
Study and modelling of the development of *Euterpina acutifrons* (Copepoda: harpacticoida)

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Abstract. The larval development of populations initially composed of nauplii N1 of *Euterpina acutifrons* (Copepoda: Harpacticoida) is studied in the laboratory. A first experiment in which temperature is the only varying parameter allows an assessment of inherent variability of development. A simple mathematical model then accounts for the effect of temperature on development. We find residence times to be almost identical for all developmental stages, and higher mortality rates in the case of stages N6 and C1. The model also accounts for latency times observed in the development of populations including larval stages. A second experiment, run at constant temperature, shows that a deficient food supply increases the average residence time of early stages, as well as their variance. Data obtained on a population bred in tanks under unregulated trophic and temperature conditions show that the variation with time of the stage composition of the population modulates the effect of external factors on the growth of the population.

Introduction

The dynamics of a population may be expressed by a few parameters, such as the number of larval stages, the residence time and death rate for each stage, the generation time, the sex ratio and the hatching rate. Most methods used in this field arise from the study of insect populations. The highly synchronous character of insect development, as well as the relative ease of sampling allow one to obtain good chronological series which in turn can be analysed by simple methods (Southwood, 1966), whether for death rate per stage (Richards and Waloff, 1954; Richards *et al.*, 1960; Dempster, 1961) or for recruitment per stage (Dempster, 1956). According to Rigler and Cooley (1974), methods designed for insect populations are not necessarily good for zooplankton and require additional data: authors assume that the rate of natural development is the same as that observed in the laboratory. All factors affecting development must therefore be measured in the field and controlled experimentally. With a critique on methods elaborated by Comita (1972), Rigler and Cooley (1974) describe a method for calculating average residence time per developmental stage on the basis of the field data (see also Hairston and Twombly, 1985). Miller *et al.* (1984) have observed in the laboratory the development of stage C4 of freshly collected copepods, assuming that the development rate which they observe is the same as that in the field (Burkill and Kendall, 1982). Complications are introduced by the presence of individual variability in residence times which causes a gradual loss of synchrony in natural populations.

We have chosen to study in the laboratory the dynamics of a population of copepods whose development may be easily controlled by acting separately on temperature and food supply. Although it is in general difficult to extrapolate directly parameter values from a laboratory study to the natural environment, the basic processes governing both situations must be similar, and laboratory studies may increase our understanding of the marine environment.

The study of the population dynamics requires frequent sampling and large numbers

of animals to reduce the effect of individual variability on population characteristics. Our large breeding tanks for the harpacticoid copepod *Euterpina acutifrons* provide us with sufficient numbers of mature females at the same time to obtain large, synchronized populations. Frequent and regular sampling is performed during the development of these populations under different conditions of temperature and food supply. A simple deterministic model developed from this data allows prediction of temperature effects under conditions in which food supply is not limiting.

Methods

First experiment: constant food supply, variable temperature

The aim of the first experimental phase is to obtain large numbers of stage N1 individuals of *E. acutifrons* in a short time. Approximately 700 gravid females from a breeding tank are put to spawn in 3 l of a suspension of the alga *Phaeodactylum tricornutum* at a concentration of 300 000 cells ml⁻¹, more than sufficient to induce a maximal hatching rate (Sciandra, 1982). The eggs are not spawned freely into the surrounding medium, but instead carried in a sac by the female until the end of embryonic development, when the sac tears open and the first nauplius stage N1 is released. The hatching rate is estimated from the population of N1 nauplii, assuming all eggs have developed. Table I shows the evolution of average hatching rate with time measured ever 12 h between the time of removal of the females from the breeding tank and 5 days later. At this time, the hatching rate is close to the maximum rate obtained in other studies in our laboratory, namely 10–12 eggs female⁻¹ day⁻¹. The nauplii which have appeared in the course of the last 12 h are isolated and placed in a suspension of 8 l of *P. tricornutum* at 250 000 cells ml⁻¹. This constitutes $t = 0$ for the second phase of the experiment. The concentration is sufficient to ensure maximal ingestion rate in *E. acutifrons* (Sciandra, 1982) whose development in this experiment will be assumed to be independent from food supply. Four times a day (at 3, 9, 15 and 21 h), the population is sampled by removing a known volume of the suspension (100 ml from day 1 to day 14, 50 ml later) after a gentle mixing of the culture to ensure homogeneity. The phytoplankton concentration is measured with a HIAC particle counter, and increased to its original level if necessary. The drop in volume caused by sampling is not compensated to avoid dilution of the population. An increasing proportion of the medium

