Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development

François Carlotti, Antoine Sciandra

**Station Zoologique, C.E.R.O.V., B.P. 28, U.A. 716, F-06230 Villefranche-sur-mer, France**

**ABSTRACT:** A mathematical model of population dynamics is proposed which embodies the principal biological processes involved in the energetic budget of *Euterpina acutifrons* Dana (Copepoda: Harpacticoida): ingestion, excretion, egestion, and reproduction. The model proposes functional connections between growth and development through the larval instars. The major hypotheses are: (1) weight and cumulated specific growth rate control the molting process; (2) molting occurs at fixed weights which are independent of temperature; (3) temperature influences only the ingestion process according to a constant $Q_{10}$ rule. Simulations fit satisfactorily with the development of *E. acutifrons* followed experimentally in different conditions of temperature and food concentration. Growth was sigmoidal, the major weight increase being between stage C5 and adult. The model reveals $Q_{10}$ values for growth and development between 10 and 25°C which are constant and similar, and higher than the $Q_{10}$ for ingestion. According to the hypotheses put forward, growth is potentially exponential over a wide range of food and temperature. Equipoportional development was found for *E. acutifrons*. The model is used to test the effects of variation of food and predators on the recruitment of a population of *E. acutifrons*. Because of the number and nonlinearity of interactions between biological processes governing development, only a sophisticated model incorporating both physiological and developmental processes is able to predict the effect of simultaneous external forcing variables on the population success.

**INTRODUCTION**

Numerous biological factors, such as food and predation, and physical factors, such as temperature, salinity and light, influence survival, reproduction and metabolic rates of copepods in culture (Marshall 1973, Corkett & McLaren 1978, Paffenhofer & Harris 1979). Food and temperature are generally considered as the most important parameters of population dynamics and individual growth (Thompson 1982). Temperature influences mortality, instar duration (Haq 1972, McLaren 1978), molting rate (Heip 1974), and reproduction (Landry 1975). Food also plays an important role in mortality (Paffenhofer 1970), instar duration (Vidal 1980b), and egg production (Zurlini et al. 1978). Often, these relations have been established in the laboratory which provides constant conditions for measurements. Only a few relationships have been estimated in situ, such as egg production (Dagg 1977). Based on this knowledge, models have been designed at different levels of complexity. The simplest show the influence of external parameters on a process involved in the dynamics such as developmental rate (Heip 1974) or egg production (Uye 1981). More sophisticated models include several processes and are based on a global representation of the population (Zurlini et al. 1978, Zurlini & Ferrari 1979); they can discriminate instars (Wroblewski 1980, Davis 1984), or age classes (Sciandra 1986a).

Relations between forcing parameters and physiological functions, especially those which are directly related to the energetic balance equation of growth (ingestion, excretion, egestion, reproduction), have been extensively studied. Temperature influences these processes according to a constant $Q_{10}$ law in the range of natural variations (Nival et al. 1974, Ikeda 1985). Food concentration influences filtration (Frost 1972), ingestion (Mullin & Brooks 1970b, Paffenhofer 1971), egestion (Gaudy 1974), excretion and respiration (Nival et al. 1974), and consequently, the growth rate (Mullin & Brooks 1970b). There are simple relationships which link processes with field parameters, such as filtration with food (Lam & Frost 1976) or ingestion with food concentration (Lehman 1976, Bartram 1980). Others
link one growth characteristic with external parameters, such as weight with food (Zurlini et al. 1978), size with food (Paffenhofer 1970), size with temperature (McLaren 1978) or weight, respiration and excretion with temperature (Nival et al. 1974). More elaborated growth models simultaneously consider ingestion, egestion, excretion and respiration (Steele 1974, Huntley & Boyd 1984, Wroblewski 1984, Wroblewski & Richman 1987).

External variations affect organisms through several biological steps, so that relations between causes and effects are rarely simple. In models of larval dynamics, development rates and external parameters are generally linked by empirical relationships, which do not take into account the functional properties of the processes involved in the dynamics. As a consequence, the field of application of these general models is restricted, especially if the external conditions of temperature and food are highly variable.

Population dynamics and individual growth are 2 different approach levels for studying copepods in their natural environment. This explains the fact that dynamics (fluxes of individuals) and growth (fluxes of matter and energy) are often modelled separately, although the latter controls the former. It is clear that a synthetic representation of population dynamics taking into account the biological characteristics of individuals would be very profitable, because of the exchange of information between the 2 different levels of knowledge.

Elaborated models of population dynamics, which embody the crucial relationships between the lower and upper trophic levels, are also useful tools for the understanding of ecosystem behavior. Representation of population dynamics in the model of Steele & Frost (1977) is not very specific since only flows of biomass were taken into account. Steele & Mullin (1977) discussed the necessity to use the number of individuals rather than the biomass to support a good description of the population dynamics. However, their model allowed only a single mean growth rate for the whole population, so that they were forced to assume a stable population structure.

This paper presents the integration of both biomass and number criteria through a unique conceptual model. The aim of this model (which is applicable to several species of copepods) is to simulate copepod population dynamics (here Euterpina acutifrons) in different conditions of food and temperature, by taking into account the processes involved in individual growth. This functional synthesis allows us to discuss hypotheses about possible relations between the different growth processes (ingestion, egestion, excretion, oogenesis, etc.) and the processes which control the time course of abundance of individuals in each instar (mortality rate, molting rate, reproduction).

**MODEL CONCEPTUALIZATION**

We consider that the development of copepods may be divided into 2 levels. The first corresponds to the natural succession of development stages: eggs (i = 1), nauplii (i = 2 to 7), copepodes (i = 8 to 12) and adults (i = 13). The second level corresponds to age classes in each instar. The number of age classes is high enough to allow the maximal duration in each instar. This division makes it possible to represent copepods of different ages and weights in a given stage. Larval dynamics within such a structure, explained in detail by Nival et al. (1988), is based on previous models (Davis 1984, Sciandra 1986a, b, Carlotti 1987).

