 6. The figure clearly showed that the snails kept at optimum temperature (25 °C) exhibited maximum condition factor which means that weight increase was more pronounced than the increase in length and that the snails were 'fatter' in this group as compared to the other groups, where a trend towards decrease in condition factor was observed.

Reproduction

In order to have the snails mature properly and reproduce continuously they were maintained for 70 weeks. This was done because of the fact that *B. bengalensis* starts reproducing between age of 50-53 weeks. The results regarding reproduction during a fortnight and cumulative reproduction have been given in Fig. 6. Reproduction increased in all the groups from the age of 70 weeks till 78-82 weeks except in snails kept at 15 and 35 °C. In other snail groups, the response was different and temperature specific. The snails kept at 30 °C exhibited a more or less constant reproduction from age 74-94 weeks and then there was an increase. In the groups kept at 20 °C, the reproduction increased till 82 weeks and then after a little decline remained constant for 12 more weeks after which it declined quite severely. In contrast to all other groups, *B. bengalensis* kept at 25 °C showed an increase with a peak observed at age 86 weeks and after a brief decline upto 94 weeks the values increased again. When the data was presented as cumulative reproduction, maximum value was observed at 25 °C followed by 30, 20, 35 and 15 °C (Fig 6).

DISCUSSION

Survival

The results of the present investigation showed that temperature exerts great influence on survival of the snails tested. It was observed that maximum survival was noted at 25 °C followed by temperatures around this maxima i.e., 20 and 30 °C. The temperatures below 20 and above 30 °C induced greater mortalities. Our present results are in close resemblance with those of Stirewalt (1954) and Michelson (1961). These authors reported that snail mortalities were higher at temperature lower than 5 °C and higher than

30 °C. Shiff and Garnett (1967) constructed various life tables for *Biomphalaria pfeifferi* at 18, 25 and 27 °C. They showed that within the range investigated (18, 25 and 27 °C) there was a little influence on the mortality rate of *B. pfeifferi* (Krauss), although the maximum survival and growth was observed at 25 °C. Similarly, while completing the life tables for the same species (*B. pfeifferi*) at different (11, 25, 30 °C) temperature, Sturrock (1966) reported, that the optimum temperature for rapid expansion of the population was 25 °C. At temperatures lower or higher (19 and 30 °C) than this, population growth was much slower. It was also observed that survival was good at 19 °C while it was poor at 30 °C, showing that the snail was not a good tolerant of high temperature. It was noted in this same study that maximum tolerance limit for this snail was 32 °C in the laboratory but Sturrock (1966) was of the view that in the nature it is doubtful whether colonies would survive temperatures much above 28 °C. He also concluded that the higher temperatures were a barrier to the colonization by *B. pfeifferi* on the coastal plains of Tanzania. Mantale (1971) noted that in snail *Cryptozonia semirugata*, the percent mortality was higher at high temperatures. He observed 100 percent mortality at 41 °C. Nagabhushanam and Azmatunnisa (1976) reported that for *Lymnaea acuminata* percent mortality increased with rise in temperature from 25 °C to 42 °C. They observed 50 percent mortality at 34.5 °C and 100 percent mortality at 42 °C in 24 hours. Nagabhushanam and Chintawar (1976) acclimatized, their snail *Indoplanorbis exustus* at 27-28°C and tested them at 34-37 °C, they observed that 24 hour survival values for *I. exustus* were 100, 80, 50 and zero percent at 34, 35, 36 and 37 °C.

Growth and Reproduction

Present results showed that growth of the snails is very much influenced by the environmental factors and that temperature is the most important of them. In the present study it was observed that the optimum temperature for the survival and growth of both juvenile and adult *B. bengalensis* was 25 °C and that any increase or decrease in the temperature from this optimum point will affects the survival and growth of the snails. Another point that emerged from these studies is that although the optimum temperature for survival and growth for the juvenile and adult snails is the same, the increase in age (size) increases the tolerance of the animal to different temperature. This was particularly obvious, when the snails were subjected to the extremes of temperature. Many reports are available on the affect of temperature on growth of different

snail species. Growth and reproduction was optimum at 25 °C for *Bulinus pfeifferi* (Krebs, 1972 ; Sturrock, 1966, Shiff and Garnett, 1967), *Biomphalaria glabrata* (Sturrock and Sturrock, 1972) and for *Bulinus globosus* (Shiff, 1964). Mousa and El-Hassan (1972) found, optimal growth and egg laying at 25 °C for *Biomphalaria alexandrina* and *Bulinus truncatus*.

