

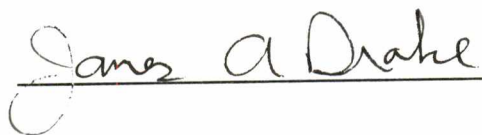
To the Graduate Council:

I am submitting herewith a thesis written by Georgios D. Kokkoris entitled "Effects of temperature on Growth and other physiological parameters of Daphnia magna". I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Mathematics.

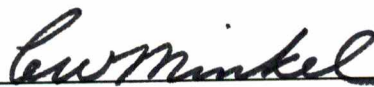


Thomas G. Hallam, Major Professor

We have read this thesis
and recommend its acceptance:



Accepted for the Council:



Vice Provost
and Dean of The Graduate School

THE EFFECTS OF TEMPERATURE ON
GROWTH AND OTHER PHYSIOLOGICAL PARAMETERS
OF DAPHNIA MAGNA

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Georgios D. Kokkoris

December 1990

This work is dedicated to Rosa Maria.

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ABSTRACT

The von Bertalanffy growth model is used to assess quantitative and qualitative effects of temperature on growth of Daphnia magna. For this, a standard regression analysis technique is used in order to utilize data on development time. The resulting function is coupled to the model and analyzed. The temperature range studied is from 10°C to 34°C whereas 35°C, the lethal thermal limit is not included.

An ordinary differential equation model capable of representing the behavior of physiological parameters over the normal temperature range of the organism is presented. The model implements the observed ideas of optimal and maximum temperatures that relate to the physiology of an organism. Then, the results are compared to the results of a previous model and the advantages of the new approach are discussed.

Some improvements of both models are suggested and some future research trends are proposed. The importance of the incorporation of the continuous model in existing individual based models is also discussed.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION AND LITERATURE REVIEW.....	1
1. Introduction.....	1
A. General.....	1
B. Experimental organism.....	3
2. Literature review.....	4
A. Scope of Review.....	4
B. General Reviews.....	5
C. Development Time, Growth and other physiological parameters.....	6
D. Growth Rates and Temperature.....	9
II. METHODS.....	13
1. The von Bertalanffy growth model.....	13
A. Derivation.....	13
B. Growth rate as function of temperature.....	17
2. An Ordinary Differential Equation model for Physiological Parameters.....	21
A. Derivation.....	21
B. The model.....	22
III. RESULTS.....	25
1. The von Bertalanffy growth rate.....	25
2. Physiological Parameters.....	26
A. Growth rate.....	26
B. Reproductive Frequency.....	28
C. Length as a function of temperature and time....	33

CHAPTER	PAGE
IV. DISCUSSION.....	37
1. The von Bertalanffy growth rate.....	37
2. Physiological parameters.....	38
3. Length as a function of both temperature and time.....	40
V. SUMMARY AND CONCLUSIONS.....	43
LIST OF REFERENCES.....	45
VITA.....	49

LIST OF TABLES

TABLE	PAGE
1. Average developmental time from birth to the end of the first adult instar for <u>Daphnia magna</u>	18
2. Values of the von Bertalanffy growth at different temperatures.....	25
3. Mean instar duration at different temperatures for <u>D. magna</u>	31

LIST OF FIGURES

FIGURE		PAGE
1.	Growth in length as a function of time resulting from the von Bertalanffy model.....	16
2.	Development time for <u>D. magna</u> at different temperatures, and the corresponding regression curve.....	19
3.	The von Bertalanffy growth rate as a function of temperature as it results from the classical von Bertalanffy model.....	27
4.	The von Bertalanffy growth rate throughout the entire temperature range of <u>D. magna</u> as it results from the differential equation model.....	29
5.	The von Bertalanffy growth rate as predicted from the Arrhenius relationship.....	30
6.	Instar duration time for <u>D. magna</u> at different temperatures, and the corresponding regression curve.....	32
7.	The reproductive frequency throughout the entire thermal range of <u>D. magna</u> as it results from the differential equation model.....	34
8.	The length of <u>D. magna</u> as a function both of temperature and time throughout its entire life span and thermal range as it results from the combination of the von Bertalanffy and the differential equation model.....	35

CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

1. INTRODUCTION

A. General

Progress in evolutionary biology during the last decades has enabled ecologists to see that within the hierarchy from cell to tissue, to individual organism, to population, to community, and finally to biosphere, the individual organism is something distinct. Ecological roles of species are determined by properties of individuals. Population level information generally must be obtained by compilation from a lower organizational level, usually the individual or aggregates of individuals (Lomnicki, 1988).

Growth of organisms is an important phenomenon, not only from a physiological point of view, but also from an ecological one. Many processes, e.g. ingestion, development and growth are associated with size, and consequently size is correlated with growth (Fabens, 1965).

Temperature has been shown to affect survival, growth, metabolism, morphology, reproduction and behavior in aquatic poikilotherms (Gophen, 1976, Goss and Bunting, 1976, Goss, 1978). The degree to which these biological processes are affected is dependent upon several factors, including range of temperatures to which an organism is exposed, time of exposure at a given temperature, developmental stage in an

organism's life history, and interaction of temperature with other environmental parameters which have profound effects on biological processes (Bunting, 1974). Over an organism's normal temperature range, i.e. the temperature at which it can grow and reproduce, the general trend is for metabolic and growth rates to increase as temperature increases. However, an upper optimal temperature is reached at which metabolic rates reverse. It is usually not far past this optimum that death is imminent (Goss, 1978).

The greatest single industrial use of water is for cooling purposes (Cairns, 1956, in Goss, 1978). Vast quantities of water are removed from natural sources, heated, and discharged back into the source, thereby abruptly increasing natural temperatures. The extent and duration of this increase depend upon a variety of factors, e.g. flow of the water body, amount of water used for cooling, etc.

Since temperature is a major factor in aquatic habitats, the need for a more thorough understanding of the behavior of aquatic organisms at different thermal environments is unquestionable. This study was undertaken to provide information about effects of temperature on growth of zooplankton, perhaps the least studied group of aquatic animals in relation to temperature (Goss, 1978).

B. Experimental organism

It is appropriate to present briefly the life history

of the organism to indicate characteristics that should be reflected in the hypotheses, input, and output of this model.

Data for Daphnia magna Straus were chosen for use in this study. Daphnia taxonomically belongs to the order **Cladocera** and to the class **Crustacea**. Cladocera have a carapace typically covering the entire body but not the head. It is the most important and successful order and often forms a large segment of the freshwater zooplankton.

Adult female D. magna vary in length from 2.5 to 6.0 mm (Green, 1956). They reproduce parthenogenetically except under conditions of stress, when males can be produced. When males are created sexual reproduction occurs, and sexual eggs, resistant to desiccation and freezing, are formed within an ephippium. The reproduction occurs at frequent time intervals. The young of Daphnia are expelled from the mother's brood pouch as miniature adults. There is no metamorphosis as growth and maturation take place. The young pass through four juvenile instars, a fifth adolescent instar, and then a sequence of adult instars when the resource levels are adequate (Anderson, 1932). They can pass through more than fifteen adult instars, releasing new broods at the end of each instar. All developmental stages may be distinguished as each is marked by ecdysis. The eggs develop without external nutrient until they are released from the brood pouch.