Table I. Evolution of the average egg-laying rate of 700 gravid females of *E. acutifrons* isolated from a breeding tank and put to spawn in 3 l of a suspension of the alga *P. tricornutum* at a concentration of 300 000 cells ml⁻¹.

Time after isolation (days)	Average egg-laying rate (eggs female ⁻¹ day ⁻¹)
2.0	1.0
2.5	1.6
3.0	2.7
3.5	3.3
4.0	2.5
4.5	6.5
5.0	9.8

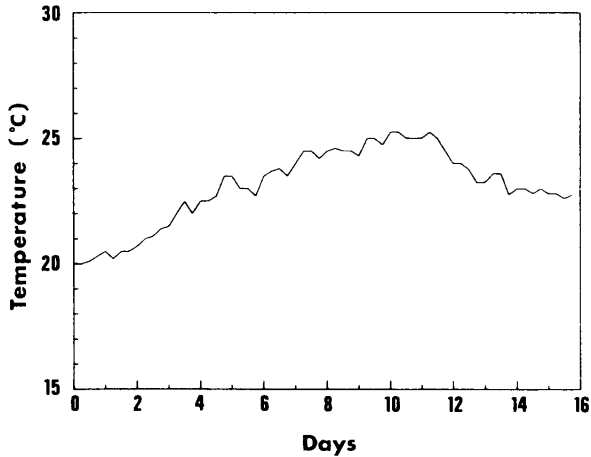


Fig. 1. Temperature during first experiment.

is thus sampled, the only changing parameter being the surface:volume ratio of the container. All developmental stages present in the samples are identified (Yassen, 1985). Number of individuals sampled is around 80 initially and around 25 by day 10. Given that copepod distribution over stages increases during development, estimates of numbers in later stages must contain higher Poisson error terms than earlier ones. Ten days after time 0, the medium is renewed. Water temperature is not controlled during the experiment (see Figure 1).

Second experiment: constant temperature, effect of food concentration

N1 nauplii are obtained as before, but hatching is allowed to carry on for 16 h instead of 12, leading to a less narrow distribution of ages at the beginning of the second phase of the experiment. The nauplii thus obtained are distributed at random between two batches of equal size at $t = 0$. One batch is fed with 200 000 cells ml^{-1} of *P. tricor-nutum* (batch A) and the other with 30 000 cells ml^{-1} (batch B). The conditions of sampling and food supply readjustment are the same as above. Temperature is maintained within 0.1 degrees of 22°C.

Results

First experiment: constant food supply

At time $t = 0$, the population is composed of N1 individuals aged between 0 and 12 h. Figure 2 shows that 1 day later, the majority of individuals has begun to moult, and that by 24 h all have become N2. The N2 population peaks when the recruitment is balanced by mortality and passage to N3. The same process applies to all subsequent stages and dictates their successive appearance in the course of development. Adults are obtained from day 8, the first eggs are visible on the females from day 10, and the first nauplii of the second generation appear on day 12.

It should be noted that the duration of the first three stages is short by comparison

