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EFFECTS OF STARVATION ON THE GROWTH AND FECUNDITY OF THE SNAIL *SUCCINEA DAUCINA:* INTERPRETATION USING GROWTH MODELS

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Abstract. The food-dependent changes in the population growth and fecundity of land snails are the primary indicators of their adaptation to environmental changes. Starvation-based changes in the growth and fecundity of the land-snail *Succinea daucina* (Pfeiffer,1855) (Gastropoda: Succineidae) substantiated this proposition. In experimental conditions, laboratory-reared and newly hatched snails were provided food regularly (control) and at a gap of 1 to 6 days per week (treatment). The increment of shell length and biomass were used as the indicators of individual growth, while the oviposition rate was considered an indicator of fecundity. A compliance with the von Bertalanffy growth equation ($L_t = L_\infty(1 - e^{-k(t - t_0)})$) was observed for the increment of shell length in all instances, but the magnitude of b (regression coefficients), $L_{maximum}$ and L_∞ (maximum and asymptotic length) decreased with increasing growth rate, as the starvation period extended. A special emphasis on b was given to predict a change in the shape of snails with starvation. Similar observations were made for fecundity, where the oviposition rate was higher in the snails that had regular food availability. As the starvation duration extended, population growth and fecundity showed a negative correspondence. Such variations in growth and fecundity reflect the specie's adaptation to cope with the environmental odds.

INTRODUCTION

Organismal growth deduced in terms of the increment in length and biomass can be explained through mathematical expressions. Amongst several mathematical models, the von Bertalanffy growth function proposed by Ludwig von Bertalanffy (von Bertalanffy 1934, 1957) enables growth prediction if length and biomass are recorded for a particular time period. As organismal growth reflects environmental adaptation, the modelling of the growth pattern enables the portrayal of the expansion of biomass and length as traits defining the fitness aspects of the species.

The application of the von Bertalanffy growth function (VBGF) appears to be a feasible option to portray growth. This is substantiated through the studies using body length and biomass as input variables in fishes (Hesp et al. 2004; Kumari et al. 2018), molluscs (Ismen et al. 2007; Fontoura-da-Silva et al. 2016) and crustaceans (Costa et al. 2020; Aydin and Tıraşın 2023). The pattern of changes in body length and biomass over time enables portraying the growth of the individuals in a population, which bears application in species conservation as well as interpreting pest biology. As indicators of individual growth, the changes in length and weight are therefore useful and can be deduced with precision following the VBGF. Any factor altering growth can be assessed through changes in length and biomass and therefore can be presented through the VBGF. In the present instance, the growth of the land snail *Succinea daucina* (Pfeiffer, 1855) (Gastropoda: Succineidae) was deduced using shell length and biomass as the indicators against a gradient of fasting conditions. Using the VBGF, the growth pattern was described and compared for the varying levels of starvation. Since *S. daucina* is a common snail occurring in the varied habitats in India (Raut et al. 1997; Nandy et al. 2023), the growth was easily monitored in the laboratory through monitoring and subsequently evaluated through the VBGF model.

Alike all animals, in snails, a variation in the availability of food and resources would lead to a deviation from the general growth. Empirical studies on the food-induced variation in growth and fecundity in different snails support this proposition (Butler 1976; Moriarty 1978; Haniffa 1982, 1987a, b; Perry 1987; Vianey-Liaud and aLancastre 1994). Two field experiments on *Helicella virgata*, one with increasing density of snails leading to the absolute food scarcity, and the second with food quality declining, resulted in the reduced growth, reproduction and survival (Butler 1976). In the fresh-water gastropod *Planorbarius corneas* (L.), shell diameter and fresh weight decreased proportionally with the starvation duration (Moriarty 1978). In the apple snail *Pila globosa,* starvation accelerates metabolism that reduces dry weight (Haniffa 1987). The fasting-dependent changes in growth and fecundity were observed for the freshwater snail *Biomphalaria glabrata* subjected to intermittent fasting (Vianey-Liaud and aLancastre 1994). In compliance with the observations made on these snails, in the present instance, the growth of the snail *S. daucina* was observed under a different intermittent feeding regime. The exposure to the varying levels of starvation may affect the growth and fecundity of the snails and therefore would provide a basis to understand the impact of the feeding on the growth and reproduction in the snail. Using the VBGF model as a standard to estimate the growth of the snails and subsequently a comparison of the growth at the different levels of the treatment would provide insights into the adaptive nature of the snails. Variation in the growth in snails and other species can be standardized through the application of the VBGF. A comparison of the growth of different land snails can be made using the VBGF as a standard equation. For a single species, the variations of growth at the intraspecific level can be made. Hence, as shown in the present instance, a comparison of growth and fecundity under varying treatments could be made.

The growth and fecundity of the land snails are the primary indicators of the fitness at the individual and population levels (Dillen et al. 2010; Proćków et al. 2013; Astor et al. 2015; Nandy and Aditya 2022a, b; Nandy et al. 2023). A reflection of adaptation to the existing habitat conditions can be observed from the growth pattern and the oviposition rate in the snails. A shortage of food resource availability or intermittent starvation may induce a change in the growth and fecundity in the snails (Butler 1976; Vianey-Liaud 1984; Vianey-Liaud and Dussart 1994; Gosselin and Chia 1995). Since *S. daucina* and similar land snails thrive in conditions where the food resource availability is partly affected by the habitat permanence (Raut et al. 1997; Nandy and Aditya 2022a, b; Nandy et al. 2023), the corresponding effect on the growth and fecundity could be deduced through the present study using the VBGF model. A link between the extent of starvation and the deviation from the normal growth could be judged through the application of the VBGF model, thereby reflecting the adaptations of the snail *S. daucina.* An overview of the changes in the key events of the life history like growth and fecundity in response to starvation or shortage of food supply can be portrayed using the parameters of the VBGF model. The inference from the present study may prove useful for understanding the adaptations of land snails requiring conservation effort or biological control.

MATERIALS AND METHODS

The snails *S. daucina* were collected from the different habitats of Khardah and Dunlop, Kolkata, India, during February 2023 and brought to the laboratory for the rearing following a standard protocol (Nandy and Aditya 2022a, b; Nandy et al. 2023). The snails were reared in three glass terraria (42 cm × 20 cm × 12 cm) with 1 cm moist soil (mixture of cocopeat, soil and sand in equal portions) as the base with the colony of mosses (1 cm^2 substrate) spread at the oviposition sites and two beakers of 25 ml filled with tap-water to maintain humidity inside the terrarium. Each terrarium was covered with a perforated polythene sheet and placed near the window for sunlight. Snails were fed slices of cucumber, bottle gourd and lettuce *ad libitum* and cleaned every 24 hours for the faecal matter and rotten food. Subsequently, after adding adequate food and sprinkling water in the terraria, the eggs, if any, were collected and placed separately in small plastic containers (100 and 200 ml volume) with 1 cm moist soil at the base. After counting, the collected eggs were separated and allowed to develop into juveniles.

The individuals reared continuously for 15 days as a large population and then emerging from the eggs (F$_1$-generation; < 12 h old) were used in the experiment. An adequate number of juveniles (7 treatments × 6 snails × 3 replicates = 126 × 2 = 252; 126 for one experiment, and another 126 for the reserve) obtained through rearing were used for the experiment. Most of *S. daucina* died due to desiccation, as they moved haphazardly in search of food.

The juveniles (F$_1$-generation) were put in seven different treatments, with three replicates for each, in 500 ml containers with about 1 cm moist soil as the base and covered with perforated polythene sheets. In the treatments, the replicate receiving food every day was considered a control set, while the rest were subjected to starvation for one to six days. In addition, at least three containers for each of these fasting regimes were present to serve as a reserve to be replaced in case of death of an individual in a container, such that the whole set is never less than the required number of individuals. In all instances, they were fed as above.

All the experimental containers were monitored every 24 hours for observing the number of snails present or the required food to be added as per the fasting regime. The shell length and biomass were noted at the end of each week for the consecutive 12 weeks, whereas the collection of eggs along with the number of eggs oviposited in a clutch and the total number of clutches were noted down every 24 hours. Fecundity was assessed by counting the total number of eggs, total number of clutches and eggs/clutch. The eggs were counted and collected after each week for each group. In order to estimate the shell shape, the measurements of shell length (SL) (from the apex to the tip of the last whorl in mm) were taken using a divider and recorded to the nearest 0.1 mm scale, and the biomass (BW) of a live snail specimen was recorded using a pan balance (Citizen®, India) to the nearest 0.1 mg. The experiment was conducted on and from 24 March 2023 till 2 June 2023.

