

NOTES

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The development and growth of *Calanus* copepodites¹

Abstract—A two-compartment model of developing calanoid copepods is proposed. One compartment is tentatively identified with the oil sac of copepodites and determines the rate of growth of the other. The developmental stage of the copepod is taken to be a measure of the second compartment. Parameter values are estimated for copepodites of *Calanus pacificus* using existing data. Respiration appears to be directly proportional to the estimated size of the second compartment.

This note describes a simple model of the growth and development of calanoid copepods. It has benefited from the comments of B. L. Bayne and J. M. Colebrook.

The data used to estimate the model parameters are those presented by Vidal (1978; see also Vidal 1980a,b,c,d) relating to the copepodite stages of *Calanus pacificus* Brodsky. These appear to represent the most detailed and comprehensive experimental study of the development of a copepod at present available. The model has been constrained by the requirement that its parameters be estimable from these data, and, while allowing for the observed variation in the mean weight and composition of stages through the year (Gatten et al. 1979), it remains readily testable.

The body of a copepod is conceived as divisible into two parts termed "store" and "structural copepod." It is postulated that, upon assimilation, food or that component of food whose supply limits development, is converted initially into some storage form—the store. This is

subsequently used in the production of the more differentiated part of the copepod's anatomy, referred to generically as structural copepod. Moulting is taken to occur at fixed weights of structural copepod. The growth rate of the structural copepod is thus equivalent to the development rate of the copepod and is dependent on the amount of store. Thus, if s , g , and w are the weights of the store, structural copepod, and total animal

$$\dot{g} = u(s) \text{ and} \quad (1)$$

$$s = w - g. \quad (2)$$

Equation 1 incorporates the strong assumption that structural growth does not depend directly upon the amount of structural copepod already present, although the accumulation of store may.

A priori it is to be expected that $u(s)$ represents a monotonically increasing function of some positive power, ϕ of s , which rises toward some upper asymptote (γ_2). For instance,

$$\dot{g} = \gamma_1 \gamma_2 s^\phi / (\gamma_1 s^\phi + \gamma_2) \quad (3)$$

in which γ_2 is a constant. However, if ϕ were < 1 , reducing the proportionate effect of the store with increasing size, its effects would tend to be confounded with those of γ_2 . This was the case for Vidal's data. For this reason these were insufficient for the simultaneous estimation of both parameters and a simpler relation was preferred:

$$\dot{g} = \gamma s^\phi. \quad (4)$$

To constrain the model sufficiently for its parameters to be estimated, a fixed relation between the levels of structural copepod at which moulting occurs is needed. An intuitively appealing assumption is that the rule associated variously with the names of Brooks, Dyar, and Przibaum

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(Miller et al. 1977; Bodenheimer 1933) applies to this portion of the copepod. That is

$$g_i^* = kg_{i-1}^* \quad (5)$$

where g_i^* is the level of g at completion of the i th developmental stage and k is a constant.

To estimate the parameters of Eq. 4 and 5 it is necessary to express Eq. 4 in terms of observable variables. If the derivative of s with respect to time (\dot{s}) were known, it could be combined with Eq. 2, 4, and 5 to provide an implicit relation between the time taken by a copepod to pass from one moult to the next and its growth. In its absence, the integration required to render this explicit is impossible. A reasonable approximation might be achieved by taking \dot{s} to be constant within each stage, but even so integration does not yield a relation which can be made explicit in any observable variable. In view of this I used a discrete approximation to apply Eq. 4 and 5 directly to observed data.

Let $\bar{g}_i = (g_{i-1}^* + g_i^*)/2$ and \bar{w}_i be the corresponding mean dry weight. Let $\Delta g_i = g_i^* - g_{i-1}^*$ and t_i be the time required to pass through the i th stage. Then Eq. 4 can be approximated by

$$\Delta g_i/t_i \simeq \gamma(\bar{w}_i - \bar{g}_i)^\phi, \quad (6)$$

which can be rearranged to give

$$1/t_i \simeq \gamma(\bar{w}_i - \bar{g}_i)^\phi/\Delta g_i. \quad (7)$$

Given k and g_i^* for one particular i , Eq. 5 yields the g_i^* , and hence the values of \bar{g}_i and g_i , for all i . Given these, together with the γ and ϕ , Eq. 7 can be used to determine the development rate ($1/t_i$) of a copepodite in any particular stage from its mean weight during that stage. Thus, between them, Eq. 5 and 7 give a four-parameter relation of development rate to mean copepodite weight for each stage over all stages.