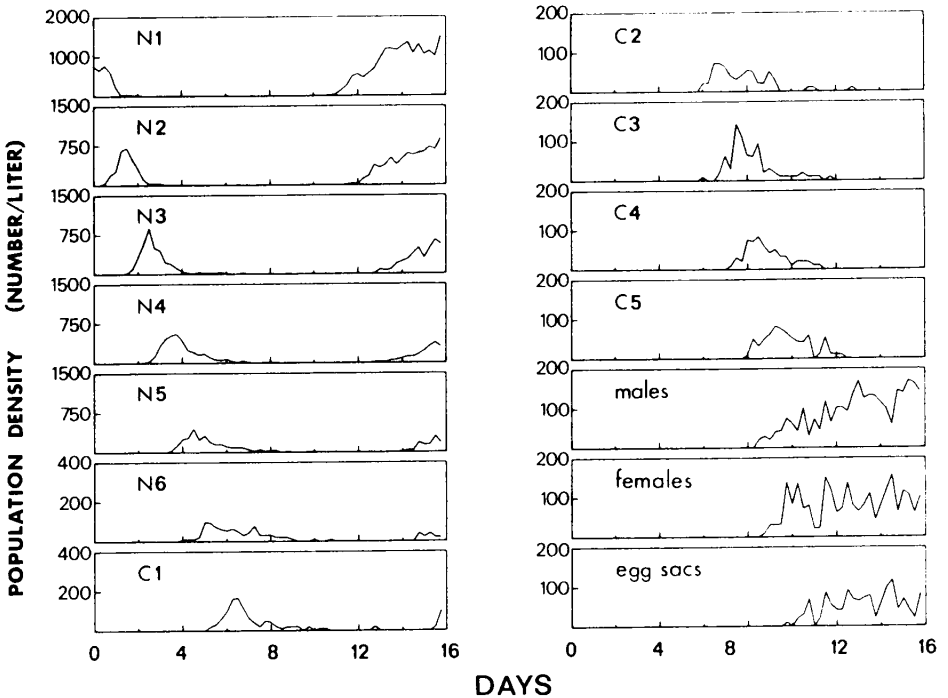


Fig. 2. First experiment: development of *E. acutifrons* through six nauplius stages, five copepodite stages, male and female, with variable temperature and constant food supply.

with the 12-day generation time, which suggests that developmental rates are homogeneous. This is not surprising, since crustacean development is precisely determined and timed. Clearly, if the N1 were all exactly of the same age at the beginning of the experiment, the transient period corresponding to the decrease in N1 and increase in N2 would be shorter still. It is worth noting that this period, ~12 h in duration, equals the time interval during which females have been allowed to spawn. The behaviour of the population is therefore partly explained by the variability in ages at the beginning of the experiment.

It is also clear that during development, peak amplitudes of different stages decrease progressively, while the curves broaden increasingly. Death causes a fall in total population, and individual variation is responsible for the broadening. Animals which, for one reason or another (genetics, competition) take longer to moult than others, reside somewhat longer in each stage and thus accumulate a delay. The dynamics of the population are therefore characterized by an asymmetry previously observed by Bermans (1981) in *Tisbe furcata*, the straight part of the curve being due to late-arriving individuals. This asymmetry is the experimental manifestation of the variation inherent in individual properties and life histories. With time, a 'sieving' of individuals takes place, the terminal part of the curves corresponding to individuals whose behaviour deviates maximally from average.

The peak of stage N6 is much lower than that of N5, which suggests that the last nauplius stage has a higher death rate. A single experiment such as this one does not

