

Model of copepod growth and development: moulting and mortality in relation to physiological processes during an individual moult cycle

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ABSTRACT: A mathematical model of copepod population dynamics coupling individual growth and development was tested. The results show in detail the effect of applying various hypotheses, particularly concerning the relationship between certain physiological processes (ingestion, egestion, excretion, oogenesis, etc.) and processes controlling the time course of abundance of individuals in each instar (mortality rate, moulting rate, reproduction). The model shows the changes in physiological processes (ingestion, growth rate, etc.) at the individual level as a function of age within stage, and consequently the probability of moulting and death. If an individual remains for some time at one stage, its growth rate decreases, weight does not increase, the ability to moult is lost and the probability of death is greater. In addition, the model gives the mean values of processes for the whole population, as could be obtained experimentally, but it also provides an explanation of the variability of processes related to the population age structure. Finally, the results of this mathematical model led to an experimental test of the validity of the hypotheses put forward. The mathematical model can be used in all conditions, since it simulates values of processes constant in time as long as the external conditions are also constant, while remaining capable of expressing the internal dynamics of a population when the environment is suddenly perturbed.

INTRODUCTION

For a better understanding of the dynamics of a planktonic population within the pelagic ecosystem, 2 types of processes should be considered: demographic (flux of animals) and biogeochemical (cycles of matter). Yet these 2 approaches are quite often modelled separately (Cale 1988) for 2 reasons. The researcher may be more interested in the behaviour of the ecosystem (flux of matter) or, on the other hand, he may focus his study on a single population or even on a particular developmental stage (e.g. recruitment). In models of larval dynamics, development and mortality rates generally are linked directly to external parameters (food, temperature) by empirical relationships, which do not take into account the energetic processes involved in dynamics (Davis 1984, Sciandra 1986). In fact, these external parameters affect the physiology of organisms in several ways, either ensuring normal development or inducing developmental difficulties, even death. Moreover, these

physiological steps act as filters for certain variations of external parameters, which are subject to strong fluctuations in the pelagic environment, and contribute to time lags observed in population dynamics.

In order to describe population dynamics in terms of individuals and biomass simultaneously, a model must take into account the energy characteristics of the individual and how they are connected with demographic processes (Steele & Mullin 1977). Successful studies are often made of the relationships between external variables and the physiological functions which control the energy budget (ingestion, excretion, egestion, reproduction), whereas relationships between energetic (growth) and demographic processes (moult, mortality) are difficult to assess experimentally.

A conceptual scheme has been proposed in the model established by Carlotti & Sciandra (1989) and Carlotti (1990), which integrates biomass and demographic criteria simultaneously. In this model, the processes involved in individual growth (ingestion,

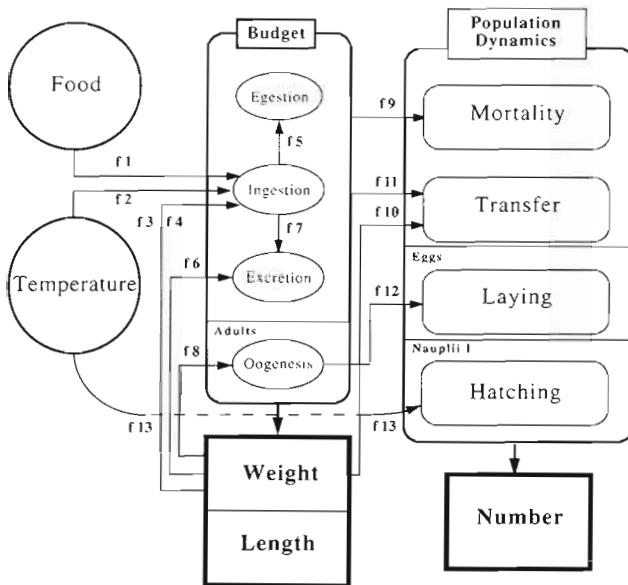


Fig. 1. Conceptual diagram of the model. Relationships (f) between external forcing variables, physiological processes and population dynamics terms are detailed in Fig. 3

egestion, excretion, oogenesis) are coupled with processes controlling the time course of the abundance of individuals at each stage (mortality, moulting and reproduction rates) (Fig. 1).

Using this model we were able to simulate the growth and development of *Euterpina acutifrons* simultaneously (quantitative validation) and to define general rules concerning the growth and development of small copepods (qualitative validation). Moreover, this model fits the time series of stages of a *Euterpina acutifrons* population raised in the laboratory (Fig. 3 in Carlotti & Sciandra 1989) better than a model using empirical formulations (Sciandra 1986; see his Fig. 5). A deterministic explanation of the asymmetry of the time course curves of abundance for each stage has been suggested. In Carlotti & Sciandra (1989), the results presented mainly concerned the time courses of the state variables: number in each stage, weight of individuals and biomass of the population.

Here, we give a description of the fundamental internal characteristics of this model and explain how it can provide the basis for an experimental study of a copepod population (Carlotti & Nival 1992). Moreover, the model permits observational access to processes and variables which cannot be assessed directly in experimentation. We indicate the time courses of the processes of mortality and transfer to the next stage (moulting) during development at each stage, and test the functional connections with the physiological processes at the individual level. The hypotheses concerning these functional connections are:

Hypothesis 1. In the absence of predators and parasites, the probability of death depends directly on the physiological state of the individual, which is a consequence of the past feeding history of the animal. This hypothesis has already been formulated for fish (Wroblewski 1984).

Hypothesis 2. Moulting occurs (1) when a given weight is reached (critical moulting weight) and (2) if the physiological state during a short period preceding the moult is favourable.

Hypothesis 3. Individual weight cannot exceed a maximum value in a stage, because the exoskeleton limits growth. Thus, if the animal goes above the critical moulting weight, ingestion decreases as a function of the excess biomass of this critical weight.

The purpose of this report is to present in detail the consequences of these biological hypotheses regarding the pattern of mortality and moulting rates during the moulting cycle. The simulations described here supplement those which have already been presented concerning the population dynamics of *Euterpina acutifrons* (Carlotti & Sciandra 1989).

THE MODEL

The conceptual basis of the model has already been described in detail (Carlotti & Sciandra 1989). In this paper, we focus on the influence of variables affecting the physiological processes involved and on the interaction of processes.

Scope of the model

The development of copepods can be divided into 2 levels (Fig. 2). The first one corresponds to the developmental instars: eggs ($i = 1$), nauplii ($i = 2$ to 7), copepodites ($i = 8$ to 12) and adults; while the second level concerns the age classes within each stage. The choice of the duration of an age class is up to the person using the model. The number of age classes within a stage must be large enough to allow maximum duration at each stage.

In each age class, the variations in mean individual weight and in the numbers of individuals are calculated as a function of various biological processes, which are linked as shown in Fig. 1. The differential equations of the model are given in Table 1, and the mathematical formulations of the processes are given with Fig. 3 (see also Table 1 in Carlotti & Sciandra 1989).

Here results are presented for the first 2 feeding stages (NI and NII) of *Euterpina acutifrons*, as it is easier to illustrate some processes of population dynamics at the early stages (see Fig. 8 in Carlotti & Sciandra 1989).