The number of individuals survived in the control and each treatment were subjected to Kendall's coefficient of concordance (W) to assess the significant effect of food on growth. The data on the shell length and biomass increments were subjected to the Kruskal-Wallis test, with the age (in weeks) and duration of starvation (in days) as the explanatory variables, and the shell length and biomass as the response variables. Similarly, the data on the eggs collected per week was also subjected to the Kruskal-Wallis test, as they did not comply with normality (Zar 1999).

Theoretical framework for VBGF

The equation proposed by von Bertalanffy (von Bertalanffy 1934) is

$$\frac{dm}{dt} = E - km \, , \tag{1}$$

where E is the constant related to anabolism, k is the constant related to catabolism, and m is body-mass (von Bertalanffy 1968).

Equation (1) on integration becomes

$$m = \frac{E}{k} - (\frac{E}{k} - m_0)e^{-tk} \tag{2}$$

when integrated from m_0 to m, and time from zero to t_0, or

$$m = \frac{E}{k}(1 - e^{-k(t-t_0)}) \tag{3}$$

when integrated from $m = 0$ to m, and time from $t = t_0$ to t.

We are considering a similar form to Equation (3) for our analysis as observed in *Drepanotrema lucidum* and *D. depressissimum* (Rumi et al. 2007), *Siphonaria compressa* (Allanson and Msizi 2010), *Trochus niloticus* (Tuhumury 2013), *Helix aperta* (Benbellil-Tafoughalt and Koene 2015), *Terebralia palustris, T. semistriata* and *T. telescopium* (Wells and Keesing 2019), and *Allopeas gracile* (Nandy and Aditya 2022a, b). However, an alternative approach is elaborated in the attached supplementary file (Supplementary File 1), which incorporates growth loss.

Growth analysis

The proposed von Bertalanffy growth model equations are

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \tag{4}$$

for shell length in mm at time t and

$$BW_t = BW_\infty (1 - (e^{-k(t-t_0)})^b \tag{5}$$

for biomass in mg at time t, where L_t and BW_t are shell length in mm and body weight in mg, respectively, at a specific time t. L_∞ is asymptotic length, k is the growth rate coefficient that describes the pace of an organism to attain its asymptotic size, t_0 is hypothetical time when size is zero. The length and biomass are subjected to power regression, as power regression fits best to the data which curves at a point. With increase in length, biomass cannot be enormously linearly increased to maintain a balance between anabolism (builds biomolecules and accumulates them to increase weight) and catabolism (breaks biomolecules to perform physiological functions like cell division that increases length):

$$BW_t - a.L_t^b \text{ (Froese 2006)}, \tag{6}$$

where a and b are the regression coefficients, a is a multiplier, and b is power. For assessing the biomass, the term in parentheses in Equation (4) is raised to the power of b, and

$$BW_\infty - a.L_\infty^b \tag{7}$$

In experimental conditions, laboratory-reared and newly hatched snails were provided food regularly (control) and at a gap of 1 to 6 days (treatment). The increment of shell length and biomass were used as indicators of growth, while the oviposition rate was considered the indicator of fecundity. L_{max} and L_∞ are considered to be different parameters in this paper. As the snails were studied under food treatment for 12 weeks, the maximum length attained after 12 weeks is denoted as $L_{max,}$ and L_∞ is the asymptotic length as considered in other literatures.

RESULTS

In experimental conditions, a few individuals of *S. daucina* died at regular intervals, providing an impression of the starvation-dependent death. A comparative account shows that the survival of the individuals varied with the length of starvation. With an increase in the time interval, the number of individuals dying increased with

Table 1. Numbers of dead *S. daucina* during the experiment with statistical analysis for survival by Kendall's coefficient of concordance (W) after a rank transformation, showing starvation does not affect growth significantly.

Week	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Control	0	0	0	0	0	0	0	0	2	7	8	10
Treatment 1	0	0	0	0	0	0	0	0	2	5	8	9
Treatment 2	0	0	0	0	0	0	0	0	0	0	3	11
Treatment 3	0	0	0	0	0	0	0	0	1	4	9	14
Treatment 4	0	0	0	0	0	0	0	0	2	6	16	17
Treatment 5	0	0	0	0	0	0	0	0	1	10	12	16
Treatment 6	0	0	0	0	0	0	0	2	0	9	11	17

Kendall's $W = 0.0195$
$P = 0.999$

the age of the cohort, as shown in Table 1. The Kendall's coefficient of concordance (W) following rank transformation showed that the survival did not vary with the treatments significantly (Kendall's W = 0.0195; $P = 0.999$).

The growth of the snails based on shell length and biomass showed a gradual increase with time. However, with the increase in the duration of starvation, there was a decrease in growth both in terms of length and biomass. The growth pattern followed the von Bertalanffy growth function in all instances, but the magnitude of $L_{maximum}$ (L_{max}) and L_∞ decreased with increased growth rate coefficient (k) as the starvation period extended.

The initial increase (Figures 1 and 2) in shell length and biomass for all the groups under study suggests continuous growth, despite varied levels of starvation. However, the variations in the relative increment of length and biomass in the seven groups were prominent reflecting that the magnitude of growth reduced to starvation gap. The data were subjected to Kruskal-Wallis test (as the data did not comply to Shapiro-Wilk test for normality), taking age (in weeks) and duration of starvation (in days) as explanatory variables, which shows the presence of significant difference ($P < 0.05$) for six treatments with the control (K = 955.872, df = 90 for shell length, and K = 968.165, df = 90 for biomass). A post hoc multiple comparison following Steel-Dwas-Critchlow-Fligner method yielded significant differences ($P < 0.05$) in most of the treatments (days of starvation).

For all the seven instances, the populations followed the VBGF curve (Figures 3 and 4), but with decreased maximum length and weight attained after 12 weeks of the study (Figure 5). The growth of the land snail *S. daucina* was affected by the extent and length of the starvation period, reflected through the increment in the shell length and biomass of the individuals over time. It was observed that $L_{maximum}$ (Figure 5a and c) and $B_{maximum}$ (Figure 5b and d), i.e. the shell length and biomass of the snails after 12 weeks, declined steadily with the increasing gap of starvation, indicating the dependence of growth on the amount of nutrients assimilated, which converted into physiological growth. Apparently with the increase in the tenure of starvation (from no starvation through starvation for a period of 6 days), the overall growth varied significantly. While for a particular starvation treatment, shell length and biomass increment corresponded positively with time (age in weeks), the extent of the increment decreased with the increase in the starvation period. The values of the growth rate coefficient (k) increased with the duration of starvation (Figure 6a) while L_∞ declined (Figure 6b) with increasing duration of starvation. The statistical comparison through the paired t-test of observed and expected values of shell length and biomass did not show significant difference (Table 2 and 3). The k is directly proportional to the duration of starvation (Figure 6a),

Table 2. The results of t-test for the comparison of expected and observed values of shell length in *S. daucina* observed in different weeks. The non-significant differences of shell length justify the fit to the von Bertalanffy growth equation by the concerned snail group.

Gap of feeding	t-value	Df	P value
0	0.16	24	0.87
1	0.1	24	0.92
2	0.08	24	0.93
3	0.07	24	0.94
4	0.01	24	0.99
5	0.03	24	0.97
6	0.01	24	0.99

Table 3. The results of t-test for the comparison of expected and observed values of biomass in *S. daucina* observed in different weeks. The non-significant differences of biomass justify the fit to the von Bertalanffy growth equation by the concerned snail group.