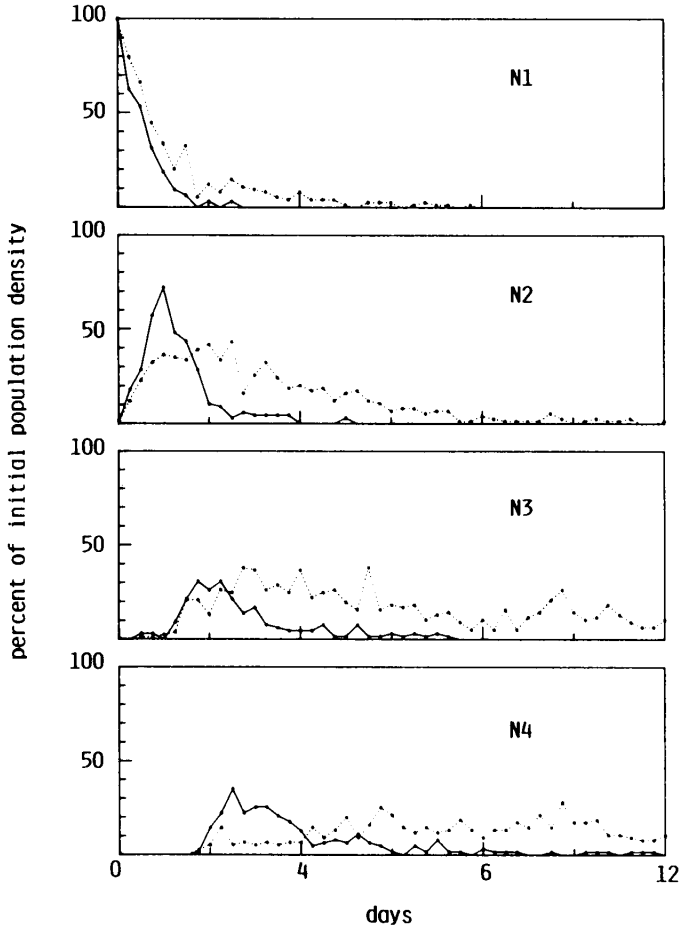


Fig. 3. Second experiment: development of *E. acutifrons* at constant temperature and at two different concentrations of *P. tricorutum*: —, 200 000 cells ml⁻¹; ·····, 30 000 cells ml⁻¹.

allow one to state with certainty that a high death is characteristic of this stage. However, D'Apolito and Stancyk (1979) report the same observation from life tables of *E. acutifrons* in its natural environment.

Second experiment: constant temperature

The experiment was principally carried out on naupliar stages. Figure 3 clearly shows that the nauplii exposed to a lower concentration of food have the longest residence times. Stage N2 individuals, for example, are present in batch B at $t = 2.5$ days, while they are absent from batch A after $t = 1.6$ days. For this batch, the peak in N2 takes place at $t = 0.7$ days, while it lies around 1.2 days for batch B. It is nevertheless remarkable that the times of first appearance of a given stage are the same for both batches. There exist in both batches animals able to develop at the fastest speed, but the lagging population is greater when food supply is deficient. A limiting food supply thus reduces average development rate by increasing individual disparities. It is likely

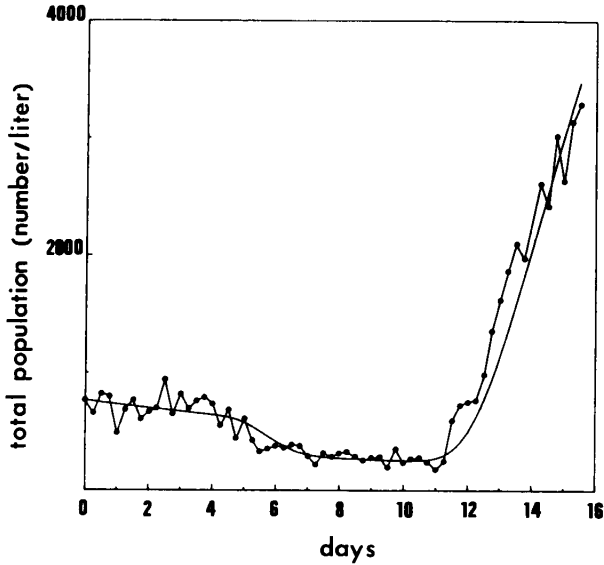


Fig. 4. First experiment: total population of *E. acutifrons* during development. Dots, experimental data; line, simulation.

therefore that food supply acts both on average residence time and on its variance. It should be noted that this influence manifests itself right from the beginning of development, which leads one to suppose that even the earliest stages of this species are able to feed.

Mathematical model

We propose a mathematical representation of development by a deterministic model. We consider here that development only depends on temperature and is independent from the available food supposed not limiting. For a small time interval dt , the variation dN_i of the population of a given stage N_i depends on recruitment, death, and transfer to the next stage. If the population is sufficiently large to smooth out all individual variation, we can write:

$$dN_i/dt = t_{i-1}.N_{i-1} - (t_i + d_i).N_i$$

where t_i is rate of transition from state i to stage $i+1$ and d_i the death rate. For the first stage N_1 , the recruitment is ensured by hatching and for adults N_{12} the only loss is due to death.

$$dN_1/dt = p_0.r.N_{12} - (t_1 + d_1).N_1$$

$$dN_{12}/dt = t_{11}.N_{11} - d_{12}.N_{12}$$

p_0 being the hatching rate and r the sex ratio. If a sex ratio r of 0.5 is assumed, the eggs are produced by half the adults during their entire life.