The change in number of individuals in each age class during each unit of time is used to count age. External parameters (temperature, food) control the individual growth rate, and consequently the variation of weight. Weight and growth rate are state variables which control the molting process. We use 2 basic hypotheses to relate growth to development. The first is that individuals of an instar i may be transferred to instar i + 1 only if they have reached a sufficient weight, called the critical molting weight (Xc). In other words, each stage of development is characterized by a period of growth bracketed by critical weights of entering and leaving this stage. McLaren (1986) observed this phenomenon in Calanus finmarchicus during the spring generation. Harris (1983) considered in his growth model a structural weight and a storage weight, and assumed that molts occur at fixed structural weights. We also make this assumption for Euterpinia acutifrons which has little ability to store material. For naupliar and first copepodite stages, the results of Paffenhofer (1971), Burkill & Kendall (1982) and Hamburger & Boettius (1987) illustrate that the mean weight range of a given instar does not overlap that of the previous or the next instar. An overlap has been observed for the C5 and adult instars (Vidal 1980a, Berggreen et al. 1988) with a noticeable diminution of the weight at low food concentrations. At different temperatures, overlaps occur only for the older stages (C4 to adult) of Acartia tonsa (Miller et al. 1977), Pseudocalanus sp. (Corkett & McLaren 1978), Acartia clausii (Landry 1978) with a marked diminution of weights at the higher temperatures. Mullin & Brooks (1970a, b) stated that temperature has a limited influence on the quantity of ingested food necessary to reach a given instar. For some other species (Calanus pacificus, Calanus helgolandicus, Eudiaptomus graciloids), the mean weight of an instar is not strongly dependent on temperature (Paffenhofer 1971, Vidal 1980b, Hamburger & Boettius 1987). We assume here that the critical molting weight is independent of the
temperature and food conditions. As will be seen in the results, this assumption does not imply that instar mean weights are independent of food concentration and temperature. Moreover, this does not affect significantly the development rate.

The first hypothesis depends on the fact that molting is possible only if a sufficient amount of matter has been assimilated since the previous molt. The cumulated weight integrates the feeding history of the stage for several days.

The second hypotheses, proposed by Nival et al. (1988) depends on the assumption that molting is also controlled by the physiological state of larvae, which can be approximated by the specific growth rate (ratio of growth rate to weight). Changes in metabolic rate may limit molting even for larvae which have reached the critical molting weight. As the effects of external stimuli on growth are not instantaneous, it is necessary to take into account the feeding history of organisms during a preceding period of time so that variability of temperature and food can be damped. We consider here that the mean specific growth rate cumulated after some hours is the critical factor to be considered, instead of instantaneous specific growth rate.

The different biological processes controlling growth and population dynamics are presented in Fig. 1. Processes taken into account are presented in Tables 1 and 2. For each age class, 2 state variables represent the number \(N_{i,j}\) and the weight \(W_{i,j}\) of individuals.

Weight is controlled by growth, which depends on food and temperature, and both growth and weight control molting rate. Differential equations apply to each age class \(j\) of an instar \(i\) (Table 2).

The growth rate is expressed in nitrogen mass units. The ingestion rate of an instar \(i\) is dependent firstly on the food concentration according to a sigmoidal function \(f_1\) (Sciandra 1982, 1986b), and secondly on temperature, following a constant \(Q_{10}\) law \(f_2\). We use the allometric relation expressed by Paffenhofer (1971), \(f_3\), in which the maximal ingestion rate increases with weight during development.

Experimental studies have shown that some species of crustaceans with normal development stop eating just before and during the molting period (Lasker 1966, Paffenhofer 1971, Harpaz et al. 1987). Harris & Paffenhofer (1976) observed in *Temora longicornis* a depression in feeding activity before molting to C1 and before the last molt to adult. Presumably ingestion decreases as weight reaches the critical weight of molt, because growth is limited by the exoskeleton. We assume that the ingestion of an instar follows a negative parabolic function \(f_4\) when the weight surpasses the critical molting weight. Such a limitation does not occur for adults for which reproduction limits weight increase.

Egested matter is the part of ingested matter which is not assimilated. We assume as a first approximation that assimilation efficiency is independent of the amount of ingested food (Conover 1966); the quantity of egested matter is simply proportional \(f_5\) to the ingestion rate.

Metabolic rate is represented by excretion rate. We suppose as Wroblewski (1984) that excretion can be separated into 2 terms (see also Steele & Mullin 1977, Vidal 1980c). The first \(f_6\) represents the routine metabolism and is proportional to weight. The second \(f_7\) refers to the active metabolism and is proportional to ingestion rate.

For mature adults, ingested matter is used for maintenance and reproduction (Sekiguchi et al. 1980). We assume that reproduction occurs when adults have accumulated a sufficient amount of matter. The relationship \(f_8\) between the egg-laying rate and the nitrogen individual weight is sigmoidal. For crustaceans, such a relationship has been shown between the egg-laying rate and the size or weight of females (Corkett & McLaren 1969, Smith & Lane 1985). Egg weight is considered here to be constant. The egg-laying rate per female \(f_{12}\) is then equal to the ratio of the nitrogen mass invested for reproduction to the weight of an egg.

Mortality rate is usually considered constant for the whole population. This approximation neglects the facts that stages may have different sensitivity during critical periods such as molt or starvation, and that individuals in a given stage may have different mortal-
Table 1. Mathematical formulations of relationships used in the model. i: stage; j: age class. F: food; Te: temperature; Wi,j: weight; Xi: critical weight for transfer; Ii,j: ingestion; SGi,j: specific growth; CSGi,j: cumulated specific growth; Pr: predator density; c: capture rate coefficient; P1, to P19; biological parameters (see their definitions in Table 3)

<table>
<thead>
<tr>
<th>Process and formulation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ingestion</td>
<td>Influence of food following an Ivlev curve</td>
</tr>
<tr>
<td></td>
<td>Influence of temperature</td>
</tr>
<tr>
<td></td>
<td>Allometric relation</td>
</tr>
<tr>
<td></td>
<td>Limitation as molting weight is reached</td>
</tr>
<tr>
<td>Egestion</td>
<td>Fraction of ingestion not assimilated</td>
</tr>
<tr>
<td>Excretion</td>
<td>Routine metabolism</td>
</tr>
<tr>
<td></td>
<td>Active metabolism</td>
</tr>
<tr>
<td>Reproduction</td>
<td>Influence of weight on the amount of matter invested for reproduction</td>
</tr>
<tr>
<td></td>
<td>If SGi,j &lt; P12, Specific growth influence if SGi,j ≥ P12;</td>
</tr>
<tr>
<td>Mortality</td>
<td>Weight influence</td>
</tr>
<tr>
<td></td>
<td>Cumulated specific growth influence</td>
</tr>
<tr>
<td></td>
<td>Laying</td>
</tr>
<tr>
<td></td>
<td>Influence of temperature</td>
</tr>
<tr>
<td>Transfer</td>
<td>Selection of eaten stage</td>
</tr>
<tr>
<td></td>
<td>Influence of predator density Pr</td>
</tr>
</tbody>
</table>

In the model, we assume that all the laid eggs are physiologically equivalent. The hatching rate (f13) is simply formulated as the inverse of the embryonic duration, that is controlled by temperature only.