Gap of feeding	t-value	Df	P value
0	0.11	22	0.91
1	0.17	22	0.87
2	0.05	23	0.96
3	0.07	23	0.94
4	0.11	24	0.92
5	0.08	24	0.93
6	0.09	23	0.93

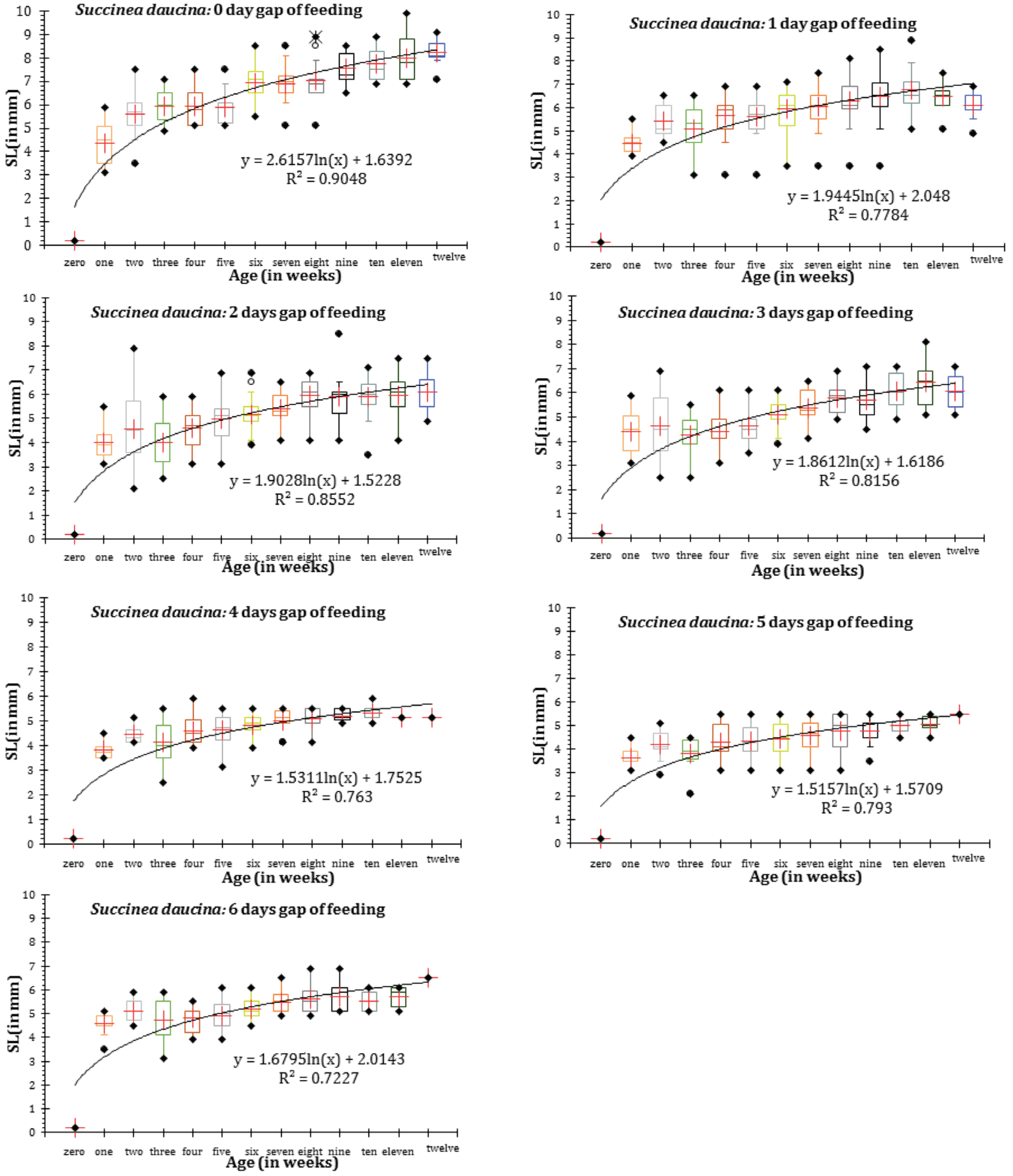

Figure 1. The box-plot representation of shell length increment of *S. daucina* in consecutive weeks for all experimental treatments: box plot – median, upper and lower quartiles; filled circles – extreme values; open circles – outliers; cross – mean value.

whereas L_∞ declined with increasing starvation gap (Figure 6b). When plotted against starvation gap, k and L_∞ showed a polynomial regression pattern ($R^2 = 0.74$ and 0.94, respectively). The change in k as a function of L_∞ (Figure 7a) follows a second-order polynomial regression ($R^2 = 0.76$). With increasing starvation, b tends to decrease ($R^2 = 0.99$) (Figure 7b), producing a negative correlation ($r = -0.99$) with time gap. The magnitude of b varies from 1.8 to 1.6 for regular feeding to a 6-day gap of feeding. The value of b for treatment with a 6-days gap of feeding were not considered due a higher rate of mortality among snails.

The outcome of the study indicates that the life history traits vary with the availability of the food. The observations on the growth were made up to 12 weeks. Individual snails showed marked variations in terms

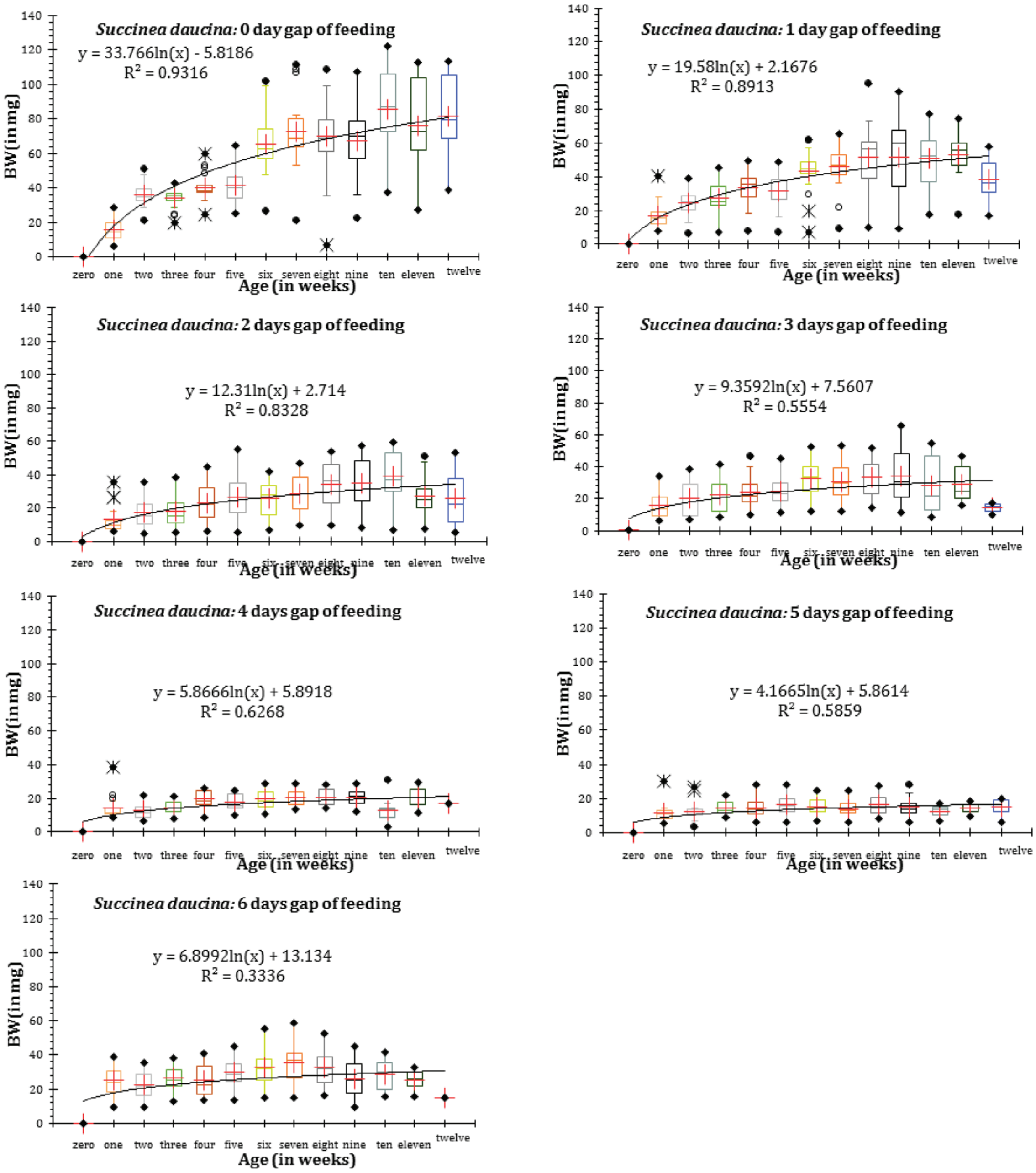

Figure 2. The box-plot representation of increment in biomass in each week for *S. daucina* exposed to different levels of fasting: filled circles – extreme values, open circles – outliers, cross – mean value, bar inside the box – median value with the upper and lower quartiles spread in the box.

of shell length and biomass. They showed the longest shell length and the largest biomass (shell length in mm, range 7.1–9.1; mean 8.225 ± 0.220 SE; biomass in mg, range 38.8–113.7; mean 81.51 ± 9.32 SE, n = 8) when they were fed regularly.

