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# Effect of Temperature on Growth, Mortality, Reproduction and Production of Adult Lymnaea obrussa Say (Mollusca: Gastropoda)

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ABSTRACT

Shell lengths and egg production were measured weekly under constant (K; 10,15,20,25°C) and varying temperature regimes during the reproductive period. Varying regimes included natural field temperature in a pond (F; diurnal and seasonal), mean daily field temperature ($\bar{F}$; seasonal) and 5 and 10°C above $\bar{F}$. Growth rate of large snails (>10 mm) was unaffected by temperature, but small snails (6-10 mm) grew fastest at 15°C(K). Growth and reproductive periods were longest, production was highest, and mortality rate was lowest at 15°C(K). Rate (per snail) of egg production increased with temperature. At equal mean temperature, regime affected growth rate only at $\bar{F}$. Regime affected the following values as shown: mortality rate, $F > \bar{F} = K$; rate of reproduction, $F > K > \bar{F}$; and total production, $K > \bar{F} = F$. The validity of extrapolation of energetic data from laboratory to field is discussed. Data relating production and temperature are valuable in thermal impact analysis.

## INTRODUCTION

Studies involving field observation of natural populations and concomitant studies in the laboratory where conditions can be controlled are vital to the understanding of the factors affecting production.[1-5] One of the most important abiotic environmental factors is temperature. Much work has been done measuring physiological rates at different temperatures. Temperature in the field varies seasonally and diurnally, however, and most laboratory work has been carried out at constant temperature. Recent work has shown that cycled temperature regimes do not always affect physiological rates that are important in production measurement in the same way as do constant temperatures;[6-11] but no comparisons of production in constant or cycled temperatures have been carried out, even though results of these comparisons are important for prediction of the environmental impact of thermal effluents. The present work was carried out to compare the production of the snail Lymnaea obrussa Say exposed to natural temperature variation (diurnal and seasonal) with that of snails exposed to seasonal and constant temperature regimes in the laboratory.

## MATERIALS AND METHODS

Specimens of the pulmonate gastropod mollusk, Lymnaea obrussa Say, were collected on April 5, 1973 at 12°C from a pord on the Energy Research and Development Administration Reservation near Oak Ridge, Tennessee, U.S.A. The pond has a surface area of about 800 $m^2$ and a maximum depth of about 3 m. Annual temperature variation is relatively small. Pond temperatures varied over a range of about 12 to 23°C for the years 1972-1973. The population of L. obrussa is limited to the area very near shore (< 50 cm depth) where the pond plants Ludwigia sp. and Elodea sp. and their associated periphyton dominate the flora. The water temperature of this area is more variable than the rest of the pond. Maximum daily variation for the period from April through August 1973 was 5.5°C; the mean was 2.1°C.

Snails were acclimated in the laboratory at a rate of less than 1°C per day to a series of constant or varying test temperatures. The constant temperatures were 10, 15, 20, 25 and 30°C. The varying regimes included the natural field temperature in the pond (F), mean daily field temperature ($\overline{F}$), and temperatures exceeding $\overline{F}$ by 5 ($\overline{F}$+5) and 10°C ($\overline{F}$+10). The latter three regimes were maintained in the laboratory. Field temperature was monitored using temperatures recorders in cages placed beside the experimental cages in the pond. Each noon (1200 hours) the mean field temperature for the previous 24-hr period was estimated from the temperature recording. Regime $\overline{F}$ was then set at the estimated mean field temperature for the next 24-hr period, and $\overline{F}$+5 and $\overline{F}$+10 were set appropriately. Mean temperatures for the total period of observation were obtained

by averaging the daily temperatures. Mean temperatures for the varying regimes were F, 17°C; $\bar{F}$, 17°C; $\bar{F}$+5, 21.5°C; and $\bar{F}$+10, 26°C. The intervals were not exactly 5°C because of differences in the length of the reproductive period. Groups of snails at regime F were exposed to both diurnal and seasonal temperature variation, while groups at $\bar{F}$, $\bar{F}$+5 and $\bar{F}$+10 were exposed to seasonal variation alone (i.e., temperatures were changed once every 24 hr).

Flow-through cages with a capacity of about 3 liters were used to hold the snails at constant or varying temperature regimes (Fig. 1). Each cage was separated into halves by a divider and covered with commercial, clear plastic "wrap." Each side contained natural pond substrate (mud and gravel) to a depth of about 3 cm and two strands each of Ludwigia sp. and Elodea sp. Four cages, each initially containing 10 snails, were maintained at each different temperature. The cages were kept in 190-liter aquaria through which ran a constant supply of well water maintained at the proper temperature (±0.3°C). Natural day length was approximated by photocell control of fluorescent lights above the aquaria; the lights were either fully off or fully on. Initial shell lengths (SL) of snails were less than 10.0 mm in two of the cages at each temperature and greater than 10.0 mm in the other two cages. Two sets of 36 cages each were used. During the week that one set of cages was being used, the second set (without snails) was held in the pond to allow accumulation of aufwuchs and settled seston. A similar food supply was thus provided for snails at all regimes. During weekly exchange of cages, (SL the distance from the apex of the shell to the farthest point on the aperture) of live snails were measured to the nearest 0.1 mm with

with a dial caliper. Eggs and dead snails were also collected. The eggs were preserved in 12% formalin saturated with $CaCO_3$ ("neutral formalin") for later counting. The live snails were transferred to the second set of cages which had been held in the pond and the "new" cages were placed in the aquaria. The "old" cages were then placed in the pond. Observation of snails at a regime was ended arbitrarily whenever either (1) only five of the original 40 snails were left alive or (2) when no eggs had been laid at that regime for two consecutive weeks. Live snails collected at the end were fixed in 12% neutral formalin.

To estimate production, it was necessary to convert growth and egg production to equivalent units. Total organic carbon of both snails and eggs was estimated using the wet oxidation method of Russell-Hunter et al.[12] Eggs (veliger stage or earlier) collected at the beginning, at about the middle and near the end of the reproduction period at 10, 15 and 20°C were analyzed. Snails held in cages like the experimental ones were sampled before (~2 weeks post-oviposition) and at about the middle (for each regime) of the reproductive period. These snails as well as those collected after the end of the reproductive period (~2 weeks post-oviposition) were also analyzed for total organic carbon.