Wroblewski (1980) used this type of differential equation to account for the dynamics of *Acartia clausi* in an ecosystem model. This formulation requires more extensive approximations to be made, since adults appear at the beginning of the simulation though

Table II. Parameter values used in the simulations.

Stage	d_i (day ⁻¹)	a_i (day °C ⁻¹)	L_i (day, at $T = 20^\circ\text{C}$)	P_o (eggs female ⁻¹ day ⁻¹)
N1	0.05	450	1.20	
N2	0.05	450	1.20	
N3	0.05	450	1.20	
N4	0.05	450	1.20	
N5	0.05	450	1.20	
N6	0.50	450	1.20	
C1	0.50	450	1.20	
C2	0.05	450	1.20	
C3	0.05	450	1.20	
C4	0.05	400	1.06	
C5	0.05	400	1.06	
Adult	0.03	1600	4.25	10.0

there are only eggs initially (see Figure 4 of Wroblewski, 1980). The time required for larval and juvenile development before the appearance of the second generation (see Figure 2) cannot therefore be reproduced by this model. The inadequacy arises from the fact that, after the k th integration step, the product $t_i \cdot N_i$, ($i = k$) is no longer equal to zero. Individuals appear in stage N_{k+1} after a time equal to k times the integration step.

To get around this difficulty, one must assume that the animals can move on to the next stage only after having stayed in one stage for the duration necessary to their development. This can be achieved by subdividing the development time of stages in age classes of a duration close to the integration step. Only animals which have reached the last age class may moult and move on to the next stage. Davis (1984) uses the same modelling technique in a finite-difference equation system coupled to a water-circulation model.

It will also be assumed that the females will lay eggs after the time necessary to their maturation. In this deterministic model, it is assumed that all individuals in an age class have identical behaviour. The system of differential equations remains the same: state variables are age classes instead of stages.

First class ($j = 1$), first stage ($i = 1$):

$$dN_{1,1}/dt = p_0 \cdot r \cdot N_{n,q(n)} - (t_1 + d_1) \cdot N_{1,1}$$

First class ($j = 1$), stages $i = 2, n$:

$$dN_{i,1}/dt = t_{i-1} \cdot N_{i-1,q(i-1)} - (t_i + d_i) \cdot N_{i,1}$$

Other classes ($i = 1, n$; $j = 2, q_i$):

$$dN_{i,j}/dt = t_i \cdot N_{i,j-1} - (t_i + d_i) \cdot N_{i,j}$$

Mature adults ($i = n$; $j = q_n$):

$$dN_{n,q(n)}/dt = t_n \cdot N_{n,q(n-1)} - d_n \cdot N_{n,q(n)}$$

with p_0 egg-laying rate; $N_{i,j}$ number of individuals in class j of stage i (number l^{-1}); $i = 1, n$ (n is number of stages); $j = 1, q_i$ (q_i is number of class in stage i); t_i transition

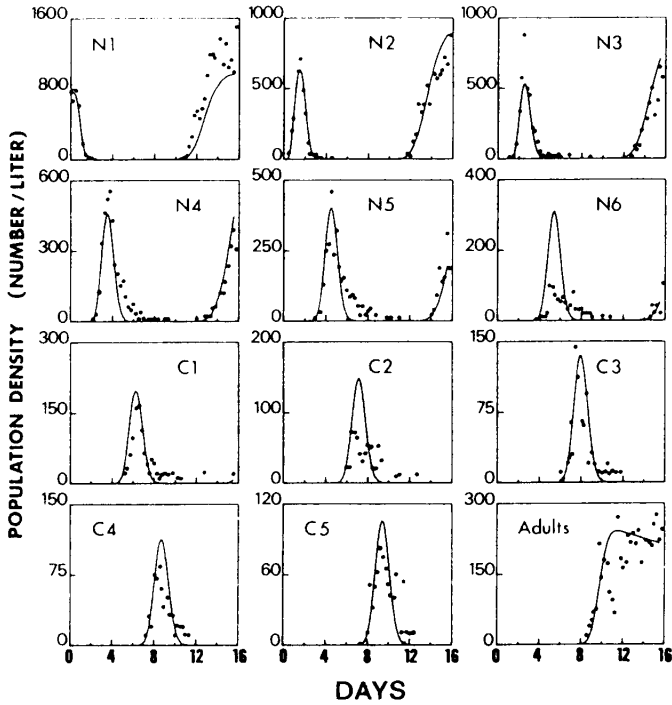


Fig. 5. First experiment: developmental stages of *E. acutifrons* during development. Dots, experimental data; lines, simulations.