The number of eggs oviposited shows a negative correlation (r = -0.88) with the extent of starvation. The numbers of eggs and clutches reduced significantly ($P < 0.0001$) with the increased extent of starvation (Figure 8). Oviposition in starved snails also delayed to the 5–6th week (first oviposition for the control was on the 4th week). As the newly-hatched snails were used to distinguish the age of sexual maturity, it was seen that the first oviposition occurred after 4 weeks in the control, whereas in the treatments the first oviposition was delayed to the 5–6th week (Figure 9). The oviposition for the control and each treatment showed the same trend for every week (Figure 10). In all instances, a significant impact was observed for the response variables, as reflected in the results of Kruskal-Wallis test (K = 89.511, df = 6, $P < 0.0001$ for eggs, and K = 106.121, df = 6, $P < 0.0001$ for clutches). During the reproductive phases, the number of eggs and clutches produced by *S. daucina* under a different duration of starvation were portrayed

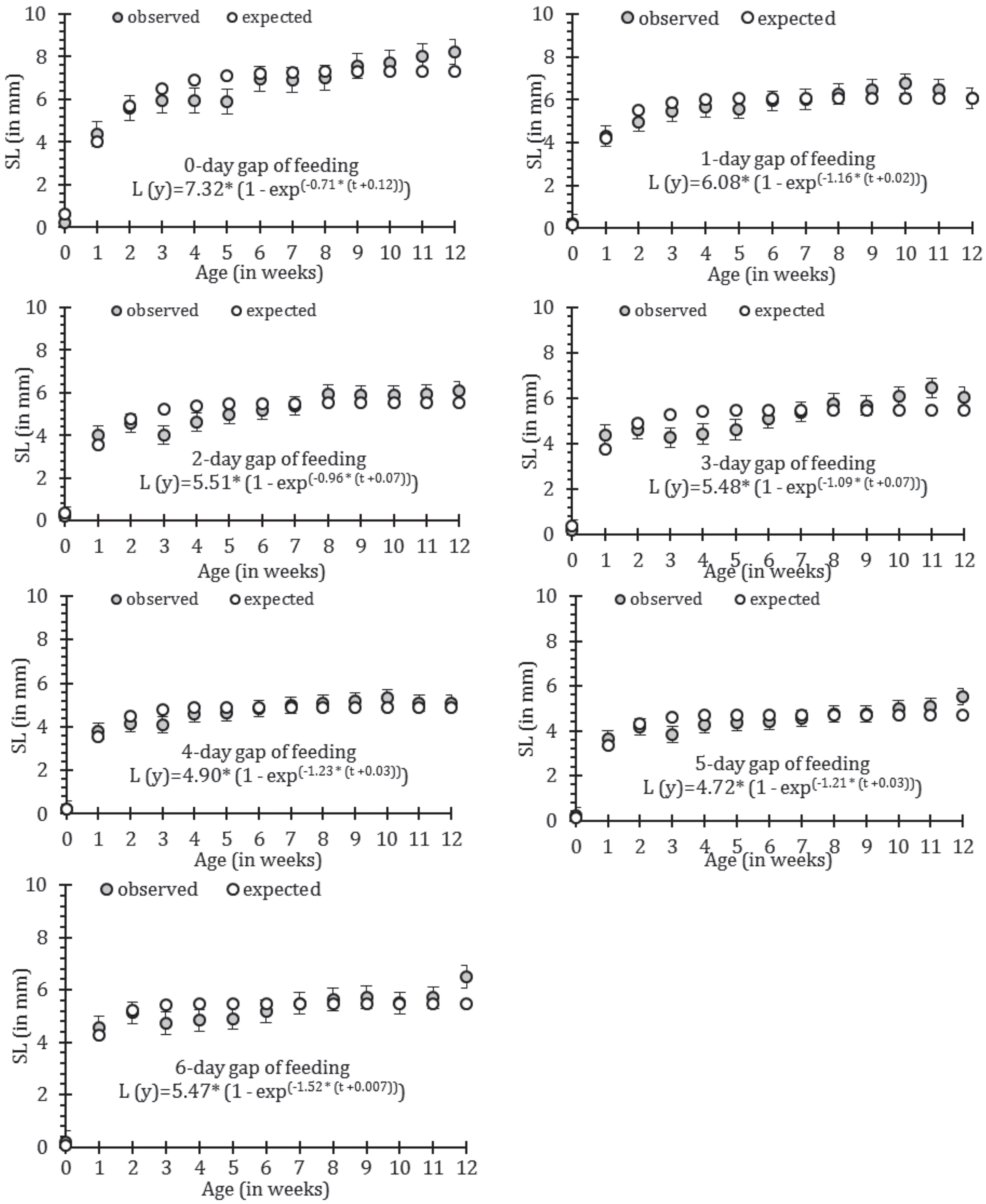

Figure 3. The compliance of *S. daucina* shell length increment with the von Bertalanffy growth equation for all experimental treatments.

as a function of the von Bertalanffy growth parameters (L_∞ and *k*) (Figure 11). In all instances, the number of eggs and clutches produced showed an increasing trend with L_∞, and a decreasing trend with *k*.

DISCUSSION

Based on the snails' biomass and shell length, their growth gradually increased over time. In contrast, growth in terms of length and biomass decreased as the length of famine increased. The von Bertalanffy growth pattern was followed in every case' however, as the famine time lengthened, the magnitude of Lmaximum (Lmax) and L∞ dropped, with an increase in the growth rate coefficient (k).

The growth pattern reflects the contribution of the food as an essential part of anabolism (Reddy and Rao 1985). Under starvation, the reduced sugar in haemolymph

