Limnol. Oceanogr., 39(7), 1994, 1528–1542

A model of growth and development in copepods

Frank van den Bosch[1] *and Wilfried Gabriel*
Max Planck Institute for Limnology, Department of Physiological Ecology, P.O. Box 165, D-24302 Plön, Germany

Abstract

We present a model for the growth and development of copepods based on the simple assumption that a constant fraction of assimilated carbon is invested in the formation of a new carapace. The individual molts into the next stage when the weight of the accumulated carapace building bricks is a fixed fraction of the body mass at the beginning of the stage. This simple stage-transition coordinating system is built into an individual growth model.

The model predicts decreasing stage duration and increasing body weight with increasing food concentrations. These trends closely agree with published data. Anisochronality, as found in many copepod species, agrees with model predictions. *Acartia* species usually show isochronal development. The model predicts isochronal development for one particular value of a parameter of the feeding process. Literature data show that this parameter value is realistic for *Acartia* spp. "Equiproportionality" is predicted by the model. The model thus shows close agreement with observed growth and development patterns.

In many freshwater and marine ecosystems, copepods are among the dominant secondary producers. Research on copepods lags work on cladocerans, especially *Daphnia* species.

Physiologically based models of individual growth have been developed for *Daphnia*. Much insight has been gained into the growth and development of *Daphnia* individuals. These individual growth models have been used to investigate the physiology of starvation (Lynch 1989; Gurney et al. 1990) and the effects of toxic substances (Kooijman and Metz 1984; Hallam et al. 1990). Some investigators have constructed population models based on such individual growth models (de Roos et al. 1992; Sinko and Steifer 1969). These models reveal how processes at the individual level influence the dynamics of *Daphnia* populations. In copepods, both the study of growth and development of individuals and of population dynamics could benefit from models of individual growth, as has been done for *Daphnia*. There are, however, major differences between growth and development of copepods and cladocerans that must be considered. These differences necessitate the development of new models. In this paper, we make a first step toward constructing a copepod life-history model. We concentrate on development within a stage and the transitions between stages.

Most *Daphnia* models assume molts occur at preset ages that are not influenced by food conditions (Lynch 1989; Hallam et al. 1990; Gurney et al. 1990). The onset of reproduction is assumed to be triggered by size (length or weight) of the animal (Kooijman and Metz 1984; Kooijman 1986; Gurney et al. 1990). These rules are questionable for *Daphnia* at low concentrations of food and are not appropriate for copepods.

In contrast to *Daphnia,* copepods reach the adult stage after a fixed number of immature stages. Molting from one stage to the next is not triggered simply by age or size of the animal. Stage duration of some species decreases with increasing food supply, thus ruling out age as the sole trigger for stage transition. Size in a stage for some species increases with increasing food supply, thus ruling out size as the sole trigger (Vidal 1980*a,b*; Paffenhöfer and Harris 1976; Elmore 1982; Berggreen et al. 1988; Santer and van den Bosch 1994). The when and why of stage transition is thus a central question in modeling the growth and development of copepods. We suggest an answer to this question by proposing a simple molting rule. Based on this idea, we present a copepod growth model.

---

[1] Present address: Department of Mathematics, Agricultural University of Wageningen, Dreijenlaan 4, NL-6703 HA Wageningen, The Netherlands.

Acknowledgments

We thank R. C. Hart for helpful discussions. We are grateful to W. R. DeMott and two anonymous referees whose comments improved the paper. We thank N. Zerbach for checking the English.

F. van den Bosch acknowledges the Alexander von Humboldt Stiftung for a research stipend and the Max-Plank-Institut für Limnologie for hospitality and support during his stay.

When to molt?

What determines the timing of stage transition in copepods if it is not triggered solely by age or size? The size of the carapace does not change within a stage, although copepods feed and gain mass between molts. Obviously, for the old carapace to be replaced during molting by a new and larger one, the building bricks of this new carapace must be synthesized. Assuming that the individual will molt as soon as the new carapace is ready, we have a simple and biologically plausible rule: an individual molts into the next stage when its new carapace is ready.

We still must define when the new carapace is ready. The animal invests a certain amount of assimilated carbon in carapace building bricks. The new carapace is ready when enough building bricks have been synthesized. Since the carapace covers the animal's surface, an obvious assumption would be that the size of the carapace building-brick compartment is proportional to the surface area of the animal. This implies that the thickness of the carapace is constant through stages. The first naupliar stage, however, has a much thinner carapace than an adult individual, so the thickness of the carapace is related to the size (length) of the animal.

Combining the arguments on surface area and carapace thickness discussed above gives a proportionality to length cubed, which is in turn proportional to volume and weight. We thus assume, as a first approximation, that carapace building-brick weight at the molt is proportional to weight of the animal. Vidal (1980*b*), the only investigator who has studied molting exhaustively, found (p. 141)

> The carbon content in exoskeletons of stages CII to CVI of *Calanus pacificus* ranged from 2.8 to 5.1% of the body carbon content of the *preceding* development stage. The mean was 3.8% and the deviations from the mean were uncorrelated with changes in temperature and *body size*.

This experimental observation is a first indication that our assumption is correct. We thus have the molting rule:

> *Molt to the next instar when and if the net accumulated carbon allocated to carapace building bricks during the current instar reaches a fixed fraction of the body mass at the beginning of the current instar.*

Notation

	Variables
$W_i(t)$	Total C content of stage i (excluding the compartment where carapace building bricks are stored) of an individual that is t time in stage i, μg ind.$^{-1}$
$S_i(t)$	C content of the carapace building-brick storage compartment at age-in-stage t, μg ind.$^{-1}$
L_i	Length of stage i, does not vary with age-in-stage, mm
t	Time since the beginning of the stage to be called age-in-stage, d
τ_i	Stage duration of stage i, d
C_i	Average C content of stage i, μg ind.$^{-1}$
	Parameters
κ	Fraction of the assimilated C channeled to biomass accumulation
ν	Parameter of the allometric length–carbon content relation, $\mu g\ (mm^{\sigma})^{-1}$
σ	Parameter of the allometric length–carbon content relation
η	Fraction of the volume of the individual reserved to store the carapace building bricks, ind.$^{-1}$
I_m	Maximum ingestion rate per unit of volume, $\mu g\ C\ d^{-1}\ (mm^3)^{\theta}$
α	Shape parameter of the functional response, ml $(\mu g\ C)^{-1}$
θ	Shape parameter of the dependence of maximum ingestion rate as related to body size
β_1	Amount of C needed for maintenance per unit of body C, d^{-1}
β_2	As β_1 but per unit of carapace building-brick C, d^{-1}
γ	C assimilation efficiency
x	Food density, $\mu g\ C\ ml^{-1}$

The model

Using the molting rule, we constructed a model that calculates, for each stage separately, the growth of the biomass of the animal and the synthesis of the building bricks of the new carapace. Feeding and assimilation as related to size of the animal are described. The model predicts stage durations and weight-in-stage as dependent on food concentration.

Variables and parameters are described in the list of notation and the model equations are summarized in Table 1.

Assimilation and allocation—A copepod in developmental stage i acquires A_i milligrams of assimilated carbon per day. A fraction, κ, is allocated to production of a new carapace. The remaining carbon, a fraction $1 - \kappa$, is channeled to accumulation of other biomass.

Denote for each stage, i, the carbon content of the carapace building bricks as S_i; the carbon content of (the rest of) the animal is denoted W_i. For both compartments, net growth is given as the balance between carbon allocation and maintenance cost. Growth in W_i and S_i is thus governed by von Bertalanffy (1934) -type equations:

$$\frac{dW_i}{dt} = [\kappa A_i - M_1]^+; \tag{1}$$

$$\frac{dS_i}{dt} = [(1 - \kappa)A_i - M_2]^+. \tag{2}$$

M_1 and M_2 are the maintenance costs of W and S, respectively. The notation $[\ldots]^+$ replaces the quantity in brackets with zero whenever it is negative, implying that the size of the animal cannot decrease. We thus consider structural biomass only.