## CALCULATIONS

### Mortality

Mortality rates were calculated from least-squares fits to the relationships between cumulative mortality (expressed as percent of the snails present at the beginning of observation) and time. Although some escape occurred, most was during the first 2-3 weeks; therefore, these snails were not counted as part of the original number. Mortality rates for each cage were included in the calculation of production. All but six of the 31 coefficients of determination ($r^2$) exceeded 0.70. Differences in mortality rate with size and temperature were tested using analysis of variance procedures (ANOVA). For comparison of mortality rates at the different temperatures, all groups at a temperature were pooled to calculate one rate.

### Growth in Terms of Carbon

Because weekly measurements were of SL, growth data were initially computed on that basis. The dividers in the cages were not perfect, and occasionally snails would move from one side to another. However, with only five snails on each side of the cage, it was possible to follow individual snails in each group. Data were converted to the average change in SL for all the snails in the group. Growth was thus

$$G = \frac{\sum_{i=1}^{i=n} (SL_{t+1} - SL_t)}{n} ,$$

where SL is the shell length at the beginning (t) and end (t+1) of the week and n is the number of snails living at the end of the week. The

growth increments were then added to the original mean SL of the group to give the estimated mean snail size at the end of each weekly interval.

These weekly mean SL were converted to units of total organic carbon using an empirical fit to data obtained from snails sampled about two weeks before initiation of egg laying. Least-squares fits to a third-order polynomial were found for snails before, during and after oviposition. The polynomial was

$$y = \alpha\chi^3 + \beta \quad ,$$

where y is total organic carbon (μg), $\chi$ is shell length (mm), and $\alpha$ and $\beta$ are constants.

Following conversion of mean SL to μg C, the growth rate was determined by calculating the best least-squares fit to cumulative carbon content over time. In most (19/31) cages, growth continued to the end of the experiment. In cases where growth stopped during the reproduction period, the end of the growth curve was truncated until the maximum coefficient of determination was obtained and the growth rate was taken as the slope of that line. Factors affecting growth rate were then determined by ANOVA.

## Reproduction in Terms of Carbon

Egg production rate (eggs per snail per week) was expressed in terms of total organic carbon (μg) using the carbon value obtained per egg. Data in terms of numbers of eggs produced were presented earlier;[9] reproductive output in terms of carbon are presented here. Confidence limits for egg carbon production used here are based on ANOVA. Means

and 95% confidence intervals for constant temperatures of 17, 21.5 and 26°C were estimated using a least-squares fit to a polynomial

$$E[Y(T)] = \alpha + \beta T + \gamma T^2 \quad ,$$

where E[Y(T)] is the expected or mean egg production rate (μgC) at constant temperature T, and $\alpha$, $\beta$ and $\gamma$ are fitted constants. Analysis of the regression indicated that the polynomial accounted for a large percentage of the variability ($R^2$ = .91) and that the lack of fit for the quadratic equation was not significant.

**Production**

Calculation of production in terms of total organic carbon was carried out for each individual cage of a regime using the growth, mortality and egg production rates and reproductive and growth period lengths observed for snails of that cage. Calculations were based on a starting snail number of 100. Carbon production of eggs and growth were calculated separately for each week. Growth and reproductive rates (as carbon) were each multiplied by the number of live snails existing at the end of the week to estimate total carbon produced in each category for that week. The sum of each of these over the weeks that they occurred gave totals for the reproductive period. Prior to calculation of total production, total growth carbon was corrected for negative growth which occurred toward the end of the reproductive period. Comparison of "before" and "end" curves relating SL to total body carbon indicated the necessity for this correction. It was assumed that this negative growth applied to all snails dying during the period. The

number dying in each weekly period was derived from the mortality rate. Size at death for each snail was derived from the growth curve. The negative growth component was taken as the difference in carbon value predicted by the "before" and "end" curves relating SL to body burden carbon for a snail of that size. The sum of these differences for snails dying during the reproductive period as well as those (of the original 100) alive at the end of the period was then subtracted from the estimate of total carbon growth as calculated above and the result (corrected carbon growth) summed with reproductive carbon to give an estimate of total production.

## RESULTS

### Mortality

Mortality rate varied significantly with temperature ($P < .01$), but not with size ($P > .75$). Minimum mortality rate was found at 15°C and increased at both higher and lower temperatures (Fig. 2). Mortality rates for groups F and $\bar{F}$+5 appeared somewhat higher than that expected for the same mean constant temperature. Variance of mortality rate increased at higher temperatures.

### Growth

For a given SL, a snail sampled during the reproductive period had a higher carbon content than one sampled before oviposition, while a snail sampled after oviposition had a lower carbon content than before oviposition (Fig. 3). The relationships between SL and total organic carbon for snails before, during and after the reproductive period were found to differ significantly ($P < .05$). The slopes ($\hat{\alpha}$) of the relationship for snails before and during reproduction were not significantly different ($P > .5$), but both differed ($P < .05$) from the slope found for snails sampled after the reproductive period. Calculation of growth as carbon is based on the relationship between SL and carbon for the preoviposition period. The rationale for this will be discussed in a subsequent section.

Results of ANOVA indicated that size affected the relationship between temperature and growth rate. There was a significant relationship ($P < .025$) between temperature and growth rate for the small snails,

but no significant relationship ($P > .75$) between temperature and growth rate for the large snails (Fig. 4). Growth rate of the smaller snails was maximum at 15°C and was significantly lower at 10 and 20°C. Growth rate appeared to level off at about 40 µg per snail per week at temperatures from above 21.5°C. No animals lived longer than 2 weeks at 30°C. Growth rates for groups F, $\overline{F}$+5 and $\overline{F}$+10 appeared to fit the relationship indicated by the results at constant temperature. Growth rate of group $\overline{F}$ was significantly lower than F and did not fit the general relationship indicated by the curve. Conversely, growth rates for the snails with larger initial SL were not significantly related to temperature ($P > .75$). The 95% confidence interval for these larger snails was ± 41 µg C.