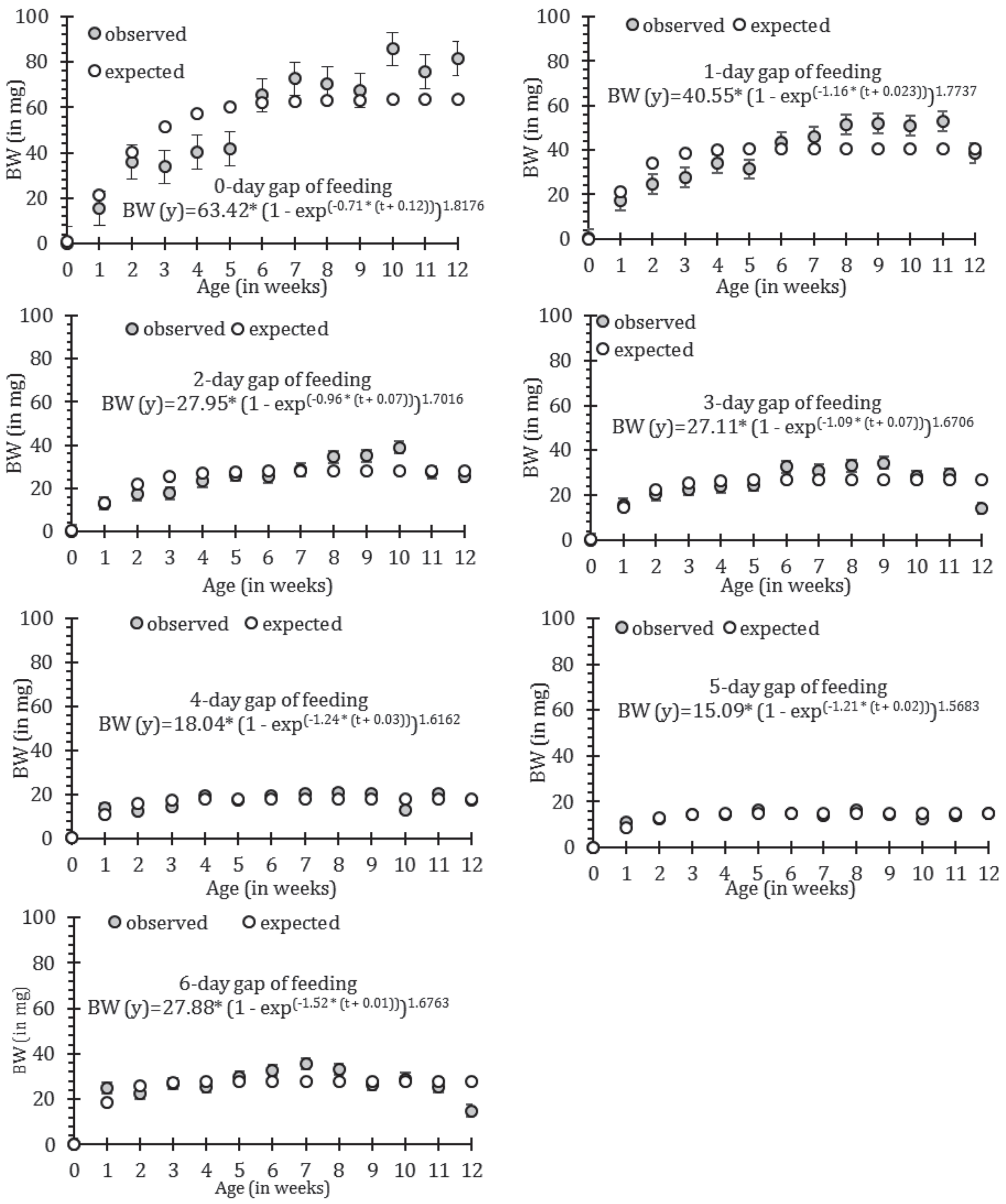

Figure 4. The compliance of biomass (BW, in mg) increment with age (in weeks) with the von Bertalanffy growth equation for *S. daucina* exposed to the varying level of the gap of feeding (seven levels of fasting, 0 through 6 days). Here also, biomass reduced with the increased gap of starvation.

lowers significantly in *Achatina fulica* (Brockelman and Sithithavorn 1980), while, glucose tolerance and incorporation of glucose in muscles are lowered in *Biomphalaria glabrata* (Liebsch and Becker 1990). The land snails possess neutral fatty acids in their gastric glands. As the snails try to cope up with the food stress, they tend to break the lipids to acquire energy for other physiological processes (Lavarías et al. 2023). A reduced level of ketone bodies in haemolymph, with a reduced oxidation rate of 3-hydroxybutyrate (Meyer et al. 1986) explain in part the reason of decreasing body length and biomass of starved snails.

With reference to the VBGF, an increase in k would mean a lesser time to reach L_{∞}, but it can also be perceived as an attempt to compensate food scarcity by reducing the asymptotic length in normal conditions to

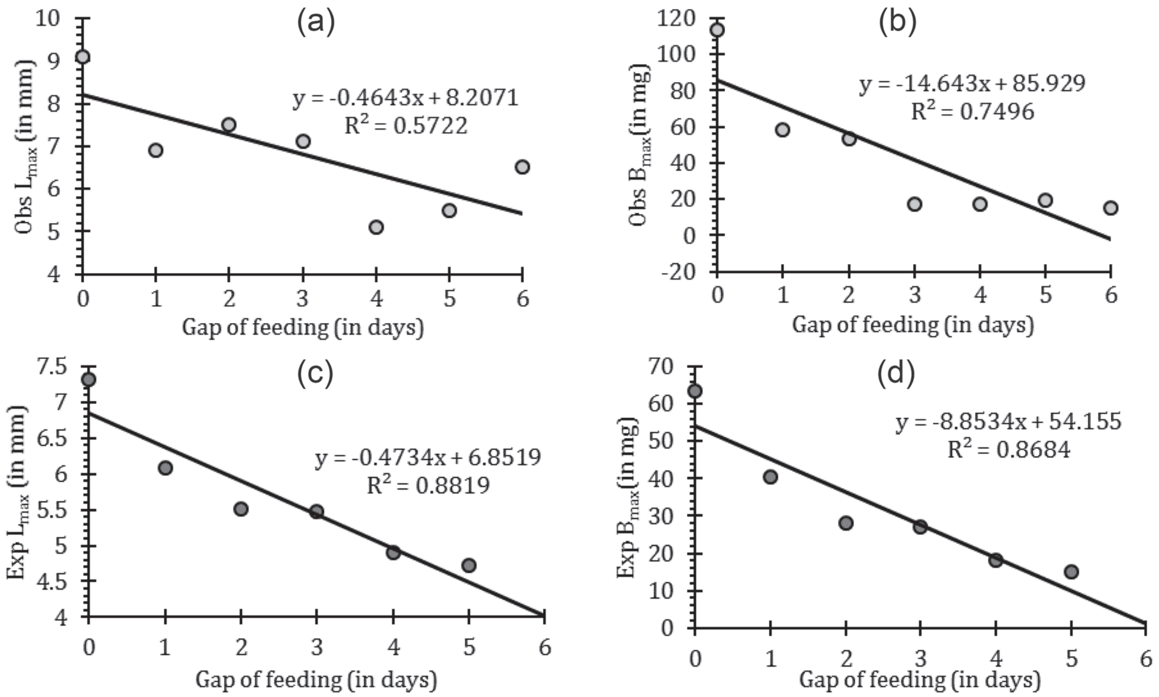

Figure 5. The regression equation representing the relationship between the treatments (as explanatory variables) and the observed growth maxima [(a)L_{max} and (b) B_{max}] along with the growth maxima obtained from the von Bertalanffy growth equation [(c)L_{max} and (d) B_{max}].

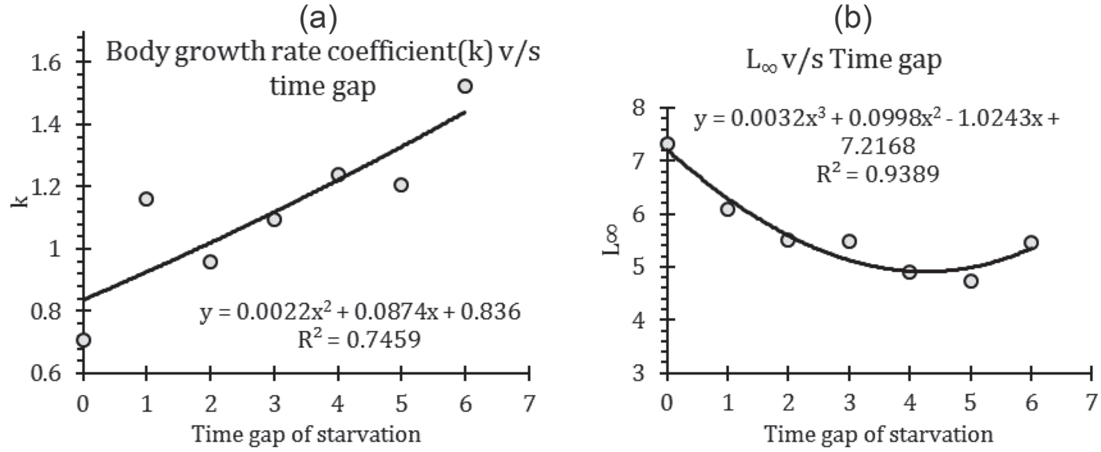

Figure 6. The regression equation describing the change in k and L_∞ with the starvation gap.

increase survivability. In terms of metabolism, which VBGF is based on, food depletion reduces anabolism, rendering the organism to survive on minimum requirements, increasing the catabolism processes which result in individual growth. They do not cope with even a slight change in the environment, as both $L_{maximum}$ (L_{max}) and $B_{maximum}$ (B_{max}) started to reduce drastically with a one-day gap of feeding ($P < 0.05$). The snails showed high mortality during rearing in laboratory conditions, which increased with the starvation period. As per data observed, both L_{max} and B_{max} (highest length and biomass of snails found after 12 weeks, respectively) tend to decrease (Figures 5a and b) indicating that *S. daucina* is very vulnerable to environment perturbation.