For a detailed account, we should also incorporate nonstructural biomass and reserves, which would allow the size of the animal to decrease. Incorporating these features makes the model much more complex, as is shown by the work on *Daphnia* (Kooijman 1986; McCauley et al. 1990; Hallam et al. 1990). Moreover, the fit to data does not improve significantly compared to much simpler models incorporating structural biomass only (Kooijman and Metz 1984; de Roos et al. 1992).

Allometric relation—Various workers have determined length-mass relations for several copepod species. These relations are satisfactorily described by (*see* McCauley 1984)

$$\text{biomass} = \nu \text{ length } \sigma. \tag{3}$$

The parameters of allometric relations are usually thought to be independent of environmental conditions (*see* McCauley et al. 1990 for a discussion on *Daphnia*), but they can be quite sensitive to food at low concentrations (Duncan et al. 1985). There is, however, not sufficient information on this point to include this aspect in the model for copepods. Between molts, copepods do not increase in length. They do accumulate biomass, however. Relation 3 is thus only an "on-average" description of the relation between weight and length. At the molt, the new length of the animal is determined from its biomass at the time of the molt. The total carbon content ($W_i + S_i$) of an animal at the end of a stage, i, thus determines its length in the following stage, $i + 1$.

Timing of the molt—During the molt, the new carapace is assembled and S_i becomes zero. The proposed molting rule can now be described by

molt if: $S_i(\tau_i) = \eta(\nu L_i^{\sigma})$;

at the molt: $S_{i+1}(0) = 0$.

Note that τ_i is the stage duration of stage i.

Ingestion and assimilation—Feeding in marine calanoid copepods has been well studied. Work on freshwater copepods, especially cyclopoids, is scarce. Feeding rates depend on food density (x) and animal size and usually increase with food density to an upper limit. Dependence of feeding rate on food density is often well described by a concave (from above) or convex (from below) curve (e.g. Fernandez 1979; Frost 1972; Ambler 1986; Santer and van den Bosch 1994). One such curve often used for feeding responses is the Holling type 2 functional response. This functional response is mathematically similar to the Monod curve and the Michaelis-Menten kinetics.

In her study on *Paracalanus*, Ambler (1986) showed that maximum feeding rate is related to the size of the animal. The curvature of the response curve is influenced by animal size only to a minor extent. Inspection of the data given by Fernandez (1979), Hansen et al. (1990), and Paffenhöfer (1984*a,b*) also shows that the relation between food density and the half-maximum feeding rate is virtually independent of size. From these observations, we assume the curvature of the functional response to be independent of size.

Maximum feeding rate, however, is strongly dependent on size. The relation between feeding rate and animal biomass on a log-log scale is usually linear (e.g. Hamburger and Boetius 1987; Harris and Paffenhöfer 1976; Paffenhöfer and Harris 1976). Therefore, we assume maximum feeding rates to be proportional to biomass to the power θ.

The rate of carbon intake, F_i, is given by

$$F_i = I_m \frac{\alpha x}{1 + \alpha x}(\nu L_i^{\sigma})^{\theta}. \tag{4}$$

x is food density. We chose to incorporate Eq. 3 into Eq. 4 because many workers give data on feeding rates vs. individual mass rather than length.

The acquired assimilated carbon, A_i, in Eq. 1 and 2 is calculated by multiplying Eq. 4 by the assimilation efficiency, γ.

Maintenance—There are two maintenance costs, one for body structure, M_1, the other for carapace building bricks, M_2. The only experimental data available is the relation between total respiration and body weight (Lampert 1984). Although the expenditure of energy on maintenance is clearly associated with respiration, the precise relation is not known. Because of the lack of accurate data on maintenance requirements, we use as a first approximation the assumption that M_1 and M_2 are proportional to W_i and S_i:

$$M_1 = \beta_1 W_i, \tag{5}$$

$$M_2 = \beta_2 S_i. \tag{6}$$

McCauley et al. (1990) concluded that for *Daphnia,* the maintenance cost is approximately linearly proportional to body weight, although some investigators have reported that respiration rates are proportional to a "<1" power of body weight.

For copepods, some workers have also reported <1 powers for respiration vs. biomass. Harris (1983), Conover and Corner (1968), and Berggreen et al. (1988) indicated that this is due to incorporation of the storage oil sac in weight measurements. Re-examination of Vidal's (1980*a*) data by Harris (1983) showed that metabolic requirements are linearly proportional to structural body mass. From this empirical evidence in the literature, we conclude that our assumption of linear dependence of maintenance on body mass is not far from the truth and is useful as a first approximation.

Model analyses

Most experimental data on copepod life history give stage duration and animal size as variables. Such experiments on growth and development are usually done for various food concentrations that are kept constant during experiments. In this section, we derive explicit solutions for our model (Table 1) for constant food abundance. Stage durations and weight for *variable* food abundance can be obtained from our model by numerical solution.

Table 1. Summary of the model equations. i indexes the life stages of the copepod from N1 until adulthood. For calanoid copepods $i = 1, \ldots, 12$; for cyclopoid copepods $i = 1, \ldots, 11$. Variables and parameters are summarized in the list of notation.

At birth:

$$W_1(0) = W_b, \text{ the carbon content at birth}$$

$$L_1 = \left(\frac{W_b}{\nu}\right)^{1/\sigma}. \tag{7}$$

Between molts:

$$\frac{dW_i}{dt} = \left[\kappa\gamma I_m \frac{\alpha x}{1 + \alpha x}(\nu L_i^{\sigma})^{\theta} - \beta_1 W_i\right]^{+}; \tag{8}$$

$$\frac{dS_i}{dt} = \left[(1 - \kappa)\gamma I_m \frac{\alpha x}{1 + \alpha x}(\nu L_i^{\sigma})^{\theta} - \beta_2 S_i\right]^{+}; \tag{9}$$

$$\frac{dL_i}{dt} = 0. \tag{10}$$

Molt if:

$$S_i(\tau_i) = \eta\nu L_i^{\sigma}. \tag{11}$$

At the molt:

$$W_{i+1}(0) = W_i(\tau); \tag{12}$$

$$L_{i+1} = \left[\frac{W_{i+1}(0) + S_i(\tau_i)}{\nu}\right]^{1/\sigma}; \tag{13}$$

$$S_{i+1}(0) = 0. \tag{14}$$

For each stage i, we calculate the stage duration, τ_i, length, L_i, and average carbon content, C_i. These three quantities can be calculated explicitly from the model for each of the subsequent stages (Table 2).

Life starts with hatching from the egg. The newly born nauplius 1 contains $W_1(0)$ µg C. Its length is calculated from Eq. 3. For stage 1 through *n,* we can subsequently calculate the three relevant quantities from

$$\tau_i = \frac{1}{\beta_2}\ln\left[\frac{A}{A - \beta_2\eta(\nu L_i^{\sigma})}\right] \tag{15}$$

$$\begin{aligned} C_i = \frac{1}{\tau_i\beta_1}\Biggl\{ & B\tau_i - \frac{1}{\beta_1}[B - W_i(0)\beta_1] \\ & \times [1 - \exp(\beta_1\tau_i)]\Biggr\} + \eta\nu L_{i-1}^{\sigma} \\ & + \frac{A}{\tau_i\beta_2}\left[\frac{1}{\beta_2} - \tau_i - \frac{1}{\beta_2}\exp(-\beta_2\tau_i)\right] \end{aligned} \tag{16}$$

Table 2. Model analysis.