Temperature also affected the length of the growth period (Fig. 5a). Three groups at 15°C, one at F (17°C) and two at $\overline{F}$ were still growing at the end of the observations. Growth period for these groups may thus be somewhat underestimated. There was no difference in length of the growth period for large and small snails.

## Reproduction

Length of reproductive period varied with temperature (Fig. 5b) in a fashion similar to that of growth period. Egg production lasted longest (25 weeks) at 15°C. Ignoring Groups F and $\overline{F}$, a relatively smooth decrease in the egg-laying period is apparent with increasing temperature. The egg-laying period for groups F and $\overline{F}$ are shorter than would be expected. Egg laying is also shorter at 10°C. Three of the four groups of snails at the F regime were still laying eggs at the time of

termination. Length of the egg-laying period for F is thus an artificial underestimate of the true value.

Egg production rate (eggs per snail per week) was expressed in terms of total organic carbon (Table 2) following estimation of the mean egg carbon content (Table 1). Carbon per egg did not vary significantly with either temperature or time ($P > .05$); therefore, only one mean (22.7 µgC/egg) was used to convert numbers of eggs to weight of carbon produced. Egg production rates in terms of carbon increased with increase in temperature, but regime also affected the value of the rate (Table 2). Egg carbon production rates by groups at F (seasonal and diurnal variation) were significantly higher and by groups at $\overline{F}$ (seasonal variation) were significantly lower than for the predicted value for 17°C constant temperature ($P < .05$). Carbon production rates by groups at $\overline{F}$+5 and $\overline{F}$+10 were lower than, but not significantly different from ($P > .05$), the corresponding mean constant temperatures (21.5 and 26°C, respectively).

## Production

Both size ($P < .05$) and temperature ($P < .005$) were found to significantly affect total production (Fig. 6). Production for the individual groups (usually four at each temperature) ranged from -32.4 µg to 889.4 µg. Two negative values were found, one at a mean temperature of 25°C and the other at 26°C. Production was highest at 15°C. Production was greater for snails initially smaller than 10 mm than for snails initially larger than 10 mm. Total production for large and small snails at $\overline{F}$+5 and $\overline{F}$+10 and for the large snails at 25°C was not significantly different

from zero. Small snails at F and $\bar{F}$ appear to fit the relationship for the large snails (lower line, Fig. 6) more closely than that for the smaller snails.

# DISCUSSION

## Shell Length - Carbon Relationship

Use of the preoviposition relationship between total body carbon and SL for calculation of growth rate assumes that no reproductive carbon is present in the snails at that time. Evidence that the increase in the relation between total body carbon and SL from before oviposition ("before") to during the oviposition period (middle") is due to an increase in reproductive carbon content of the snails is circumstantial. The "middle" snails analyzed for total organic carbon averaged about 11 mm SL. The difference in total carbon predicted from "before" and "middle" curves (Fig. 1) for an 11 mm snail is 396.4 µg. A weighted mean for weekly production of egg carbon based on the number of snails analyzed from each temperature and the corresponding carbon per adult per week value from Table 2 gave a mean and 95% confidence interval of 378.3 ± 40.8 µg. The most logical reason for the lack of significance between these figures is that the "middle" snails contained eggs and "before" ones did not. Increase in reproductive tissue is not limited to eggs (sperm must comprise some of the increase) or even to gametes. However, few snails would probably be full of completed egg masses; egg membranes are added in the oviduct. The closeness of the carbon values (378 and 396) may thus be somewhat fortuitous, but the increase from "before" to "middle" periods probably is due mostly to reproductive carbon.

Depletion of body carbon apparently occurs (1) rapidly and (2) near the end of the reproductive period. Both of these assumptions are critical to use of the preoviposition curve in calculating growth rate.

The rapidity with which the decrease occurred in snails at 25°C and F+10°C (3 weeks or less) indicates the probability of the first assumption. As for the second, there is only one other explanation for the carbon increase from "before" to "middle": reproductive carbon is stored prior to initiation of oviposition, and egg production continues until it is depleted. However, this would require that snails of 8 mm SL store double their body carbon in about two weeks. This does not seem very likely. Rapid depletion in the last weeks of oviposition is more reasonable.

The changes in the relation between total carbon and SL have implications for future studies of production in populations which are short-lived and have a relatively prolonged reproductive period. The continuous intake of food and release of eggs indicate that measurement of snail weight or carbon change over the reproductive period underestimates production since only the reproductive carbon contained by the snail at the moment would be measured. Thus, a constant weight could be measured over a period of weeks while the carbon released in the eggs could be over 500 µgC per snail per week (at 25°C). The amount of error involved in the production estimate would depend on the length of the reproductive period and the difference between the eggs (or sperm) held in the animal at one time and the total released. To avoid error this requires that organisms of this type be treated as having continuous reproduction.

## Effect on Production

### Size

The lower production of large snails in relation to small ones implies a decreased ability to obtain food and/or a decreased efficiency in utilizing it. The difference reflects differences in growth since no relation was found between size and either mortality or egg production. Evidence exists that feeding rate,[13] assimilation efficiency,[9] growth rate[14] and conversion efficiency[15] can decrease with increasing animal size, but data presented here do not allow decision as to the applicability of any or all of these to Lymnaea.

### Temperature

Production exhibits the general rule of increase with temperature to a maximum followed by a decrease at higher temperatures.[16] Growth rate, survivorship (inverse mortality) and lengths of growth and reproductive periods also follow this rule. All are optimal at 15°C. Other Lymnaeid species have also been found to have optima between 12 and 20°C.[17-18] These optima are relatively low compared to other snails. Conversely, egg production rate was found to increase from 10 to about 25°C. Since no eggs were laid at 30°C, the decrease following an optimum somewhere near 25°C must have been rapid. This increased egg production rate at the high temperatures was, however, accompanied by a shortened reproductive period so that total egg production was maximum at 15°C. The effect of temperature on production probably revolves around differential effects on physiological rates such as feeding[13] and respiration, both of which strongly influence various ecological

efficiencies. The concurrence of all the optima at 15°C suggests a rather stenothermal organism which would be highly susceptible to thermal pollution. This may account for its wide range and sporadic occurrence.[19]

Temperature Regime

Comparison of the production estimates at the different temperature regimes indicates that some factor connected with exposure to daily and/or seasonal regimes negatively influences production. There is little question that the decrease in production at $\overline{F}$ is real; growth and reproduction were consistently and significantly lower than at the constant regime. However, results at $\overline{F}+5$ and $\overline{F}+10$ suggest that increase in temperature decreases the difference between the constant and seasonal regimes. Production at F is apparently also low. However, the significantly greater egg production and growth rates found at F, as compared to $\overline{F}$, imply that there are differences in the effect of these two regimes even though the production values were not significantly different. The decrease in production is thus not simply a result of temperature variation per se, but is influenced by the type of variation as well.