rate from class j to class $j + 1$ in a class i (day^{-1}); d_i death rate in stage i (day^{-1}); r sex ratio.

The transition rate from one age class to the next is inversely proportional to the residence time l_i in a given class: $t_i = 1/l_i$ with $l_i = L_i/m_i$ and $L_i = a_i \cdot T^b$ where L_i is the residence time of stage i at temperature T and m_i the number of classes in this stage.

The influence of temperature on development speed is expressed by the formula suggested by Heip (1974), which requires fewer coefficients than the expression derived by Belehradek (1935) found in McLaren (1963). The negative b coefficient which describes the degree of influence of temperature on development has been determined for *E. acutifrons* by Heip and Smol (1976) from data reported by Haq (1972). This coefficient is a characteristic of a given species, and is constant for all stages. We shall assume that a_i can vary from one stage to the next.

Simulation

The system of differential equations is solved by fourth-order Runge–Kutta numerical integration with a time step of 0.5 h. The number m_i of age classes per stage is set to 15 (between 10 and 15, results differ little, and not at all for more than 15).

The vector of initial population values is set to zero at the start of the simulation for all stages and age classes, except for the nauplii which are evenly distributed among

the first eight age classes of stage N1. The program for the calculations is written in Fortran and run on an IBM 3033.

Parameter values are shown in Table II. The parameter set was obtained by trial and error until the fit between simulations and chronological series was satisfactory. a_i was first changed so that stage $i + 1$ appears at the appropriate time. Afterwards, both this parameter and especially death rate d_i were changed to adjust the height of the i th stage peak. Figure 4 shows that the high death rates given to stages N6 and C1 produce a distinct inflexion on the curve during the transition from nauplius to copepodite. The simulated series which gives a good fit to the experimental results clearly shows the existence of three developmental periods with differing death rates, the higher corresponding to morphological changes (D'Apolito and Stancik, 1979). Adults which no longer moult have the lowest death rate.

As is apparent from Figure 5, the phases of appearance of the individuals in successive stages of the simulated series match the experimental ones. The amplitude of the peaks is well adjusted for most stages except for stage N6 for which the model predicts an abundance twice as large as the experimental value. The fact that the time evolution of the following stages are well predicted by the model suggests that this discrepancy may be due to imperfect sampling or identification errors, stages N5 and N6 being very similar.

The terminal part of the population curves is not well reproduced by the deterministic model which assumes an equal transition probability from age class j to age class $j + 1$ for all individuals. The simulated curves show little dissymetry.

The coefficients a_i are very similar for all larval stages, indicating an isochronous development [Haq (1972); Neunes and Pongolini (1965) quoted in Bergmans (1981)]. The high a_i value for the adults reflects the time necessary for females to lay eggs and for the latter to hatch (gamete maturation, encounter with a male and spermatophore fixation, fertilization, egg-laying and embryonic development).

Discussion

The methods described in the Introduction are useful to extract information from data acquired either in the natural milieu or in laboratory experiments. This information is commonly displayed as a life table for the species under study.

Other authors have chosen to manipulate this information by subjecting it to mathematical treatments of varying sophistication. Manly's (1974) model, initially conceived to describe the development of insects through larval stages, is an example of a purely descriptive model, which assumes a normal distribution of transition probabilities from one stage to the next. Aside from this biological assumption, which has not in any event been satisfactorily verified (Stinner *et al.*, 1975), the model makes no further assumptions about the process itself. In view of its simplicity, it is only applicable to a single generation with a death rate identical for all developmental stages.