Both differential Eq. 1 and 2, with 5 and 6 respectively, have the form:

$$\frac{\mathrm{d}y_i}{\mathrm{d}t} = D - By_i.$$

Therefore, the solutions are (e.g. *see* Boyce and DiPrima 1977):

$$y_i(t) = \frac{1}{B}[D - \exp(-Bt)\exp(-BC)]$$

where the integration constants C are calculated by filling in the appropriate initial conditions. For Eq. 2, $y_i(0) = 0$ and therefore $c = 0$. Filling in the appropriate forms of B and D, we see that the solution of Eq. 2 is

$$S_i(t) = \frac{(1-\kappa)}{\beta_2}\gamma I_m \frac{\alpha x}{1+\alpha x}(\nu L_i^\sigma)^\theta[1 - \exp(-\beta_2 t)].$$

With the initial conditions Eq. 12 and the appropriate forms of B and D we find

$$W_i(t) = \frac{1}{\beta_1}\{D - [D - \beta_1 W_i(0)]\exp(-\beta_1 t)\}$$

$$\text{where } D = \kappa\gamma I_m \frac{\alpha x}{1+\alpha x}(\nu L_i^\sigma)^\theta.$$

τ_i is calculated by applying the molt-criterion Eq. 11 to the equation for W_i. Rearranging the resulting relation gives Eq. 15. Filling in Eq. 15 in the equation for W_i we find expression 19 for $W_i(\tau_i)$, and therewith Eq. 18 is completely defined. The length-in-stage expression 17 can now be calculated for each stage.

The average carbon content of a stage is given by

$$\mathrm{C}_i = \frac{1}{\tau_i}\int_0^{\tau_i} W_i(t)\,\mathrm{d}t + S_{i-1} + \frac{1}{\tau_i}\int_0^{\tau_i} S_i(t)\,\mathrm{d}t$$

which is a standard integration that yields Eq. 16. Realizing that there is no further growth after the molt out of the stage into the adult stage finally leads to Eq. 22.

$$L_i = \left[\frac{W_i(0) + \eta\nu L_{i-1}{}^\sigma}{\nu}\right]^{\frac{1}{\sigma}} \tag{17}$$

where

$$W_i(0) = W_{i-1}(\tau_{i-1}), \tag{18}$$

and

$$W_i(\tau_i)\beta = W_i(0) + \frac{\kappa\beta_2}{(1-\kappa)\beta_1}\eta\nu L_i^\sigma - \frac{\beta_2 W_i(0)\eta\nu L_i^\sigma}{A}, \tag{19}$$

in which

$$A = (1-\kappa)\gamma I_m \frac{\alpha x}{1+\alpha x}[\nu L_i^\sigma]^\theta \tag{20}$$

$$B = \frac{\kappa}{1-\kappa}A. \tag{21}$$

Finally, the carbon content of an adult is calculated from

$$\mathrm{C}_{\text{adult}} = W_n(\tau_n) + S_n(\tau_n). \tag{22}$$

Qualitative model behavior

In this section, we make a qualitative comparison of the model output with published data sets. This comparison serves as a first step in verifying the model. The model outputs to be considered are stage duration, weight-in-stage, and length-in-stage, as given by formulae 15–22. We compare model output with two well-established copepod development patterns. First, we consider the dependence of stage duration and animal size on food concentration. Second, we consider anisochronality as discussed by Hart (1990). Finally, we also consider Hart's equiproportional development.

The model needs input parameters. Table 3 discusses a default parameter set to be used throughout this section. We note here that the model output has been studied for other biologically reasonable parameter sets, but no significant deviations are found from the qualitative model behavior as described later.

Stage duration, size, and food—The first test of our model concerns the dependence of development time and size-in-stage on food concentration. Stage duration is inversely related to food concentration and is more pronounced in later developmental stages (Vidal 1980*b*; Hart 1990; Berggreen et al. 1988; Santer and van den Bosch 1994). It is well established that body size increases as food concentration increases but only to some saturation level. As with stage duration, the effect of food on size is more pronounced in late than in early developmental stages (Mullin and Brooks 1970; Vidal 1980*a*; Berggreen et al. 1988; Santer and van den Bosch 1994). These patterns have been observed for marine as well as freshwater species, for calanoids as well as cyclopoids.

The decrease of stage duration with increasing food density is obvious from the model structure (Eq. 15). The carapace building-brick storage compartment is filled sooner if more food is available. The dependence of size on food concentration, however, can be used as a

Table 3. The default parameter set.

Free-living calanoid and cyclopoid copepods have six and five naupliar stages respectively, followed by five copepodite stages and the adult stage (Kiefer 1960, 1973). Because most of the literature to be used is on marine calanoids we use six naupliar stages in our examples.

- *Allometric relation:* McCauley (1984) lists the parameter values of the length vs. dry-weight relation for 39 freshwater copepod species. Most of the exponents σ have values between 2 and 3 with an average of 2.3. If we assume a conversion factor of 0.4 for dry weight to carbon content (Peters and Downing 1984), ν has values between 1 and 3 with an average of 1.9.
- *Food intake:* For nauplii and copepodites, Berggreen et al. (1988), Ambler (1986), Hamburger and Boetius (1987), Harris and Paffenhöfer (1976), Paffenhöfer and Harris (1976), and Santer and van den Bosch (1994) give values of the exponent θ which vary between 0.79 and 1.0 and average 0.85. Using the exponents given by these investigators and the conversion factors given by Peters and Downing (1984), we calculated (for the various food concentrations) the factors,

$$\frac{F_i}{(\nu L_i^{\sigma})\theta} = I_m \frac{\alpha x}{1 + \alpha x},$$

  on a carbon-to-carbon basis. I_m and α are estimated by nonlinear least-squares. (Food concentrations used by Harris and Paffenhöfer were too low to allow estimation of θ.) The values estimated for I_m are 0.45, 1.07, 1.4, 9.6, and 1.9. Those for α are 8.1×10^{-3}, 1.3×10^{-2}, 5.6×10^{-3}, 10.0×10^{-3}, and 8.0×10^{-3}. There is thus considerable variation depending on food species and copepod species as was to be expected. As our default parameters we take $I_m = 1.5$ and $\alpha = 6.0 \times 10^{-3}$.
- *Assimilation efficiency:* Corkett and McLaren (1978 and references therein), Hamburger and Boetius (1987), and Berggreen et al. (1988) report assimilation efficiencies ranging from 0.4 to 0.8 with an average of ~0.6. A similar range and average is found for *Daphnia.*
- *Allocation and molt:* There is little information from which we can "guesstimate" κ and η. Vidal (1980*b*) calculated growth rates and rates of loss of body carbon due to molting. Comparing these rates, we find $1 - \kappa$ is ~0.05. Mullin and Brooks (1970) found the C content of the exoskeleton to be 10% of the total body C of *Rhinocalanus nasutus.* Vidal (1980*b*) found 2.8–5.1% for *Calanus pacificus.* We use $\eta = 0.05$ as our default value.
- *Maintenance:* As already stated, the relation between maintenance and respiration is complex. From Lampert (1984) we find a respiratory coefficient of 0.1 μg assimilated C per μg body C per day at 12°C. We take this as an approximation of maintenance. Furthermore, due to the lack of any information we take β_1 and β_2 to be equal.
- *Initial weight:* For the initial weight we take 0.2 μg C, which amounts to an average-sized copepod species.

first test of the model. More food availability, which increases growth rate, is opposed by shorter development time. These two opposite effects can result in increasing, decreasing, or constant size as food availability increases. From Fig. 1, we see that the increase of size with food concentration is accurately predicted by the model. As is found in experimental work, the model predicts that the effect of food density on development and growth is more pronounced in later stages (Fig. 1).