Apart from the studies cited above there is some reported information which shows that the optimum temperature for growth and reproduction was different. For *B. glabrata* optimum temperature for growth was 30 °C and for reproduction 25 °C (Michelson, 1961). For *Helisoma duryi*, *B. alexandrina* and *Bulinus truncatus*, optimum temperature for growth and reproduction was 26—28 °C (El-Emam and Madsen, 1982). In *H. trivolvis*, *H. anceps* and *H. campanulatum*, this temperature was 30 °C for growth and 24—26 °C for reproduction (van der Schalie and Berry, 1973).

The reasons that for the same snail species different optimum temperatures for growth have been reported is that most probably different races of these species have been employed. Secondly, that the previous temperature history (acclimation temperature) of the species should be kept in mind, thirdly the size (age) of the species at the time of the experiment may have implication in this regard and lastly the nutritional status and history of the animal also have its importance. All these factors must be kept in mind while planning the experiments.

The question as to why the growth become slow at lower or higher temperatures than the optimum temperature also warrants further comments. At lower temperature in the present study we observed that due to diminished activity the food intake of *B. bengalensis* was very low. This means that appetite play an important role in this regard. This has been shown in *Lymnaea truncatula* (Hodasi, 1976). This appetite in turn may depend upon the metabolic rate of the snail. It is a quite well known fact that lower temperatures decrease the metabolic rate of these animals (Tanveer, 1991). In our studies on *B. bengalensis* it was noted that oxygen consumption (metabolic rate) of snails kept at lower temperatures is lower than at higher (near optimum) temperatures; while at very high temperatures the oxygen consumption declined again (Tanveer, 1991). At very high temperatures, apart from appetite factor, oxygen content of the environment also become a limiting factor regarding growth.

The effect of temperature on the growth and survival of *B. bengalensis* has been discussed above. Apart from these, effect of different temperatures on the reproduction (number of young one produced/snail) was also studied. The observations showed 25 °C as the optimum temperature for reproduction (Fig. 6). This observation differs from many studies made on different snails where the optimum temperature for growth is different from the temperature for reproduction. Michelson (1961) found optimal growth of *B. glabrata* at 30 °C and egg laying was maximum at 25 °C. While El-Emam and Madsen (1982) reported that optimum temperature for growth and survival for *H. duryi*, *Biomphalaria alexandrina* and *Bulinus truncatus* was 28 °C while the same temperature for reproduction was 26 °C. These studies probably points to the fact that reproduction in certain snails needs a temperature gradient. It may also be pointed out that in snails where reproduction occur at low temperatures, higher temperature bring problems. Michelson (1961) reported that higher temperature caused thermal castration of the female reproductive system and various pathologies including that of the albumin glands were observed. Similarly *H. duryi* snail swere able to survive at 33 °C but reproduction in these snails was depressed and egg laying took place later than the snails which were at lower temperatures. El-Emam and Madsen (1982) thought that this delay was caused for the abnormal development of the gonads.

Apart from the changes in the reproductive potential, changes in the egg laying and hatchability of the eggs are also effected by high temperatures. Aboul-Ela and Beddiny (1980a) found that no egg of *H. duryi* hatched at 35 °C whereas 90 percent hatched at 30 °C. Mousa and El-Hassan (1972) found that at 35 °C no egg of *B. alexandrina* hatched but eggs of *Bulinus truncatus* did hatch after 5 days of incubation. At 30 °C both species had their eggs hatched normally. However, Joubert and Pietorius (1986) reported that sustained temperatures below 16 °C and above 30 °C are detrimental to the developing and hatching of *B. glabrata* eggs. Suliman *et al.* (1987) also reported that hatchability of *Lymnaea acuminata* was 0% at 10 and 35 °C and was very high (99.9%) at 24–27 °C.

In the present experiment *B. bengalensis* maintained at different temperatures (between 15 and 35 °C), showed maximum reproduction at 25 °C when studied between the age of 70 weeks to 98 weeks. During this

time the reproduction was continued, though at a lower level at 20 and 30 °C but the reproduction ceased in group kept at 15 and 35 °C after 12 and 8 weeks. This means our results are in line with the results reported above that higher temperature are more detrimental for reproduction. Secondly, in *B. bengalensis* lower temperatures are comparatively less detrimental. It was seen that reproduction in 35 °C snails increased quickly and was higher than the snails kept at 15 °C. It is also interesting to note that the reproduction ceased about 2 months before the death of all the snails in this group. It is not clear at this moment that what would have happened if the snails kept at 15 and 35 °C would have returned to optimum temperature of 25 °C. This type of information may be very important. Apart from the observation reported above, the snails kept at 20 and 30 °C (two temperatures around the optimum temperature) were also compared regarding survival, growth and reproduction. These comparisons showed that all the parameters studied were higher in snails kept at 30 °C as compared to 20 °C (Fig. 1-6). This means that *B. bengalensis* showed best performance between 25 and 30 °C.