Predators are forcing variables in this study. Their action is formulated by functions f14 and f15 which respectively take into account the instars and the number of predators.

### CALIBRATION

Table 2. Processes and system of differential equations. $N_{ij}$: abundance

<table>
<thead>
<tr>
<th>Process</th>
<th>Units</th>
<th>Formulation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Growth</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ingestion (I)</td>
<td>μg-at N d$^{-1}$</td>
<td>$I_{ij} = f_{1i} + f_{2ij} + f_{3ij} + f_{4ij}$</td>
</tr>
<tr>
<td>Egestion (EG)</td>
<td>μg-at N d$^{-1}$</td>
<td>$E_{G ij} = f_{5ij}$</td>
</tr>
<tr>
<td>Excretion (EX)</td>
<td>μg-at N d$^{-1}$</td>
<td>$E_{X ij} = f_{6ij} + f_{7ij}$</td>
</tr>
<tr>
<td>Matter for reproduction (MR)</td>
<td>μg-at N d$^{-1}$</td>
<td>$M_{R ij} = f_{8ij}$</td>
</tr>
<tr>
<td>Growth (G)</td>
<td>μg-at N d$^{-1}$</td>
<td>$G_{ij} = I_{ij} - E_{X ij} - E_{G ij}$</td>
</tr>
<tr>
<td>Specific growth (SG)</td>
<td>d$^{-1}$</td>
<td>$S_{G ij} = \frac{G_{ij}}{W_{ij}}$</td>
</tr>
<tr>
<td>Cumulated specific growth (CSG)</td>
<td>d$^{-1}$</td>
<td>$C_{S G ij} = \frac{1}{\Delta t} \int_{t-t_{0}}^{t} S_{G ij} , dt$</td>
</tr>
<tr>
<td><strong>Dynamics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transfer (T)</td>
<td>d$^{-1}$</td>
<td>$T_{ij} = f_{10ij} \cdot f_{11ij}$</td>
</tr>
<tr>
<td>Laying (L)</td>
<td>d$^{-1}$</td>
<td>$L_{ij} = f_{12ij}$</td>
</tr>
<tr>
<td>Hatching (H)</td>
<td>d$^{-1}$</td>
<td>$H_{ij} = f_{13ij}$</td>
</tr>
<tr>
<td>Mortality (M)</td>
<td>d$^{-1}$</td>
<td>$M_{ij} = f_{9ij}$</td>
</tr>
<tr>
<td>Predation (P)</td>
<td>d$^{-1}$</td>
<td>$P_{ij} = f_{14ij} \cdot f_{15ij}$</td>
</tr>
</tbody>
</table>

**Differential equations**

Growth

Eggs (i = 1)

$$\frac{dW_{i1j}}{dt} = 0$$  \hspace{1cm} (13)

N1 to C5 (i = 2 to 12)

$$\frac{dW_{i2j}}{dt} = G_{ij}$$  \hspace{1cm} (14)

Adults (i = 13)

$$\frac{dW_{i13j}}{dt} = G_{13j} - M_{R13j}$$  \hspace{1cm} (15)

Dynamics

Eggs (i = 1)

$$\frac{dN_{i1j}}{dt} = L_{13j} \cdot N_{13j} - (H_{1j} + M_{1i} + P_{1i}) \cdot N_{1i}$$  \hspace{1cm} (16)

N1 (1st age class)

$$\frac{dN_{1i1j}}{dt} = H_{1i} \cdot N_{1i1} - (T_{2i} + M_{2i} + P_{2i}) \cdot N_{2i}$$  \hspace{1cm} (17)

N2 to C5 (1st age class)

$$\frac{dN_{i2j}}{dt} = \sum_{i=1}^{2} T_{i,j-1} \cdot N_{i,j-1} - (T_{i,j} + M_{i} + P_{i}) \cdot N_{i}$$  \hspace{1cm} (18)

N1 to C5 (next age class)

$$\frac{dN_{1i3j}}{dt} = -(T_{ij} + M_{ij} + P_{ij}) \cdot N_{ij}$$  \hspace{1cm} (19)

Adults (1st age class)

$$\frac{dN_{1i13j}}{dt} = \sum_{i=1}^{2} T_{i2j} \cdot N_{1i12j} - (M_{13j} + P_{13j}) \cdot N_{13j}$$  \hspace{1cm} (20)

Adults (next age classes)

$$\frac{dN_{i23j}}{dt} = -(M_{13j} + P_{13j}) \cdot N_{13j}$$  \hspace{1cm} (21)

**Coefficients of growth and egg-laying processes**

In the Ligurian Sea, *Euterpina acutifrons* lives at temperatures between 10 and 25 °C. All the relations used in this model are valid within this scale of variation.

The values of ingestion, egestion and excretion coefficients ($P_1$ to $P_{10}$) were found in the literature for copepodid and adult stages. Very little information is available for naupliar stages of *Euterpina acutifrons*. We assume that the coefficients for naupliar stages can be approximated by extrapolating from the relationships demonstrated for copepodids and adults.

The values ($P_1$, $P_2$ and $P_3$) of Ivlev curve $f_1$ for adults fed with the diatom *Phaeodactylum tricornutum* at 20 °C were obtained from Sciandra (1982) for adults. According to the review by Kremer & Nixon (1978) on *Acartia clausi*, the maximal ingestion rate increases exponentially with temperature following a $Q_{10}$ varying from 1.6 to 3.3. We use an intermediate value of 2.6 to estimate the $P_5$ coefficient. Coefficient $P_4$ is calculated so that $f_2$ is equal to 1 at 20 °C. Fernandez (1979) observed that the ingestion rate per individual increases during the development of *Calanus pacificus*. For N1 to C3 instars, we have extrapolated the coefficient $P_1$ considering a similar increase. Coefficients $P_2$ to $P_5$ are identical for all stages. The exponent $P_6$ of the allometric relation between weight and ingestion generally lies between 0.6 and 0.8 for copepods (Sushchenya 1970, Paffenhofer 1971). Because of the ab-
Table 3. *Euterpina acutifrons*. Parameters used in the model