Anisochronality—When the duration of all juvenile stages is equal, development is called isochronal. Miller et al. (1977) described isochronal development in a marine calanoid copepod. Although Landry (1983) subsequently commented on the inapplicability of isochronal development for marine calanoids in general, the concept has persisted. Hart's (1990) review showed apparent isochronality in only four of 38 species. He showed that, with occasional exceptions in the N3 stage, stage duration increases with developmental stage (Fig. 2A). Our model with the default parameter set, also predicts longer stage durations in later developmental stages (Fig. 2B).

In our models, ingestion rates increase with the power $\theta < 1$ of body size, whereas maintenance increases linearly with body size. Therefore, a larger individual has a higher maintenance expenditure relative to its ingestion compared to a small individual, implying longer stage durations in later developmental stages. Thus, development is not isochronal. Note, however, that this depends on the value of the parameter θ. Experimental data show that θ is usually smaller than unity.

There is a remarkable exception to the rule. Hart (1990) found that isochronality is closely approached in species of the genus *Acartia.* He listed three independent papers that report isochronal development in *Acartia.* Considering the discussion above, our model thus predicts that θ should be close to unity for *Acartia* spp. The paper by Berggreen et al. (1988), not mentioned by Hart, confirms iso-

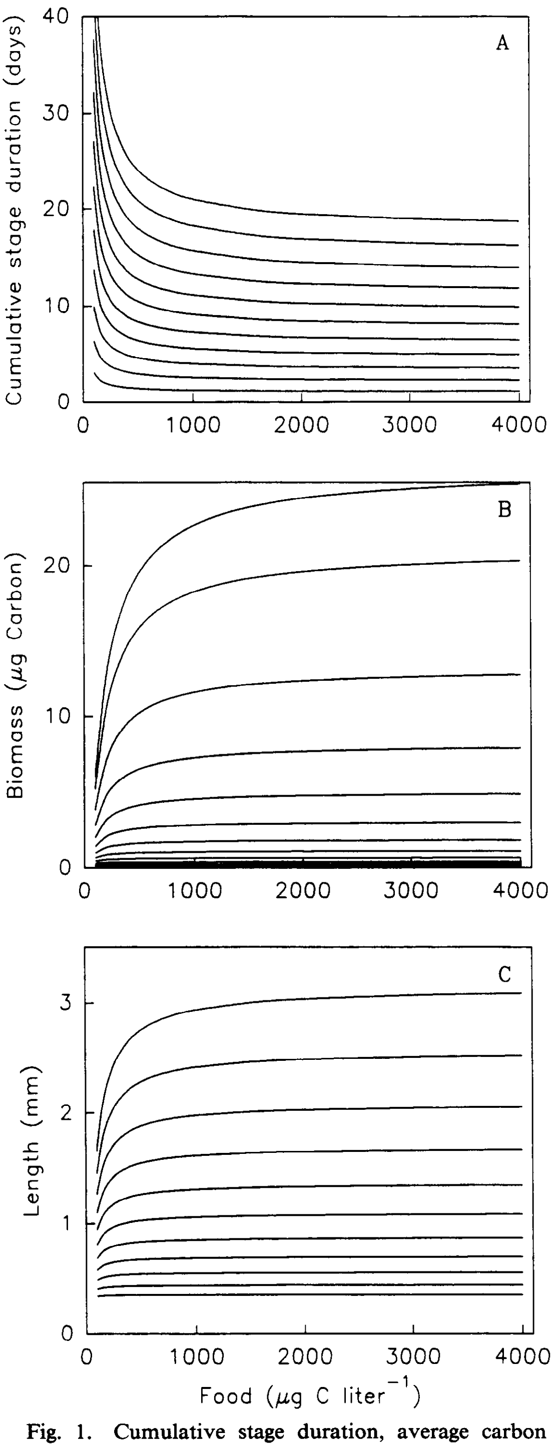

Fig. 1. Cumulative stage duration, average carbon content, and length within a stage as a function of food concentration, calculated from the growth and development model. A. All individuals are adults above the upper curve, all are C5 between the upper and the second curve, etc. B., C. Upper curve for adults, second from top for C5 stage, etc. Parameter values are the default values discussed in Table 3.

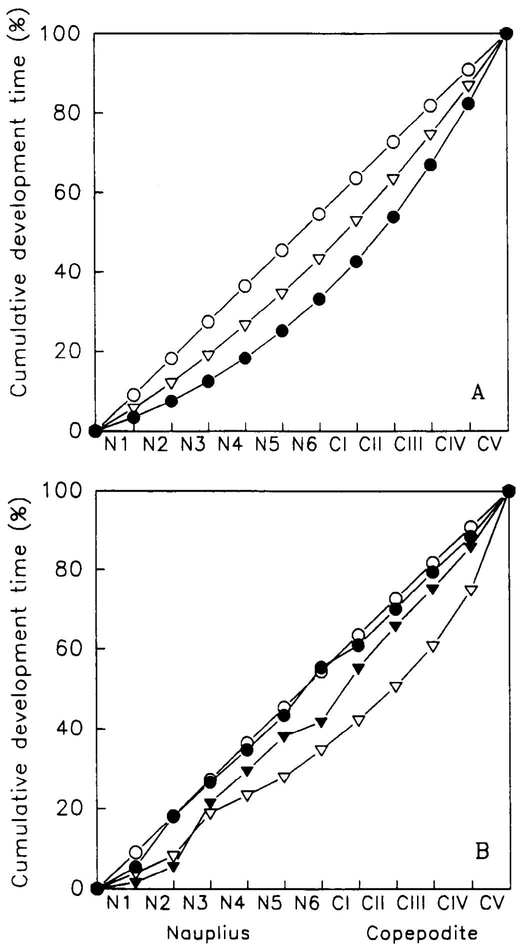

Fig. 2. Anisochronal and isochronal development in copepods. A. Model calculations with default parameter values; pure isochronal development—○; development pattern with $\theta = 0.85$—▽; development pattern with $\theta = 0.70$—●. B. Data given in the literature; pure isochronal development—○; *Acartia clausi* (Landry 1978)—●; *Pseudocalanus* spp. (Thompson 1982)—▼; *Calanus pacificus* (Landry 1983)—▽.

chronality again. Berggreen et al. also measured the dependence of ingestion rates of eight algal species on body weight in *Acartia tonsa.* Averaged over all eight species, Berggreen et al. reported an average value of θ of 1.08. For only one algal species is θ markedly smaller than unity. All others are very close to unity.

We can thus conclude that our model predicts the general pattern described by Hart. Moreover, our model provides an explanation of anisochronality based on the parameters involved in ingestion and maintenance.

Equiproportional development—Hart (1990) concluded that isochronality is the exception rather than the rule. He searched for other patterns in copepod development and proposed the equiproportional rule of development. Equiproportionality means that the duration of each developmental stage is a fixed percentage of the total postembryonic development time, independent of food density (and other environmental factors). The number of studies on which he based this proposal is small. Therefore, it cannot yet be considered a generally applicable rule, as Hart also indicated. It is, however, tempting to compare the predictions of our model with this rule.

From Fig. 3, we see that the model predicts relative stage duration to be independent of food density in the range of 0–4 mg C liter^{-1}. Only at food concentrations <200 μg C liter^{-1} is there a barely perceptible increase in the relative duration of the earlier stages. The difference in relative stage duration between lowest and highest food concentrations is maximally 5%. Other biologically reasonable parameter sets give similar results. These results indicate that Hart's equiproportionality rule is a relevant generalization of observed life histories in copepods.