D. magna has a reported average life span of forty days at 25°C (Anderson and Jenkins, 1942).

D. magna occurs sporadically over a wide latitudinal range in northern and western North America and most of Europe and Asia and in Africa, north of Sahara.

2. LITERATURE REVIEW

A. Scope of Review

Over the past several years a significant amount of literature has been published dealing with the effects of temperature on aquatic organisms and some reviews which condense and summarize the contents of this literature have been compiled. Also some attempts have been made for the construction of mathematical models which describe these effects.

Unfortunately, it seems that there is a relatively small amount of experimental work dealing specifically with the thermal effects on the class of Cladocera. The same holds clearly for the efforts pertaining to the development of mathematical models describing these effects.

This literature review undertaken here, has as scope to concentrate and summarize the existing results in the study of thermal effects on zooplankton and the attempts for mathematical modelling of those.

B. General Reviews

The effects of temperature on aquatic life has been an area in which comprehensive literature reviews have been published regularly over the past years. A widespread intense interest has been developed recently in this particular area. As a result, much of the research work pertaining thermal effects has been conducted only relatively recently.

Altman and Dittmer (1966) reviewed the effects of temperature on animals and plants, both terrestrial and aquatic. A specific section was presented, devoted to the tolerance of aquatic invertebrates at temperature extremes. This indicates the particular importance of this specific issue in the study of thermal effects. Bush, et al. (1974), developed tables pertaining to the same subject and included data on freshwater invertebrates. McLaren (1963) reviewed the literature on the effects of temperature on the growth of zooplankton. Goss and Bunting (1976) summarized results of thermal tolerance studies on zooplankton. Goss (1978) also presented a complete review of studies on temperature effects on Cladocera. Presented data in this review cover effects on growth, development, reproduction, temperature tolerance and respiration on several different species without attempting any conclusions.

C. Development Time, Growth and other physiological parameters

Kryuchkova (1973) summarized most of the available data on the effects of temperature on the duration of Cladocera development. She concluded that the development rate of Cladocera clearly depends on temperature. Pratt (1943) studied the development of Daphnia magna populations under conditions with different temperatures. He found that mean population size at 18°C was two and one-half times as great as at 25°C. This result referred to the size of the overall population and did not relate to rates of reproduction. Brown (1929a, in Goss, 1978) found that generation time for D. magna was less at 25°C than at 20°C but greater at 30°C than at 25°C. The organism would not live and reproduce at 35°C. Identical results were found for D. magna by Goss (1978).

McMahon (1965) found that filtering and feeding rate for the same taxon increased up to 24°C but then rapidly decreased at higher temperatures. Hall (1964) experimented with populations of D. galeata mendotae and found that frequency of molting, duration of egg development and physiological life span were affected mainly by temperature. Reproduction occurred every 2.0 days at 25°C, every 2.6 days at 20°C and every 8.0 days at 11°C. Brood size he concluded was primarily influenced by the amount of food.

Brown (1929b, in Goss, 1978) found that summer and

southern Cladocera displayed higher temperature coefficients (Q_{10}) for development than did those of more general distribution.

Kooijman (1988) found results which followed the general pattern of those above but the optimal temperature and the lethal temperature limit for populations of D. magna in northern Europe, were considerably different. He reported that the minimum generation time appears at 27.5°C and that the organism dies at 29°C. This may be possibly explained by existing evolutionary adaptations between the sibling species in the two continents.

One of the most interesting problems encountered in the study of data presented on development time at different temperatures, is that of their representation through an appropriate regression equation. Data on development time are often obtained from a few temperatures, usually four or five. To facilitate interpolation and possible extrapolation to other temperatures, the dependence of the duration or rate of development has been usually assumed to follow some simple model.

Sarvala (1979) reviewed the literature on this subject. He presented and studied six different equations, widely used in the studies of development time. These were:

$$1/D=a+bT \quad (1.I)$$

which is a linear relationship between temperature T and the rate of development (reciprocal of the development time D). This has been widely used but Bottrell (1975) showed that the assumption of linearity is not generally warranted.

Another model is the Belehradek's equation which in a $\ln$ -transformed form is:

$$\ln D = \ln a + b \ln (T - \alpha) \quad (2.I)$$

where α is the temperature at which the development time D is 0 ("biological zero").

Another simpler model is the simple power function which in logarithmic form is:

$$\ln D = \ln a + b \ln T \quad (3.I)$$

Other models used include:

$$\ln D = \ln a + T \ln b + T^2 \ln c \quad (4.I)$$

$$\ln D = \ln a + b \ln T + c (\ln T)^2 \quad (5.I)$$

$$\ln D = \ln a + b (\ln T)^2 \quad (6.I)$$

Other equations suggested include Krogh's normal curve which has been criticized by many authors. Bottrell (1975)

showed its poor predictive ability especially at low temperatures.

Sarvala tested the previous models using data on seven different species of freshwater benthic **copepoda**. The fourteen data sets presented, related to development times of the egg, nauplius and copepodite stages of the organisms. His results indicated that the relationship between rate of development and temperature was not linear. None of the curvilinear temperature functions tested was statistically adequate in all cases. However, three of the models, equations (4.I), (5.I), (6.I) gave a reasonable fit to all egg development data, and one of these, the semilogarithmic quadratic equation (4.I), also satisfactorily described postembryonic development. He theorized that this model accommodates the retardation of development at higher temperatures and can therefore be recommended for further testing.

Goss (1978) used the simple equation (3.I) to describe the development time from birth to the end of the first instar for D. magna and D. pulex. Vijverberg (1980) studied thirteen different species that belonged to the orders of Cladocera and Copepoda. He used equation (6.I) since he found no evidence for retardation of development at higher temperatures.

D. Growth Rates and Temperature

Kooijman (1988) believes that the way growth rates

depend on temperature is usually well described by the **Arrhenius relationship**. This equation states that the logarithm of the growth rate depends linearly on the inverse of the absolute temperature, i.e.

$$j_T = j_{298} \exp\{T_A(1/298 - 1/T)\} \quad (7.I)$$

where 298°K or 25°C has been chosen as a reference. This relation holds in a species-specific tolerance limit; that is, T takes values from a range, specific to each species. The **Arrhenius temperature** T_A which is the slope of the line in the Arrhenius plot of ln-transformed equation (7.I) can be estimated in the case of several different types of growth. Kooijman in the same study, found this value for D. magna to be 6400°K, using the von Bertalanffy growth rate. The usual values for this temperature are between 5500 to 15000°K (Glasstone et al., 1941, in Kooijman, 1986).

Another common way to correct temperature differences in the values of physiological parameters is to use the so-called Q_{10} value, i.e. a factor that is applied for every 10°C increase in temperature. The equation that describes this has the form:

$$j_T = j_{298} Q_{10}^{(T-298)/10} \quad (8.I)$$

Because the range of relevant temperatures is only from

about 0 to 40°C, this way to correct differences is for practical purposes indistinguishable from that using the Arrhenius relationship. The usual value for Q_{10} is between 2 and 3 (Stanier et al., 1984, in Kooijman, 1986) and corresponds to an Arrhenius temperature T_A between 5000 and 10000°K. The Q_{10} value is different for different physiological parameters of the same organism. For growth, they are in the upper end of the range mentioned before and somewhat beyond; about 1500°K (Kooijman, 1986).

