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Moulting and mortality rates of copepods related to age within stage: experimental results

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ABSTRACT: Patterns of copepod mortality and moulting related to age within stage, described by a mathematical model of population dynamics, were tested experimentally on *Centropages typicus*. Individuals of the same brood were observed separately at regular time intervals from copepodite I to adult, sorted as living or dead, and checked for stage. The results obtained for the pooled copepods enabled a reconstruction of the mean durations of each stage for the whole cohort, and to interpret them with respect to the information acquired for each individual. Probabilities of moulting and dying were not constant but depended on age within stage. In all copepodite stages, the distribution of durations in relation to age within stage was asymmetrical around a mode. A minimum mortality rate (0.01 to 0.02 d^{-1}) was present before the mode of the duration distribution. Beyond the mode, mortality increased up to a maximum of 0.1 for those individuals which stayed in a stage twice as long as normal. A conceptual model of moulting and mortality rates during the moult cycle is proposed. Modelling and experimentation suggest that the variable development of copepods bred from a synchronous cohort does not proceed as a purely random phenomenon, but seems to be determined by the diverse physiological conditions displayed by different members of the same population. We show here that modelling does not only have a quantitative purpose – it should also lead to a better understanding of the phenomena involved.

INTRODUCTION

Herbivorous copepods are the main consumers of phytoplankton in large parts of the oceans, and it is necessary to know the relationship between their production and environmental conditions. It is important to be aware of the development times and mortality rates of copepods when calculating the production of a population, and to understand the populations dynamics (Landry 1978, 1983, McLaren 1978, Aksnes & Magnesen 1983, Vidal & Smith 1986, Davis 1987). Different methods of assessing instar durations have been worked out in the last decade with a view to constructing life tables (Bergmans 1981, Landry 1983, Hairston & Twombly 1985). Conceptual models of development have been proposed, concerning isochronal (Miller et al. 1977, Uye 1980, Landry 1983) and equiproportional (Corkett 1984, Corkett et al. 1986) development, as well as the sigmoidal pattern of development (Peterson 1986). Nevertheless, no method can be truly infallible, owing to the combined effects of varying recruitment in instars and mortality rates (Matthews et al. 1978), so that researchers have to find the technique most suited to their particular purposes (Peterson & Painting 1990). Usually, mortality rates are estimated throughout the development of an entire cohort (Paffenhöfer 1970, 1976). Nevertheless, stage-specific mortality rates are often difficult or impossible to measure (Fager 1973, Myers & Runge 1983). For this reason Landry (1983) assumed that an error in the estimation of stage-specific mortality rates would be proportional to the error in assessing the difference in duration between adjacent instars, i.e. influenced by isochronal development.

Current methods of calculating production and models of population dynamics are based on the following assumptions:

(1) In constant environmental conditions, mortality rates vary among the instars, but they are considered to be constant within each instar (see Matthews et al. 1978, Wroblewski 1982, Peterson 1986, Sciandra 1986). They have been seen to vary with food (Paffenhöfer 1970) and temperature (Tande 1988).

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(2) Stage durations can be estimated in reverse ratio to moulting rates and are determined by incubating samples of single stages in static cultures of natural seawater, for a given period immediately after capture (Burkill & Kendall 1982, Falkowski et al. 1983, Miller et al. 1984, Runge et al. 1985, McLaren et al. 1989). Consequently, moulting rates in population dynamics models are formulated as being inversely proportional to instar durations (Wroblewski 1980, 1982, Sciandra 1986, Davis 1987, Hofmann & Ambler 1988). Sometimes, Belehradek's relationship between stage durations and temperature (McLaren 1978) can be introduced into the formulation of moulting rates vs instar durations (McLaren et al. 1989). In other words, these assumptions mean that age structure within a life-history stage is uniform, recruitment into the stage is constant and all individuals have the same duration in this stage (no variability).

In fact, however, individual variability does occur in the development and growth of copepods (Thompson 1982, Miller et al. 1984, Carlotti & Nival 1991), due to individual variability of the bioenergetic processes (Båmstedt 1988). The latter author indicates furthermore that once this variability has been defined, new models can be set up [see also the Marine Zooplankton Colloquium 1 (1989)].

The deterministic model presented by Carlotti & Sciandra (1989), Carlotti (1990) and Carlotti & Nival (1992) combines several hypotheses on the functional relationships between 2 representation levels: the individual and the population. Hypotheses concerning the parameters of population dynamics (mortality rate, moulting rate, i.e. transfer rate) are related to biological criteria (growth rate, weight). Time and age do not intervene in these processes. On the other hand, simulated growth and development results can be explained as a function of age within stage and of time (see Figs. 7 & 10 of Carlotti & Nival 1992), and their time course can then be interpreted in relation to the conceptual scheme proposed.