The complexity of the effect of regime on production is emphasized by the differences in response of some of the important parameters of production. Rates of growth and reproduction were affected differently by the different regimes. Regime affected only the rate of growth of small snails at $\overline{F}$ (a decrease). On the other hand, regime strongly affected egg production rate, with snails at F laying eggs most rapidly and those at $\overline{F}$ least rapidly. Burky[20] found that egg-laying intensity of Ferrissia rivularis, a pulmonate snail, was directly related to short-term temperature fluctuations. The diurnal regime may be a

reproductive stimulus in an area of relatively small temperature change such as the pond. However, this would not account for the lowered egg production rate at $\overline{F}$ or the differences in growth rate between groups at F and $\overline{F}$. The similarity in growth and reproductive period lengths and the differences in mortality are also difficult to fit into an hypothesis for regime effect.

The complexity, as well as the occurrence, of the above effects indicates need for caution in extrapolating production data obtained under constant temperature conditions to field situations. Snails at $\overline{F}$ had lower growth rates, shortened growth and reproductive periods, and lower reproduction rates than those at constant temperature. They also had lower growth and reproductive rates than those at F. These differences imply that an organism which has evolved under relatively strong diurnal temperature regimes may be dependent on them for certain facets of its physiology.

## Applicability of Production vs Temperature Data

Data on production at different temperatures are useful in predicting the impacts resulting from thermal releases to the environment. Accurate predictions are important in decision-making processes (e.g., siting power plants). At present, it is not possible to accurately predict effects on the ecosystem as a whole; and predictions based on individual tolerance data bog down in the extrapolation of percent mortality. Interpretation of effects on populations, especially of important or representative species, is probably the best available alternative. Population production is of importance for prediction because it gives a first estimate of the importance of the population to the ecosystem. In the case

of L. obrussa adults, increase in summertime environmental temperature would probably result in a decrease in production since the optimum temperature (about 15°C) is so low. The relative effect on the population would vary with the actual temperature change and the range over which it occurred. A small change occurring near 25°C could have a strong effect on the population.

The results presented here apply to L. obrussa adults exposed to different temperatures as adults. Pre-reproductive exposure to the same temperatures could also affect fecundity.[16] Studies are needed comparing total lifetime population production with both constant and varying temperature regimes to yield information of importance in predicting thermal impact.

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## Figure Titles

Figure 1. Protocol for the experiment involved four cages at each temperature regime and two sets of cages. Measurements of shell length and count of eggs laid and snails dead were made each week. Each set of cages was stored in the pond on alternate weeks to collect natural food. For further discussion see text.

Figure 2. Mortality rate and 95% confidence intervals shown for the various mean temperatures. Confidence intervals were calculated from a least-squares fit of % total snails (of those alive at the start) dead versus time. The line connects mean mortality rates at constant temperature.

Figure 3. Relationships between shell length and total body carbon found by fitting a third-order polynomial $y = \alpha \chi^3 + \beta$ ($y$ = total body carbon and $\chi$ = shell length) to data for snails sampled two weeks pre-oviposition ("before"), during oviposition ("middle") and two weeks post-oviposition ("end"). Curve parameters are also shown.

Figure 4. Mean carbon growth rate and 95% confidence interval for the various temperatures for two size classes of snails. Results for the varying temperature regimes are shown at the mean temperature over the reproduction period. Lines connect the mean rate obtained for each temperature. Confidence intervals (C.I.) were calculated from the pooled error mean square obtained from one-way ANOVA for each size. C.I. (not shown) for the large snails was ± 41 μgC.

Figure 5. Mean weeks of (a) growth and (b) reproduction during the reproductive period at the various temperatures. Times for the varying temperatures are shown at the mean temperatures for the reproductive period.

Figure 6. Mean total production and 95% C.I. in terms of carbon at the various temperatures for two size classes of snails. Production for the varying temperatures is shown at the mean temperature for the reproductive period. Points for large snails at F and $\overline{F}$ (17°C) have been displaced slightly for clarity. Confidence intervals for large and small snails were calculated separately from the error mean square found through one-way ANOVA. Mean production values at constant temperatures are connected by the upper line for small snails and by the lower line for large snails.