A uniquely extensive set of suitable data concerning the development of *C. pacificus* at three temperatures and under various feeding regimes is provided by Vidal (1978). The experimental conditions are described by Vidal (1980a).

Table 1. Approximate ANOVA of the relation of development rate (days^{-1}) to dry weight through Eq. 5 and 7 for *C. pacificus* data derived from Vidal (1978).

Source of variation	Approx df	Approx variance ($\times 10^4$)
Improvement of 12-parameter model over mean	11	611.6
Effect of temp on		
moulting parameters	4	14.3
γ	2	32.2
ϕ	2	5.2
Joint effect of temp dependence of moulting parameters and ϕ	6	14.4
Residual	100	8.5
Deviations from mean	111	68.3

Rather than using the estimates of inter-moult period and moulting weights tabulated by Vidal (1980b: table 3), I re-estimated values from the original data. Times of moulting were estimated using a probit analysis of numbers of individuals past each moult. The square root of moulting time was generally found to be satisfactorily normal; in instances where this was not the case deviations were not systematic and all data concerning that moult in that experiment were discarded. Moulting weights, used to calculate the \bar{w}_i , were derived by inserting these times in Chapman-Richards growth functions which had been fitted to the weight data for each experiment (Vidal 1980b).

Marquardt's method (Marquardt 1963) was used to determine parameter values which minimized the sum of squared deviations of the observed values of $1/t_i$ for each copepodite stage represented (copepodites 2–5 inclusive) in each experiment from those derived under Eq. 5 and 7. This was done initially with all four parameters allowed to vary independently with temperature (giving, for data at three temperatures, a 12-parameter model), then both parameters of Eq. 6, followed by each of the remaining parameters in turn constrained to be independent of temperature. The effects on the approximate mean-square deviations are presented in Table 1. The nonlinearity of

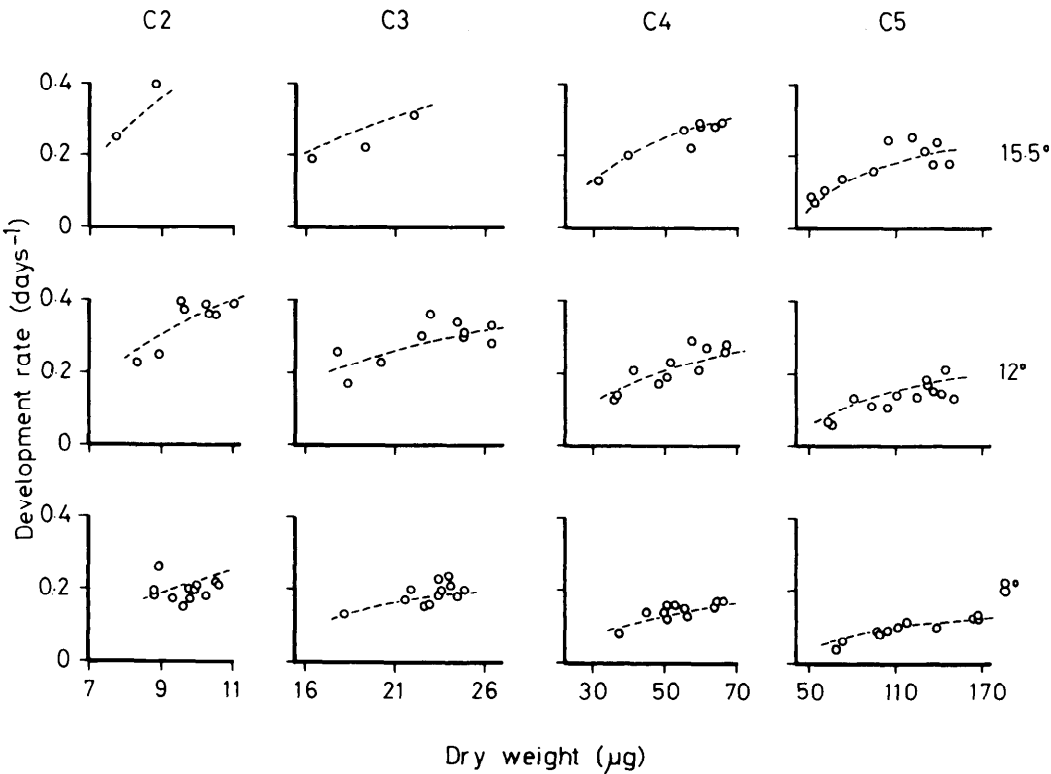


Fig. 1. Relation between development rate (reciprocal of intermolt period) and mean weight for stage shown by data of Vidal (1978) for *C. pacificus*. Dotted lines indicate least-squares fits of Eq. 7 and 5, with common parameter values apart from γ , which varies between temperatures.