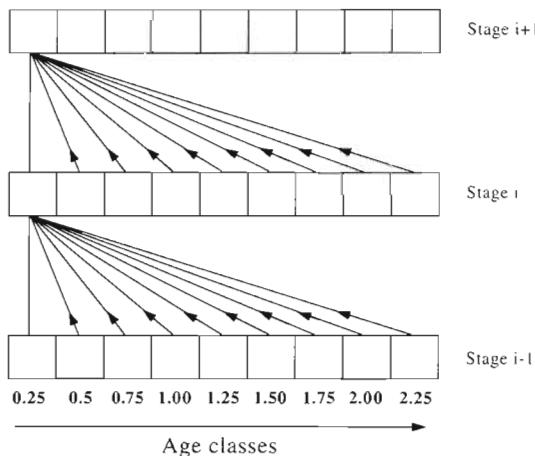


Fig. 2. Conceptual framework of the model. Copepod development can be divided into stages (natural partition), and each stage can be divided into age classes all having the same duration (artificial partition). Duration of age classes was chosen as 0.25 d in the simulations. Arrows denote that a proportion of larvae can reach the first age class of the next stage. This transfer depends on physiological factors, which only become adequate for some age classes (see 'Simulations')

Indeed, these stages closely reflect egg production pulses, whereas at later stages this correspondence becomes damped by variability due to the asynchronous development of individuals, which increases progressively (Carlotti & Nival 1991). Nevertheless, we could have chosen another stage for presenting these results, because the mechanical representation (the mathematical functions as a whole) of the growth and development in the different stages is the same.

Physiological processes

The choice of the mathematical formulations of physiological processes is justified in Carlotti & Sciandra (1989) with regard to the literature. Fig. 3 shows the plots of the functions presented in Fig. 1.

At any given time, 3 variables influence ingestion (Fig. 3A to D): food concentration (F), temperature (T_e) and mean individual weight (W) in an age class. This representation is a simplification of the factors known to influence ingestion (Huntley 1988). The relationship between ingestion and food concentration (Fig. 3A) has been studied experimentally for *Euterpina acutifrons* by Sciandra (1982), who determined the sigmoidal function f_1 .

Temperature affects enzymatic reactions and hence bioenergetic processes. Experiments on copepods have shown its impact on ingestion (Mullin & Brooks 1970, Kiørboe et al. 1982, Thébault 1985), assimilation (Conover 1966), excretion (Ikeda 1985) and respiration

(Huntley & Boyd 1984, Ikeda 1985). However, the effect of temperature is rarely estimated by the activity of the enzymes involved in a given process, but by the variation in the flux of matter generated by the activity of enzymes. In fact, the influence of temperature on only one of these processes can be limiting for the general functioning of the matter budget. Concerning copepods, there are 2 opposing points of view in this respect: the first is that copepod growth can be described by temperature alone (Paffenhöfer & Harris 1976, McLaren 1978), whereas the second considers food as a limiting factor (Mullin & Brooks 1976, Checkley 1980, Huntley & Boyd 1984). In fact, the response to these parameters is more complex, as the effect of temperature may differ with food concentration (Thébault 1985).

For a parameter with such a complex influence as temperature, the modeller has to answer 3 questions: (1) Which processes are likely to be modified by temperature? (2) Which coefficients of the mathematical functions of processes change with temperature? (3) Which mathematical representation should be used for the effect of temperature on the coefficients chosen?

To simplify matters, we considered the action of temperature on the ingestion rate only (Fig. 3B), since catabolic processes are related to ingestion and therefore indirectly to temperature. This implies that ingestion rate limits the whole budget. The influence of temperature on the maximum ingestion rate can be expressed as an exponential within the range 10 to 25 °C, which is not extreme for *Euterpina acutifrons* (see Carlotti & Sciandra 1989).

The influence of weight on physiological processes has been widely demonstrated. In the present model, weight is linked with ingestion, excretion and reproduction.

Two weight functions (f_3 and f_4) which account for different phenomena influence the ingestion rate (Fig. 3C, D). The allometric law (function f_3) is determined experimentally by analyzing the total growth of the copepod. This signifies that the ingestion rate per unit weight decreases as weight increases (Paffenhöfer 1971, 1984). This empirical relation is due to complex genetical and physiological phenomena occurring as the individual grows older, and is quite often used in models (Steele 1974, Kremer & Nixon 1978). The second function (f_4) concerns the copepod's mode of life during the moulting cycle. It was not included in previous versions of the model (Carlotti 1986, 1987, Nival et al. 1988). The results obtained with these versions have revealed a certain abnormality: some individuals in a given stage, i.e. those which developed slowly, continued to grow within that stage. Obviously, however, copepods are prevented by their exoskeleton from growing indefinitely in one stage, as moulting is the only way in which the organism can keep growing. For individuals

Table 1. Processes and system of differential equations describing dynamics of copepod individuals and populations. i: stage; j: age class; $W_{i,j}$: weight; $N_{i,j}$: abundance

Process	Units	Formulation	
Growth			
Ingestion (I)	$\mu\text{g-at. N d}^{-1} \text{i}^{-1}$	$I_{i,j} = f1_{i,j} \cdot f2_{i,j} \cdot f3_{i,j} \cdot f4_{i,j}$	(1)
Egestion (EG)	$\mu\text{g-at. N d}^{-1} \text{i}^{-1}$	$EG_{i,j} = f5_{i,j}$	(2)
Excretion (EX)	$\mu\text{g-at. N d}^{-1} \text{i}^{-1}$	$EX_{i,j} = f6_{i,j} + f7_{i,j}$	(3)
Matter for reproduction (MR)	$\mu\text{g-at. N d}^{-1} \text{i}^{-1}$	$MR_{13,j} = f8_{13,j}$	(4)
Growth (G)	$\mu\text{g-at. N d}^{-1} \text{i}^{-1}$	$G_{i,j} = I_{i,j} - EX_{i,j} - EG_{i,j}$	(5)
Specific growth (SG)	d^{-1}	$SG_{i,j} = \frac{G_{i,j}}{W_{i,j}}$	(6)
Cumulated specific growth (CSG)	d^{-1}	$CSG_{i,j} = \frac{1}{\Delta t} \cdot \int_{t-\Delta t}^t SG_{i,j} \cdot dt$	(7)
Dynamics			
Mortality (M)	d^{-1}	$M_{i,j} = f9_{i,j}$	(8)
Transfer (T)	d^{-1}	$T_{i,j} = f10_{i,j} \cdot f11_{i,j}$	(9)
Laying (L)	d^{-1}	$L_{13,j} = f12_{13,j}$	(10)
Hatching (H)	d^{-1}	$H_{1,1} = f13_{1,j}$	(11)
Differential equations			
Growth			
Eggs ($i = 1$)		$\frac{dW_{1,1}}{dt} = 0$	(12)
N1 to C5 ($i = 2$ to 12)		$\frac{dW_{i,j}}{dt} = G_{i,j}$	(13)
Adults ($i = 13$)		$\frac{dW_{13,j}}{dt} = G_{13,j} - MR_{13,j}$	(14)
Dynamics			
Eggs ($i = 1$)		$\frac{dN_{1,1}}{dt} = L_{13,j} \cdot N_{13,j} - (H_{1,1} + M_{1,1}) \cdot N_{1,1}$	(15)
N1 (1st age class)		$\frac{dN_{2,1}}{dt} = H_{1,1} \cdot N_{1,1} - (T_{2,1} + M_{2,1}) \cdot N_{2,1}$	(16)
N2 to C5 (1st age class)		$\frac{dN_{i,1}}{dt} = \sum_{j=1}^n T_{i-1,j} \cdot N_{i-1,j} - (T_{i,1} + M_{i,1}) \cdot N_{i,1}$	(17)
N1 to C5 (next age class)		$\frac{dN_{i,j}}{dt} = -(T_{i,j} + M_{i,j}) \cdot N_{i,j}$	(18)
Adults (1st age class)		$\frac{dN_{13,1}}{dt} = \sum_{j=1}^n T_{12,j} \cdot N_{12,j} - M_{13,1} \cdot N_{13,1}$	(19)
Adults (next age classes)		$\frac{dN_{13,j}}{dt} = -M_{13,j} \cdot N_{13,j}$	(20)

which stay too long in one stage, therefore, the model must simulate a stabilization of growth, hence a growth rate of zero. As the model takes into account critical moulting weights during ontogenetic development (see Carlotti & Sciandra 1989), function f4 limits ingestion when this weight is reached (Hypothesis 3). This phenomenon is hypothetical, as is its mathematical formulation. We assume that ingestion in one stage follows a negative parabolic function (Fig. 3D) when the weight exceeds the critical moulting weight of stage i: X_i . To avoid introducing an additional coefficient, we decided that function f4 would cross the abscissa at the weight corresponding to the critical moulting weight of the subsequent stage. This hypothetical function is obviously an

important one in the model, both for physiological processes and for population curves, and we discuss below its biological significance.