Now the question arises as to what are the reasons for the diminished reproduction at temperatures other than the optimum temperature. The answer to this question is not simple and clear at this moment but some comments can be made at this point. Firstly, photoperiod can be an important factor in this regard but in the present study the photoperiod was kept constant, it may be possible that the photoperiod kept in the present study interacted with the temperature more at lower and higher temperatures than the optimum temperatures. More quantitative studies are needed in this direction. The studies of El-Emam and Madsen (1982) on the planorbid snails, *H. duryi*, *Biomphalaria alexandrina* and *Bulinus truncatus* showed that photoperiod will have effect on growth, survival and reproduction in snails, as complete darkness was shown to be very detrimental to the above mentioned snails.

Secondly, at lower or higher temperatures the role of appetite, discussed above in connection with the growth, is also important. The food is very important in channeling the energy for the development of gonadal products. In this connection further factor is the quantity and quality of the food given or available in nature. Lower and higher temperatures decrease the food intake there by decreasing growth. It is however, not clear whether

the decreased reproduction is indirectly due to decreased growth of the snails or is affected directly due to decreased energy inputs. This of course is another field to be explored. Cossins and Bowler (1987) stated that for complete understanding of the effect of temperature on growth, a detailed knowledge of its effects upon the processes of ingestion, digestion and assimilation of food, as well as its metabolic interconversion, is essential. They further quoted that if these processes have different thermal optima or dependences then the resulting effect of temperature on growth may be complex, rather than simple.

In connection with the above discussion the studies reported by El-Emam and Madsen (1982) on the effects of starvation and different food types on the growth and reproduction of planorbid snails are quite pertinent and important. Growth and egg laying seem to be higher in groups given protein-energy rich diets than carbohydrate rich diets (Jennings *et al.*, 1970 ; Milward-de- Andrade *et al.*, 1978 ; Stanislawski and Becker, 1979). In studies performed in the natural habitats of different snail species there are indications that quality of food, rather than quantity, plays more important role in the regulation of snail population communities (Eisenberg, 1966, 1970 ; Skoog, 1978).

Some comments on the behaviour of B. bengalensis

when exposed to different temperatures.

It was observed during the present investigation that at extreme temperatures (lethal or sub lethal such as 10, 15 or 35, 40 and 45 °C) the snail populations showed very diminished activities, they lay inactive with operculum closed and without feeding. At temperatures between 20-30 °C *B. bengalensis* resume their normal activities of feeding and active crawling in the aquaria. Earlier workers dealing with snail ecology and biology have observed similar behavioural pattern in snails species. Wrede (1927) reported that at 4-6 °C *Physa fontinalis* (L) is contracted and motionless and on this state feeding and growth was certainly out of question. The observations taken at higher temperatures (upper lethal temperature) i.e., above 40 °C showed that *B. bengalensis* could not survive and a complete atrophy of the tissues was found. The operculum were shed. Although the reproduction is out of question at these extreme temperatures nevertheless it was observed that when *B. benga-*

lensis a viviparous snail, kept at extreme temperatures, they become inactive, motionless and after shedding their operculum their soft body also came out of the shell and after sometime the juvenile (successive stages from eggs to embryos & juvenile) present inside the uterus were also shed in the surrounding water. If these juvenile were kept at optimal temperatures some of them continued their growth and $3.5 \pm 2.5\%$ of them also reached the age of maturity. It was not checked whether the juveniles were precocious and whether they reproduced also when matured. It was also observed that snails kept at low temperatures did not show any change in their gonads (i.e., no atrophy was found, unpublished). Although their growth and reproduction ceased when kept longer than 2 weeks, but these snails resumed feeding and growth when transferred to normal temperatures.

Similar result have been reported by Bouillon (1956) and Michelson (1961) for *Cepea nemoralis* and *Australorbis glabratus*. Both of these authors suggested that low temperatures stimulate oogenesis and reproduction. Hodasi (1976) pointed out that young *L. truncatula* profit by long-term exposure to low temperatures in winter months. On return of favourable conditions the snails become very active, feed voraciously and grow rapidly. These snails tended to live longer and produce more offsprings. While on the other hand, low temperatures have adverse effects on the subsequent growth and reproduction of older snails.

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