Fig. 1

ORNL-DWG 74-7854R

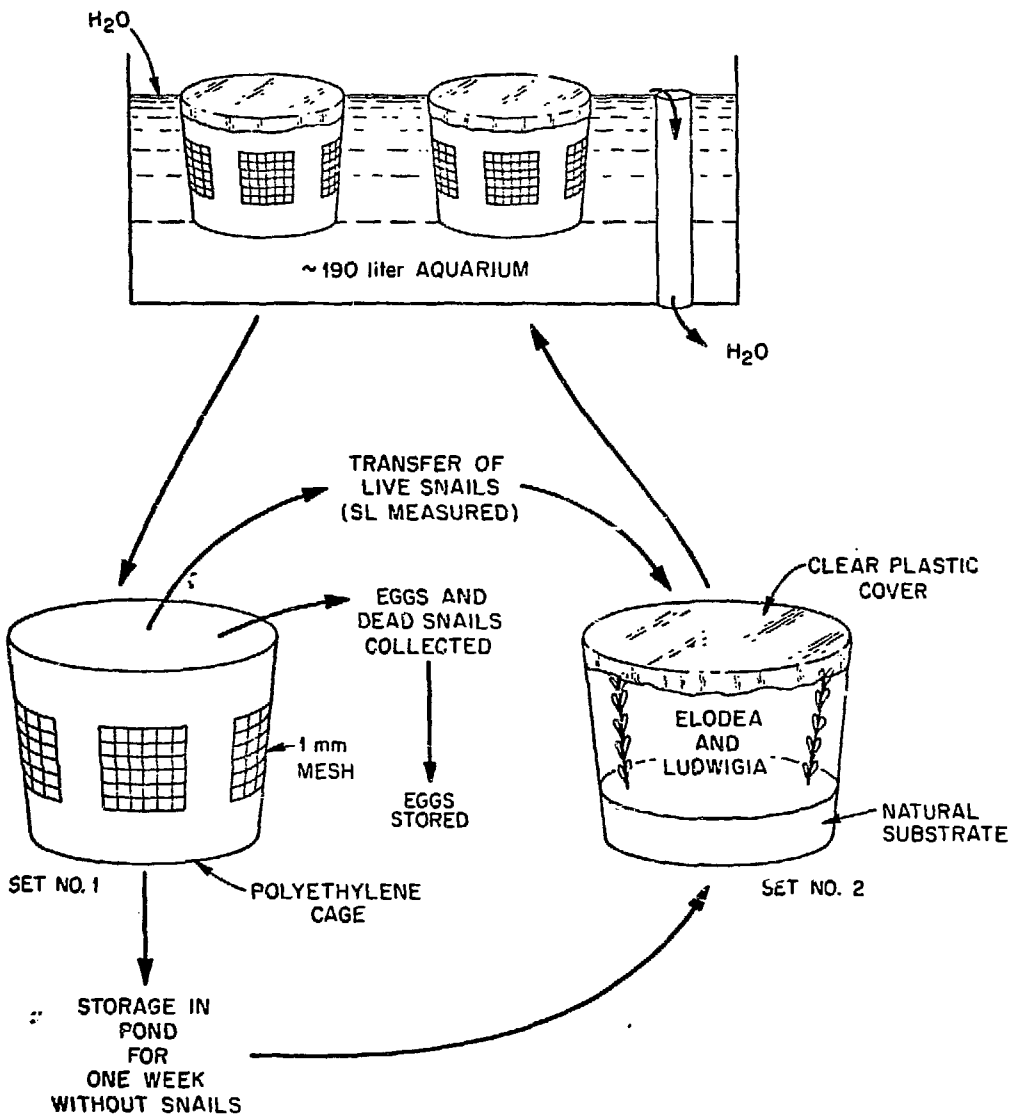


Fig. 2

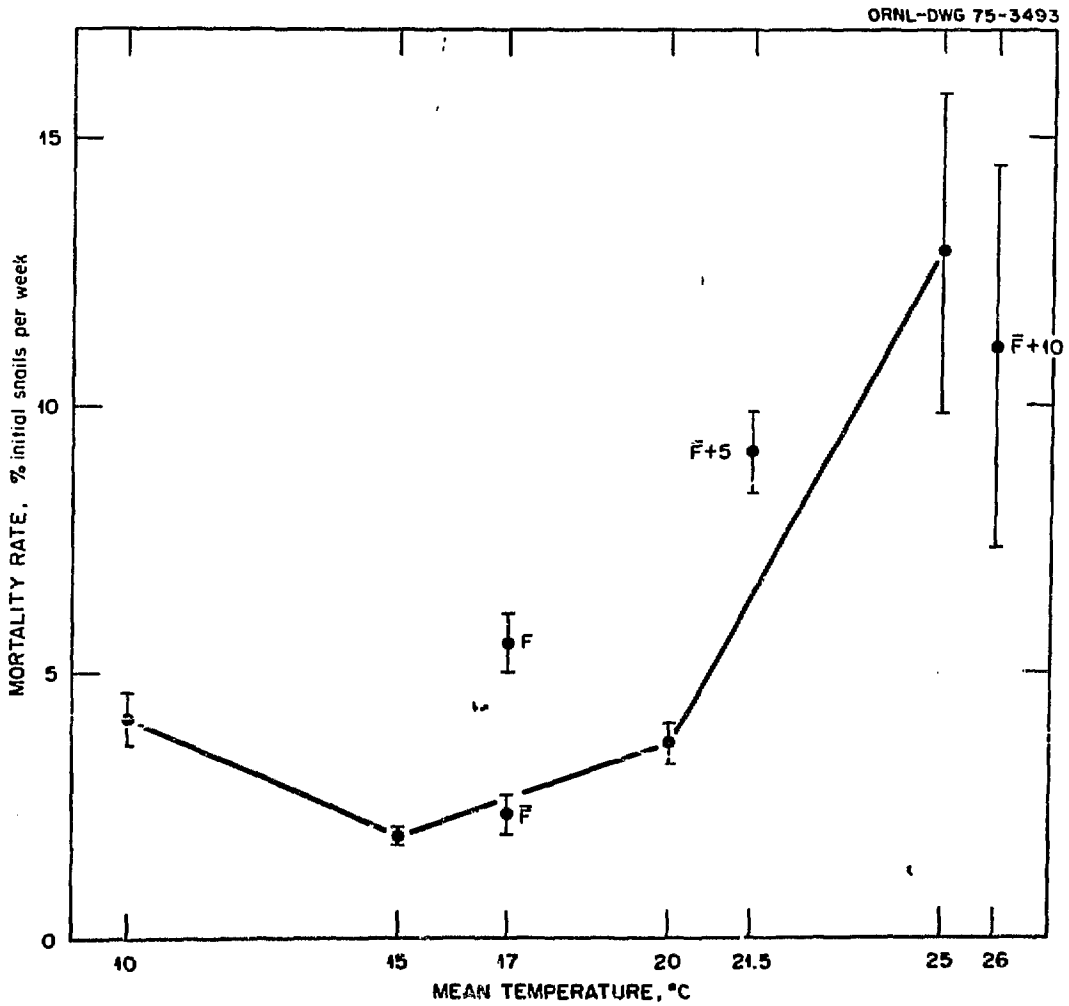

ORNL-DWG 75-3493
MORTALITY RATE, % initial snails per week
0
5
10
15
10
15
17
20
21.5
25
26
MEAN TEMPERATURE, °C
F
F
F+5
F+10