Two kinds of losses were distinguished in the model: those proportional to the ingestion rate (feces, activity, metabolism) and those related to routine metabolism, which are considered proportional to weight (Fig. 3E to G). We assume that egested matter (f5) is a constant ratio of ingested matter (Fig. 3E). Although the allometric relation of excretion or respiration to weight is frequently used (Ikeda 1974, Conover 1978), we do not introduce it directly. We suppose that it operates through the ingestion function f7 (Fig. 3G). However, even when ingestion is low or equal to

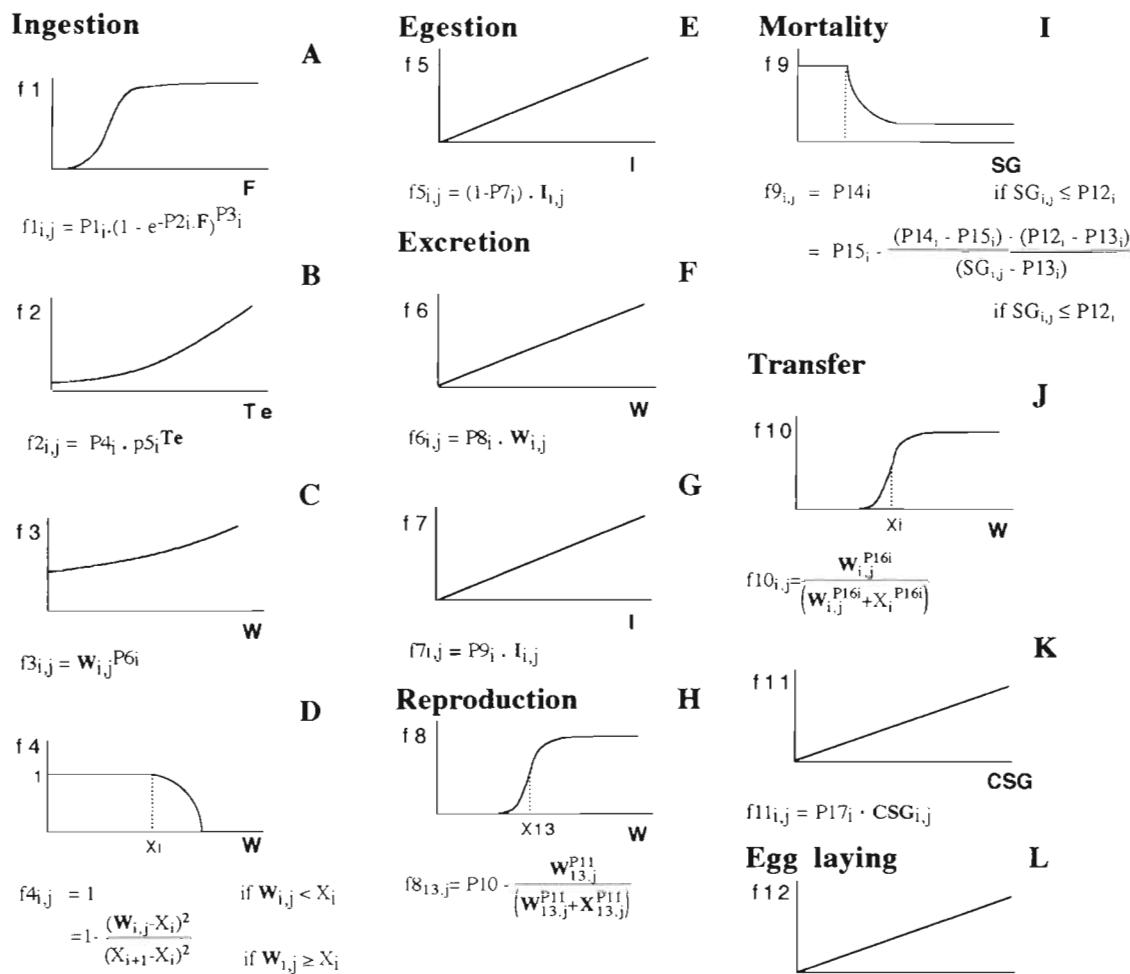


Fig. 3. Mathematical curves and formulations of copepod physiological relationships and population dynamics terms used in the model. (A) Influence of food concentration on ingestion following an Ivlev curve. (B) Influence of temperature on ingestion. (C) Allometric relation of ingestion with weight. (D) Limitation of ingestion as moulting weight is reached. (E) Fraction of ingested matter not assimilated. (F) Excretion from routine metabolism. (G) Excretion from active metabolism. (H) Influence of weight on the amount of matter invested for reproduction. (I) Influence of specific growth rate on mortality. (J) Weight influence on transfer rate. (K) Cumulated specific growth influence on transfer rate. (L) Laying rate influenced by matter invested for reproduction. (M) Influence of temperature on hatching rate. i: stage; j: age class; X_i : critical weight for transfer in stage i; X_{13} : critical weight for reproduction; P1 to P19: biological parameters [see Table 3 in Carlotti & Sciandra (1989) for definitions]

zero, the animal must maintain minimum metabolic processes, i.e. basic metabolism and 'routine' metabolism, in order to survive. Wroblewski (1984) uses a constant term, but the function f6 (Fig. 3F) proportional to weight (Corkett & McLaren 1978) seems to us more appropriate.

By combining functions f1 to f7, we obtain the distribution of consumed matter among the different bioenergetic processes at different food levels for a nauplius II with a given weight (here, 0.78×10^{-3} µg-at. N) and at a constant temperature (Fig. 4A). This type of partitioning is well known for zooplanktonic grazers

(see Fig. 2 in Checkley 1985). The consumed matter is not used entirely for growth. There is a threshold food concentration below which the growth rate is negative. In the case of nauplius II, we find that all processes stay more or less constant beyond $8 \mu\text{g-at. N l}^{-1}$. Fig. 4B, C shows the budget partitioning in the likely weight range of nauplii II of *Euterpinia acutifrons* for 2 food concentrations, one high ($13 \mu\text{g-at. N l}^{-1}$) and one low ($2 \mu\text{g-at. N l}^{-1}$). For both concentrations all processes, including growth, increase slightly up to a limit situated just above the critical moulting weight (around 0.8×10^{-3} µg-at. N). Beyond this limit, the ingestion decrease induces a