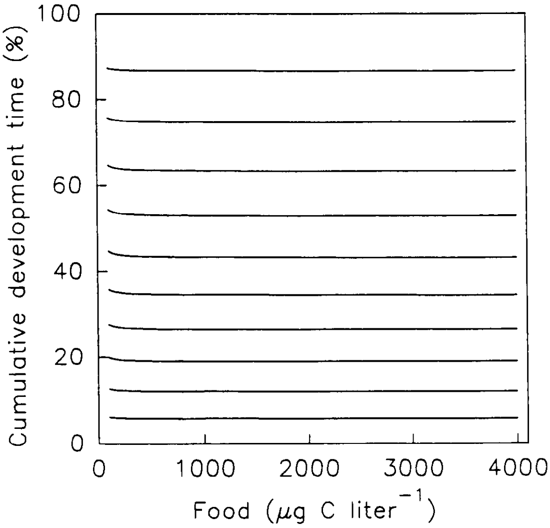

Fig. 3. Cumulative relative development time as dependent on food concentration. Parameter values are the default values discussed in Table 3. The figure illustrates that relative stage duration is virtually independent of food concentration. This is called equiproportional development.

Quantitative model behavior

In this section, we consider the quantitative fit of the model to published data on copepod development and growth. The purpose of this analysis is to get a first impression of the quantitative performance of our simple model. We use data from two species sufficiently studied to test the model on the copepodite stages. Data on nauplii are not available or are too scarce to be included. For both species, the parameters of the allometric length–weight relation, the starting weight of the first stage, and the parameters of the functional response can be estimated from published data. Five parameters for which sufficient experimental data are not yet available must be determined by fitting to the data.

A simple model, as developed here, is not expected to give a detailed quantitative fit; our goal is not fine-tuned data fitting. What we are interested in is more modest. Given estimates from published data of some of the parameters, the model is fitted (with respect to the remaining parameters) to data on stage duration and body size as a function of food concentration. Our test criterion, then, is whether the simultaneous fit to stage duration and size is good. Given the structure of the model, it is possible, for example, that stage durations or body size are underestimated in some stages and overestimated in others. If we had fitted the model to stage durations only or to animal sizes only, the five free parameters would give the model sufficient flexibility to fit any data set accurately. Even with five free parameters, a simultaneous fit (in which such diverse characteristics as development time and size are fitted by a simple model) fails if the model structure is incorrect. Another possibility is that to get a good fit, the parameters attain values which are not biologically reasonable. In such situations, the model structure is not correct.

Experimental data—Calanus pacificus: Runge (1980) gave a dry weight vs. prosome length relation. Parameters of the allometric length–weight relation were estimated from a dry weight to carbon conversion factor of 0.4 (Peters and Downing 1984) and a ratio of prosome to total length of 0.75 (Landry 1978).

Mullin and Brooks (1970) gave data on the ingestion rate (μg C d^{-1}) of *Calanus finlandicus* fed on *Thalassiosira fluviatilis* for animals of various body carbon contents. From a log-log plot, we estimate θ with linear least-squares. We know of no such data for *C. pacificus*. Paffenhöfer (1971) gave body weight vs. grazing rate log-log plots for *Calanus helgolandicus* fed on various algae and included the data from Mullin and Brooks (1970). The lines in these log-log plots are parallel. From this observation, we feel confident about using the estimated θ from *C. finlandicus* for *C. pacificus*.

Frost (1972) gave data on the ingestion rate (cells ind.$^{-1}$ h^{-1}) of adult female *C. pacificus* fed on various concentrations (cells ml^{-1}) of *T. fluviatilis*. The F factors [$=I_m\alpha x/(1 + \alpha x)$] were calculated from the carbon content of *T. fluviatilis* (9×10^{-6} μg C cell^{-1}, Frost 1972; Runge 1980), the well-fed adult female carbon weight (100 μg C ind.$^{-1}$, Vidal 1980*a*), and the estimated θ. I_m and α are estimated by nonlinear least-squares.

The average dry weight of C2 stages is given by Vidal (1980*a*). The carbon content was calculated with the 0.4 factor used as initial weight.

Vidal (1980*a,b*) gave data on duration and dry weight of copepodite stages fed on various concentrations (ppm) of *Thalassiosira eccentrica* and *Thalassiosira angustii*. We use his experiments with a temperature of 12°C because this is close to the temperature used in the feeding experiments cited above. Cell concentrations are recalculated to carbon concentrations by using the relation of ppm to carbon concentration as given by Vidal (1980*a*). Dry weights were again converted with the 0.4 factor.

We note that the data for *C. pacificus* stem from various literature sources, so experimental conditions vary. To estimate θ, we had to resort to data on *C. finlandicus*.

Cyclops vicinus: The parameters of the allometric length–weight relation are adopted from Santer and van den Bosch (1994), who also gave data on the ingestion rate (μg C ind.$^{-1}$ d^{-1}) of *Chlamydomonas reinhardii* for various food concentrations (μg C liter^{-1}) and various stages. We calculated a log-log plot of body C content vs. ingestion rate for each food concentration. To estimate θ, we fitted parallel lines to these data (Draper and Smith 1981). Using the estimated θ, we calculated the F factors [$=I_m\alpha/(1 + \alpha x)$]. I_m and α are estimated by nonlinear least-squares.

The average length of the C1 stage as reported by Santer and van den Bosch (1994) is used as the initial length (birth length). Stage duration and length-in-stage of *C. vicinus* for 10 concentrations of *C. reinhardii* are given by Santer and van den Bosch (1994).

We note that all data for *C. vicinus* result from one large set of experiments done with animals from the same culture, with the same algal species, and under the same experimental conditions. This data set is thus more consistent than the one for *C. pacificus*.

Fitting the model—To estimate γ, β_1, β_2, κ, and η, we fitted model equations to the data described above. This fitting is a nonlinear problem with respect to the parameters. The errors of the experimental data points vary considerably. Further, because of the experimental design, not all data points are statistically independent. If we assume a Gaussian error distribution of the data points, maximizing the logarithm of the likelihood function is equivalent to minimizing (e.g. *see* Richter and Söndgerath 1990)

$$G = \sum_{i=1}^{n} \frac{1}{\sigma_i^2}[y_i - f_i(x_i, \Psi)]^2, \qquad (23)$$

with x_i the independent variables, y_i the dependent variables, Ψ the parameter vector (γ, β_1, β_2, κ, η), and σ_i^2 the variance of the error distribution of y_i. The f_i functions are given by the model equations. Obtaining a maximum likelihood estimation is therefore formally equivalent to a weighted nonlinear least-squares problem. The data available are not always accurate enough to use standard errors as estimates for σ_i. As expected from the dependence of later instars on previous ones and because of the decreasing number of replicates, σ_i increases with increasing instar number for fixed food concentrations. Within one instar, however, the standard errors of the data are quite independent of food concentration. Separated for each variable and species, we estimated σ_i and its dependence on instar number.

Even drastic artificial changes in σ_i have very little effect on the parameter estimates but do, of course, influence the error bounds of these estimates. The errors of the estimated parameters must be taken carefully because of the nonlinearity of the model. They are calculated from the inverse of the second derivative of the likelihood function at the maximum, which implicitly assumes a quadratic behavior of the likelihood function at the maximum.

Table 4. Parameter values estimated from the literature and obtained by fitting the model to data for *Cyclops vicinus* and *Calanus pacificus*.