The k and L_∞ are inversely proportional (Gubiani et al. 2012) to each other, as seen in Figure 7a. With the increasing starvation, the growth rate coefficient increased, whereas L_∞ shows a polynomial regression with time gap. Such relationship is observed for the length and weight relationship in animals, like fish (Froese 2006). With the scarcity of food, organisms tend to reduce anabolism, which in turn reduces the body-mass along with L_∞ due to a reduction in catabolism, i.e. they get to survive at the cost of size. When L_∞ is reduced, the time to reach this length also reduces, justifying the increased magnitude of k. The relation between k and L_∞ is not linear, it rather follows a curvilinear graph. The relation between these two parameters is expressed by a second order polynomial equation of

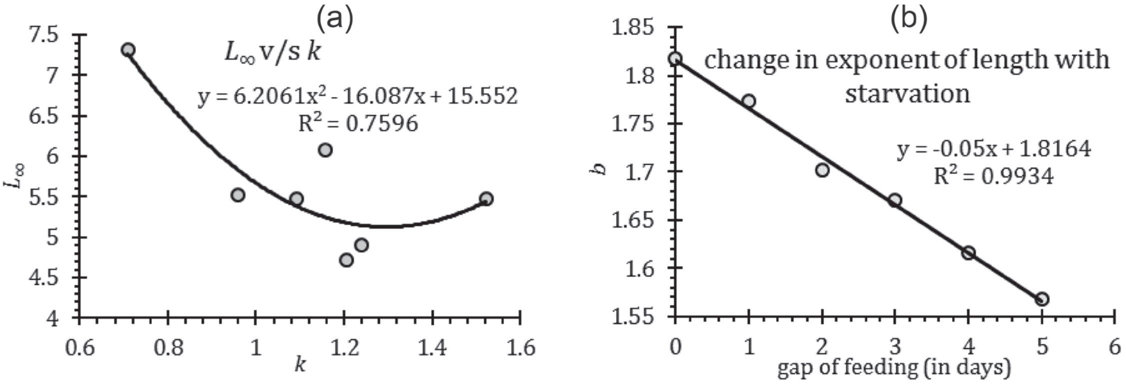

Figure 7. (a) The dependence between *k* and L_∞ shows a polynomial regression of second order. (b) The magnitude of exponent *b* declines with increasing starvation linearly. Here, the value of *b* from the sixth set was not considered due to high mortality among snails.

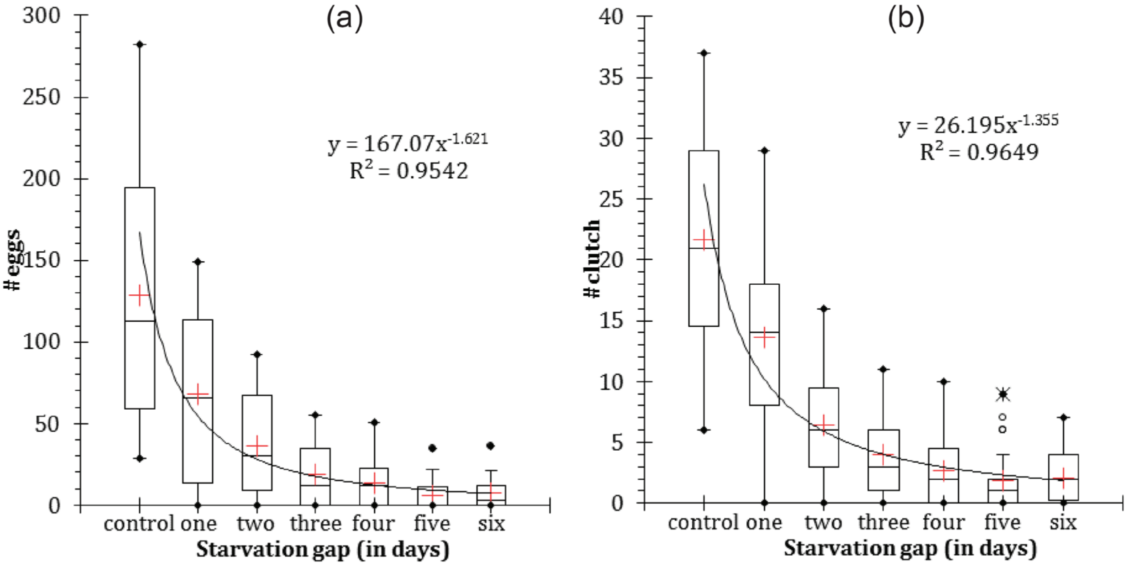

Figure 8. The number of eggs laid by the control and each treatment of *S. daucina* regressed with increased gap of starvation: (a) Oviposition gradually decreased for treatments with a higher extent of starvation, whereas it peaked somewhere in the middle of the experiment (around 7 to 10 weeks) for all seven cohorts, then decreased. The average yield of eggs decreased significantly ($P < 0.05$) with increased extent of starvation. Even a single-day gap made a huge impact ($P = 0.003$), although fecundity for treatments with 4-, 5- and 6-days gaps of feeding did not vary significantly ($P = 0.13$). (b) The number of clutches also reduced significantly ($P < 0.05$) with the increased duration of starvation. For treatments getting 5 and 6 days of starvation per week, the mean clutch increased for the latter with an insignificant difference between them ($P = 0.81$).

the type, $L_\infty = a_0 - a_1k + a_2k^2$, where L_∞ and *k* have the same meaning discussed earlier, and a_0, a_1, a_2 are the linear coefficients showing a quadratic curve fitting ($R^2 = 0.7596$), inferring the growth of *S. daucina* is not affected by growth rate alone, but there are other factors affecting it. As shown in Figure 7a, *k* always increases with increase in time gap, while L_∞ first decreases, then tends to increase (Figure 7b), which may infer a non-realistic phenomenon, where the organism tries to regain its normal anabolic rate in starvation conditions to reach the former L_∞ but cannot cope up as with increased *k* the metabolism rate increases, but the provision of food decreases, leading to a fallacy, which is not physiologically supported and is eventually leading to death.

The focus on the exponent *b* in Equations 6 and 7 illustrates the growth pattern of an organism, whether to be slender, proportionate or obese, depending on the value of *b* (Froese 2006). The biomass, as deduced from length, states that the dependence of biomass on length is raised to a certain power coefficient. The exponent *b,* as decreases with time gap, says the reduced dependence of biomass on length. If the magnitude of *b* is less than 3, the increase in length is more than width for large specimens, and small specimens had better nutritional conditions during the sampling, and vice versa $b = 3$ signifies no difference of forms between large and small specimens while collected (Froese 2006). We have analysed the change in *b* with increasing starvation, which shows a linear decrease in its magnitude, which results in slender snails with reference to biomass. But in real-