Fig. 3

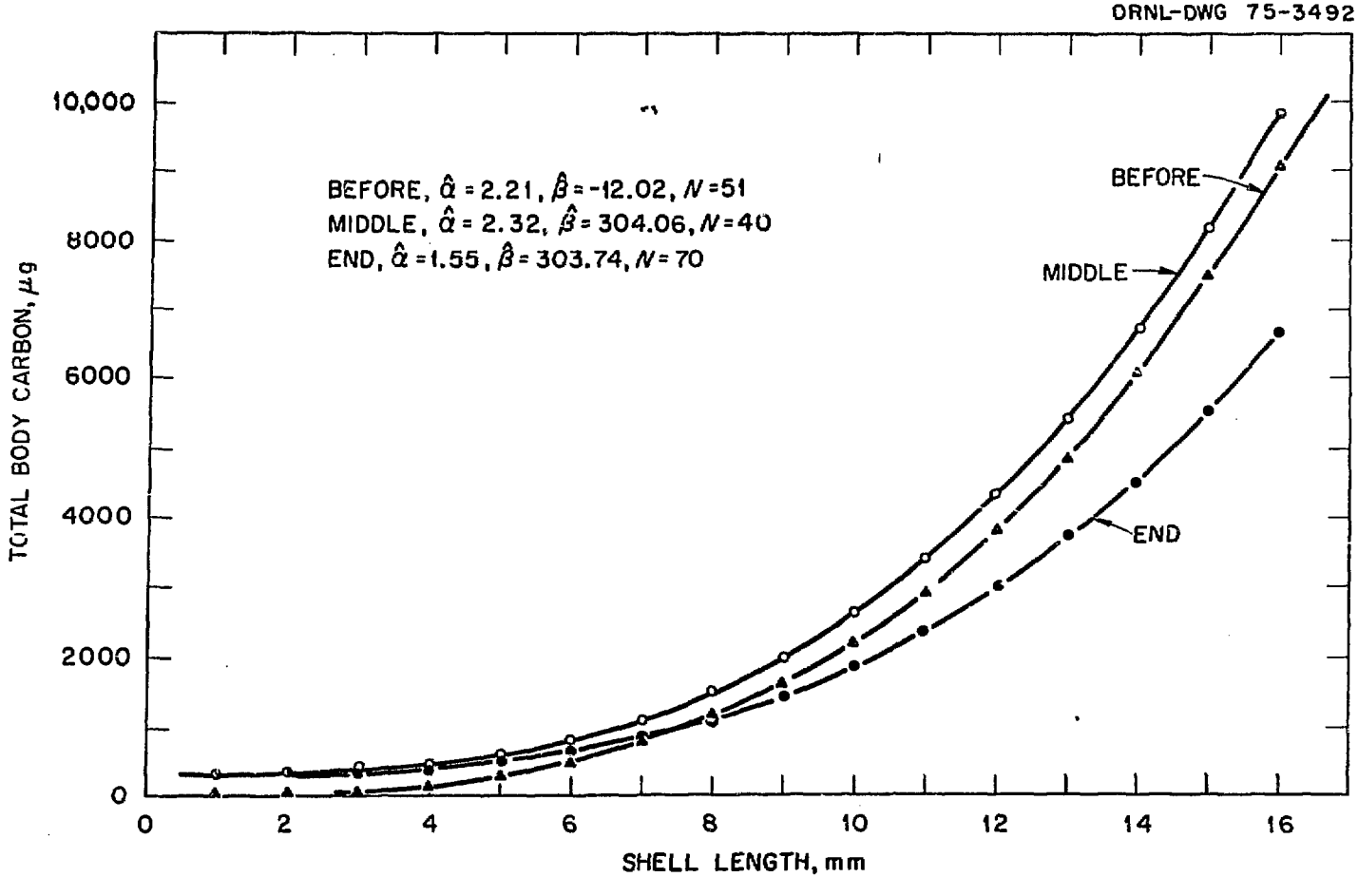