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Units</th>
<th>Definitions</th>
<th>Eggs</th>
<th>N1</th>
<th>N2</th>
<th>N3</th>
<th>N4</th>
<th>N5</th>
<th>N6</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>C4</th>
<th>C5</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ingestion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P1</td>
<td>d⁻¹</td>
<td>Maximal ingestion rate</td>
<td>0.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.16</td>
</tr>
<tr>
<td>P2</td>
<td>μg-at. N⁻¹</td>
<td>Ivlev curve coefficient</td>
<td>0.61</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P3</td>
<td>wd</td>
<td>Ivlev curve coefficient</td>
<td>1.64</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P4</td>
<td>wd</td>
<td>Temperature coefficient</td>
<td>0.120</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P5</td>
<td>wd</td>
<td>Temperature coefficient</td>
<td>1.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P6</td>
<td>wd</td>
<td>Exponent of allometric relation</td>
<td>0.75</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Egestion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P7</td>
<td>wd</td>
<td>Assimilation efficiency</td>
<td>0.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Excretion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P8</td>
<td>d⁻¹</td>
<td>Routine excretion rate</td>
<td>0.04</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P9</td>
<td>wd</td>
<td>Coefficient of proportionality</td>
<td>0.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Reproduction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P10</td>
<td>μg-at. N⁻¹ d⁻¹</td>
<td>Maximal reproduction rate</td>
<td>0.0039</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P11</td>
<td>wd</td>
<td>Exponent</td>
<td>10</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>X₁₃</td>
<td>μg-at. N⁻¹</td>
<td>Critical weight for maturation</td>
<td>0.930</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mortality</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P12</td>
<td>d⁻¹</td>
<td>Threshold of specific budget</td>
<td>0.01</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P13</td>
<td>d⁻¹</td>
<td>Shape factor</td>
<td>0.008</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P14</td>
<td>d⁻¹</td>
<td>Maximum rate</td>
<td>0.50</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P15</td>
<td>d⁻¹</td>
<td>Minimum rate</td>
<td>0.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Transfer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P16</td>
<td>wd</td>
<td>Exponent</td>
<td>30</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>X₁₆(x0.01)</td>
<td>μg-at. N⁻¹</td>
<td>Critical molting weight</td>
<td>0.063 0.078 0.095 0.103 0.107 0.205 0.255 0.280 0.335 0.395 0.490 0.930</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P17</td>
<td>d</td>
<td>Coefficient of proportionality</td>
<td>7.2 5.6 5.6 4.0 4.6 8.0 10.5 14.0 11.0 11.0 14.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Δt</td>
<td>d</td>
<td>Cumulation time</td>
<td>1.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hatching</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P18</td>
<td>d⁻¹</td>
<td>Hatching rate at 20 °C</td>
<td>5.78</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>P19</td>
<td>wd</td>
<td>Shape factor</td>
<td>0.94</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Predation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>c</td>
<td>i. pred⁻¹ d⁻¹</td>
<td>Capture rate</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

- : same value as on the left

wd: without dimension
Carlotti & Sciandra: Growth and development of Euterpinia acutifrons

Fig. 2. *Euterpinia acutifrons*. Total population during development with variable temperature and constant food supply. (△) Experimental data from Sciandra (1986a); (—) simulations. The simulation starts with Nauplii I having identical weights \(0.5 \times 10^{-3}\) mg-at. N ind.\(^{-1}\) and ages.

presence of data for *Euterpinia acutifrons*, we adopt a value of 0.75 for all the instars.

An average value of 0.7 is generally considered as representative of the assimilation rate \(P7\) of copepods (Conover 1966, Steele 1974).

Supposing first that 30% \(P9\) of the ingested matter is used for metabolism and is excreted, and second, that the ratio of maximum ingestion rate to weight averages 20% \(P8\), a daily excretion rate of 6% of weight may be attributed to the active metabolism. To adjust total metabolic losses to an average value of 10% of weight per day (Corkett & McLaren 1978, Miller & Landry 1984), we estimate that excretory wastes due to minimal metabolism \(P8\) represent 4% of the body weight.

We assume a sex ratio of 0.5. Yassen (1979) estimated egg weight to \(3 \times 10^{-4}\) mg-at. N. Considering an optimal egg-laying rate ranging from 10 to 13 eggs female\(^{-1}\) d\(^{-1}\) (Zurlini et al. 1978, Sciandra 1986a), the maximal amount of matter that can be invested daily per female for reproduction \(P10\) approaches \(39 \times 10^{-4}\) mg-at. N.

**Coefficients of developmental processes**

The coefficients of the relationships between growth and development are unknown, because of the theoretical nature of the assumptions put forward. So they have been determined by fitting simulations to chronological series of data. We have used a set of data obtained by Sciandra (1986a) on the development of *Euterpinia acutifrons* at variable temperature with constant food supply (16 mg-at. N 1\(^{-1}\)). Mortality rate coefficients \(P12, P13, P14,\) and \(P15\) have been estimated using the total population (Fig. 2) and the stage curves (Fig. 3), i.e. 13 chronological series. Densities of N6 are lower than those of N5 and C1, so that a higher death rate has been attributed to stage N6. With a simple model, Sciandra (1986a) came to the same conclusion. He also pointed out that instars N5 and N6 are very difficult to distinguish, suggesting that some confusion may exist between these stages. It has also been shown that molting from instar N6 to C1 may be a critical period of development (Paffenbogeer 1970, Haq 1972, D'Apolito & Stancyk 1979).

Molting rate coefficients \(X1, P16\) and \(P17\) were estimated successively for each stage curve. The critical weight of molting \(X1\) for each instar i and the critical weight of laying \(X13\) influence the position of the beginning of the stage curves (see the sensitivity analysis in Nival et al. 1988). The exponent \(P16\) and the coefficient of proportionality \(P17\) respectively influence the initial slope and the end of the curve. The part of the total variance in abundance explained by the model in the 2 fits (Figs. 2 and 3) are respectively equal to 0.98 and 0.92.

**SIMULATIONS AND APPLICATIONS**

The system of differential equations is solved by fourth-order Runge-Kutta numerical integration with a time step of 1 h. Simulations presented in Figs. 2 and 3 reproduce satisfactorily the principal aspects of the...
Fig. 4. *Euterpina acutifrons*. Simulated time courses of stage weights during total development. Curves are stopped when stage sizes represent less than 0.5% of the total population. The curve of mean weight is obtained by averaging weights of all individuals. (A) Weights of individuals at their maximum stage dynamics: timing of appearance and disappearance of copepods in their developmental stages, and time of generation. In particular, the asymmetry of stage distributions is well represented, which was not possible with the model of Sciodra (1986a). Nevertheless, some discrepancies appear for the maximal amplitude of the early stages. The second generation is well represented suggesting a good representation of the egg-laying process.