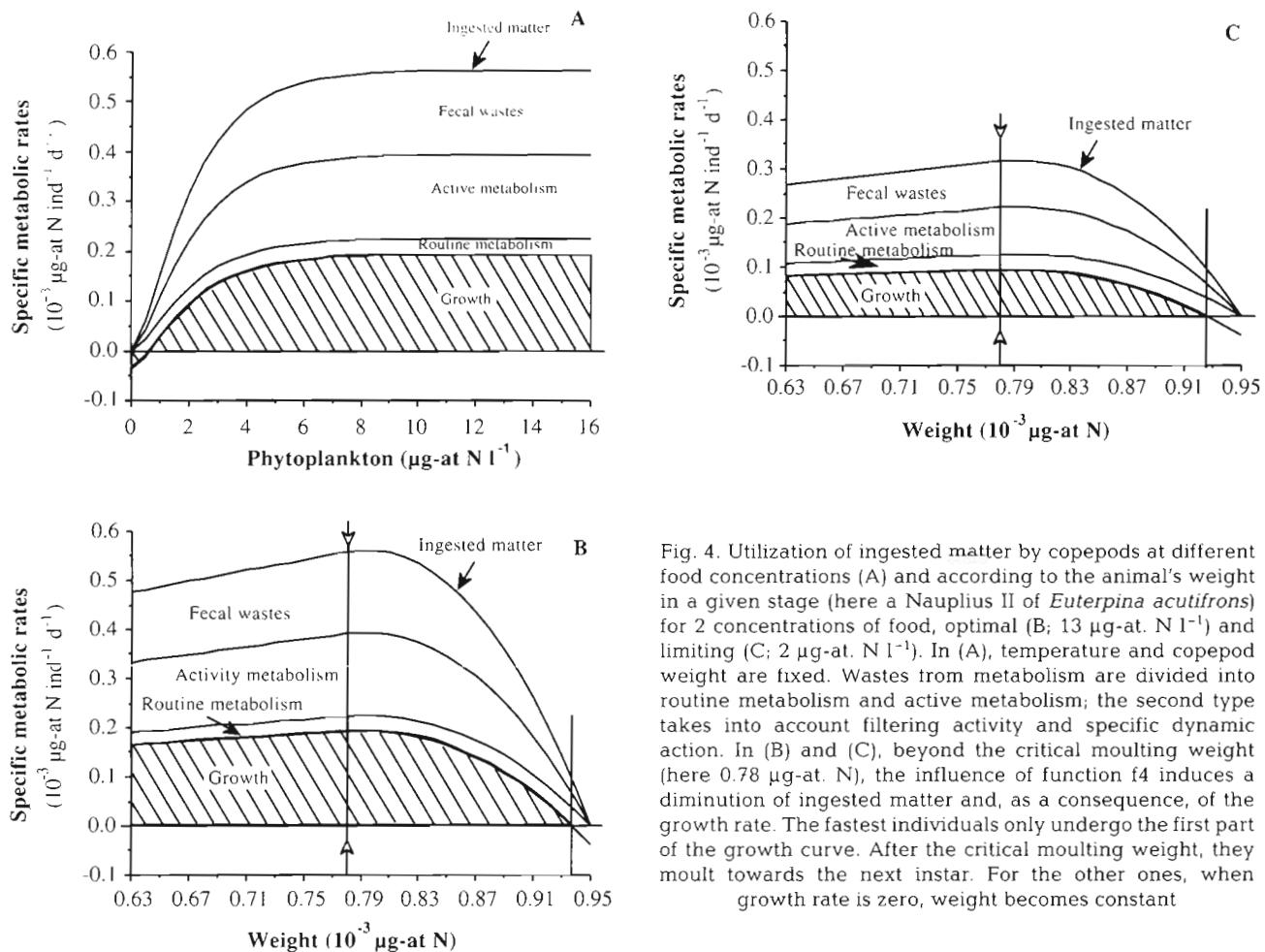


Fig. 4. Utilization of ingested matter by copepods at different food concentrations (A) and according to the animal's weight in a given stage (here a Nauplius II of *Euterpina acutifrons*) for 2 concentrations of food, optimal (B; 13 $\mu\text{g-at N l}^{-1}$) and limiting (C; 2 $\mu\text{g-at N l}^{-1}$). In (A), temperature and copepod weight are fixed. Wastes from metabolism are divided into routine metabolism and active metabolism; the second type takes into account filtering activity and specific dynamic action. In (B) and (C), beyond the critical moulting weight (here 0.78 $\mu\text{g-at N}$), the influence of function f4 induces a diminution of ingested matter and, as a consequence, of the growth rate. The fastest individuals only undergo the first part of the growth curve. After the critical moulting weight, they moult towards the next instar. For the other ones, when growth rate is zero, weight becomes constant

decrease of activity and feces production, whereas the basic losses remain constant. When growth rate reaches zero, weight is at a standstill.

In our model, eggs are laid at the expense of somatic growth; this is a usual pattern in copepods with few reserves (Kiørboe et al. 1985, Berggreen et al. 1988). We have introduced a function representing the matter invested in egg laying as a function of weight (Fig. 3H). We used a sigmoidal function (Hill's function), which has in fact been observed in female crustaceans (Corkett & McLaren 1969, Smith & Lane 1985, Dailey & Ralston 1986). The coefficient P10 corresponds to the maximum amount of matter a female can invest in egg laying. For a given weight, function f8 presents the amount of matter to be invested in reproduction. As this amount is taken out of the budget, it limits the gain in weight. The animal's weight is stabilized when the whole material budget is used for reproduction (Fig. 5). Two conclusions can be drawn from this simple scheme: (1) the higher the budget (in Fig. 5, as a function of temperature), the more important is the amount of organic matter invested in egg laying; and conse-

quently (2) the weight of eggs laid by females stabilizes at a higher value.

Processes of population dynamics

Mortality rate is usually considered as constant for the population as a whole. In fact, though, it varies according to growth stage (Paffenhofer 1970), and within each stage, according to the physiological condition of the organism. In recent models of population dynamics of zooplanktonic organisms, some authors have introduced mortality functions which depend on the ingestion rate (Davis 1984, 1987) or on the material budget (Wroblewski 1984). We used an increasing hyperbolic function (Fig. 3I), which allows for a high mortality rate when budgets are unfavourable and a low mortality when they are favourable (Hypothesis 1).

Moult determination is complex, but it is reasonable to believe that moulting occurs only when a set of fundamental biological conditions are combined. Two factors were distinguished (Hypothesis 2). In our

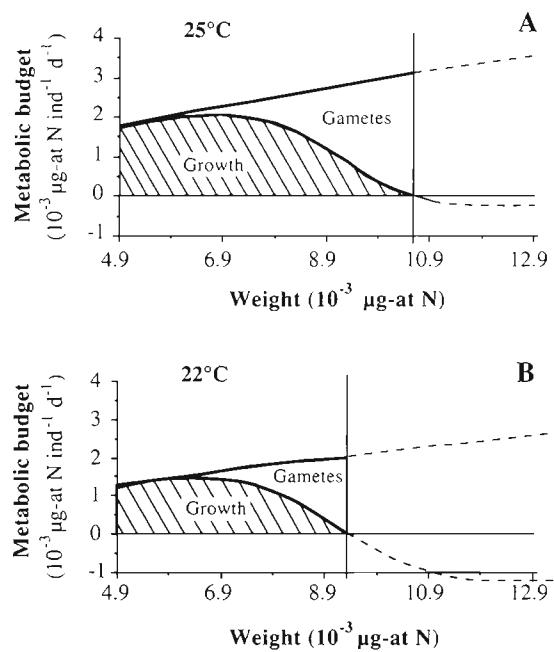


Fig. 5. Transition of budget investment from growth to reproduction as a function of copepod weight. When growth is zero, the animal's weight stops increasing and the egg-laying rate is constant. Such a representation enables a greater egg-laying rate when the budget increases (here under the effect of temperature). (A) 25 °C; (B) 22 °C

model, the transfer rate from one stage to the next (i.e. moulting) depends first of all on weight (Fig. 3J). We suppose that the animals can moult from stage i to stage $i+1$ only after having reached a critical weight X_i (function f_{10}). On the other hand, moulting also depends on the physiological condition of the organisms, and we assume that the material budget provides a good indication of these conditions (function f_{11}). As the moulting rate is not immediately influenced by variations in external patterns we used an average value of the instantaneous budgets for the hours immediately preceding moulting (Fig. 3K), which represents accumulated energy or an energy deficit, as explained in Nival et al. (1988).