The purpose of the present experiment was to determine the time course of moulting and mortality rates as a function of age within stage, and to compare the experimental results with those from the model. Individuals from the same brood were selected shortly after having entered a given stage, then put separately in identical small bowls and submitted to the same constant conditions of food and temperature. They were then observed at regular time intervals, sorted into living or dead and checked for stage. The overall results obtained for the copepods made it possible to reconstruct the mean durations in each stage for the whole cohort, and to interpret them in light of the information acquired for each individual. The results produced by the model raised a certain number of questions which we attempted to answer: (1) How does the individual variability of life duration in each stage develop, i.e. what is the time course of the probability of moulting as a function of age within stage? (2) At what moment in the stage duration does the death of an individual take place?

MATERIALS AND METHODS

Wild *Centropages typicus* (Copepoda, Calanoida) were collected at the entrance to the Bay of Villefranche in spring 1987. Water temperature and salinity were 15 °C and 38 ‰ respectively. Adults of both sexes were sorted and placed into a cool room (15 °C) in 5 l beakers, where the females could lay their eggs. To prevent the eggs from being eaten by the adults, they were put inside a plastic cylinder, closed at the bottom by a 300 µm mesh net, and suspended inside the beaker. Food was added in excess (16000 cells ml^{-1} of the haptophycean *Hymenomonas elongata*, ca 12 µm in diameter). We transferred the adults into other beakers every 12 h, so as to obtain synchronous egg-layings. The largest clutch was chosen for the experiment.

The cohort was observed every day until naupliar stage V (NV). 260 NV were then isolated by groups of 5 in 120 ml bowls, in order to facilitate the observation of the moulting from NV to copepodite I (CI). As soon as the first CI appeared, the bowls were checked at 4 h intervals and the freshly moulted CI were put into 20 ml bowls. A total of 129 CI were sorted out from the different 120 ml bowls over 4 d, and we observed them throughout their development. The same quantity of food was added daily to each small (20 ml) individual bowl, in order to assure that food was not limiting. Fecal pellets, exuviae, and uningested sedimented food were carefully removed daily from the bottom of the bowls, and the water and algae were renewed every other day. The bowls, protected with aluminum foil, were kept at 15 °C under a natural diel light rhythm. Observations of *Centropages typicus* were made at 4 h intervals for the first 2 stages (CI, CII), then at intervals of 12 h for the following stages, until adult.

RESULTS

Developmental stage durations at 15 °C

The development of each copepodite was known to an accuracy of 12 h (4 h for CI and CII). Thus it was possible to calculate the mean duration and standard deviation for each stage of the whole cohort (Table 1). Development was not isochronal, since the mean durations of the stages were unequal and the duration of

Table 1 *Centropages typicus*. Mean durations of copepodite stages at 15 °C, calculated for isolated individuals. The number of individuals which died in each instar is also shown. The experiment began with 129 individuals at stage NVI

Stage	Mean durations (d)	SD	n	No. of dead copepods
CI	2.73	0.58	112	17
CII	2.21	0.91	90	22
CIII	2.48	1.47	76	14
CIV	2.93	1.17	64	12
CV	3.47	1.32	52	12
Adult males	16.27	3.80	24	
Adult females	14.80	4.59	28	

the naupliar phase was less than 54.5 % of the total development time (see Landry 1983). Duration of life for males was appreciably longer than for females. Of the copepods which reached adulthood, 46 % were males.

Other authors have estimated life durations for stages or groups of stages (Table 2). We found rather short durations compared to those reported by Smith & Lane (1987) for mass cultures at the same temperature. However, these authors found quite different values of life durations depending on which method they used for estimation (see Table 2).

Moulting related to age within stage

In all copepodite stages, the distribution of durations in relation to age within stage was asymmetrical (Fig. 1). After a minimum length of time spent in the stage, a large proportion of the individuals changed stage at the same time, and the rest then moulted progressively. Some individuals were found to remain in a stage 4 times longer than most of the others (see e.g. CIII). This phenomenon strongly affected the mean calculated duration (Table 1). For copepodite III, the mean duration was 2.5 d, whereas the mode was 2 d. The mode of this distribution apparently provides a more realistic value of the stage duration than does the mean (see Carlotti & Nival 1991 for details).