**Individual and population growth**

The model allows us to present 3 sets of results (Fig. 4): (1) the mean weight of the whole population; (2) the weight of individuals at their maximal abundance in successive stages; (3) the mean weight of individuals in each instar. These results are obtained from the simulations presented in Fig. 3. The curve of the population mean weight is sigmoidal suggesting more or less exponential growth in the nauplius and copepodid stages, followed by saturation as adults appear. Similar curves have previously been obtained in the laboratory for *Pseudocalanus elongatus* (Paffenhofer & Harris 1976), *Temora longicornis* (Harris & Paffenhofer 1976), *Acartia clausi* and *A. tonsa* (Miller et al. 1977), *Calanus pacificus* and *Pseudocalanus* sp. (Vidal 1980a), *Calanus finmarchicus* (Corner et al. 1967, McLaren 1986), *Eudiaptomus graciloides* (Hamburger & Boëtius 1987). Fig. 4 shows that growth is maximal between copepodid V and adult stages. Some copepod species such as *Temora longicornis* (Harris & Paffenhofer 1976, Razouls & Razouls 1976) have the same pattern of growth.

Fig. 4 shows that the mean weight of an individual during its complete development cannot be correctly estimated by simply weighing copepods at their maximal abundance in successive stages. The overestimation due to this method in comparison with the true estimation (mean curve) increases as new stages appear. This is explained by the fact that stages overlap more and more as development completes, leading the population to be less homogeneous in its stage composition. By taking into account only individuals at maximum stages, individuals lighter in weight which remain in previous stages are neglected. Fig. 4 also shows that the mean growth, which seems to be continuous on the overall development, is in fact the sum of the discontinuous growths of successive stages. For each of them, weight cannot exceed a given value, so that copepods continue to grow only if they succeed in molting into the next instar.

Simulated weights are in good agreement with the weight of *Euterpina acutifrons* measured by Zurlini et al. (1978), Yassen (1979) and Moreira et al. (1985) (Table 4). The marked difference between C5 and female weights reproduced by the model can also be observed for other harpacticoids (Herman & Heip 1985).

Fig. 5 clearly demonstrates that the time variation of the total population biomass results from the combination of dynamics (Fig. 2) and growth processes (Fig. 4). Until Day 5, population biomass increases because individual weight gain compensates mortality. Total biomass decreases during the time where N6 and C1 stages are preponderant in the population, because of their higher mortality rate. Between Days 10 and 13 the rapid weight increase is primarily due to adult growth. It is also clear that copepods which remain late in each stage may constitute an important proportion of total population weight, which explains the discrepancy cited above.

**Influence of temperature**

The model was used to simulate the effect of temperature on the development of *Euterpina acutifrons* between 10 and 25 °C. Fig. 6 shows that with non-limiting food, naupliar and total development times expressed on a log scale (Fig. 6) decrease approximately linearly as temperature increases, suggesting a constant $Q_{10}$ between 10 and 25 °C. The experimental results on the same species given by Bernard (1963, his Table 3), Haq (1972, his Fig. 1) and D’Apolito & Stanczyk (1979, their Table 5) are in good agreement with the present simulations (Table 5). $Q_{10}$ calculated between 10 and 20 °C for naupliar and total development is respectively 3.52 and 3.44, of the same order as $Q_{10}$ measured by Haq (1972) (respectively 4.20 and
Table 4. *Euterpina acutifrons*. Instar mean weights (10\(^{-3}\) µg-at. N ind.\(^{-1}\)) obtained by the model and from the literature after conversion from dry weight into nitrogen content. Values of Yassen (1979) were obtained from mean weights of several stages in the same culture.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Model results (20–25 °C)</th>
<th>Yassen (1979) (18 °C)</th>
<th>Zurlini et al. (1978) (18 °C)</th>
<th>Moreira et al. (1985) (22 °C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N1</td>
<td>0.5</td>
<td>0.72</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N2</td>
<td>0.98</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N3</td>
<td>1.26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N4</td>
<td>1.60</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N5</td>
<td>2.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N6</td>
<td>2.54</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1</td>
<td>2.84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C2</td>
<td>3.35</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C3</td>
<td>3.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td>4.78</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult females</td>
<td>10.31</td>
<td>9.48</td>
<td>11.00</td>
<td>11.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Females with eggs

4.10). It is higher than the Q\(_{10}\) adopted for ingestion (2.6). The calculated stage durations at 18 °C are consistent with the results of Neunes & Pongolini (1965) obtained with *E. acutifrons* in culture.

Although our representation of the temperature effect is very simple, the model is able to reproduce the most important features of its action on the development rate. Generally, temperature is hypothesized to influence several processes involved in the metabolism such as filtration, ingestion, excretion, or more global processes such as growth or development. Our results show that the effect of temperature on ingestion only, which has an indirect effect on excretion and assimilation, is sufficient to simulate correctly the action of temperature on the development rate. This is not surpr-

![Fig. 5. *Euterpina acutifrons*. Simulated distribution of biomass among stages during total development. Upper limit represents total biomass of the population.](image)

![Fig. 6. *Euterpina acutifrons*. Simulated durations of naupliar (N; □) and total (T; ■) development under different temperature and non-limiting food conditions](image)

![Fig. 7. *Euterpina acutifrons*. Simulated time-courses of stage weights during development at different temperatures, and with non-limiting food. Growth rates are estimated from exponential adjustments, and are reported for the different temperatures. A Q\(_{10}\) of 3.47 is evaluated in the range of temperature studied. Reported adult weights are those calculated at the beginning of egg-laying](image)
Table 5. *Euperna acutifrons*. Development time at various temperatures based on the literature and from the present study