Egg-laying rate depends directly on the matter invested for reproduction at any time (Fig. 3L). The eggs are assumed to have the same weight, to be physiologically equivalent, and without any phenomenon of ageing or loss of ability to hatch. Consequently, the hatching rate (Fig. 3M) is considered to be the inverse of embryonic duration, controlled by temperature (McLaren et al. 1989).

Regarding simulations, we will discuss the influence of the 3 underlying hypotheses on the functioning of population dynamics and their links with physiological processes.

SIMULATIONS

The simulations presented here complement those given by Carlotti & Sciandra (1989) and the coefficient values remain unchanged (see their Table 3). The system of differential equations is solved by a fourth-order Runge-Kutta numerical integration with a time step of 1 h.

Time course of processes as a function of age of individuals within a stage

Fig. 6 shows the dynamics of the developmental stages of a *Euterpinia acutifrons* population beginning with 100 eggs, in optimal conditions (22 °C temperature, 8 $\mu\text{g-at N l}^{-1}$ food concentration), for the first generation.

The model can give at any time the rates of the biological processes and the values of state variables in each age class at every stage. Thus a considerable amount of information is obtained rapidly. We have therefore chosen to present the values of the main processes as a function of age within stage for only 2 successive stages. Fig. 7 shows the values of abundance, individual weight, and rates of ingestion, growth, mortality and moulting for each age class of naupliar stages 1 and 2 (NI and NII), at Days 1, 2, 3 and 4 (see Fig. 6).

Day 1

On Day 1, there are individuals in the first 4 age classes of NI and in the first 3 of NII. At the NI stage, the '0.75' age class (individuals hatched between '0.75' and '0.5' d) is the most abundant, first because fewer

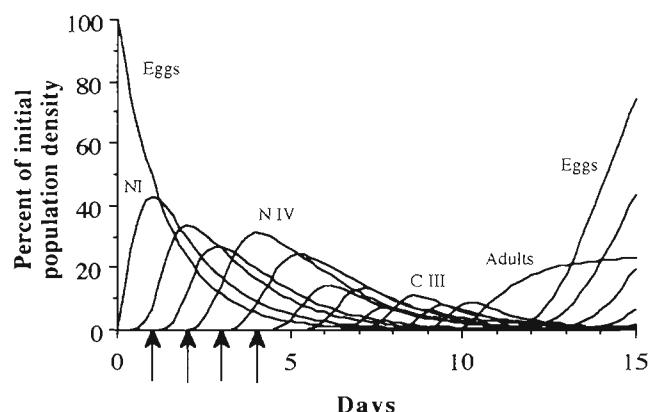
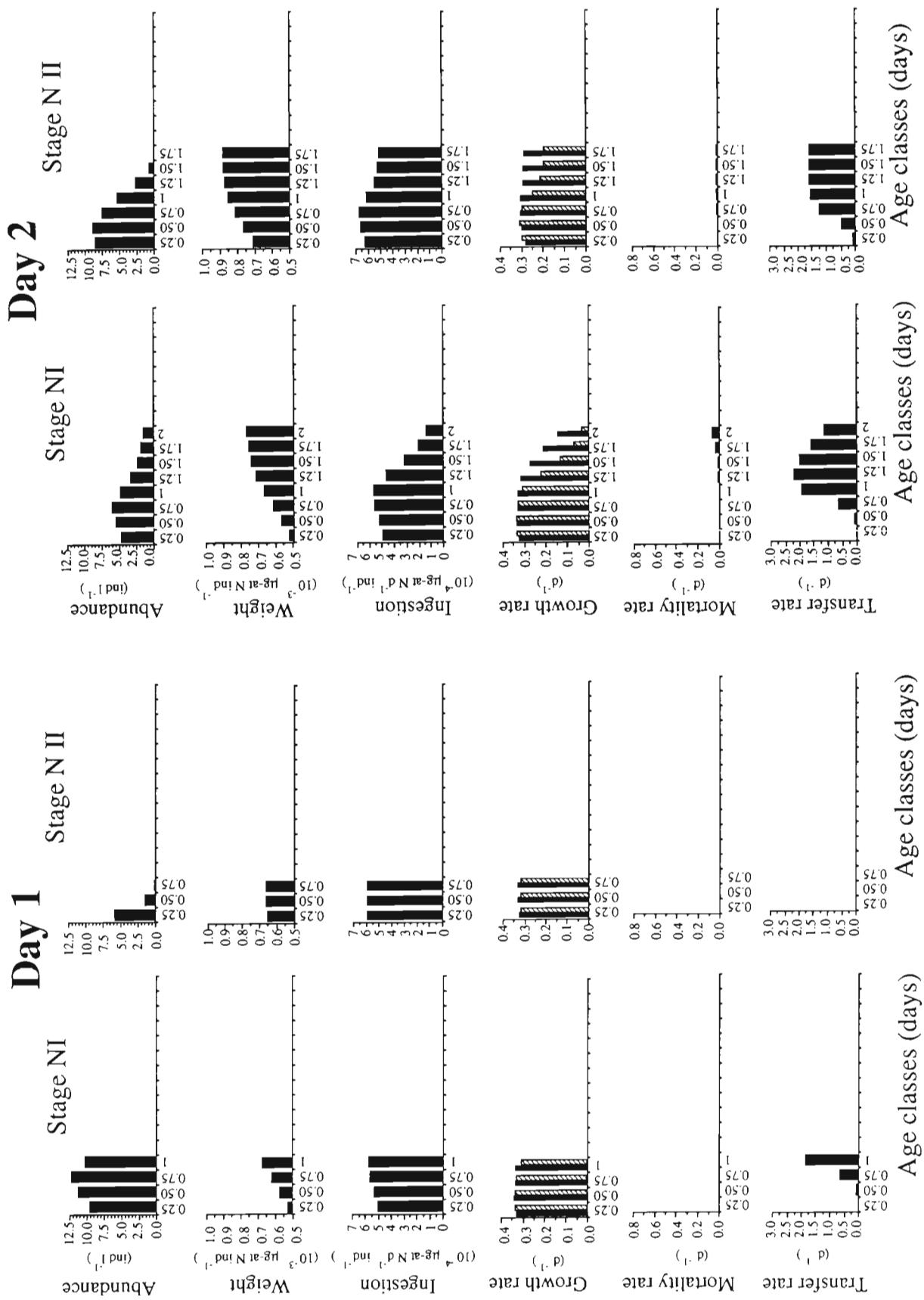


Fig. 6. *Euterpinia acutifrons*. Simulated time courses of stage abundances (eggs, 6 nauplii, 5 copepodites and adults) under constant temperature and food supply (22 °C and 8 $\mu\text{g-at N l}^{-1}$). The simulation starts with 100 eggs having identical weights ($0.5 \times 10^{-3} \mu\text{g-at N}$)