Sutcliffe et al. (1981), studied the effects of temperature on growth rates of the amphipod Gammarus pulex. They first defined the percentage growth rate which was:

$$G_s = \ln(W_t/W_0) t^{-1} \cdot 100 \quad (9.I)$$

where W_0 is the weight at birth and W_t is the weight at any given time. The range of the temperature T was up to 20.4°C. Their relationship was curvilinear on arithmetic scales but linear on logarithmic scales. This relationship could be approximated by a power equation:

$$G_s = aT^b \quad (10.I)$$

where a and b are constants with values 0.37 and 0.993 respectively. They also found that the equation:

$$W=W_{\max}/\{1+\exp[-g(t-t_0)]\} \quad (11.I)$$

where g was defined to be the **overall growth constant**, described well the mean growth in body weight.

Swartzman and Bentley (1979) reviewed eight plankton simulation models. In those models, temperature affected the growth of phytoplankton, and grazing and respiration of zooplankton. In the formulations of these effects several factors were included: critical water temperature for growth, temperature above which no growth occurs and Q_{10} coefficients. In the most of the models individual zooplankton weight gain was not considered and growth was lumped as biomass. This growth was measured in $\text{mg/m}^3/\text{day}$.

CHAPTER II

METHODS

1. THE VON BERTALANFFY GROWTH MODEL

A. Derivation

The rate of growth in weight of an animal is the difference between an **anabolic** and a **catabolic** rate. It is natural to assume that the rate of breaking down of tissue for maintenance and reproduction would be approximately constant so that the rate of total weight loss of the animal due to catabolism would be proportional to the weight of the animal. One might also assume that new tissue construction is restricted by the capacity for respiration and ingestion and hence by the external surface area of the organism and the surface area of the lungs, guts, etc. Thus, if it is also assume that the shape of the organism does not change as it grows, the anabolic growth rate would be proportional to the two-thirds power of the weight (Fabens, 1965).

If it is also assumed that the food density in the environment is constant and that the reduction in the ultimate length of the endotherm organisms due to the energy drain in heating is negligible, then these assumptions constitute the von Bertalanffy first metabolic type model. This may be expressed:

$$W' = \eta W^{2/3} - \mu W \quad (1.II)$$

where W is the total weight of the animal, W' is the rate of change of weight with time, and η and μ are the anabolic and catabolic constants for the particular taxon under study.

Since the model assumes that the shape of the animal does not change, we may also assume that any linear dimension as length or the cube root of volume will be proportional to the cube root of weight, i.e. that

$$W=qL^3 \quad (2.II)$$

where q is a constant which is characteristic of the taxon¹ and it is called **shape coefficient**. The value q differs when considering dry or wet weight, and for the particular taxon under study when L is length takes the value:

$$q_{\text{wet}}=0.526 \text{ and } q_{\text{dry}}=0.6$$

(In Kooijman (1988) and in Hallam (1990)).

We can rewrite the differential equation (1.II), in terms of the variable L , instead of the weight W , and solve it as a linear differential equation. Thus we obtain the formula:

$$L=q^{-1/3}\eta/\mu - (q^{-1/3}\eta/\mu - c)\exp(-\mu t/3) \quad (3.II)$$

The new parameter c arises in the solution of the

¹This is a special case of the length-weight hypothesis which is represented by the allometric law $W=qL^v$, $q>0$, $v>0$. When $v=3$ we have what is called isometric growth.

differential equation. The form of the equation (3.II) has been chosen so that:

$$c=L \text{ when } t=0$$

This is the size of the organism at birth.

We can simplify the formula (3.II) by choosing a new parameter L_i and relabel c and μ such that:

$$L_i = q^{-1/3} \eta / \mu, \quad L_0 = c, \quad j = \mu/3 \quad (4.II)$$

The transformations (4.II) have the advantage of acquiring descriptive significance giving asymptotic size and initial length.

$$L = L_i - (L_i - L_0) \exp(-jt) \quad (5.II)$$

The graph of the growth curve for length has the appearance indicated in Figure 1. The growth rate is highest at birth and decreases continually. The size approaches an asymptote whose value is the ultimate length the organism can attain, L_i .

If we take the natural logarithms of both sides of the equation (5.II), and solve for the growth rate j , we find:

$$j = t^{-1} \ln \{ (L_i - L_0) / (L_i - L) \} \quad (6.II)$$

Here, the growth rate j is represented as a function of the

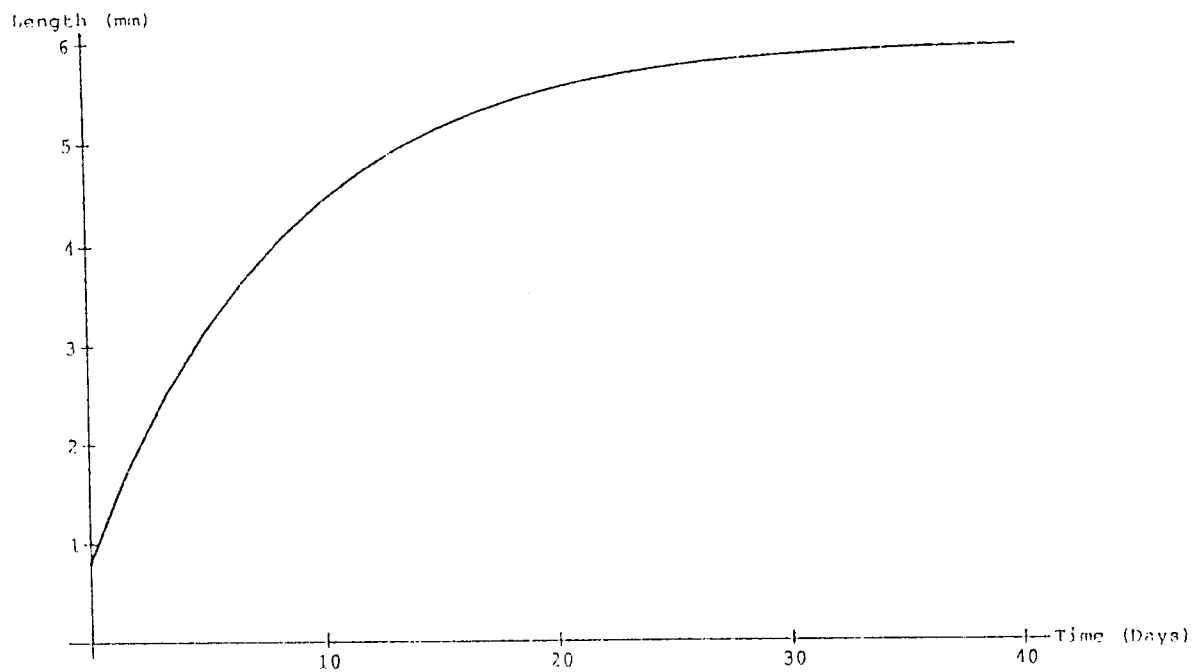


Figure 1. Growth in length as a function of time resulting from the von Bertalanffy model.

age t of the length L of the organism.

B. Growth rate as a function of temperature

To get a direct estimate for the value of the growth rate j from equation (6.II), the organism has to be followed during its entire life span and measures have to be taken pertaining to its length at several different times. Then statistical methods have to be used in order to fit the data. This procedure has been successful in the past, (Fabens, 1965).