Mortality related to age within stage

One of the aims of our experiment was to observe whether the death rate remains constant throughout the duration of a stage, or increases at certain times during the moulting cycle. Although the number of copepods observed was high (129), the number of dead copepods in each stage was too small (12 to 22) to provide sound information for every stage (Fig. 2). At best, we can note that the number of dead copepods was about the same on both sides of the duration distribu-

Table 2. *Centropages typicus*. Comparison of durations (in d) of development obtained in different studies. A: Duration calculated from differences in time of first individual's entering each stage; B: calculated from the day when 50 % of individuals entered each stage; C and D are 2 different cultures (see Fryd et al. 1991). Generation time is time from egg to egg. Values in parentheses are ranges

Study:	Present	Smith & Lane (1987)		Gaudy (1976)	Miller et al. (1984)	Lawson & Grice (1970)	Nassogne (1972)		Fryd et al. (1991)	
Culture:	Individual	Population		*In situ*	–	Population	Population	Individual	Population	
Food:	*Hymenomonas elongata*	*Thalassiosira weissflogi*		–	–	–	Mixture	Mixture	*Rhodomonas baltica*, *Oxyrrhis marina*	
Temperature:	15 °C	15 ± 1 °C		18 °C	15 °C	18–19 °C	18 °C	18 °C	17 ± 0.5 °C	
		A	B						C	D
Egg to NVI	12	14.1	16.4	8			8 (6–15)	8 (6–10)		
NII to NVI									5.46	5.99
CI	2.73	1.9	2.3	2					1.26	1.29
CII	2.21	2.9	4.2	3					1.38	1.91
CIII	2.48	3.5	4.7	4					1.58	1.31
CIV	2.93	4.8	4.9	5	5				2.18	2.04
CV	3.47	3.5	0.5	6					2.70	2.29
Adult males	16.27									
Adult females	14.80									
CI to adult	13.82						12 (8–14)	11 (6–14)		
Egg to adult	25.82	30.7	33.0	28					16.16	
Generation time		33				22	38 (29–44)			

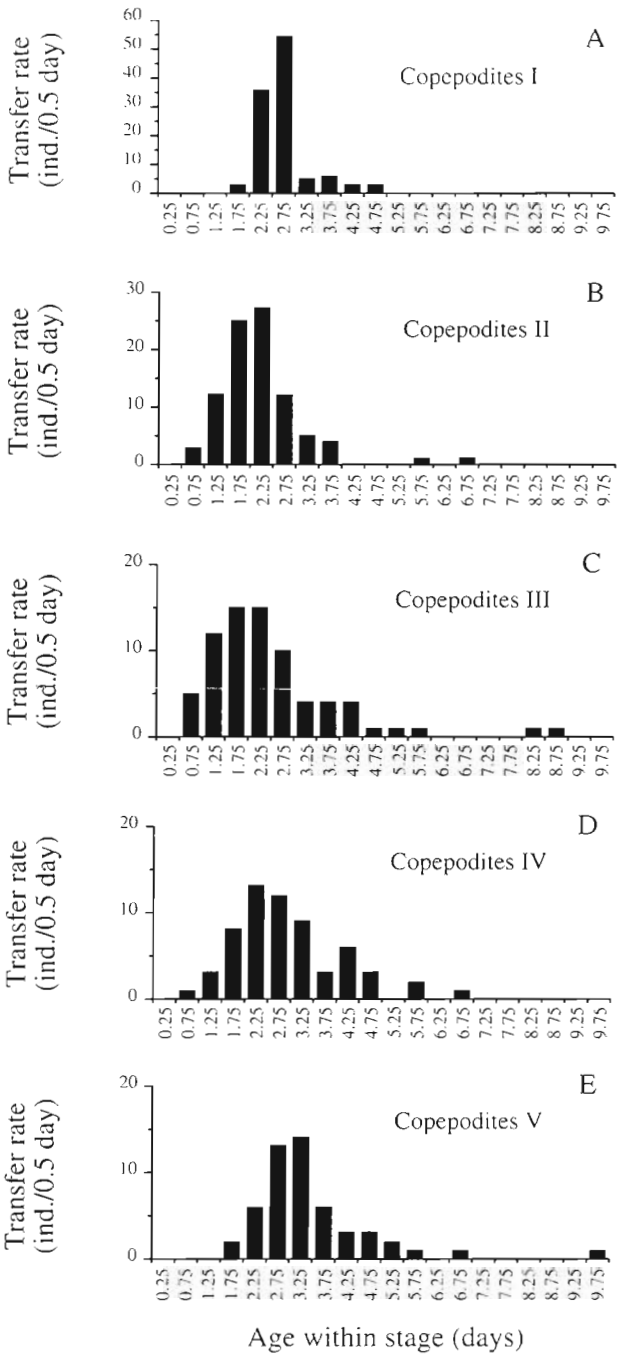

Fig. 1 *Centropages typicus*. Number of individuals moulting from one copepodite stage to the next as a function of age within stage. The transfer rate is expressed as individuals per 0.25 d