the model and the correlations between the intermolt times from any one experiment render this analysis approximate at best; however, it appears to be only the removal of temperature dependence from γ which has any noticeable impact, and removal of the temperature dependence of all the remaining parameters has little effect on the overall goodness-of-fit. Allowing only γ to vary with temperature yields an apparently adequate description of the data (Fig. 1), giving the parameter estimates shown in Table 2. While exact confidence limits cannot be placed on these, all plane sections of the approximate 95% confidence region taken through the minimum parallel to the axes are virtually elliptical, so that there is probably little error in considering their distribution to be multivariate normal. On this basis the covariance matrix of the parameters was estimated by $(\mathbf{J}'\mathbf{J})^{-1}q/(n -$

$m)$, where \mathbf{J} is the matrix of numerically estimated partial derivatives of the expected values with respect to the parameters when the sum of squared deviations of the observations from expectations

Table 2. Estimates of the parameters of Eq. 5 and 7 for *C. pacificus* data derived from Vidal (1978), with measures of their error (see text).

Parameter	Least-squares estimate	SE of estimate	Approx 95% C.L.	Principal eigenvector of absolute covariance matrix
γ ($\mu\text{g}^{0.62} \cdot \text{days}^{-1}$)				
at 8°C	0.638	0.083	± 0.165	0.161
at 12°C	1.032	0.134	± 0.265	0.263
at 15.5°C	1.211	0.172	± 0.341	0.339
ϕ	0.379	0.034	± 0.068	0.062
$\ln(g^*_1)^\dagger$ (μg)	1.557	0.065	± 0.129	0.123
k	1.928	0.033	± 0.066	0.043

[†] $\ln(g^*_1)$ was estimated rather than g^*_1 since its error distribution was more nearly normal.

Table 3. Correlation matrix of estimates of parameters of Eq. 5 and 7 for *C. pacificus* data derived from Vidal (1978).

Parameter	γ			ϕ	$\ln g^*_1$
	at 8°C	at 12°C	at 15.5°C		
γ					
at 12°C	0.968				
at 15.5°C	0.959	0.971			
ϕ	-0.889	-0.900	-0.878		
$\ln g^*_1$	0.944	0.952	0.929	-0.925	
k	-0.643	-0.644	-0.602	0.866	-0.800

takes its minimum value (q); n is the number of observations and m the number of parameters (e.g. see Himmelblau 1970). From this the standard errors, confidence limits, and correlations (Tables 2 and 3) were derived in the usual way.

As might be expected from the model structure, all the parameter estimates are highly interdependent (Table 3); about 95% of the error variance in their estimation lies along a single axis. This may be judged from Table 2, in which the principal eigenvector of the absolute covariance matrix of the parameters is scaled to represent the projection of the 95% limits along this axis onto the original axes. Only for k does this markedly underestimate the confidence limits. It is clear that increasing the precision of estimation of any one parameter would improve that of all the remainder.

Although the detailed form of Eq. 4 and 5 may be open to question, it seems that the concept encapsulated in Eq. 1 and 2 is consistent with the observed data. It remains to place it in a context of copepod structure and physiology. The copepodite stages of many species of calanoid copepods possess an oil sac adjacent

to the gut which is generally regarded as representing a food reserve. The extent to which this can be identified with the hypothetical storage component might be suggested by its size. This is quite variable according to feeding conditions (Petipa 1964) but may represent a considerable proportion of the volume of an individual (Arnaud et al. 1980). Although the calculated mean store weights over all experiments for each stage are rather higher than those implied by the oil sac volumes determined by Petipa (1964) (Table 4), the wide scatter of individual values comfortably includes Petipa's figures. The oil sac contains largely, if not exclusively, wax ester (Lee et al. 1970; Benson et al. 1972), so that an alternative measure of sac size, or identity for the store, would be the copepod's wax ester content. Amounts found in fifth stage copepodites by Sargent et al. (1977) are compatible with the volumes given by Petipa. However, the levels found by Gatten et al. (1980), which show a considerable range, are more comparable to the mean level determined here.

If the store were the contents of the oil sac, it would exert little or no metabolic

Table 4. Store weights (in μg) determined from the data of Vidal (1978) for *C. pacificus* for comparison with oil sac weights derived from daily means of volumes found for *C. helgolandicus* by Petipa (1964) (assuming sp gr of 0.91; Petipa 1964).