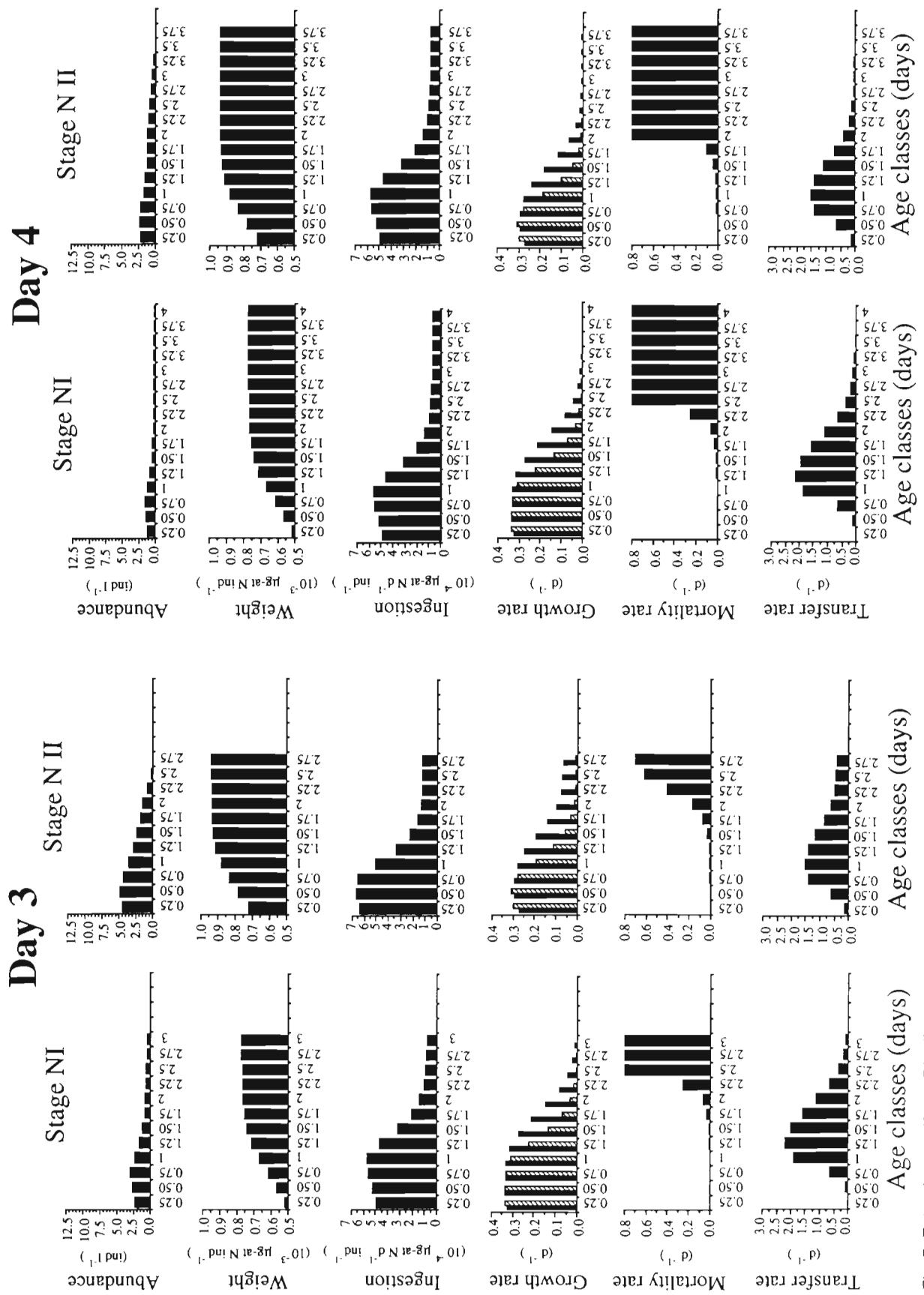


Fig. 7. *Euterpina acutifrons*. Distribution of abundances, weights, specific growth rates (black columns), cumulated specific growth rates (hatched columns), mortality rates and moulting rates in the age classes of stages NI and NII. These distributions are presented for Days 1, 2, 3 and 4 of the simulation shown in Fig. 9. See explanations in text

eggs were hatched in age classes '0.25' and '0.5' (see Fig. 7) and second because some individuals in age class '1' have already molted to stage NII (see transfer rate).

The copepods hatch at stage NI, having the same weight as their eggs (considered as constant), then start growing. Ingestion rate increases with age, but this can only be attributed to weight increase, since the trophic conditions are constant. As ingestion rate shows a negative allometric relationship with weight, the intrinsic growth rate decreases slightly, but still remains quite sufficient for the survival of the copepods, and mortality rates are minimal. In contrast to stage NI, age classes at stage NII have practically the same weights on Day 1. However, weights upon entering stage NII are different for each of these classes. An individual having molted precociously to stage NII (i.e. in the '0.75' age class) has a lower weight at molt than an individual which has just molted on Day 1. Nevertheless, most of the individuals of age class '0.25' in NII (just molted) issue from age class '1' of NI, so the weights of individuals in these 2 classes are similar.

In other words, the earlier the individuals enter stage NII, the lower is their weight, but the amount of matter which has not been gained in one stage is gained in another. This phenomenon also occurs for growth and metabolic rates. Mortality and transfer rates are zero because NII individuals weigh less than the critical molting weight and metabolic rates are high.

Day 2

For each time interval of 0.25 d, the individuals of a given class, with all their characteristics, transfer to the next age class. From Day 1 to Day 2, 4 new age classes appear at each stage (NI and NII), shifting the '0.25' to '1' age classes of Day 1 to '1.25' to '2'. This shows that abundances spread among age classes at stage NI, owing to egg-hatching and the molting of old individuals within a stage. Whereas there is a gain in weight with young age classes, the weights of the old individuals within a stage reach a maximum. These individuals have overlapped the critical molting weight and their growth and ingestion rates decrease rapidly, due to function f4 (see Hypothesis 3). Consequently, the oldest age classes show some mortality (see Hypothesis 1). The molting rate decreases more gradually, as it is related to the cumulative growth rate over the preceding hours (see Hypothesis 2), and not to the instant growth rate.

In stage NII, the most recently recruited age classes ('0.25' to '1') are more abundant than classes '1.25' to '2'. The total number of NII nears a maximum on Day 2 (see Fig. 6). The weight in the first class at stage NII ('0.25') has shifted towards an opti-

mal value, due to the new age structure in stage NI (compare Days 1 and 2).

Age classes '0.25' to '1' show a linear increase in weight. The first age classes ('1.25' to '2') reach the critical molting rate to stage NIII and their metabolic rates start decreasing. However, the growth rate stays very high and the transfer rate is maximum, whereas mortality is zero.

Days 3 and 4

The tendencies observed on Day 2 are confirmed: the abundances of age classes keep spreading, due to the fact that hatchings become scarcer. The weight histograms show the growth phase of the individuals as they enter a given stage, followed by their stabilization. When the organisms weigh more than the critical weight for molting to the next stage, their ingestion rate decreases to the minimum needed to balance the basic needs, and instant growth rate falls to zero (combination of Hypotheses 1, 2 and 3). As a result, the probability of death rises and the probability of molting (transfer to the next instar) diminishes more and more.

Time course of processes for a complete instar

Most of the time, laboratory experiments, conceived to determine biological processes, are conducted on whole populations. We were able to represent this with the model (all the age classes of a stage were grouped together and we obtained mean values for the processes). Fig. 8 shows the time courses of mean rates of ingestion, growth, mortality and molting. The curves are a combination of these various rates and of abundance values for age classes. As there are always some individuals in each age class, the mean rates decrease slowly.