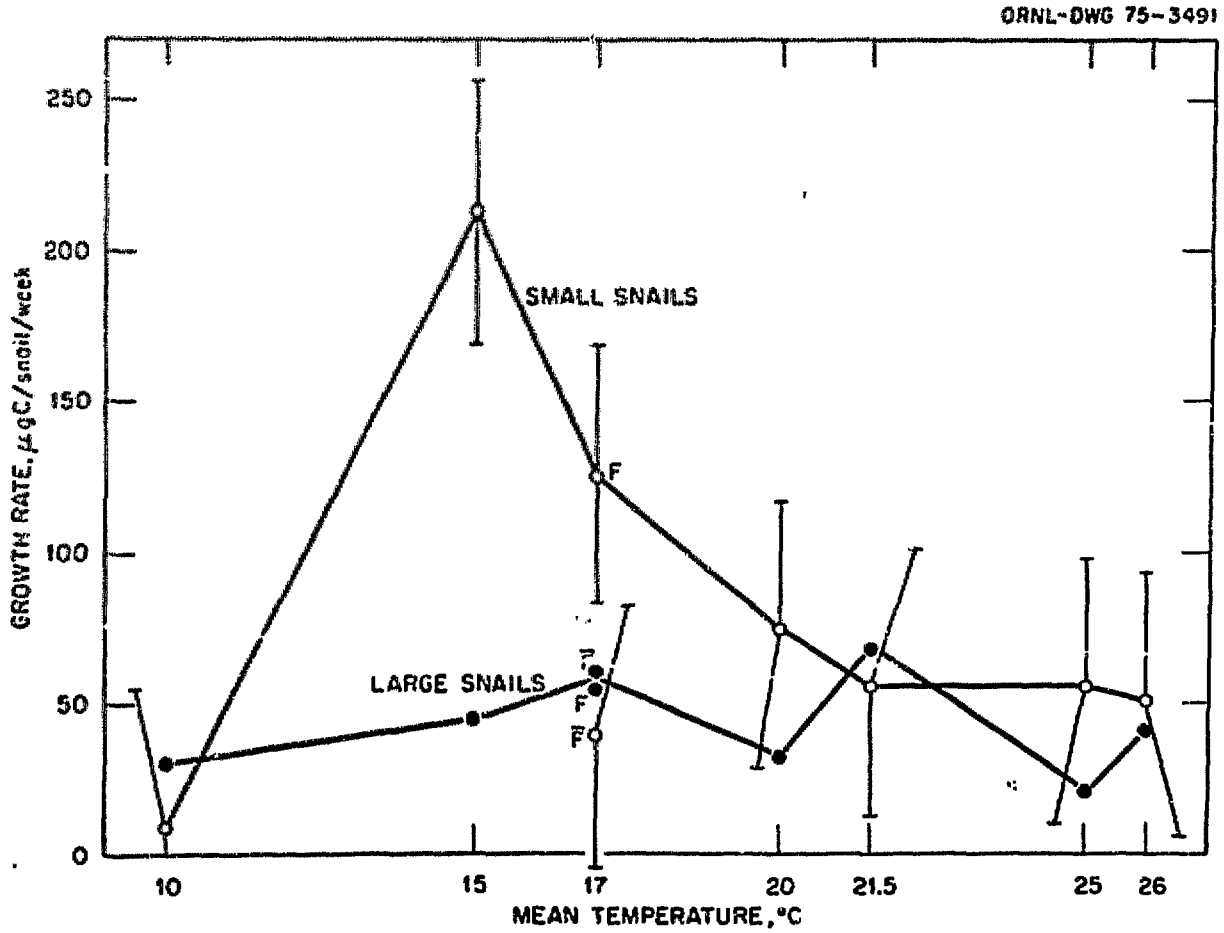
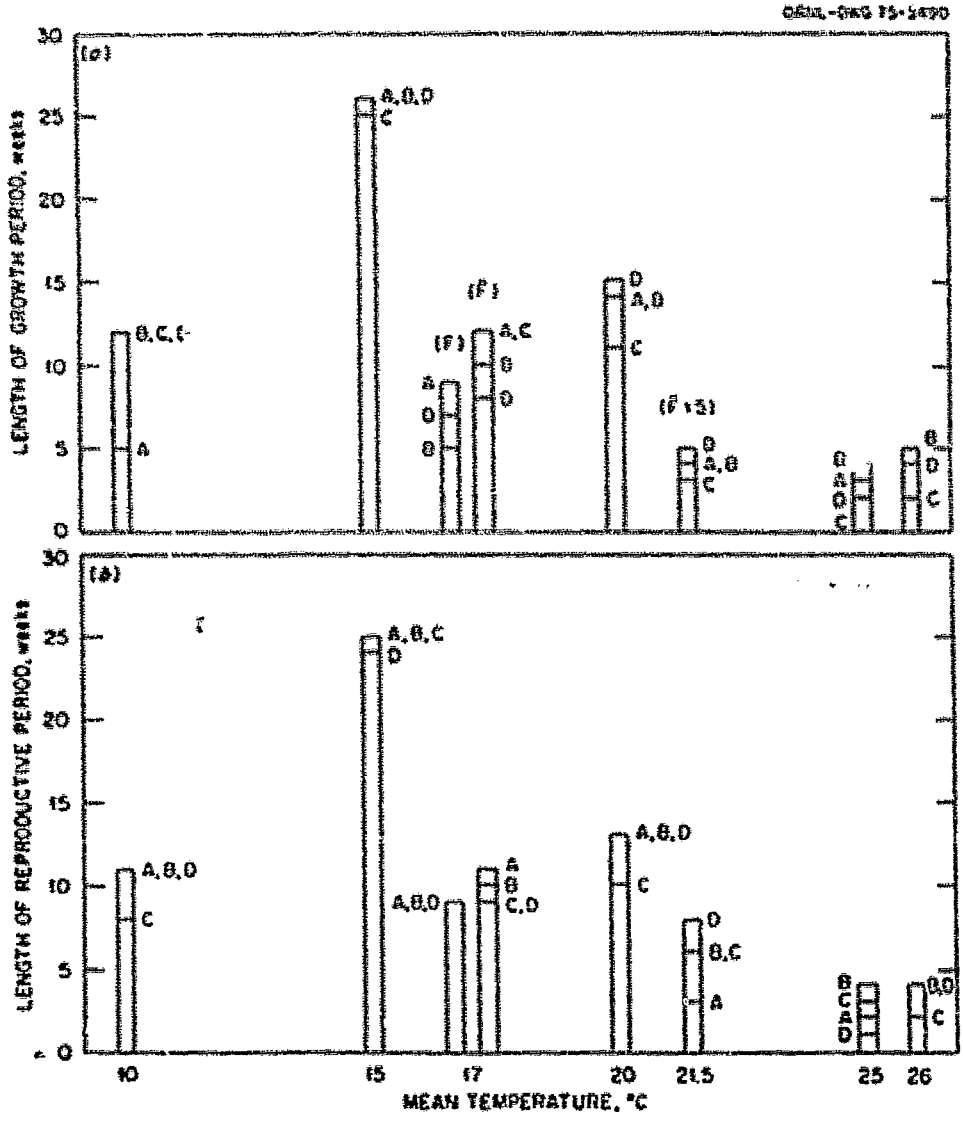