	Parameter	*C. vicinus*	*C. pacificus*
Parameters estimated directly from data	σ	2.10±0.02	2.50
	ν	2.98±0.02	3.88
	Θ	0.85±0.04	0.71±0.01
	I_m	0.45±0.08	1.07±0.07
	α	0.0081±0.0016	0.013±0.001
Parameter estimates resulting from model fit	γ	0.788±0.055	0.274±0.005
	β_1	0.073±0.005	0.017±0.001
	β_2	0.059±0.006	0.069±0.005
	κ	0.91±0.027	0.938±0.004
	η	0.091±0.020	0.021±0.002

Results

Parameter estimates from data—The allometric ln-length ln-weight relation is well established in the literature (McCauley 1984), and our estimated parameters are well within the range cited (Fig. 4, Table 4).

The same holds for the relation between body weight and feeding rate. θ estimated from the data agrees well with values found for other species (Tables 3 and 4).

The fit of the Holling functional response to the data is less satisfactory (Fig. 4). The data on *C. vicinus* show a great deal of scatter, resulting in large (compared to the parameter value) standard deviations of the parameters. For *C. pacificus,* there seems to be a systematic deviation of the data from the fitted curve (Fig. 4). We will return to this point in the discussion.

Parameter estimates from fitting the model—We used a χ^2 test to evaluate the fit of the model to the data. The results must, however, be viewed with caution. Within one experiment, the stage duration and size of a given stage can be influenced by the stage duration and size of the preceding stage. The data for one food concentration are thus not independent as required for the χ^2 test. Therefore, the critical region may be somewhat shifted in our case, and we can accept the fit as good only if the level of significance is much smaller than the value we would consider in case of independent data.

For the fit of the model to the *C. vicinus* data (Fig. 5), we find a level of significance of $P < 0.001$. No systematic deviation is found. For the fit to the *C. pacificus* data (Fig. 5), we find $P < 0.01$. There is, however, a systematic deviation of the data from the model predictions. The major difference between data and model fit is that the curves level off at food concentrations too high or are not steep enough at low food concentration. Most of the parameter values that result from the fit (Table 4) are well within the range found in the literature.

Discussion

We have proposed a simple model for the growth and development of copepods. The model can be used to study copepod life-history traits. We made a first start by comparing development patterns with those found in the work of Hart (1990).

The model is also a first step toward a complete individual growth model that can be used in ecophysiological studies. To this end, the model must be supplemented with a reproduction model and a model describing mortality. For reproduction, the model by Sciandra et al. (1990) seems useful. Mortality in copepods has been widely discussed, but no models yet exist. The model of individual copepods can be built into a population model with the methodology developed by Metz and Diekmann (1986). Furthermore, the model can be built into birth- and death-rate estimation procedures. The present study is only a first step toward these applications; there is still a long way to go.

The stage-structured approach to growth and development dates to the 1960s and has been applied to a variety of taxa. In this paper, we applied this method to copepods for the first time. The main feature of the model, new to individual growth models, is the timing of the molt. We assume that a fixed fraction of the

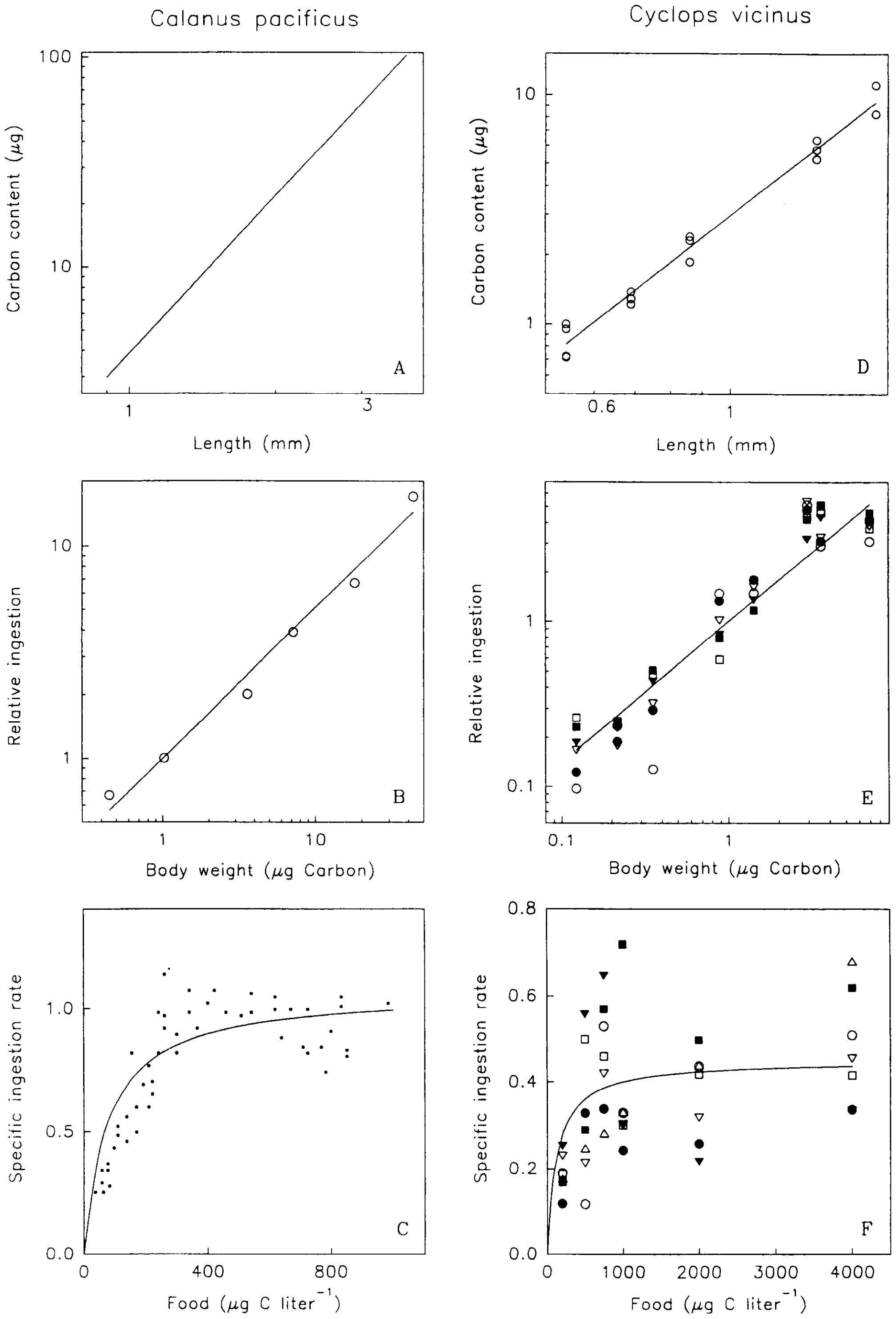

Fig. 4. Data from which parameters are estimated. Symbols are data points; lines are fitted relations as explained in the text. For *C. vicinus* relative ingestion: food concentration 0.2 mg C liter^{-1}—○; 0.5—●; 0.75—▽; 1.0—▼; 2.0—□; 4.0—■. For *C. vicinus* specific ingestion rates: N1–N2—○; N3–N5—●; N5–N6—▽; C1—▼; C2—□; C3—■; C4—△.