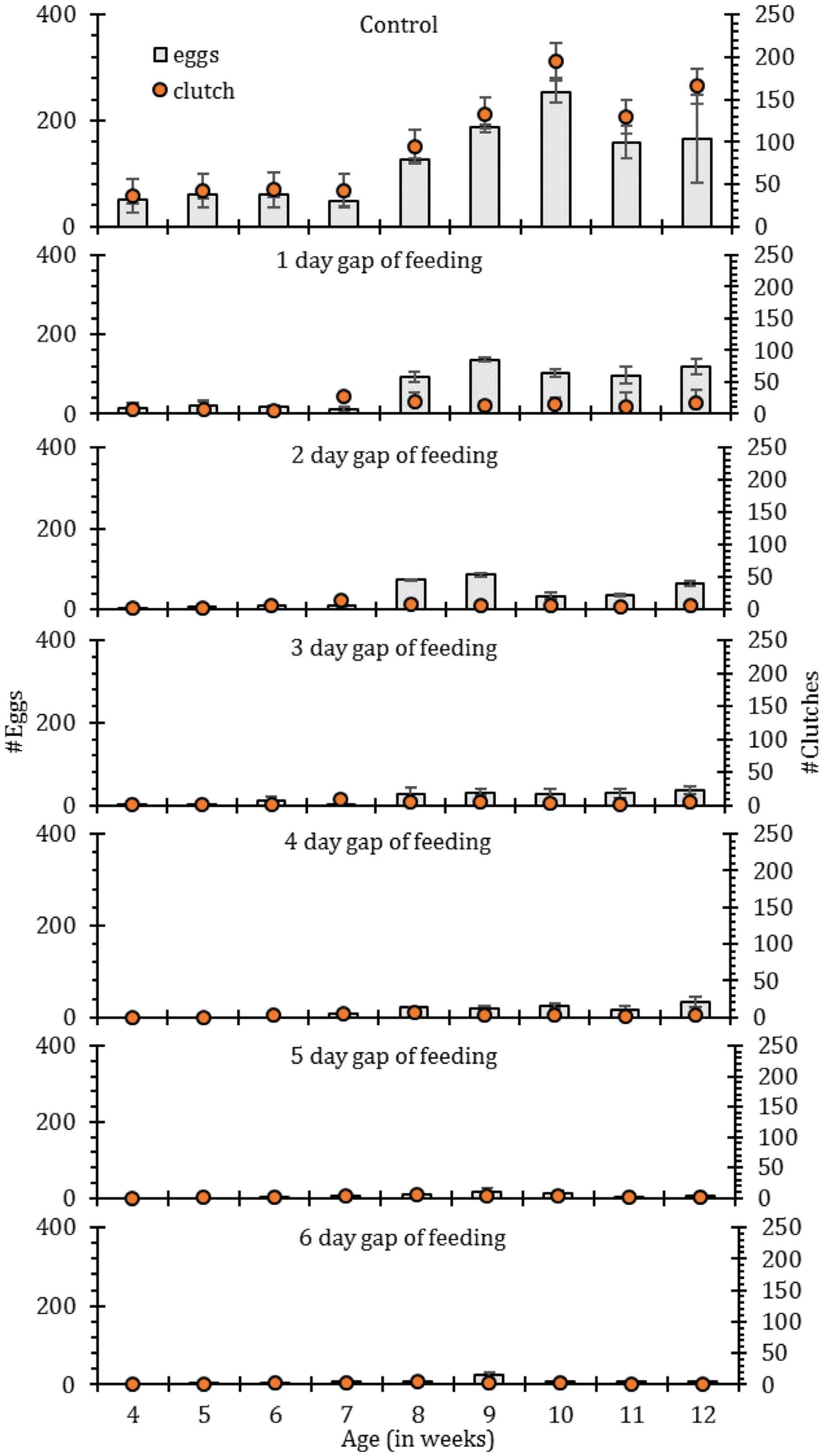

Figure 9. The number of eggs and clutches reduced significantly with increased extent of starvation. There are some instances showing clutches without eggs when snails starved for 4, 5 and 6 days per week. It was also observed that oviposition was delayed by a few weeks, and even when eggs were laid, the quantity nearly got halved even with a single-day gap of feeding, and it gradually decreased from the maximum of eggs (254.67 ± 21.61) and clutches (195.87 ± 80.41) at the 10th week for the control to the maximum of eggs (23.00 ± 7.00) and clutches (3.00 ± 1.00) at the 9th week for the treatment with 6 days of starvation per week. Oviposition took a surge at about 8–9th week, then reduced again, with an exception of treatments having 2-, 3- and 4-day gaps of feeding.

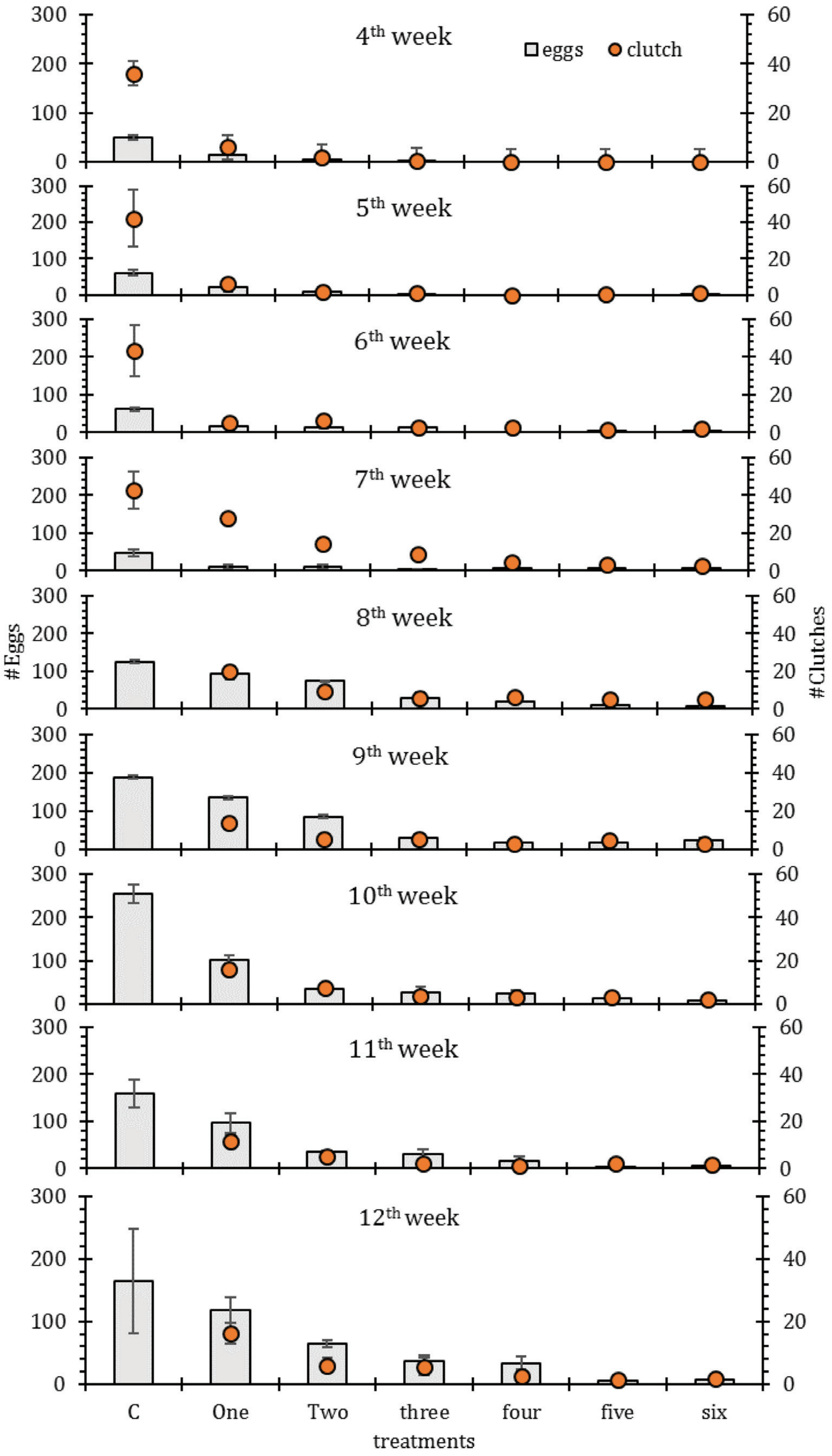

Figure 10. The number of eggs laid along with the clutches for the control and each treatment reduced gradually for each week (4th week onward). Though excessively starved snails laid clutches, they contained no eggs, and delay in oviposition was a result of starvation. The snails lacked the required energy to produce eggs at such early ages, which delayed their sexual maturity.