A very important factor which has not been given very much attention is the modelling of the effect of temperature on the growth rate. Growth rate, as is the case for many physiological parameters, is greatly affected by changes in the temperature of the habitat of an organism.

Here, a method is presented which formulates the von Bertalanffy growth rate as a function of temperature. It utilizes data on development time from birth to the end of the first adult instar for Daphnia magna Straus, (Goss, 1978). These are presented in Table 1, slightly modified from their original version; here the **development time** is measured in days instead of hours.

Table 1. Average developmental time from birth to the end of the first adult instar for Daphnia magna.

Number of organisms	Temperature (°C)	Development Time (Days)
39	10	34.875
39	15	16.342
37	20	10.184
38	25	6.517
22	30	7.288

In Figure 2 the results of a regression analysis applied to the data above are presented. The development time can be approximated quite satisfactorily ($R=0.99$) by the quadratic equation:

$$t_p = 0.1184T^2 - 6.0453T + 82.5718 \quad (7.II)$$

where t_p is the time needed for maturation at the corresponding temperature T . According to the above quadratic equation, the minimum time required for the organism to reach its reproductive period occurs at about 25.5°C.

The time of reproduction for D. magna is independent of the age of the organism. What determines the beginning of

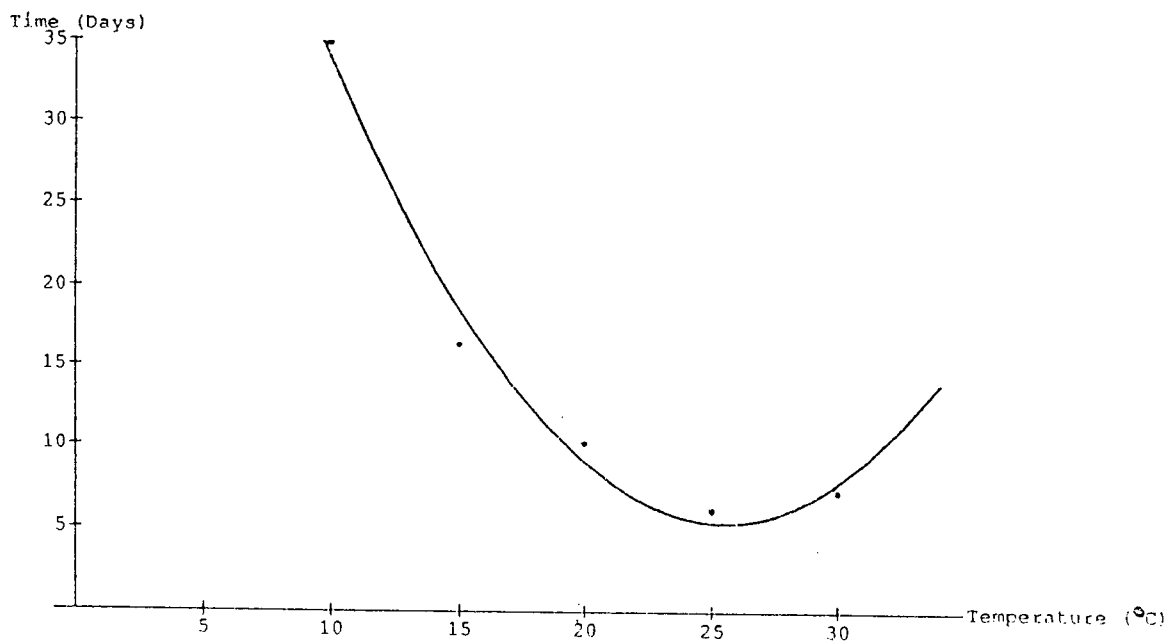


Figure 2. Development time for D. magna at different temperatures, and the corresponding regression curve.

the reproductive period is its length² rather than age (Goss, 1978). It is well documented in the literature that the specific length for reproduction is:

$$L_R = 2.5 \text{ mm}$$

(Kooijman, 1986). Also, the length at birth is

$$L_0 = 0.8 \text{ mm}$$

(Goulden et al., 1982).

If the values above are substituted into the equation (6.II), taking into consideration that the maximum length the organism can attain is:

$$L_i = 6 \text{ mm}$$

(Hallam, 1990) and equation (7.II) is used as well, a representation for the von Bertalanffy growth rate j is obtained. The growth rate in this form depends solely on temperature and is:

$$j = \ln\{(L_i - L_0)/(L_i - L_R)\} / (0.1184T^2 - 6.0453T + 82.5718) \quad (8.II)$$

Although for the regression equation (7.II), only the time needed for maturation at different temperature levels is used, the results can be extrapolated since the von Bertalanffy growth rate remains constant throughout the entire life of organism, and equation (8.II) can be used for the entire life span of D. magna, (Fabens, 1965).

²This may not be true for organisms living in temporary ponds (Lynch et al., 1986).

2. AN ORDINARY DIFFERENTIAL EQUATION MODEL FOR PHYSIOLOGICAL PARAMETERS

A. Derivation

In the previous section, an indirect method for estimating the von Bertalanffy growth rate as a function of temperature was presented.

Here, a more generic, ordinary differential equation model for the study of the behavior of several different physiological parameters at different temperatures is presented.

Observations in the literature (Goss, 1978) and Lassiter (personal communication, 1990) indicate that, the following statements concerning the effects of temperature on physiological parameters of an organism are valid:

- 1) There exists a unique optimal temperature T_{opt} where the physiological parameter takes its optimal value.
- 2) An increase in the temperature throughout a temperature range below the optimal will cause an increase in the value of the physiological parameter.
- 3) There exists a maximum temperature T_{max} greater than T_{opt} , which if approached for T greater than T_{opt} causes a decrease in the value of the physiological parameter. Above this temperature, the organism dies immediately.
- 4) The temperature range and in particularly the optimum and the maximum values are usually distinct for different organisms.

5) The rate of change of the physiological parameters as a function of T is not solely a function of temperature change but depends upon the value of the temperature itself as well as the magnitude of the parameter when the change occurs.

B. The model

Based on these observations, it is assumed that the model describes the rate of change of a physiological parameter with respect to temperature with the following properties:

- a) It is proportional to the value of the physiological parameter k .
- b) It is proportional to a deviation of temperature T from the optimal temperature T_{opt} with a rate of change that is positive with increasing temperatures T for values below T_{opt} and negative for values above T_{opt} .
- c) It is inversely proportional to a deviation from the maximum temperature T_{max} , i.e. large deviation from T_{max} results in small rates of change for the physiological parameter k , and as T approaches T_{max} the rate of change of k decreases substantially; namely, k approaches zero.

Therefore an equation that represents the model described above may have the form:

$$dk/dT = ak(T_{opt} - T) / (T_{max} - T) \quad (9.II)$$

where a is a constant of proportionality. The parameter a is

a function of the particular species and the particular physiological parameter.