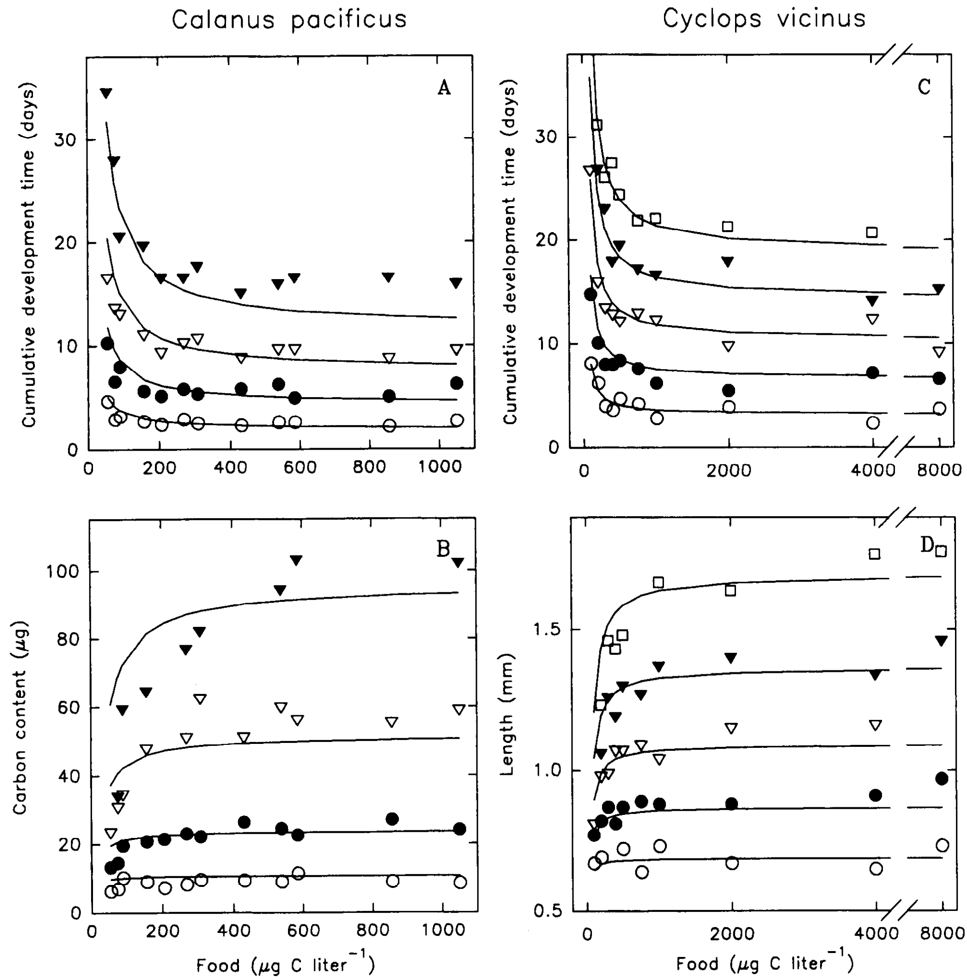

Fig. 5. Fitting the model. Development times and body size of the various developmental stages of *C. vicinus* and *C. pacificus* as dependent on food concentration. Symbols are data points; lines are the fit of the model. For *C. pacificus*: C3—○; C4—●; C5—▽; adults—▼. For *C. vicinus*: C2—○; C3—●; C4—▽; C5—▼; adults—□.

assimilated energy is allocated to the development of a new carapace. An individual molts into the next stage when its new carapace is ready. Given this development-coordinating mechanism, we made the various parts of the model as simple as possible. Certainly, many aspects of the model are open to improvement. Our main question was whether this development-coordinating system is able to explain observed patterns in stage duration and size as a function of food concentration.

To test the model, we compared both qualitative and quantitative predictions with published data. Anisochronality, reported by various investigators, is also found in our model. Our model also explains the observed isochronality for *Acartia* species. Thus, the qualitative predictions of the model are in line with observed patterns in various copepod species.

The quantitative test of the model needs more discussion. The ultimate test of the model would be to estimate all input parameters from the literature, substitute these in the model, and compare the predicted with the estimated size-in-stage and development times. We have not been able to find such a data set. We had to restrict our quantitative testing to the copepodite stages only because data on naupliar growth and development are virtually absent. Usually, only total time to the first copepodite stage is given, and this is insufficient for a model test. More experimental work must be done before a rigorous quantitative test of the model is feasible.

Concerning the parameters estimated directly from literature data, only the functional response shows some problems. As for *Daphnia,* the mathematical description of the functional response is not yet well developed. Some investigators use the bilinear filter-feeder functional response, while others use the Ivlev curve or the Holling functional response. A better mathematical description of functional responses for copepod feeding is needed. Ambler (1986) made a first step in this direction. For the time being, we can only choose a functional response that reasonably fits the data. Our purpose here is to test whether the set of assumptions on molting and growth of copepods can explain observed patterns in individual development. The mathematical details of the functional response can result in quantitative deviations from observations but are not essential for testing our simple model. In the future, a more realistic functional response can easily be inserted in both the model equations (Table 1) and the size and stage duration formulae (Eq. 15–22).

The test of the fit of the model to the stage duration and body size data has very small *P* values, which gives us confidence in the model. The small systematic deviation observed for the *C. pacificus* data can be attributed to three causes. First, the input parameters for this species are estimated from a diverse set of papers. Each researcher used different culturing methods and experimental techniques. Moreover, there could be large differences between the races of *C. pacificus* used by the various investigators. The θ was calculated from data for *C. helgolandicus.* This diverse data set could influence the fit to the data. Second, as discussed above, the Holling functional response does not fit the feeding data well. Another functional response that better fits the feeding data might cause the model to better fit the stage duration and size data. We tried using a bilinear functional response, but this did not result in an essentially better fit to the stage duration and size data. Third, as discussed at several places in the paper, improvements in the model are possible. It might be that a more detailed and complex model can adjust for the small systematic deviation of the fit to the *C. pacificus* data.

A second test criterion is whether the resulting parameters are within biologically reasonable bounds. From Table 4, we conclude that most parameter estimates resulting from the model are within biologically reasonable ranges. The assimilation efficiency of *Chlamydomonas* is large, as expected for such flagellate green algae. Assimilation efficiency for *Thalassiosira* is, however, low compared to the values found in the literature. For both species, the maintenance energy is smaller than that calculated for *Daphnia* species (Gurney et al. 1990). This finding is in line with the observation that copepods are resistant to starvation. The maintenance energy for the carapace building bricks and the energy allocation to the new carapace are similar, giving us the impression that our description of the molting process is applicable across species. The maintenance energy for structural biomass of *C. vicinus* is within a biologically reasonable range. For *C. pacificus,* the maintenance energy for structural biomass is, however, very small. Especially compared to the maintenance energy for the carapace building bricks, this parameter deviates significantly.

The parameter κ is close to the value reported by Vidal (1980*b*). The storage space for the carapace building bricks is larger for *C. vicinus* than for *C. pacificus*; that can be explained with geometrical relations. The ratio of surface area to volume is larger for small species. Assuming that the thickness of the carapace is dependent only to a minor extent on species size, we expect η to be larger for smaller species. The fact that most parameters resulting from the model fit are within reasonable ranges and that the differences between species have biological explanations gives confidence to our model formulation.

We have been able to describe the essential features of growth and development in copepod species as dependent on constant food concentration. Fluctuating food conditions are easily simulated, but the model must be extended to incorporate changing temperature before it can be applied to studies conducted in field situations.

Although we provided tests of the whole model based on available literature data, the molting rule itself is untested. The molting rule implies that stage duration is a function of food density and size-in-stage but not of feeding history during previous stages. This suggests a simple and convincing test of the molting rule. A group of animals is raised at a constant food level through the first i instars. Immediately upon molting to instar $i + 1$, the animals are distributed over a range of food concentrations. If the molting rule is an accurate description, the duration of instar $i + 1$ should depend on food concentration as given in Eq. 15–20, implying a threshold food concentration for further molts and a dependence of stage duration τ on food x as

$$\tau \sim \ln[x/(cx - d)],$$

where c and d are constants. We intend to perform such tests for several copepod species in further experimental research.