Copepodite stage	8°C		12°C		15.5°C		Wt of oil sac (μg)
	Mean	SD	Mean	SD	Mean	SD	
2	2.7	0.6	2.8	0.9	1.3	0.8	0.6
3	9.6	1.8	9.5	3.1	5.8	2.9	2.2
4	28.5	8.4	26.6	11.1	27.4	12.0	7.9
5	69.9	34.0	63.9	30.0	51.0	36.2	45.4

demand, so that respiratory rate might relate more simply to the structural weight (g) than to the total dry weight (w) of the copepod. This view is consistent with the interpretation of their data by Conover and Corner (1968) to indicate that, whereas increased nitrogen content tends to increase specific respiration, increased fat reduces it. For his experimental *C. pacificus*, Vidal (1980c) estimated that the total respiratory rate of a copepod was proportional to the 0.824 power of its dry weight, with a constant of proportionality dependent on temperature. Double logarithmic regression of the rates implied by this relation (Vidal 1980c: eq. 3) on the structural weights at moult given by the parameter values of Table 2 implies that the two are directly proportional (the exponents are estimated as 1.06, 1.03, and 1.02 at 8°C, 12°C, and 15.5°C, none differing significantly from unity), although Vidal still finds an exponent of less than unity when respiration is related to lipid-free dry weight (B. W. Frost pers. comm.).

If the division of the developing copepodite into store and structural parts is accepted, the mechanism already suggested, relating the rate of accretion of the latter to the amount of the former, is clearly not the only possibility. Sharpe and Hu (1980) suggested that, in poikilotherms in general and the boll weevil (*Anthonomus grandis* Boh) in particular, growth and development are limited by different dietary constituents. They suggested that, whereas the former was energy (carbohydrate) limited, the latter was limited by the supply of protein. In the present context the growth of store and structural copepod might reflect separate aspects of the copepod's nutrition, related by their correlation in its food. The copepod retains the excess lipid, which it takes up in association with the requisites for its development. The respiratory constant of proportionality, estimated as the mean ratio of respiratory rate to structural weight, varies with temperature in parallel with the developmental constant, γ (Fig. 2). This might be interpreted as the inevitable result of the rate of respiration determining the excess of its

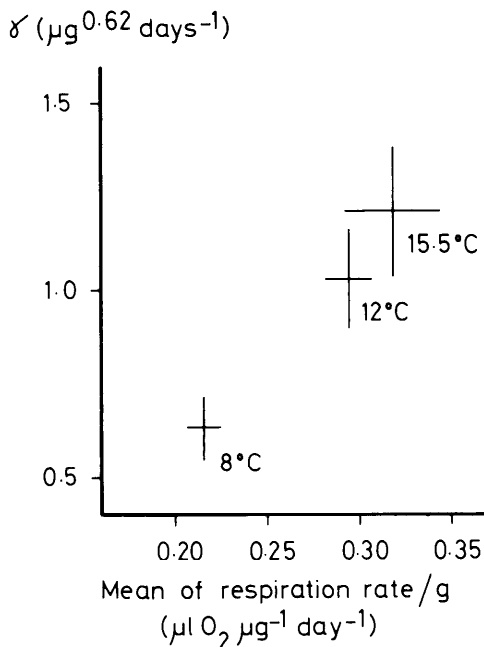


Fig. 2. Relation between development constant, γ (Eq. 4), and constant of proportionality of respiratory rate to structural weight (g) with varying temperature. Bars indicate 95% confidence limits.

substrate available for storage. Assuming that the components of food which limit development are not used by other metabolic processes, such a mechanism might be expected to lead to an effectively constant food requirement for any particular phase of development, independent of the rate at which it is obtained, as has been found, for example, for one spider species (Turnbull 1962). This is not the case for *Calanus helgolandicus* (Paffenhöfer 1976).

The concept upon which the development of the model was based, that development rate is limited by the rate of supply of material from the store (effectively energy if this were the oil sac), is more direct. This is a view exactly analogous to that presented by Caperon (1968) and Droop (1968) for algae, and similar to that given for higher plants by Thornley (1977). If structural growth were limited by its supply of energy the similar temperature relation of γ and the respiratory constant of proportionality would be a direct result. The overall relation of

respiration to structure weight would tend to imply that the allocation of respiratory energy to structural growth is small. The decline in the proportionate rate of use of the store for development with increased size ($\phi < 1$) might be taken to reflect the tendency to incorporate lipid reserves into wax esters of increasing chain length as their amounts increase (Lee et al. 1970).

It is clear that the view of copepod development which has been presented here is neither complete nor unequivocal; however, it does appear that the interrelations of growth and development in copepods may be explicable within a very simple scheme.

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