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N1</td>
<td>4.3</td>
<td>2</td>
<td>2</td>
<td>1.8</td>
<td>1.6</td>
<td>1.3</td>
<td>1.3</td>
<td>0.8</td>
</tr>
<tr>
<td>N2</td>
<td>4.1</td>
<td>1</td>
<td>1.8</td>
<td>1.4</td>
<td>1.5</td>
<td>1.2</td>
<td>1.2</td>
<td>0.9</td>
</tr>
<tr>
<td>N3</td>
<td>3.2</td>
<td>1</td>
<td>1.8</td>
<td>1.3</td>
<td>1.3</td>
<td>1.0</td>
<td>1.0</td>
<td>0.7</td>
</tr>
<tr>
<td>N4</td>
<td>4.8</td>
<td>1</td>
<td>2.2</td>
<td>1.5</td>
<td>1.8</td>
<td>1.5</td>
<td>1.5</td>
<td>0.9</td>
</tr>
<tr>
<td>N5</td>
<td>5.2</td>
<td>1</td>
<td>2.4</td>
<td>1.5</td>
<td>1.8</td>
<td>1.4</td>
<td>1.4</td>
<td>0.9</td>
</tr>
<tr>
<td>N6</td>
<td>4.6</td>
<td>1</td>
<td>1.8</td>
<td>1</td>
<td>1.5</td>
<td>1.2</td>
<td>1.2</td>
<td>0.9</td>
</tr>
<tr>
<td>Naupliar development</td>
<td>26.2</td>
<td>12.0</td>
<td>8.5</td>
<td>5 to 7</td>
<td>9.5</td>
<td>6.3</td>
<td>7.6</td>
<td>4.9</td>
</tr>
<tr>
<td>C1</td>
<td>5.0</td>
<td>1</td>
<td>2.0</td>
<td>1.6</td>
<td>1.5</td>
<td>1.2</td>
<td>1.2</td>
<td>0.8</td>
</tr>
<tr>
<td>C2</td>
<td>5.0</td>
<td>1</td>
<td>1.3</td>
<td>1.7</td>
<td>1.1</td>
<td>0.9</td>
<td>0.9</td>
<td>0.4</td>
</tr>
<tr>
<td>C3</td>
<td>3.8</td>
<td>1</td>
<td>1.7</td>
<td>1.9</td>
<td>1.3</td>
<td>1.1</td>
<td>1.1</td>
<td>0.7</td>
</tr>
<tr>
<td>C4</td>
<td>2.6</td>
<td>1.5</td>
<td>1.6</td>
<td>1.6</td>
<td>1.3</td>
<td>1.0</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>C5</td>
<td>3.8</td>
<td>2</td>
<td>1.8</td>
<td>2.2</td>
<td>1.3</td>
<td>1.0</td>
<td>1.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Copepodite development</td>
<td>20.2</td>
<td>8.4</td>
<td>9</td>
<td>6.5</td>
<td>8.8</td>
<td>5.2</td>
<td>5.2</td>
<td>3.0</td>
</tr>
<tr>
<td>Pre-adult life span</td>
<td>46.4</td>
<td>13.5</td>
<td>20.2</td>
<td>17.5</td>
<td>9 to 12</td>
<td>16</td>
<td>15.1</td>
<td>12.8</td>
</tr>
<tr>
<td>Generation time</td>
<td>52 to 55</td>
<td>56</td>
<td>20</td>
<td>25</td>
<td>20 to 21</td>
<td>14 to 16</td>
<td>20</td>
<td>19.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12 to 14</td>
<td>15</td>
<td>9</td>
<td>10.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.6</td>
</tr>
</tbody>
</table>
with experiments on *Acartia tonsa*. The present Fig. 7 suggests that the development of *Euterpina acutifrons* is equiproportional (sensu McLaren 1986), since temperature variation does not modify the ratio between the different stage lengths.

### Influence of food concentration

The ability of the model to simulate the influence of different food concentrations was tested by comparing simulations with 2 sets of data obtained by Sciandra (1986a). Development was only followed in the first 4 naupliar stages at constant temperature (22 °C) and for 2 concentrations of the diatom *Phaeodactylum tricornutum*: 2 and 13 µg-at. N l⁻¹ (Fig. 8A, B). Model coefficients remain unchanged.

Fits are good for the high food series. Timing of development stages and amplitude of maximal abundance are well reproduced by the model. For the low food series, adjustments are acceptable for stages N1 and N2 for which simulated curves have the same asymmetry as in experimental results. For stages N3, the initial slope is well represented, but the terminal part of the curve is too low. Nevertheless, the model is able to simulate 2 important properties at low food level: first the lower speed of development (stage peaks occur later in Fig. 8B than in Fig. 8A); second the greater proportion of individuals which stay a longer time in the stages.

Low food conditions seem to have another effect which was discussed by Sciandra (1986a), and cannot be accomodated in a deterministic model. Variability in Fig. 8B is much greater than in Fig. 8A. The part of the total variance explained by the model is respectively 0.94 and 0.84 for the high and low food conditions. Our model, which only explains the deterministic properties of individuals, is unable to account for the effect of variability on the population development. This can be seen from the increasing discrepancy between simulations and experiments for the N3 and N4 stages. Limitations of deterministic representations have to be kept in mind to clearly identify what part of the population properties may be attributable to individual properties.

Fig. 9 gives a synthetic representation of the influence of food concentration on the duration of the naupliar and total development, simulated at a constant temperature of 22 °C. For concentrations higher than about 4 µg-at. N l⁻¹, there is no marked influence because of the saturation of the ingestion process formulated by the Ivlev relationship. Between 1 and 3 µg-at. N l⁻¹, development is strongly affected by the variation of food level. For concentrations lower than 0.5 µg-at. N l⁻¹, copepods die before reaching their total development. Similar results have been obtained experimentally on *Calanus helgolandicus* (Paffenröder 1970, 1971), *Calanus pacificus* (Vidal 1980b), and a cladoceran species, *Eudiaptomus graciloides* (Weglenska 1971).

Fig. 10 shows that growth is fairly exponential for high as well as for low food levels. Growth rates are reduced especially for concentrations lower than 3 µg-at. N l⁻¹. Experiments by Berggreen et al. (1988, their Figs. 4 and 5) show that
growth of *Acartia tonsa* is exponential and constant throughout development at all food concentrations, although Miller et al. (1977) observed the contrary for the same species at very low food concentrations. Our results are also in good agreement with experiments of Harris & Paffenröder (1976) on *Temora longicornis*, Hamburger & Boetius (1987) on *Eudiaptomus graciloides*, and Tessier & Goulden (1987) on *Daphnia magna*.