Parslow *et al.* (1979) take this approach further and derive two models from it: the 'lag-Manly', and the 'lag' models, the first being usable only for one generation. They also describe a 'linear transfer model' which bears some analogies to the mathematical model which we have described. These models have as an aim the determination of population parameters by matching the simulation to the experimental data. Sonntag

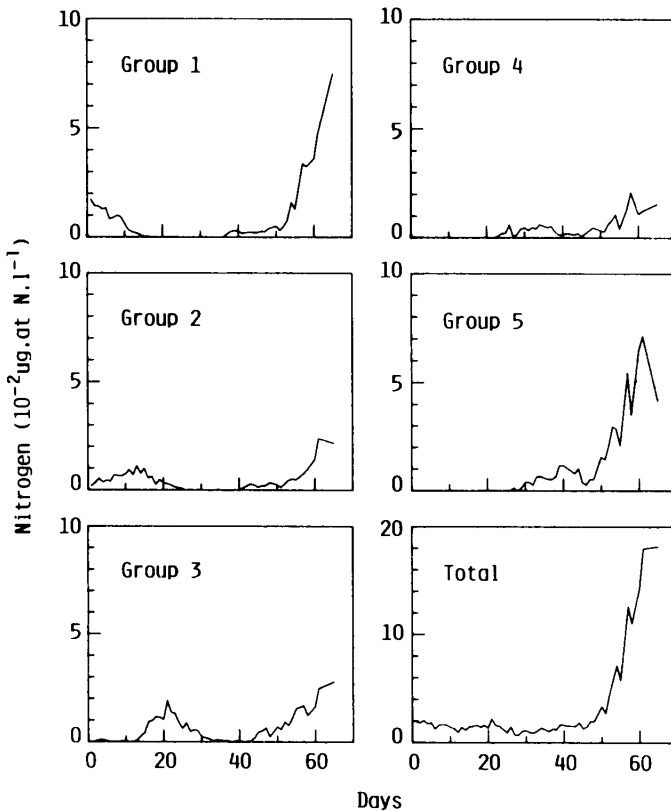


Fig. 6. Evolution of a population of *E. acutifrons* bred in a tank. Group 1: nauplii 1, 2 and 3; group 2: nauplii 4, 5 and 6; group 3: copepodites 1, 2 and 3; group 4: copepodites 4 and 5; group 5: males and females.

and Parslow (1981) use this approach to estimate these parameters and evaluate secondary production of *Paracalanus parvus* in an isolated mass of water (CEPEX). In the same way, Matthews *et al.* (1978) use Manly's model to determine stage-by-stage death rates of *Calanus finmarchicus* in the Korsfjorden (Western Norway).

Our model also allows the determination of typical parameters of population dynamics. We have found it easy to adjust the simulation to the experimental data without resorting to identification methods which tend to give biologically extreme values of coefficients. This empirical approach has led us to assign a high death rate to stages N6 and C1 which may be due to the morphological changes, and otherwise to assume isochronous development (Miller *et al.*, 1977). It remains of course to be proven that the high observed mortality is not an experimental artefact.

The chief interest of this model, however, lies in its analytical representation of population dynamics. The use of differential equations allows us to represent model parameters by continuous functions expressing environmental influences. This presents two advantages: firstly, the model is no longer merely descriptive, but instead embodies mechanistic assumptions susceptible to independent experimental test, such as the influence of temperature on development speed, differential death rate as a function of

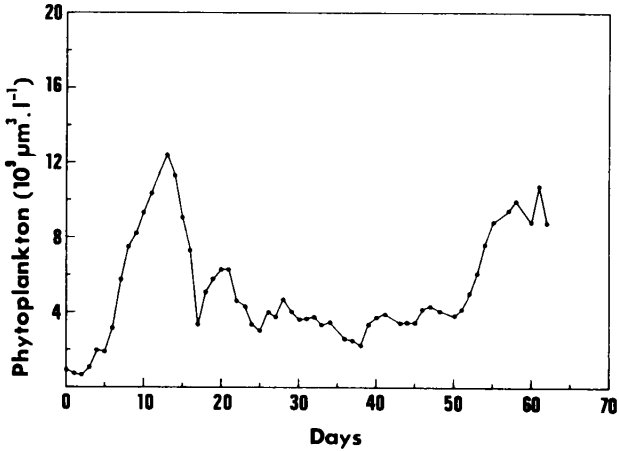


Fig. 7. Evolution of the total particulate volume (principally *P. tricorutum*) in the breeding tank of *E. acutifrons*.