Solving the above ordinary differential equation as a boundary value problem with k_{opt} taken as the optimum value of the physiological parameter when $T=T_{opt}$ the expression below is found:

$$k=k_{opt} \exp[a(T-T_{opt})] [(T_{max}-T)/(T_{max}-T_{opt})]^{a(T_{max}-T_{opt})} \quad (10.II)$$

If the effect of a unit deviation from T_{opt} is compared to the effect of a unit deviation from T_{max} and these are found to be different, this does not affect the validity of the model is provided that the coefficients for the effects are simple proportionality constants. They are a simple quotient and are included together with the coefficient of k into a single new constant a . Thus, another form of the model (9.II) is:

$$dk/dT=a_1k[a_2(T_{opt}-T)]/[a_3(T_{max}-T)] \quad (11.II)$$

If $a_1a_2/a_3=a$ the equation above becomes equation (9.II).

The differential equation (9.II) with the condition $k(T_{max})=0$, is a singular boundary value problem since as T approaches T_{max} from the left, the fraction $(T_{opt}-T)/(T_{max}-T)$ approaches $-\infty$. Therefore it is necessary to investigate the situation.

Substituting the solution (10.II) into (9.II) we find:

$$k' = ak_{opt} e^{a(T-T_{opt})} (T_{max} - T)^{a(T_{max}-T_{opt})-1} \cdot (T_{opt} - T) (T_{max} - T_{opt})^a (T_{opt} - T_{max}) \quad (12.II)$$

As T approaches T_{max} from the left, the term

$$ak_{opt} e^{a(T-T_{opt})}$$

is always positive. The term

$$(T_{opt} - T) (T_{max} - T_{opt})^a (T_{opt} - T_{max})$$

is always negative. We investigate the term

$$(T_{max} - T)^{a(T_{max}-T_{opt})-1}.$$

If $a(T_{max} - T_{opt}) - 1$ is greater than 0 then k' approaches 0.

If $a(T_{max} - T_{opt}) - 1$ is less than 0 then k' approaches $-\infty$.

If $a(T_{max} - T_{opt}) - 1$ is equal to 0 then k' approaches a constant number.

The above results interpreted for the constant a show that:

if a is less than $(T_{max} - T_{opt})^{-1}$ then k' approaches $-\infty$.

if a is greater than $(T_{max} - T_{opt})^{-1}$ then k' approaches 0.

if a is equal to $(T_{max} - T_{opt})^{-1}$ then k' approaches a constant.

CHAPTER III

RESULTS

1. THE VON BERTALANFFY GROWTH RATE

Using equation (8.II) of the previous chapter and substituting the corresponding values of temperature that were used in Table 1 we are able to find the values of the von Bertalanffy growth rate at these temperatures:

Table 2. Values of the von Bertalanffy growth rates at different temperatures.

Temperature (°C)	von Bertalanffy Growth Rate (/Day)
10	0.01181
15	0.02142
20	0.04399
25	0.073
30	0.05107
35	0

The value zero of the growth rate at 35°C presented in Table 2 is not evaluated using equation (8.II). According to Brown (1929a, in Goss, 1978) and Goss and Bunting (1976), the organism does not live and reproduce at that temperature. Therefore, it is safe to assume for the purpose of the

model, that its value equals 0.

In Figure 3 a graph of the function:

$$j(T) = 0.397 / (0.1184T^2 - 6.0453T + 82.5718) \quad (1.III)$$

is presented.

It is the von Bertalanffy growth rate as function solely of temperature. The value 0.397 results from substitution of constant quantities particular for this species in equation (8.II). The maximum value of this function is encountered at 25.5°C. The range of validity of the function is from 10 to 34°C.

2. PHYSIOLOGICAL PARAMETERS

A. Growth Rate

Equation (10.II) can be used to determine the values of several different physiological parameters over their temperature range. If the values of the optimal and the maximum temperature for the particular species and the particular parameter, the optimal value and the value of the parameter at any other temperature over the temperature range of the organism are known then the behavior of the parameter can be determined over the entire temperature range of the organism. This represents sufficient data so that the value of the constant of proportionality, **a**, can be found. Thus, every term in the right side of equation

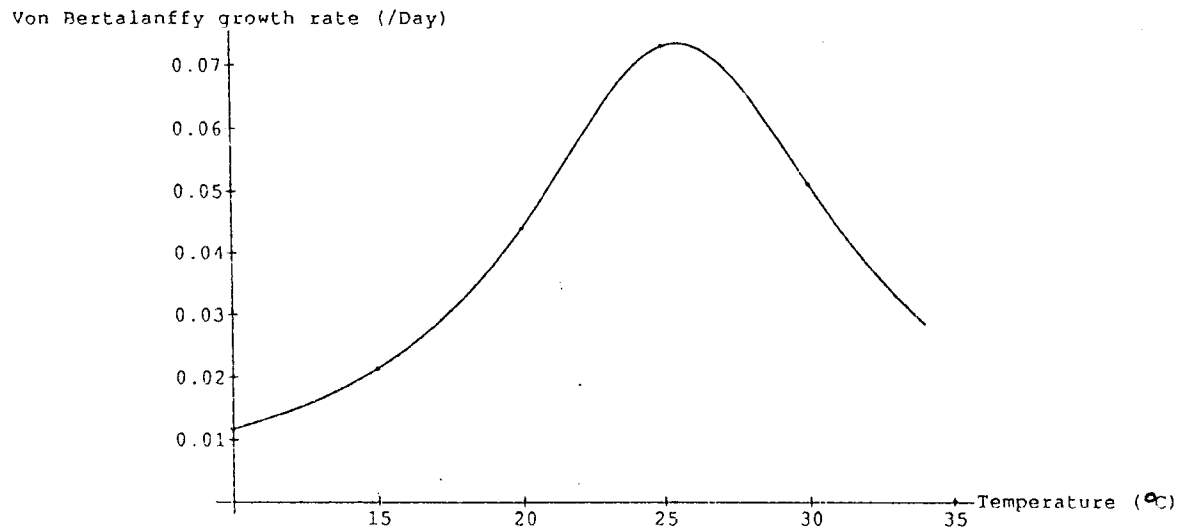


Figure 3. The von Bertalanffy growth rate as a function of temperature as it results from the classical von Bertalanffy model.

(10.II), k_{opt} , a , T_{max} , T_{opt} is known.

In Figure 4, the behavior of the von Bertalanffy growth rate is presented. The values of the parameters and constants used are the results of the model described in the previous section:

$k_{opt}=0.07343/\text{Day}$ at $T_{opt}=25.5^{\circ}\text{C}$, $T_{max}=35^{\circ}\text{C}$ and

$k=0.04399/\text{Day}$ at $T=20^{\circ}\text{C}$.

The value obtained for the constant of proportionality a using the values above is:

$$a=0.44$$

A graphical representation of equation (10.II) for the specific values mentioned above is presented in Figure 4. A more correct way to estimate the value of a for theoretical observations could be the averaging of the different values obtained by the application of the same procedure as above to different growth rate values. Our results show the value of a to be 0.37 plus or minus 0.07. This value of a is well above the critical value predicted by equation (12.II). The critical value of a is for the growth rate 0.105.

For comparison reasons the values:

$k_2=0.073/\text{day}$ from Table 2, and $T_A=6400^{\circ}\text{K}$ (Kooijman, 1988)

are applied to the Arrhenius relationship (7.I), presented in Chapter I. The graphical result of this is presented in Figure 5.