The model allows us to calculate simultaneously the time courses of metabolic (Fig. 11A) and molting rates from N2 to N3 stage (Fig. 11B). Molting rate curves have the classical shape reported by Sulkin & Van Heukelem (1986). The asymmetry due to the terminal part of the curves was experimentally observed by Miller et al. (1984). The period during which molting occurs is longer for low food level, but the maximal rate of molting is higher for high food level. The explanation is given by the specific growth rate curves. For the high food level, specific growth rate is optimal so that weight of Nauplii 2 increases rapidly, leading to the molting rate to become maximal in a short time. As weight reaches the maximum value possible in stage N2, specific growth rate tends to zero because ingestion activity diminishes according to the relationship f4. Consequently, molting rate decreases following the relationship f11. Individuals which have not molted although having reached their critical weight are represented by the tail of the simulated distribution. At this time, the peak on Fig. 11B corresponds to the slope discontinuity on Fig. 11A.

For low food level, the specific growth rate is lower, leading to slower development of weight and molting rate. Clearly, the shape given to the relationships between the molting rate and both the weight and growth rate strongly influences the shape of the specific growth and transfer curves.

The model is also able to calculate the weight distributions of stages. Such distributions for successive instars clearly show that the use of critical molting weights in the model does not imply that all the individuals molt at these weights (Fig. 12). At the stage...
peak (C4 in Fig. 12), the weight distribution is shifted towards higher values when the food concentration increases. This is the reason why the mean weights increase when growth rate increases (cf. Figs. 7 and 10).

**Applications**

The model can be used to test the effect of variation of forcing variables such as food and predators, which are complex in time and space and may act simultaneously on populations. If only the overall population is considered, their effects on the dynamics are unpredictable since they can occur at different periods of the development, characterized by different stage compositions (Nival et al. 1988). Fig. 13 shows the effects of different patterns of food deprivation and predator occurrence, simulated by the model. In the reference situation (A1), the decrease of total population is only due to natural mortality which is more important during the N6 to C1 transition period. If a starvation period occurs, development time and recruitment (% of initial individuals becoming adults) are changed. Recruitment is more affected when starvation occurs during the naupliar (A2) than during copepodid development (A3), because of the higher mortality rates of stages N6 and C1. Absence of food increases the duration of affected stages. According to the selectivity of predators and the time of their occurrence, recruitment may be more or less changed. If predator action and starvation period coincide (B2), effects may be much more dramatic than if they do not (B3).

**Basic hypotheses of coupling between growth and dynamics**

The model allows us to test hypotheses on the connections between growth rate and development. The connections were formulated theoretically, because of the lack of knowledge on the relations between molting and growth. Good fits between experimental and simulated data are encouraging. It has to be noted that...
the diversity of available particles, and the selectivity of molting occurs when a certain hormonal metabolism of crustaceans seems complex (Skinner 1985a, b). Numerous studies have shown that nutritive pre-\textsuperscript{a}mendment rates (here greater than 5 \(\mu g\)-at. N \textsuperscript{b}1-') suggested the influence of an hormonal control leading to a process taking into account a different and supplementary physiological process. Miller et al. (1977) according to which the structural growth rate becomes asymptotic at food levels that permit maximal development, but the important fact is that the development is not affected. Development times in the different instars remain nearly unchanged. The part of the total variance in abundance explained by the modified model is equal to 0.96 and 0.91 respectively for the experimental data of Figs. 2 and 3, whereas it was 0.98 and 0.92 for the initial model.

DISCUSSION

There is a hierarchy between processes in that both food and temperature act on ingestion which, in turn, influences the rate of excretion, so that excretion rate is not directly influenced either by temperature or by food (Fig. 1). This assumption results logically from the fact that excretion is a physiological process induced by other metabolic activities. Since the routine metabolism has been supposed to be independent of the temperature, the \(Q_{10}\) law used for the ingestion process applies directly to the whole metabolic rate. This assumption holds for animals whose different enzymatic activities are similarly influenced by variations of temperature.

The \(Q_{10}\) for growth is equal to 3.47 and is in the same range as those calculated for naupliar (3.44) and total weights, at least in a certain range of variation, since this assumption is of prime importance in the model.

It has been demonstrated for small species that temperature is negatively correlated with weight, especially for the last instar (McLaren 1963, Landry 1975, 1978, Miller et al. 1977, Corkett & McLaren 1978, Durbin & Durbin 1978, Vidal 1980a, Durbin et al. 1983). Heinle (1969) and Corkett & McLaren (1978) showed that body size is not affected below a given temperature, but decreases as temperature exceeds this given value. McLaren (1963) showed that the final size of adults depends on the mean temperature during the whole lifetime (cf. his Fig. 3). By considering firstly that the critical weight of molting is constant, and secondly that temperature influences only ingestion and excretion rate, the model cannot reproduce the relation between temperature and weight. This means that long-term effects of temperature should be represented by a process taking into account a different and supplementary physiological process. Miller et al. (1977) suggested the influence of an hormonal control leading to uncoupled growth and development. Although hormonal metabolism of crustaceans seems complex (Skinner 1985a, b), molting occurs when a certain hormone exceeds a threshold (Anger 1987, Anger & Spindler 1987).

We modified our model by adding an empirical relationship in which the critical molting weights of the oldest instars decrease when temperature exceed a given value. Simulations obtained at different temperatures (as for Fig. 7) reproduce this effect (Fig. 14), but the important fact is that the development is not affected. Development times in the different instars remain nearly unchanged. The part of the total variance in abundance explained by the modified model is equal to 0.96 and 0.91 respectively for the experimental data of Figs. 2 and 3, whereas it was 0.98 and 0.92 for the initial model.
stages. We have assumed here that every stage can efficiently collect food particles. The real problem is to know if the particle spectrum measurable in the seawater is wide enough to provide each stage with its optimal food condition, so that individuals can grow exponentially. Since temperature acts on different stages following the same law, its influence is easier to study theoretically and experimentally.

Tande (1988) found a relation between temperature variation and mortality rate in Calanus finmarchicus. It would be interesting to determine how the metabolic rate varies in such conditions. Since the model is applicable for other crustaceans, more appropriate species than Euterpina acutifrons could be chosen, on which biological processes and dynamics are easier to measure.

The equiproportionality rule is applicable for species whose stage durations change in the same proportion as temperature varies (Corkett & McLaren 1970, McLaren & Corkett 1981, Corkett 1984, Corkett et al. 1986). Isochronality (Miller et al. 1977, Klein Breteler 1980) is a particular case of equiproportionality applicable to species whose stages have identical durations (Uye 1980, Landry 1983), and is not always observed (Landry 1983). Generally, equiproportionality is observed in well-fed animals. Our model demonstrates that this is also theoretically possible when food limits growth, and that equiproportionality is not restricted to saturating conditions of food. It confirms also the assumption of McLaren (1986) according to which equiproportionality and exponential structural growth are associated, if fixed structural molting weights are considered (Harris 1983).