Time course of processes for a population with a stable structure

A 100 d simulation of *Euterpinia acutifrons* population dynamics showed that variability in development of individuals results in a progressive distribution of the individuals among all stages (Fig. 9A). In a steady environment, therefore, the population shows a stabilization of its age structure. In other words, the frequencies of the various stages become constant. During the first 40 d, fluctuations in abundances marked the successive stages, owing to the initial condition (i.e. egg-laying was synchronous). Four generations are easily distinguishable, but after that are difficult to detect. Zurlini & Ferrari (1979) cultivated *E. acutifrons* over

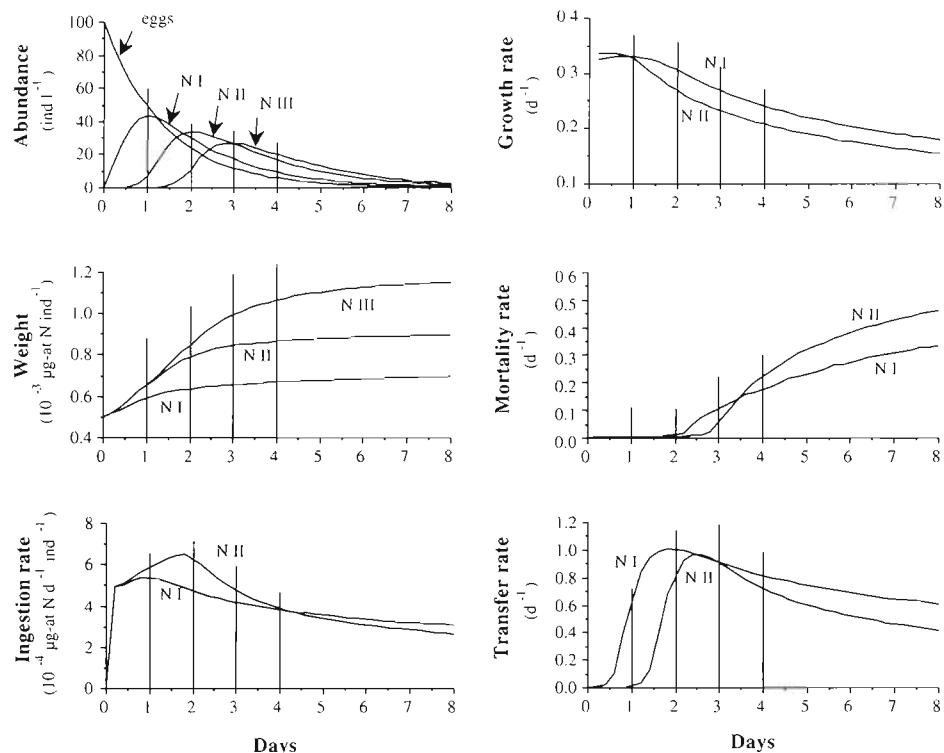


Fig. 8. *Euterpinia acutifrons*. Time courses of average values of abundance, weight, ingestion rate, specific growth rate, mortality rate and moult rate, at stages NI and NII. At any time, each curve corresponds to the average of age class values

several generations, at 18 °C, starting with 3 mature females. The population structure also stabilized after 60 d and at the fourth generation.

We focused on the time course of processes during the first 2 naupliar stages between Days 58 and 60, i.e. when the age structure of the population begins to stabilize (Fig. 10). With the model, we can take a 'snapshot' of all the processes in each age class of NI and NII. The profiles of metabolic rates and of moulting and mortality rates are

obtained as a function of age in stages NI and NII, and are similar to those already observed and commented on during the first days (see Fig. 7). At Day 60, the age structure is still the same, although absolute abundances have increased. Other variables and processes keep the same values as on Day 58 in all age classes.

The constancy of the age structure induces a constant rate of processes for each stage. Let $N_{i,j}(t)$ be the number of individuals of class j in stage i at time t, and $N_{i,j}(t+1)$

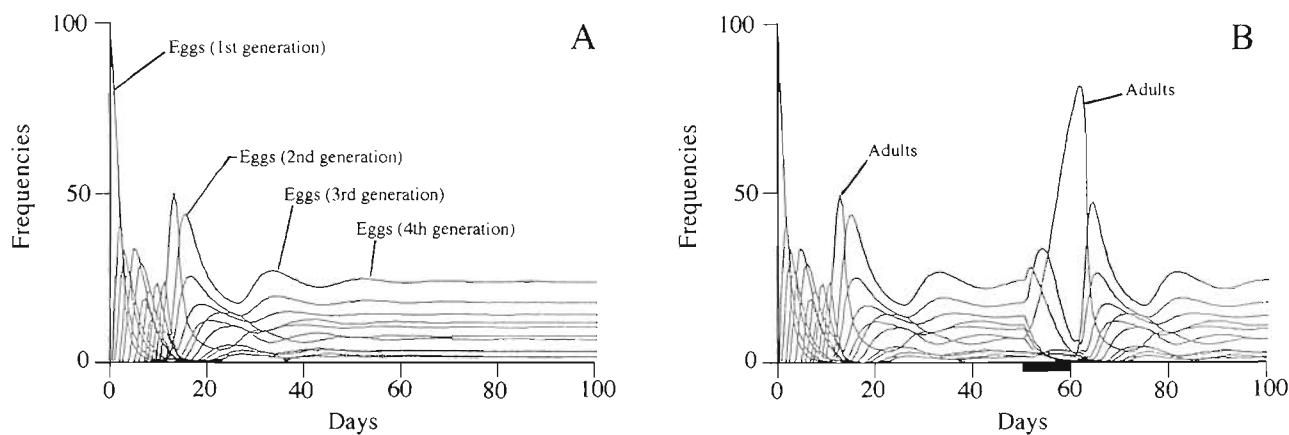


Fig. 9. *Euterpinia acutifrons*. (A) Time course of the stage structure (%) in the population over 100 d. Relative abundances of stages in the whole population become constant after the 4th generation, i.e. 60 d. Food and temperature values are those of the simulation in Fig. 6. (B) Effect of food deprivation (heavy horizontal line) between Days 50 and 60 on the population structure; the stability of the population structure is perturbed. *In situ*, such variability in external parameters would continuously perturb the population structure

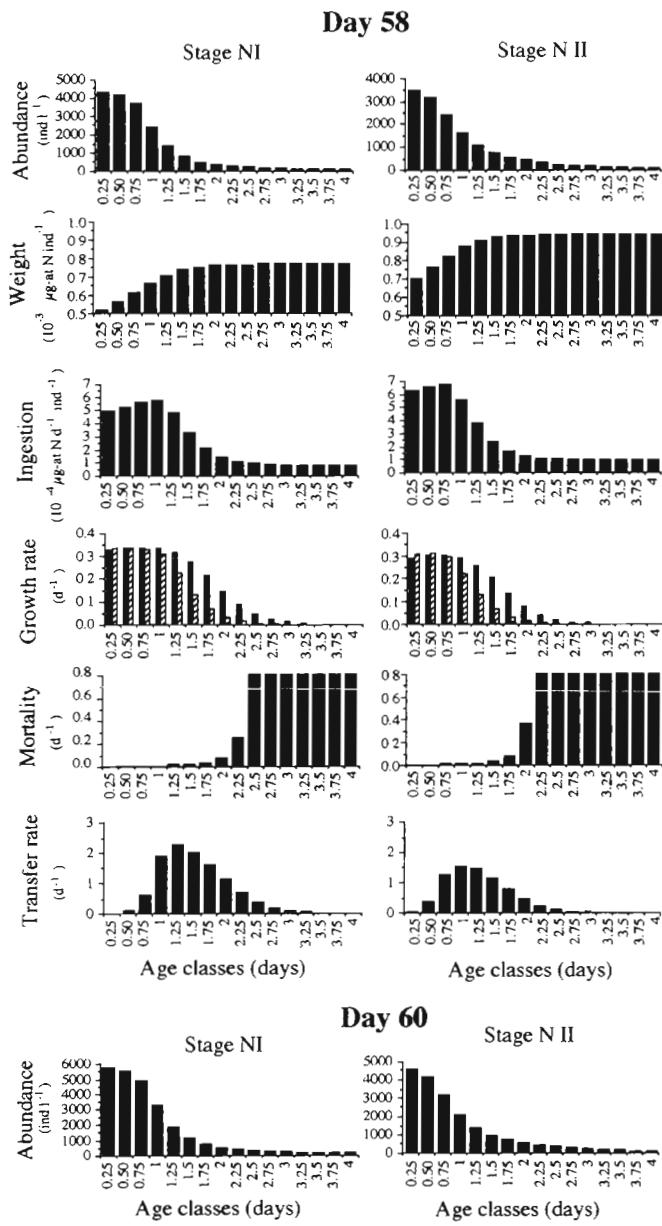


Fig. 10. *Euterpinia acutifrons*. Distribution of abundances, weights, ingestion rates, specific growth rates (black columns), cumulated specific growth rates (hatched columns), mortality rates and moulting rates among the age classes of stages NI and NII, at Day 58. Abundances at Day 60 are higher than at Day 58, but relative abundances of each age class are the same