ORNL-DWG 75-3492
BEFORE, $\hat{\alpha}$ = 2.21, $\hat{\beta}$ = -12.02, $N$ = 51
MIDDLE, $\hat{\alpha}$ = 2.32, $\hat{\beta}$ = 304.06, $N$ = 40
END, $\hat{\alpha}$ = 1.55, $\hat{\beta}$ = 303.74, $N$ = 70
BEFORE
MIDDLE
END
TOTAL BODY CARBON, μg
SHELL LENGTH, mm
0
2000
4000
6000
8000
10,000
0
2
4
6
8
10
12
14
16

Fig 4


ORNL-DWG 75-3491
GROWTH RATE, μgC/snail/week
250
200
150
100
50
0
SMALL SNAILS
LARGE SNAILS
F
F
F
10
15
17
20
21.5
25
26
MEAN TEMPERATURE, °C


ORNL-DWG 75-1490
(a)
LENGTH OF GROWTH PERIOD, weeks
30
25
20
15
10
5
0
A,B,D
C
B,C,D
A
(F)
A,C
B
D
(F)
A
D
B
(F)
D
A,B
C
(F)
B
A,B
C
B
A
D
C
B
D
C
(b)
LENGTH OF REPRODUCTIVE PERIOD, weeks
A,B,C
D
A,B,D
C
A,B,D
A
B
C,D
A,B,D
C
D
B,C
A
B
C
D
C
10
15
17
20
21.5
25
26
MEAN TEMPERATURE, °C

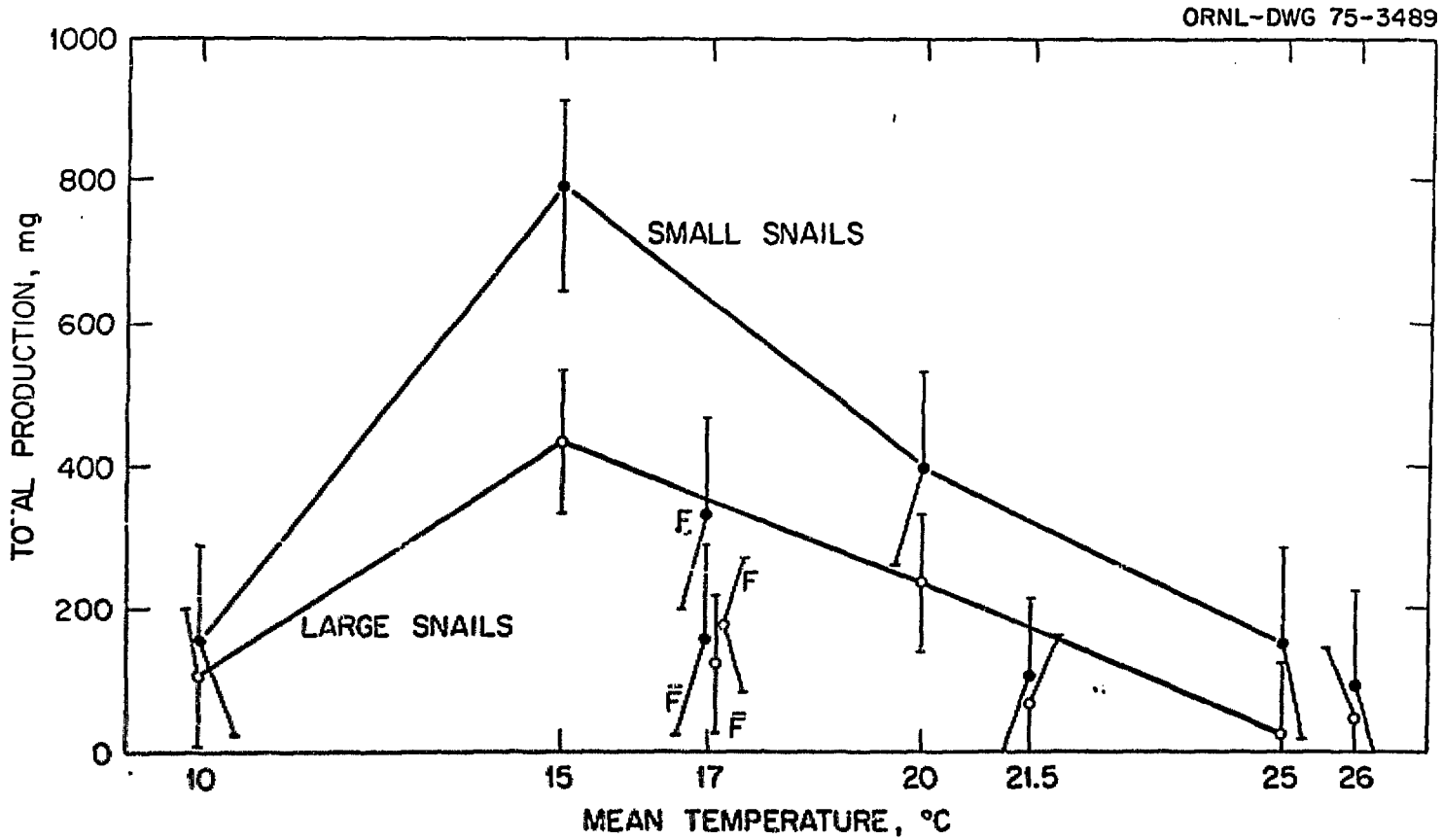

ORNL-DWG 75-3489
1000
800
600
400
200
0
TOTAL PRODUCTION, mg
SMALL SNAILS
LARGE SNAILS
F
F
F
F
10
15
17
20
21.5
25
26
MEAN TEMPERATURE, °C

TABLE 1. Mean carbon (μg) per egg and 95% confidence intervals for eggs collected at different times during the period of oviposition at three temperatures.

| Temperature | Period[1] | | |
|---|---|---|---|
| | Early | Middle | Late |
| 10°C | 22.7 ± 5.4 | 28.2 ± 10.1 | 22.4 ± 7.4 |
| 15°C | 22.7 ± 2.6 | ——— | 19.7 ± 4.6 |
| 20°C | 24.8 ± 8.8 | 18.1 ± 3.27 | 19.0 ± 4.4 |
| | Grand Mean 22.7 ± 1.91 | | |

[1]Early, middle and late are in relation to the reproductive period at the temperature given; actual dates of sampling differ.

TABLE 2. Rate of Egg Production (μgC/snail/week) at different temperatures and temperature regimes.

| Regime | Mean Temperature | | | | | | |
|---|---|---|---|---|---|---|---|
| | 10 | 15 | 17 | 20 | 21.5 | 25 | 26 |
| Diurnal | | | 406[2] | | | | |
| Constant | 208 | 259 | | 322 | | 507 | |
| Constant[1] | | | 273[3] | | 379[4] | | 540[5] |
| Seasonal | | | 166 | | 275 | | 493 |

[1] Predicted from polynomial - see text.

[2] Except where indicated 95% CI = ±86 µgC.

[3] 95% CI = ±33 µgC.

[4] 95% CI = ±37 µgC.

[5] 95% CI = ±57 µgC.