Because physiological connections are numerous and non-linear, it is difficult to clearly discern the consequences induced by an hypothesis in relation to a given process. Deterministic models have 2 features: first, because individual variability is not taken into account, their results are not subject to variation; second, because of their associative structure, modifications performed on one of its components clearly influence the rest of the system. This study suggests that the Q10 of ingestion, growth and development have to be determined simultaneously in experiments in order to compare them to the simulated values, respectively 2.6, 3.47 and 3.48. The difference between ingestion and growth Q10 values is surprising and interesting. It may be explained by the representation chosen for the influence of temperature on the processes involved in the nitrogen growth rate, and by the respective parts attributed to routine and active metabolism. In like manner, the similarity between Q10 of growth and of development has to be verified experimentally for Euterpina acutifrons. Heinle (1969) observed that for Acartia tonsa the Q10 of development and the Q10 of growth are equal below 15 °C. Above, the growth Q10 becomes lower than the development Q10.

In the natural environment, variability of temperature and food induces complex responses in copepods which have to adapt in order to optimize their growth, reproduction and development. Their reaction in a fluctuating environment can be really understood only if the critical mechanisms stimulated by the perturbations are identified. Since several external factors vary simultaneously, and since biological processes are coupled by complex and non-linear interactions, it is not possible to predict easily the dynamics of a population without a conceptual structure which embodies the biological properties of copepods. Our model is a first step in this direction.

Empirical relationships traditionally used to represent the influences of food or temperature on development rate do not take into account intrinsic properties of animals, so their applications are limited. More especially, latency times are not reproduced by such models. It is clear that delays observed in physiological responses are of prime importance in population dynamics, since they may damp effects of external variations. We have represented very simply this faculty of living organisms, by considering that the cumulated specific growth rate averaged over a certain time interval was an appropriate criterion to represent the influence of growth rate on the molting process. It is clear that this representation is itself empirical. It could be refined by including in the model a supplementary variable representing internal storage. In any case, an interesting application of the model will be to see how population dynamics changes when the value of the cumulated time is modified. The more this value is increased, the more will high frequencies of variation be damped. This would permit evaluation of the robustness of the population development within several regimes of external fluctuations of food and temperature.

Acknowledgements. We thank Prof. P. Nival for discussions and criticisms of the manuscript.

LITERATURE CITED


copépode pélagique de Méditerranée Euterpina acutifrons
Clas. Pelagos 1 (2). 35–48
Burkill, P. H., Kendall, T. F. (1982). Production of the copepod
21: 21–31
Carlotti, F. (1987). Modèles de recrutement de larves d’or-
ganismes marins. J. Rech. oceanogr. 12: 12–16
Conover, R. J. (1966). Factors affecting the assimilation
of organic matter by zooplankton and the question of super-
copepods. Studies on Copepoda II. Proceedings of the First
Crustacea, Suppl. 7: 130–133
storage by the copepod Pseudocalanus in the laboratory.
development rate of eggs and older stages of copepods. J.
rearing of the marine calanoid copepods Calanus limmar-
chus (Gunnerus), C. glacialis Jaschnov and C. hyper-
boreus Kreyer with comment on the equiproportional rule
(Copepoda). Syllogeus (Nat. Mus. Can.) 58: 539–546
the nutrition and metabolism of zooplankton. V. Feeding efficiency of
Calanus finmarchicus J. mar. biol. Ass. U.K. 47:
259–270
Euterpina acutifrons (Copepoda, Harpacticoida) from
North Inlet, South Carolina, with references to dimorphic
relationships of Acartia clausii from Narragansett Bay, R. I.
Limnol. Oceanogr. 23: 958–969
Durbin, E. G., Durbin, A. G., Sneyd, T. J., Verity, P. G.
(1983). Food limitation of production by Acartia tonsa in
Narragansett Bay, Rhode Island. Limnol. Oceanogr. 28:
1199–1213
Fernandez, F. (1979). Nutrition 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
particles on the feeding behavior of the marine planktonic
zooplankton and the adaptive value of vertical migration.
Hag, S. M. (1965). Development of the copepod Euterpina
acutifrons with special reference to dimorphism in the
Hag, S. M. (1972). Breeding of Euterpina acutifrons, a harp-
acticoid copepod, with special reference to dimorphic males.
Mar. Biol. 15: 221–235

behavior of the Malaysian prawn Macrobrachium rose-
bergii (DeMan) during the molt cycle (Decapoda, Caridea).
Crustacea 52: 53–60
copepods, Limnol. Oceanogr. 28: 142–147
Harris, R. P., Paffenbörger, G. A. (1976). Feeding, growth and
reproduction of the marine planktonic copepod
Temora longicornis Müller. J. mar biol. Ass. U.K. 56:
575–590
Chesapeake Sci. 10: 186–209
influence of temperature on the development rate of copepods.
harpacticoid copepod Parachnocampa nanus in a brack-
ish-water habitat. Limnol. Oceanogr. 30: 1060–1066
zooplankton, Am. Nat. 124: 455–478
Ikeda, T. (1985). Metabolic rates of epipelagic marine zoo-
plankton as function of both mass and temperature. Mar.
Biol. 85: 1–11
pelagic copepods in the presence of heterotrophic dinoflagellates.
Springer-Verlag, Heidelberg
response to changes in size and concentration of food.
Limnol. Oceanogr. 21: 490–500
Landry, M. R. (1975). Seasonal temperature effects and pre-
dicting development rates of marine copepod eggs. Lim-
ol. Oceanogr. 20: 434–440
planktonic marine copepod, Acartia clausii, in a small temperate lagoon on San Juan Island, Washington. Int.
copepods with comments on the isochronal rule. Limnol.
Oceanogr. 28: 614–624
23: 1291–1317
Lehman, J. T. (1976). The filter-feeder as an optimal forager
and the predicted shapes of feeding curves. Limnol.
Oceanogr. 21: 501–516
McLaren, I. A. (1963). Effects of temperature on growth of
copepods with comments on the isochronal rule. Limnol.
Oceanogr. 23: 1291–1317
Aquat. Sci. 38: 77–83
rates of ammonium excretion by the copepod Calanus
collection molting rates of planktonic marine copepods:
measurement, applications, problems. Limnol. Oceanogr. 29: 1274–1289
Vidal, J. (1980c). Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size


This article was submitted to the editor


Manuscript first received: August 29, 1988

Revised version accepted: May 18, 1989