B. Reproductive frequency

Goss (1978) presented data on mean instar durations of

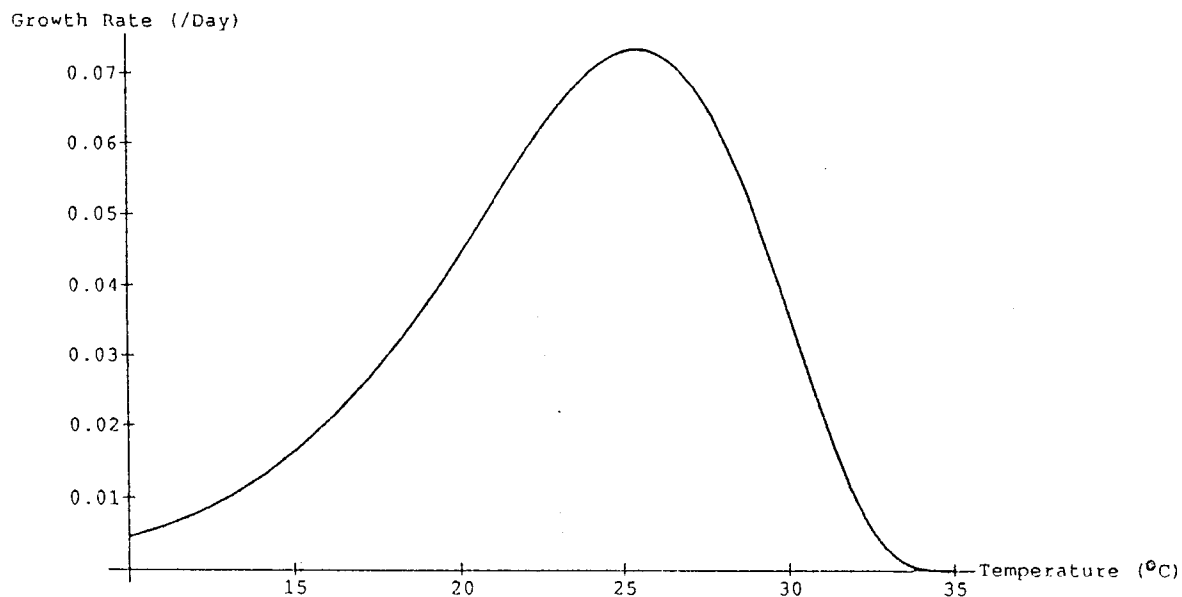


Figure 4. The von Bertalanffy growth rate throughout the entire temperature range of D. magna as it results from the differential equation model.

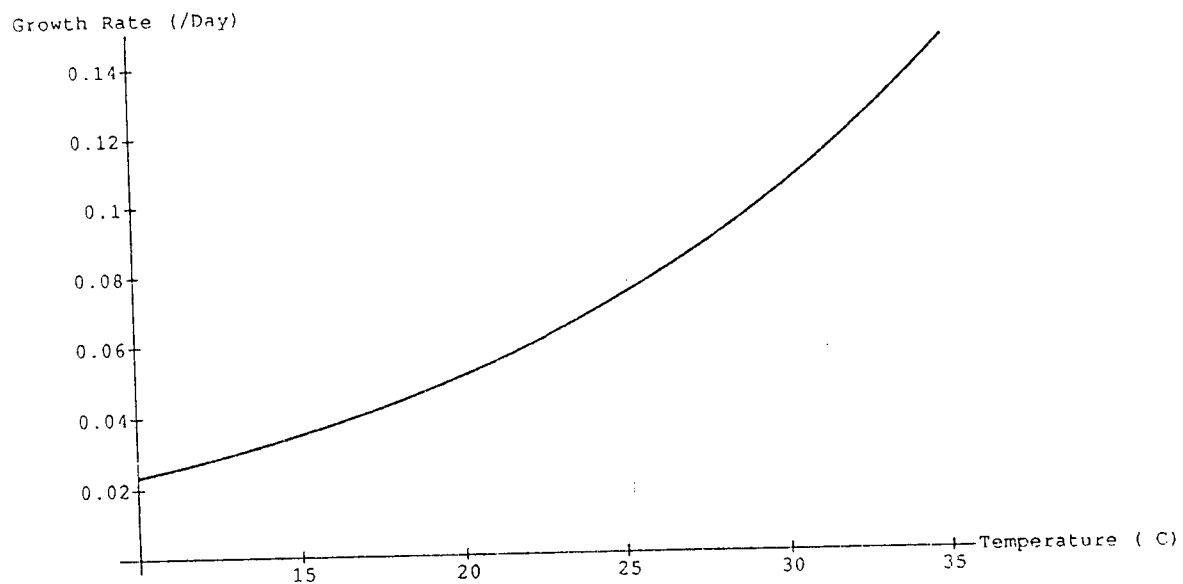


Figure 5. The von Bertalanffy growth rate as predicted from the Arrhenius relationship.

D. magna at different temperatures. At the end of each adult instar phase the organism reproduces. Hallam (1990) assumes that these reproductive periods are periodic. This is supported by the data utilized here. In Table 3 the mean instar duration is presented. This is extracted by averaging the durations of the first and second adult instar.

Table 3. Mean instar duration at different temperatures for D. Magna.

Temperature (°C)	Mean Instar Duration (Days)
10	9.876
15	5.323
20	3.207
25	2.265
30	2.182

The values above, can be approximated quite satisfactorily ($R=0.99$) by the quadratic regression equation:

$$t_r = 0.0288T^2 - 1.5248T + 22.063 \quad (2.III)$$

where t_r is the instar duration time, and T is the temperature in °C.

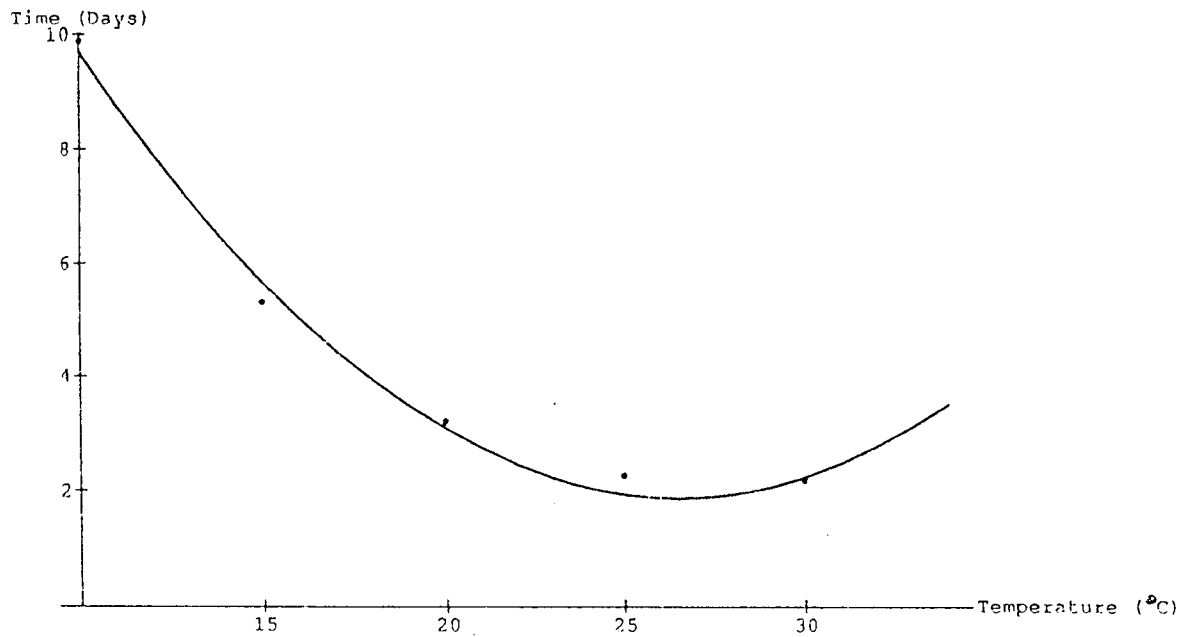


Figure 6. Instar duration time for *D. magna* at different temperatures, and the corresponding regression curve.