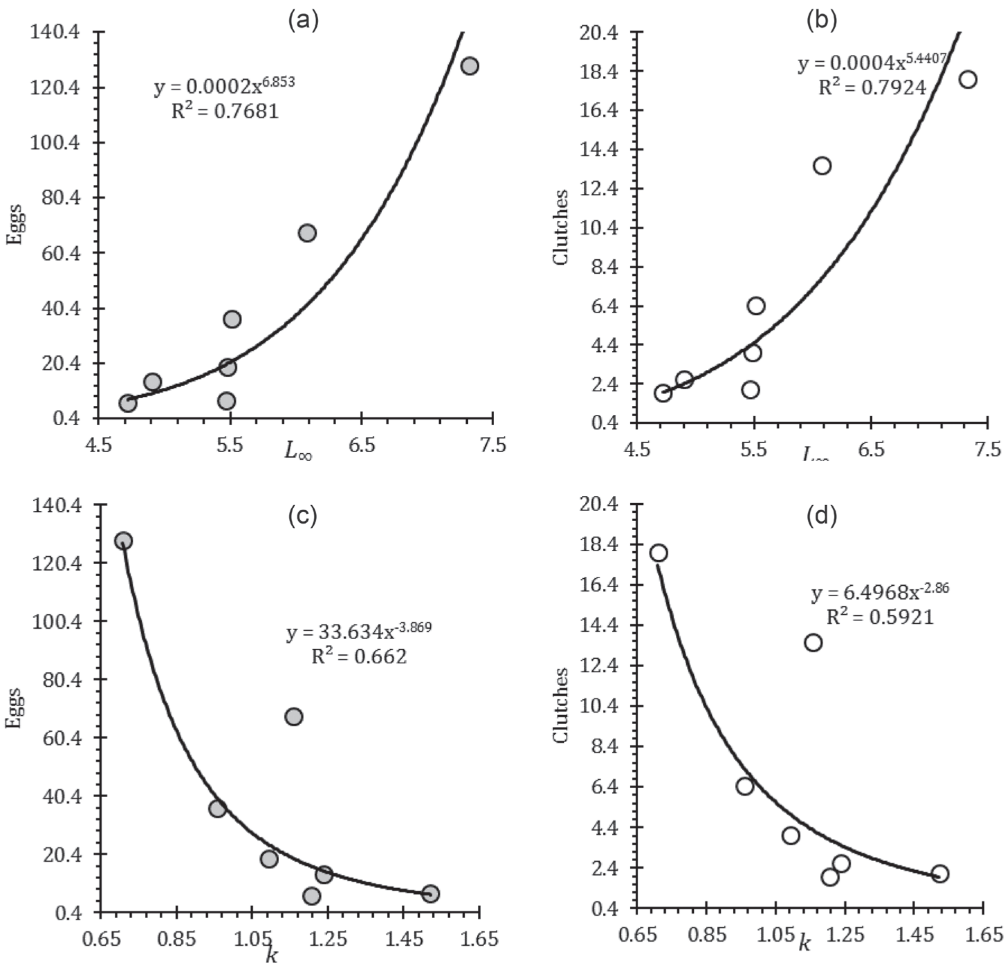

Figure 11. The magnitude of L_∞ decreased and k increased with extent of starvation. The number of eggs declined with decreasing L_∞ (a) and k (b). The number of clutches also declined with the same parameters in the same pattern (c and d), but the dependency of eggs and clutches was more inclined to L_∞ as assessed from R^2 values.

ity, it was seen that with increased time gap, L_∞ actually decreases; as b is reducing continuously, it forces the specimens to increase in length. Considering nutritional deficiency, the required building of biomolecules that will add up to length are absent, satisfying the reduction in length. So, complying with allometry (Froese 2006), the slenderness with respect to b only applies for abundant conditions of food. In the food scarcity state, even with decrease in the magnitude of b, the length of the organisms is reduced. The observation made on the cohort fed every six days was not considered for this regression analysis due to a higher rate of mortality seen in the snails.

In case of the freshwater or terrestrial snails, the starvation-induced physiological changes are quite prominent. For instance, the food utilization pattern of the apple snail *Pila globosa* was affected by the length of starvation (Haniffa 1987a). Similarly, the digestive gland function was altered due to prolonged starvation in the snail *Helix aspersa* (Porcel et al. 1996). The evidence of starvation-induced alteration in the use of the allosperm in *Biomphalaria glabrata* (Vianey-Liaud and Dussart 1994) and the mortality induced by starvation in the parasite-infested *Potamophyrgus antipodarum* (Jokela et al. 1999) are suggestive of the prospective impact of starvation in the snails at the proximate level. In the snail *Monacha cartusiana,* the changes in the carbohydrate and protein content in the digestive gland cells indicated the impact of starvation (Sharaf 2009). In case of *Eobania vermiculata,* it was evident that with starvation the acetylcholinesterase activity and metallothionein content were significantly higher (Moschovaki-Filippidou et al. 2013). In such starved *E. vermiculata,* the stability of lysosomal membrane in digestive gland cells were lower and cAMP content showed no significant change compared with that of control groups (Moschovaki-Filippidou et al. 2013). In the present study, the change in the growth pattern can therefore be considered as an effect of alteration in the physiological processes of snails induced by the length of starvation.

Apart from growth, the fecundity of *S. daucina* was affected by starvation. With the increasing gap of starvation, the number of eggs laid decreased significantly, along with a delayed sexual maturity and the reduction in the number of clutches (Figure 8). If an organism faces unfavourable conditions, it becomes necessary to spend less energy for reproduction than earlier seeking to survive (Reddy and Rao 1985; Haniffa 1987a, b). The conditions put forth here in the experiment evidently bring up the fact that, under paucity of food, *S. daucina* snails alter their metabolism and expenditure of energy if they need to survive and reproduce simultaneously. For this property, they can be used as bio-indicators to conclude if an area is under any environmental stress. If the local flora on which they feed is jeopardized for any reason with the decreasing value of snail size and number, pollution can be inferred.

In order to reach the target shell length, the snails may have to allocate more energy even with the constraint food, which in turn reduces energy expenditure for reproduction, which explains partly the reduction in eggs production after attaining maturity (Figures 8, 9 and 10). Fecundity can be related to L_∞ and k (Figure 11), where it shows to be more affected by L_∞, which may be explained through the metabolic activity, i.e. asymptotic length is directly linked to catabolism (Czarnołęski et al. 2008, 2016) that is reduced with starvation, whereas the growth rate depends on the initial and final length alone, not directly affected by metabolism. Though VBGF does not take fecundity into account, an indirect effect of metabolism on fecundity connects them on a fine line, which we tried to analyse. Fecundity has to be sacrificed to attain the proper body size, and the genes have to express their character, instead of their urge to propagate, i.e. the next-generation population may shrink but the allele quality remains the same. The idea swings here in between attaining encrypted body size and fecundity to adapted physiological responses with food stress. With starvation, different organisms react differently. Snails are species with varieties, their response must be unique as they do not have much capacity to store food for future (Meyer et al. 1986; Lavarías et al. 2023), but the urge to complete the life cycle to propagate genes to the next generation compels them to renounce body size as well as fecundity. Thus, the observations suggest that the snail *S. daucina* exhibits a growth pattern that complies with the VBGF and the parameters obtained showed correspondence with the starvation period. The growth and fecundity of *S. daucina* in the background of starvation was also reflected through the differences in the L_∞ and K values of the equations. Although further explanations regarding the effect of starvation on the growth and fecundity of the land snails can be deduced through the assessment of the physiological and genetic factors. Nonetheless, the present study provides evidence to quantify the differences in the pattern of the growth of the snails under a varied starvation situation.

CONCLUSION

The field-collected land snails *S. daucina* were maintained and reared in a laboratory for studying their response to starvation (food stress) in terms of the growth and fecundity variations. Using the variations in the parameters of the von Bertalanffy growth equation (VBGF), k, L_∞ and b were measured through shell length and biomass, along with fecundity. The growth pattern for the snails both in the control and treatments complied with the VBGF but varied in the parameters indicating the impact of starvation on the pace of growth and fecundity. The increment in shell length and biomass reduced with the increase in the starvation duration and matched similarly with the observed L_{max} and $B_{max,}$ respectively. The parameters k and b showed a positive increment with the time gap of starvation. The clutch number and eggs oviposited increased with the L_∞ and k values. Thus, the observations on the growth and fecundity of *S. daucina* at the varied duration of starvation indicates considerable adaptation to cope up with the disturbed conditions. This pattern can be used as a model to understand starvation-induced effects on snail growth and fecundity.

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Author's contribution

Conceptualized by Gautam Aditya; Experiment execution and data collection by Abhijit Sikary, Gargi Nandy, Ashmita Chakraborty, Suparna Mandal,Tanisha Ghosh, Sabarni Chakraborty; data analysis and model assessment by Gargi Nandy, Sabarni Chakraborty, Gautam Aditya and Abhijit Sikary; Model evaluation Gargi Nandy, Sabarni Chakraborty; manuscript preparation; Gargi Nandy, Sabarni Chakraborty, Gautam Aditya.

Conflict of Interest

As authors we declare no conflict of interests

Data disclosure

Elaboration of a part of the equation is presented in the Supplementary File 1. The data may be provided upon authentic request.

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SUPPLEMENTARY FILE 1