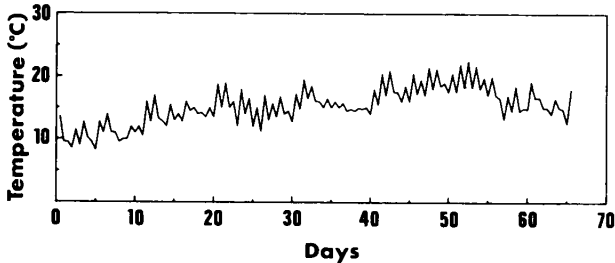


Fig. 8. Evolution of the temperature in the breeding tank of *E. acutifrons*.

developmental stage, variations in egg-laying rate, etc. Secondly, it allows a synthetic approach to data obtained in variable environments. For example the influence of temperature was studied in the first series by letting temperature vary naturally with time instead of repeating the experiment at several fixed temperatures. Only a continuous model allows quantitative parameter estimation from this type of experiment.

Nevertheless, it is clear that a deterministic model can only give a limited match to experimental data, since it fails to take into account the underlying demographic randomness [in the sense of May (1973)]. As an example of this approach, we may mention the stochastic representation of development through various stages by Read and Ashford (1968), and the Monte-Carlo approach to effect of temperature on rate of development of insect populations (Hardman, 1976). This author compares deterministic to stochastic models and concludes that the latter, though more effective, are only feasible for small populations since they require independent calculation of the transition probability for the change of age class or death event for each individual in the population at each time iteration. As a result, this type of model becomes unwieldy in use, and difficult to incorporate into a larger model using other biological variables (Sciandra, 1986) or physical processes (Wroblewski, 1980; Davis, 1984).

The developmental dynamics of a given copepod species, for example, clearly indicates the existence of time variation in its trophic relationships due to changes in differential preferences of different stages for particulate matter (Nival, 1976; Nival and Nival, 1976). Only by considering as a whole all interactions of all stages at a given time does it become possible to account for the instantaneous growth rate of the population. As an example, one may mention chronological series obtained in large-volume tanks (Sciandra, 1982). Figure 6 illustrates the dynamics of *E. acutifrons* in which all stages have been grouped together in order to transform their counts into nitrogen weights. Figure 7 gives the total mass of particulate matter (principally *P. tricornutum*) as a function of time. Figure 8 gives temperature during the same period. If one looks at the total zooplankton mass, there is a striking discontinuity around day 50, separating a phase of steady population biomass from a phase of population increase, indicating that the intrinsic growth rate in biomass is not constant. The stage composition provides an explanation for this phenomenon: at the beginning of the series, only early larval stages (nauplii N1 to N5) are present. The weight gain is limited to individuals introduced at the start of the culture, and whose number decreases by natural mortality. After day 35, the individuals of the second generation begin to appear, but one has to wait until day 45 for the population to increase markedly. From this time, trophic conditions (Figure 7) favour egg-laying and the increase in temperature (Figure 8) accelerates development. One sees on the other hand (Sciandra, 1982) that the first egg sacs appear after day 40, while females and males are present from day 30. This effect confirms the influence of temperature and food supply on reproduction.

It is therefore clear that the temporal variability of forcing variables (here temperature and food supply) acting on *E. acutifrons* and the evolution in stage composition which these cause are together responsible for the changes in the rate of increase in population. The growth of a population thus depends on its age composition, and it would be of interest to describe analytically their relationships to the environment. Every time the environment causes a synchronization of the population, for example if egg-laying is stopped for a time, latency times as described above may develop.

If this is not the case, the variability in larval development times will lead to a stable distribution of stages, by overlapping of successive cohorts. In this situation, the population can be represented by an 'average individual' and its growth will be unrelated to internal dynamics, and will depend instead on global mass.

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