According to the equation above the minimum instar duration time appears at 26.5°C and is equal to:

$$t_{26.5}=1.8806 \text{ Days}$$

The results above appear in Figure 6.

Taking the inverse of the values predicted from the equation (2.III) a new rate can be created. This may be called **reproductive frequency**. The biological interpretation of this rate may be the reproductive effort allocated by the individual organism at each time unit over each instar period.

Since the **reproductive frequency** is a rate, the equation (10.II) can be applied. For this reason values for the parameters have been chosen to be:

$$k_{opt}=0.5317/\text{Day at } T_{opt}=26.5^{\circ}\text{C}, \quad T_{max}=35^{\circ}\text{C}$$

$$k=0.3239/\text{Day at } T=20^{\circ}\text{C}.$$

In this case the value obtained for the constant of proportionality a is:

$$a=0.296$$

The graphical representation of the reproductive frequency as a function of temperature can be seen in Figure 7.

C. Length as a function of temperature and time

We are seeking a relationship that will provide us with the length of D. magna at any time during its lifetime at different temperatures.

Substituting the value of growth rate from equation

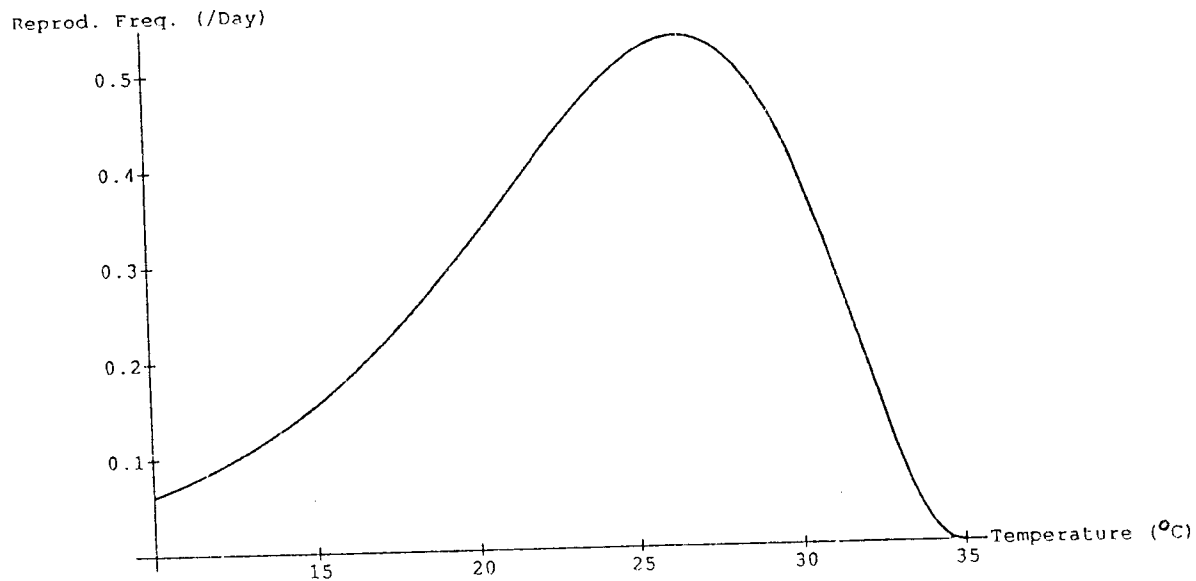


Figure 7. The reproductive frequency throughout the entire thermal range of *D. magna* as it results from the differential equation model.

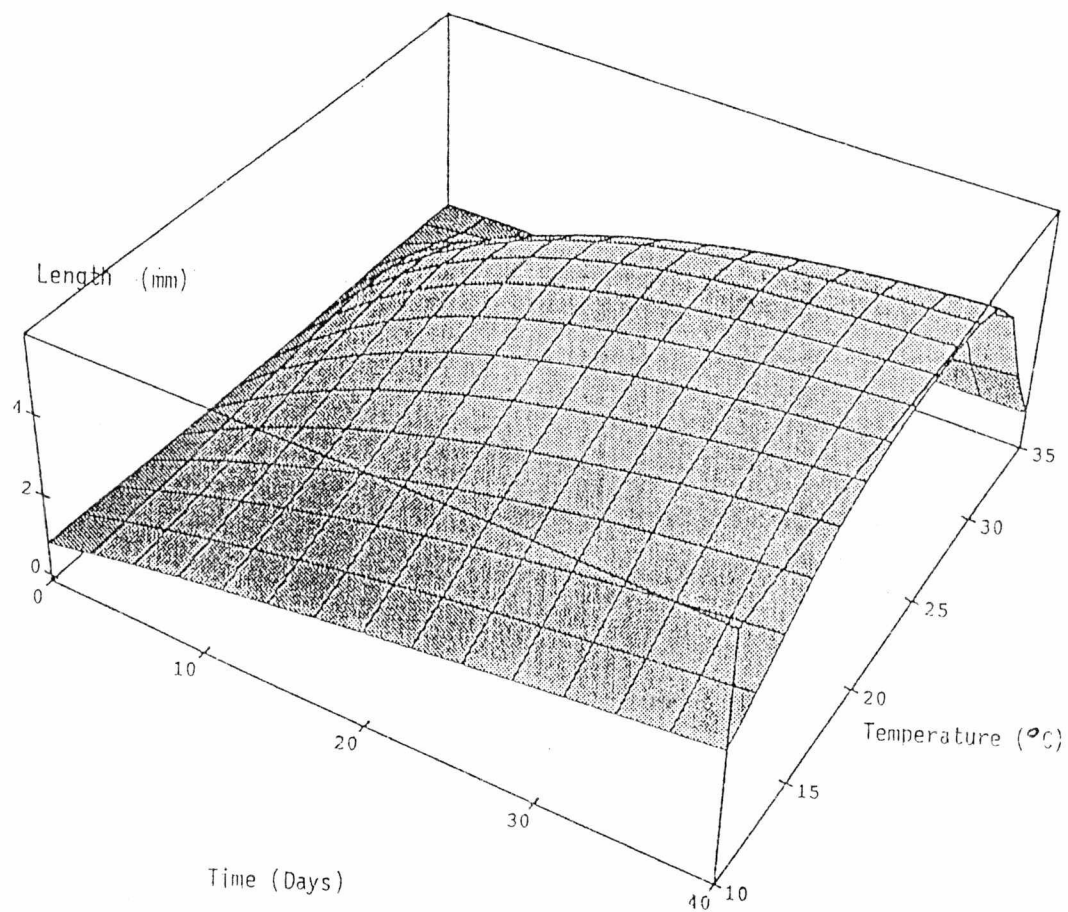


Figure 8. The length of *D. magna* as a function both of temperature and time throughout its entire life span and thermal range as it results from the combination of the von Bertalanffy and the differential equation model.

