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A COMPARISON BETWEEN MODELS DESCRIBING THE INFLUENCE OF TEMPERATURE ON THE DEVELOPMENT RATE OF COPEPODS

by

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ABSTRACT. — Four mathematical expressions relating development time to temperature are compared. All four yield good predictions of the development rate of the copepod *Tachidius discipes*. The use of the equation of BELEHRADEK is criticized. It is concluded that the power equation $D = aT^b$ gives the best approximation in this case.

INTRODUCTION

Temperature is probably the most important single parameter influencing developmental rates of aquatic invertebrates and its role has been the subject of innumerable studies. The purpose of this study was to compare some mathematical models which have been proposed to quantify the relationship between temperature and development time. The criterion used was the agreement between observed values for developmental rates of the harpacticoid copepod *Tachidius discipes* (GIESBRECHT, 1882) and calculated values from regression analysis, as measured by a χ^2-test.

MATERIAL AND METHODS

The methods used for the cultivation of the copepod will be described in detail elsewhere (SMOL and HEIP, 1974). For the purpose of this study it suffices to say that copepods were cultivated, starting from wild females carrying egg-sacs, at 0, 5, 10. 15, 20 and 25° C in glass tubes with food in excess. Temperature was controlled with a precision of approximately 0.1° C. As a measure of the development time we took the generation time, defined as the mean time between the appearance of females with egg-sacs in consecutive generations. Regression analysis was performed as simple linear regression with the aid of a HEWLETT-PACKARD 9810-A desk calculator.

RESULTS AND DISCUSSION

The observed values for the generation time of *Tachidius discipes* are taken from the study of HEIP and SMOL (in preparation) and are presented in the first column of table 1.

Table 1

Observed and expected values of the generation time of Tachidius discipes *(in days) at different temperatures*

Temperature °C	Observed	Eq. (1)	Eq. (2)	Eq. (3)	Eq. (4)
25	13.9	13.4	13.9	11.9	13.9
20	17.3	17.7	17.9	18.6	17.7
15	25.1	25.1	24.7	29.0	24.3
10	41.5	40.1	39.1	43.4	38.9
5	83.0	83.1	85.5	70.8	97.0
	x^2	0.08	0.25	3.14	2.23

The traditional equation used to represent the relationship between development time and temperature for marine copepods has been the equation of BELEHRADEK (1935):

$$D = a(T - \alpha)^b \qquad (1)$$

where D is the development time, T is temperature and a, b and α are constants. The use of this equation originates with MCLAREN (1963) who, in subsequent years, tried to give a biological interpretation of the parameters. b is a measure of the degree of curvilinearity, it is the slope of the plot of log $(T - \alpha)$ versus log D. When b is considered as being the same for different species, application of this "universal value" shows that a is nearly proportional to egg-diameter, and α is linearly correlated with the environmental temperature for different species and is therefore a simple index for temperature adaptation (MCLAREN, 1963, 1966, 1974; MCLAREN *et al.*, 1969; CORKETT and MCLAREN, 1970; CORKETT, 1972). α is called the biological zero, because development time is infinite for $T = \alpha$.

However, the application of this equation is subject to a serious disadvantage due to the calculation of the parameters from series of values of only two variables. The method used by these and other authors (e.g. GEILING and CAMPBELL, 1972) consists in holding α constant in each calculation of a and b and then selecting the value of α which yields the largest correlation coefficient. It is clear however that each α corresponds with a different pair of values for a and b. Holding b constant, as is done by the authors mentioned, is therefore an arbitrary act with no computational justification. I think that this procedure is unsatisfactory and results obtained do indeed suggest some strange phenomena : values of α are often less than —5° C (e.g. —7.5° C for *Calanus helgolandicus*, —13.4° C for *Pseudocalanus minutus* and —10.4° C for *Eurytemora hirundoides* as calculated by CORKETT (1972)) and it appears to be a somewhat low biological zero that would prevent copepods from reproducing completely only in nearly deep frozen ice.

Calculations on *T. discipes* show that values of a and b vary considerably with different α's. (table 2). In this case a value of α = —2° C yields the largest correlation coefficient and it is for this value that expected values according to BELEHRADEK's equation have been calculated (column two in table 1).

Table 2

Values of a and b of Belehradek's equation and correlation coefficient r^2 for different values of α

α	a	b	r^2
—5	3667	—1.65	0.9976
—4	2490	—1.55	0.9983
—3	1692	—1.45	0.9987
—2	1149	—1.35	0.9988
—1	779	—1.24	0.9984
0	527	—1.13	0.9972
1	354	—1.01	0.9946
2	234	—0.89	0.9892
3	152	—0.75	0.9782
4	92	—0.58	0.9529

A special case of BELEHRADEK's equation is α = 0, which yields

$$D = a\ T^b \qquad (2)$$

This is a power series and here the coefficients a and b can be calculated without ambiguity with a regression analysis. The meaning of the coefficients are clear : b is the slope of the plot of log D versus log T, and a is the development time for $T = 1°$ C. This equation is easy to calculate but it has the disadvantage that for $T = 0°$ C, D will always the infinite. For species who reproduce at temperatures of 0° C or lower the equation can not be used. This is not the case for *T. discipes* : expected values of the generation time of this species according to (2) are given in the third column of table 1.

Another possible candidate to fit the observed values is obviously the exponential function :

$$D = a\, e^{bt} \tag{3}$$

where a and b are constants, and $e = 2{,}72$ ... is the base of natural logarithms. When $T = 0$, $D = a$, so $a = D_0$, the development time at 0° C. This equation does not suffer from the disadvantage of the previous one. b is the slope of the plot of log D versus T. Values for *T. discipes* as calculated from (3) are given in the fourth column of table 1.

Finally, we consider an equation which, in a way, combines (1) and (2). Calculation of b according to (2) for three copepod species showed b to be close to minus one in all cases. Taking $b = -1$, the equation of Belehradek reduces to :

$$D = \frac{a}{T - \alpha} \tag{4}$$

which is the formula of a hyperbola. Here again there are only two parameters to be obtained from a regression analysis and no ambiguity results. α can, as in the case of Belehradek's equation, be conceived as a biological zero, because for $T = \alpha$, D becomes infinite. Values of α as obtained for three copepod species by HEIP and SMOL (in preparation) are 0.24° C for *Paronychocamptus nanus*, 1.65° C for *Tachidius discipes* and 4.33° C for *Nitocra typica*. These values are positive and are in accordance with the observed temporal distribution of these species in nature (HEIP, 1973). $T = \alpha$ is an asymptote of the hyperbola, the other asymptote is $D = 0$. Equation (4) can be moditied to provide for a minimum development time larger than zero simply by putting :

$$D = D_{min} + \frac{a}{T - \alpha} \tag{5}$$

However, the same difficulty arises as in the use of BELEHRADEK'S equation, i.e. the necessity to calculate three parameters from series of observations of two variables.

Values for the expected generation time of *T. discipes* according to (4) are given in the fifth column of table 1. From this table we can conclude that all equations yield expected values which are in close agreement with observed values, χ^2 being much smaller than 9.49 (d.f. = 4) in all cases. The best fit is obtained with equation (1) for $\alpha = -2^{\circ}$ C. The second best fit is obtained with the power equation (2), but the fit with either the exponential (3) or the hyperbola (4) is still quite satisfactory. Predictions are less accurate for 5° C only in these last two cases. As all these equations are empiric formulae, no one should be preferred a priori. In view of its simplicity we used the power equation (2) in further calculations in the case of *T. discipes*.

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