the equivalent number at time $t+1$. Let P be a given biological process (e.g. ingestion, respiration) influenced by environmental variables (food, temperature) but not by demography, and let $P_{i,j}(t)$ and $P_{i,j}(t+1)$ be the values of this process P at times t and $t+1$. When the population structure is steady, $N_{i,j}(t+1)$ is proportional to $N_{i,j}(t)$ and $P_{i,j}(t)$ is constant, thus the average biological process P_i in stage i at time $t+1$ is expressed as follows:

$$\begin{aligned} P_i(t+1) &= \frac{\sum_{j=1}^n P_{i,j}(t+1) \cdot N_{i,j}(t+1)}{\sum_{j=1}^n N_{i,j}(t+1)} \\ &= \frac{\sum_{j=1}^n P_{i,j}(t+1) \cdot \alpha N_{i,j}(t)}{\sum_{j=1}^n \alpha N_{i,j}(t)} = P_i(t), \end{aligned}$$

where α is a constant. This clearly shows that, if environmental conditions remain constant, the average rates of processes at each stage are stable, due to the steady state of the population structure, but rates of individual processes vary according to the age class.

DISCUSSION

A process observed at the population level is the result of the physiology of individuals, which depends on external (food, temperature, etc.) and internal (ageing, etc.) parameters, and on the asynchronous development of individuals, a phenomenon linked with the dynamics of the population.

Thus the model can be used as a tool for interpreting the mean values of processes at the population level (Fig. 8) with the events at the individual level (Fig. 7). It describes the time course of the processes throughout an individual's life and the variability in the individual's growth. In optimal conditions, most of the individuals grow until they reach the critical moult weight at each stage, and then moult. Owing to function f_3 , these individuals show exponential growth throughout the development from egg to adult (see Fig. 4 in Carlotti & Sciandra 1989). They therefore do not show a decrease in ingestion. Some copepods do not moult immediately upon reaching the critical weight. Their growth is reduced, because of decreased ingestion (Hypothesis 3), and their development is delayed (Hypothesis 2), or they can even die (Hypothesis 1).

In sub-optimal conditions, only a few copepods display normal development, but for most of them, the moult is slower and more difficult. For them, growth may not be exponential and mortality rate is high. Thus the model explains an important experimental finding: why is it that exponential growth can be observed in optimum conditions (McLaren 1986) but not in limiting conditions (Miller et al. 1977)?

The significance of Hypothesis 3, which assumes a decreased ingestion when the copepod is about to moult to the next stage (function f_4), is supported by the model. Under favourable conditions, this decrease only lasts a very short time, after which most of the animals moult rapidly and resume normal feeding. On

the other hand, when conditions are poor, this process plays an important role. It prevents an abnormal weight increase in the organisms which do not moult and consequently increases their death rate as grazing decreases. For decapods, which are easier subjects for the study of moulting processes, it has been shown that ingestion stops during moult (Lasker 1966, Harpaz et al. 1987, Anger et al. 1989), because mandibular appendages and the exoskeleton, which is part of the digestive tract, are replaced. Anger & Dietrich (1984) even observed that ingestion decreases early in the intermoult phase, and they adjusted the maximal ingestion rate as a function of age, by means of a decreasing parabola (see also Fig. 1 in Anger 1990). Regarding copepods, some isolated observations of individuals close to moulting describe a stoppage of filtration and ingestion before and during the moult (Paffenhofer 1971, Harris & Paffenhofer 1976), but there has been no clear demonstration of this. It is perhaps difficult to show experimentally such a decrease in ingestion by copepods, since presumably the individuals are not synchronously influenced by it. The ingestion rate should therefore be measured continuously on isolated animals.

Thus, variability of development within a cohort can be explained by the model: some individuals develop at a maximum rate throughout their existence, and others delay development to a variable extent. This has been clearly observed in experiments (Carlotti & Nival 1991).

Among the variables shown in Fig. 8, the only one frequently found in the literature is transfer rate. This is in fact easy to determine experimentally, by taking individuals recently moulted into a stage and measuring the time until they moult to the next one. The moulting rates obtained here by simulation are similar to experimental results (Sulkin & Van Heukelom 1986, Carlotti & Nival 1992). Thus the model suggests a deterministic explanation for the shape of this curve. The transfer rate depends on the weight of organisms and their physiological state (Hypothesis 2). The ascending part of the curve is the consequence of a rapid increase in the probability of moulting beyond the critical moulting weight. The decreasing portion is the result of a progressive loss of the ability to moult, which has a physiological basis (ageing). If an individual stays too long in a stage, its growth rate decreases (due to Hypothesis 3), its weight does not increase, and the probability of dying increases (due to Hypothesis 1).

Under such conditions, from the modeller's point of view, it is not necessary to have a large number of age classes at each stage (see Fig. 2), and it is quite justifiable to group in a last age class those individuals with similar characteristics which will play no further part in the development of the population.

At any time, the population structure has an influence on the overall mean value of processes or variables (weight, etc.), which makes it difficult to obtain information on these processes and variables at specific levels. The only way to improve our knowledge of the processes is to observe the organisms individually, or a very closely clustered cohort, i.e. to disturb the steady state and study the dynamics of a cluster of individuals.

However, processes or variables inaccessible to the experimenter may exist, such as a decrease in ingestion (f_4), because their fluctuations are hidden by other processes, or even by individual variability. They are then omitted from the conceptual schemes drawn from experimentation. A mathematical model can offer conceptual diagrams of functional relationships which govern growth and development phenomena and can test them.

The pattern suggested by the model for mortality rate as a function of age seems quite new. It results from the relationship between mortality rate and growth rate (Hypothesis 1) and from the decrease of ingestion (Hypothesis 3) beyond the critical moulting weight. We have confirmed experimentally the increase of mortality with age within stage (Carlotti & Nival 1992).

When the development of a population under optimal conditions of temperature and food is simulated (see Fig. 9A), the percentages of the abundance of individuals in the various stages tend towards steady values, and the population structure is stabilized. If a temporary low concentration of food is simulated (Fig. 9B), the population structure is immediately disturbed; afterwards it tends to return to a steady structure once again. In the marine environment, this sort of disturbance is very frequent, and the population cannot be represented by a mean individual with constant rates of biological processes (see Båmstedt 1988).

Most ecosystem models use constant values and do not take into account population dynamics, which have a strong influence on the dynamics of the ecosystem (Hassel & May 1985). Yet it is necessary to take into account the population level, between the individual and the ecosystem, as has been pointed out previously [Marine Zooplankton Colloquium 1 (1989); see also De Angelis (1988)]. The difficulty lies in setting up the real rules connecting the individual, the population and the ecosystem. Our model, which couples individual growth and population dynamics, can simulate values of processes steady in time if the external conditions are also steady, though potentially it maintains the ability to express the internal dynamics of the system if the environment is suddenly disturbed.

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