(10.II) into equation (5.II) we can obtain the desired relationship for the length of the organism.

This result can be seen in Figure 8. The particular values used for this application are:

$L_i = 6 \text{ mm}$, $L_o = 0.8 \text{ mm}$, $a = 0.239$,

$T_{\text{opt}} = 25.5^\circ\text{C}$, $T_{\text{max}} = 35^\circ\text{C}$, $j_{\text{opt}} = 0.07343/\text{Day}$, which have been used as parameters previously or are the results from the models above.

CHAPTER IV

DISCUSSION

1. THE VON BERTALANFFY GROWTH RATE

As can be seen in Figure 3 the model (1.III) describes the behavior of the von Bertalanffy growth rate throughout a wide temperature range. The model fails to predict a 0 value for the growth rate at the temperature of 35°C. This is a result of the method that was followed for the estimation of the equation fitting the experimental data. The temperature range covered the range from 10 to 35°C. It is impossible to include the information about the behavior of D. magna at temperature 35°C in the equation (7.II). The organism dies; therefore it is meaningless to refer to Development Time. The result confirms what has been observed in experiments and has appeared in the pertinent literature up to this point.

The minimum value of the quadratic regression equation for the Development Time, occurred at the temperature of 25.5°C. This result served as the point at which the highest growth rate appeared. The method provides a function that can be used to describe the behavior of the von Bertalanffy growth rate over almost the entire temperature range of the organism under study. Also, the von Bertalanffy growth rate results from a differential equation model which has been formulated by taking into consideration physiological

aspects of the development of the organism, and this model gives results in a continuous time scale, as opposed to a usual curve fitting.

This method can be utilized whenever data on development time for sufficient temperature points are available. More experimental work is needed, especially in the direction of collecting data at more temperature points so that we can develop more statistically suitable, development time functions.

2. PHYSIOLOGICAL PARAMETERS

The model (9.II) suggested in this study is an effort to present an ordinary differential equation capable describing the effects of temperature on the physiological parameters of an organism.

Previous attempts were based on models that converted experimental data into equations using techniques of regression analysis. A typical example of this procedure is the resulting model in this study discussed in the previous section.

The model proposed here, manages to describe the behavior of physiological parameters over the temperature range of the organism under study. This temperature range is the one in which the organism functions normally plus the lethal temperature limit. An equation that has been widely used in the past is the **Arrhenius relationship** (7.I) and a

similar equation involving the Q_{10} value, (8.I). These have the disadvantage of not taking into consideration the quantitative and qualitative changes that appear in the physiology of an organism as the temperature increases.

An important characteristic of the model is a result of its formulation as a differential equation. Because of this form, it can be more easily incorporated into already existing individual based models. As an individual progresses from egg to juvenile to adult instar, **temperature** as well as **pH** plays a very important role in its life history.

Hallam (1990) proposed a model to describe the growth of female daphnids. The individual is viewed from the physiological perspective and is divided into two compartments: storage and structure. Growth is viewed on a continuous time scale. Environmental factors such as temperature and pH are recognized as important growth factors since they affect filtering, feeding and reproductive frequency rates. However the modifications necessitated by these factors are reflected in parameter values in a process formulation rather than in the process itself. A representation like (10.II) will enable incorporation of these factors in a continuous way and may result in their representation in a more unified way.

The value of the parameter **a** seems to be different for different physiological parameters. It appears that it plays

a role similar to the one that Q_{10} plays in equation (8.I).

The model needs further testing utilizing data for other physiological parameters. Further investigation needed to determine more effective ways for the estimation of the value of the constant of proportionality a . Equation (11.II) provides one way to accomplish that. This assumes that detailed experiments have to take place in order to determine the specific effects of the deviations from T_{max} and T_{opt} and the effect of the value of the physiological parameter itself.

3. LENGTH AS A FUNCTION OF BOTH TEMPERATURE AND TIME

The graph on Figure 8 shows the length of a D. magna that lives **40 days**. At the lethal temperature of **35°C** the figure predicts no growth. This is a numerically acceptable result. The organism does not grow at this temperature because it dies instantaneously.

The model predicts that the organism will reach the length of **2.5 mm** necessary for reproduction, if it actually lives the time period of 40 days theorized here. Usually, this is not the case, especially for the temperatures at the left of the interval studied here. We believe that at temperature values below 10°C the physiology of the organism changes drastically. The female daphnids reproduce sexually and lay resting eggs that survive over the winter.

The model assumes constant temperature for the entire

life span of D. magna. This is not the case in reality for the organism. During its lifetime it encounters temperature oscillations that are not taken into consideration in the formulation suggested here. A more realistic approach would assume a temperature that is variable with time. This could be a suitable function that would properly represent accumulated meteorological data for the period of the year into consideration. In this case the initial assumption for the von Bertalanffy growth model for the length of an organism can be formulated using the following differential equation:

$$dL/dt = j[T(t)](L_i - L) \quad (1.IV)$$

where $j[T(t)]$ is the von Bertalanffy growth rate as a function of temperature T that is also a function of time t . The equation above that is also known as **growth in length hypothesis** states that the rate of growth in length is directly proportional to $L_i - L$, the length yet to be achieved.

The solution of the above equation is given by:

$$L(t) = L_i - (L_i - L_0) \exp\left\{-\int_0^t j[T(s)] ds\right\} \quad (2.IV)$$

The latter representation of the classical form of (5.II) includes temperature as a function of time, a factor

that has been neglected thus far in the applications of the von Bertalanffy model. It is also an extension of the equation that gave the graphical results of Figure 10.

Future directions in research related to this area should include studies in temperature patterns and search for proper mathematical functions that fit this patterns.

CHAPTER V

SUMMARY AND CONCLUSIONS

The current study was undertaken to quantitatively assess and propose mathematical models to investigate the effects of varying temperatures on growth rate and other physiological parameters of Daphnia magna. Results obtained provide information that can be applied in understanding the role temperature can play in regulating aquatic ecosystems.

The classical von Bertalanffy model has been revised by taking into consideration the effects temperature has on growth. Data on development time have been represented by a quadratic regression equation. Results show that temperature affects the von Bertalanffy growth rate and the maximum length. In the lower and higher temperatures, the organism does not live long enough to attain a length close to its maximum length. Finally, a more realistic version of this model is proposed where the temperature is a function of time.

A completely new model suggested by Dr. R.R. Lassiter for the incorporation of thermal effects into the behavior of physiological parameters is studied. To our knowledge, for the first time the idea of optimal temperature and lethal temperature limit are implemented into an ordinary differential equation model for the study of the physiology of an organism. The model describes physiological parameters

as a function of temperature over almost the entire thermal range of the taxon under study. This differential equation model is generally preferred more than a model that results from a regression analysis because it does not require as many data points.

The trends found in this study are considered representative for Cladocera and perhaps numerous other aquatic invertebrate poikilotherms. A natural continuation of this work would be the quantification of the affects of temperature on other physiological parameters. The effects of pH can probably be studied in an analogous manner. Such efforts should assist the studies in areas like ecotoxicology where individual physiology is fundamental.

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