References

AMBLER, J. W. 1986. Formulation of an ingestion function for a population of *Paracalanus* feeding on mixtures of phytoplankton. J. Plankton Res. **8:** 957–972.

BERGGREEN, U., B. HANSEN, AND T. KIØRBOE. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. Mar. Biol. **99:** 341–352.

BOYCE, W. E., AND R. C. DIPRIMA 1977. Elementary differential equations. Wiley.

CONOVER, R. J., AND E. D. CORNER. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. J. Mar. Biol. Assoc. U.K. **48:** 49–75.

CORKETT, C. J., AND I. A. MCLAREN. 1978. The biology of *Pseudocalanus*. Adv. Mar. Biol. **15:** 1–231.

DE ROOS, A. M., O. DIEKMANN, AND J. A. J. METZ. 1992. Studying the dynamics of structured population models: A versatile technique and its application to *Daphnia*. Am. Nat. **139:** 123–147.

DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis, 2nd ed. Wiley.

DUNCAN, A., W. LAMPERT, AND O. ROCHA. 1985. Carbon weight on length regressions of *Daphnia* spp. grown at threshold food concentrations. Int. Ver. Theor. Angew. Limnol. Verh. **22:** 3109–3115.

ELMORE, J. L. 1982. The influence of food concentration and container volume on the life history of *Diaptomus dorsalis* marsh from subtropical Florida. Hydrobiologia **89:** 215–223.

FERNANDEZ, F. 1979. Nutritional studies in the nauplius larva of *Calanus pacificus* (Copepoda: Calanoida). Mar. Biol. **53:** 131–147.

FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. **17:** 805–815.

GURNEY, W. S. C., E. MCCAULEY, R. M. NISBET, AND W. W. MURDOCH. 1990. The physiological ecology of *Daphnia*: A dynamic model of growth and reproduction. Ecology **71:** 716–732.

HALLAM, T. G., R. R. LASSITER, J. LI, AND L. A. SUAREZ. 1990. Modelling individuals employing an integrated energy response: Application to *Daphnia*. Ecology **71:** 938–954.

HAMBURGER, K., AND F. BOETIUS. 1987. Ontogeny of growth, respiration and feeding rate of the freshwater calanoid copepod *Eudiaptomus graciloides*. J. Plankton Res. **9:** 589–606.

HANSEN, B., K. S. TANDE, AND U. C. BERGGREEN. 1990. On the trophic fate of *Phaeocystis pouchetii* (Hariot). 3. Functional responses in grazing demonstrated on juvenile stages of *Calanus finmarchius* (Copepoda) fed diatoms and *Phaeocystis*. J. Plankton Res. **12:** 1173–1187.

HARRIS, J. R. W. 1983. The development and growth of *Calanus* copepodites. Limnol. Oceanogr. **28:** 142–147.

HARRIS, R. P., AND G.-A. PAFFENHÖFER. 1976. Feeding, growth and reproduction of the marine planktonic copepod *Temora longicornis* Müller. J. Mar. Biol. Assoc. U.K. **56:** 675–690.

HART, R. C. 1990. Copepod post-embryonic duration: Pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodid-naupliar duration ratio. Hydrobiologia **206:** 175–206.

KIEFER, F. 1960. Ruderfußkrebse (Copepoden). Kosmos.

———. 1973. Vergleichende Studien an Nauplien verschiedener Cyclopiden (Crustacea, Copepoda). Mem. Inst. Ital. Idrobiol. **30:** 45–60.

KOOIJMAN, S. A. L. M. 1986. Population dynamics on the basis of budgets, p. 266–297. *In* J. A. J. Metz and O. Diekmann [eds.], The dynamics of physiologically structured populations. Lecture Notes Biomath. 68. Springer.

———, AND J. A. J. METZ. 1984. On the dynamics of chemically stressed populations: The deduction of population consequences from effects on individuals. Ecotoxicol. Environ. Safety **8:** 254–274.

LAMPERT, W. 1984. The measurement of respiration, p. 413–468. *in* J. A. Downing and F. H. Rigler [eds.], A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell.

LANDRY, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia tonsa,* in a small temperate lagoon on San Juan Island. Int. Rev. Gesamten Hydrobiol. **63:** 77–119.

———. 1983. The development of marine calanoid copepods with comments on the isochronal rule. Limnol. Oceanogr. **28:** 614–624.

LYNCH, M. 1989. The life history consequences of resource depression in *Daphnia pulex* Ecology **70:** 246–256.

MCCAULEY, E. 1984. The estimation of abundance and biomass of zooplankton in samples, p. 228–265. *In* J. A. Downing and F. H. Rigler [eds.], A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell.

———, W. W. MURDOCH, R. M. NISBET, AND W. S. C. GURNEY. 1990. The physiological ecology of *Daphnia*: Development of a model of growth and reproduction. Ecology **71:** 703–715.

METZ, J. A. J., AND O. DIEKMANN [EDS.]. 1986. The dynamics of physiologically structured populations. Lecture Notes Biomath. 68. Springer.

MILLER, C. B., J. K. JOHNSON, AND D. R. HEINLE. 1977. Growth rules in the marine copepod genus *Acartia*. Limnol. Oceanogr. **22**: 326–335.

MULLIN, M. M., AND E. R. BROOKS. 1970. Growth and metabolism of two planktonic, marine copepods as influenced by temperature and type of food, p. 74–95. *In* J. H. Steele [ed.], Marine food chains. Oliver & Boyd.

PAFFENHÖFER, G. A. 1971. Grazing and ingestion rates of nauplii and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar. Biol. **11**: 286–298.

———. 1984*a*. Does *Paracalanus* feed with a leaky sieve? Limnol. Oceanogr. **29**: 155–160.

———. 1984*b*. Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. Mar. Biol. **80**: 323–333.

———, AND R. P. HARRIS. 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. J. Mar. Biol. Assoc. U.K. **56**: 327–344.

PETERS, R. H., AND J. A. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnol. Oceanogr. **29**: 763–784.

RICHTER, O., AND D. SÖNDGERATH. 1990. Parameter estimation in ecology: The link between data and models. VCH.

RUNGE, J. A. 1980. Effects of hunger and season on the feeding behavior of *Calanus pacificus*. Limnol. Oceanogr. **25**: 134–145.

SANTER, B., AND F. VAN DEN BOSCH. 1994. Herbivorous nutrition of *Cyclops vicinus*: The effect of pure algal diet on feeding, development and reproduction and life cycle. J. Plankton Res. **16**: 171–195.

SCIANDRA, A., J.-L. GOUZE, AND P. NIVAL. 1990. Modelling the reproduction of *Centropages typicus* (Copepoda: Calanoida) in a fluctuating food supply: Effect of adaptation. J. Plankton Res. **12**: 549–572.

SINKO, J. W., AND W. STEIFER. 1969. Applying models incorporating age-size structure to a population of *Daphnia*. Ecology **50**: 608–615.

THOMPSON, B. M. 1982. Growth and development of *Pseudocalanus elongatus* and *Calanus* sp. in the laboratory. J. Mar. Biol. Assoc. U.K. **62**: 359–372.

VIDAL, J. 1980*a,b*. Physioecology of zooplankton. 1. Effects of phytoplankton concentration, temperature and body size on the growth rate of *Calanus pacificus* and *pseudocalanus* sp. 2. Effects of phytoplankton concentration, temperature and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. **56**: 111–134, 135–146.

VON BERTALANFFY, L. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. Teil 1. Allgemeine Grundlage der Theorie: Mathematische und physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. Arch. Entwicklungsmech. Org. **131**: 613–652.

Submitted: 9 February 1993
Accepted: 10 November 1993
Amended: 18 July 1994