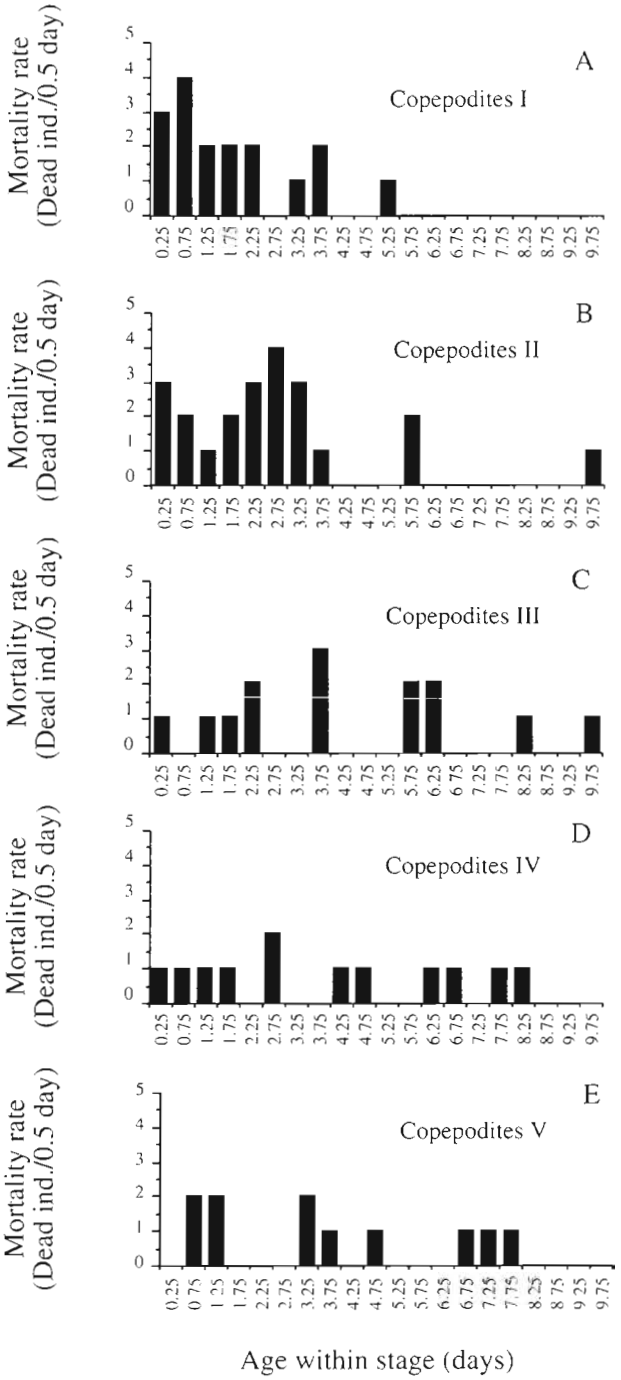

Fig. 2. *Centropages typicus*. Number of dead individuals as a function of age within stage. The mortality rate is expressed as individuals per 0.25 d

tion, except for CI, which implies that the intrinsic mortality rate (number of dead in each class / number of survivors) is higher for individuals which stay in a stage for longer than the mean duration. The higher mortality rate at the beginning of stage CI can be attributed to the NVI–CI metamorphosis.

Pattern of moulting and mortality rates in copepodite stages

With a view to establishing rules, we can assume that moulting and mortality functions are the same for all copepodite stages. As a matter of fact, development

of copepodite stages is subdivided into moults, and physiological processes follow the same rules (Vidal 1980a, b, c). Thus we cumulated the values obtained in all stages (Fig. 3) after having normalized them, i.e. after having divided the ages of transfer or death in each stage by the distribution mode shown in Fig. 1. The reference unit thus becomes the 'life duration unit'. The durations obtained were arranged in groups of one fourth of the life duration unit.

When a large number of individuals is observed, we can refine the shape of the curves representing the survival (Fig. 3A) and the transfer function (Fig. 3B) according to the copepods age. Two parts can be distinguished: after a compulsory period of time in the stage, the probability of passing to the next one increases exponentially, goes through a maximum, then decreases again exponentially, but with a more moderate slope than for the increase. The specific transfer rate (Fig. 3D) follows a pattern similar to the transfer rate, with the second part decreasing more slowly. The variability in the last few values is due to the small number of individuals (see Fig. 3 legend).

The number of copepods which died during each period of time decreased with age (Fig 3C), but the intrinsic mortality rate increased (Fig. 3E). Starting at a value of 0.02, it reached a maximum of 0.1 for individuals which stayed in a stage twice as long as normal. The final fluctuations after 2 life duration units are attributable to the small numbers of copepods remaining (e.g. 1 dead animal for 3 survivors = 0.33). We can estimate graphically the mean of this maximum death rate at around 0.1 to 0.12.

DISCUSSION

If the copepods are considered individually, moulting and death are discrete events compared to life duration, and their probability varies with biological characteristics. For copepods, these biological characteristics are not well known and account for the hypothesis that growth and development may be uncoupled by a hormonal mechanism (Miller et al. 1977; see their Fig. 8). This is due to the difficulty in experimentally estab-

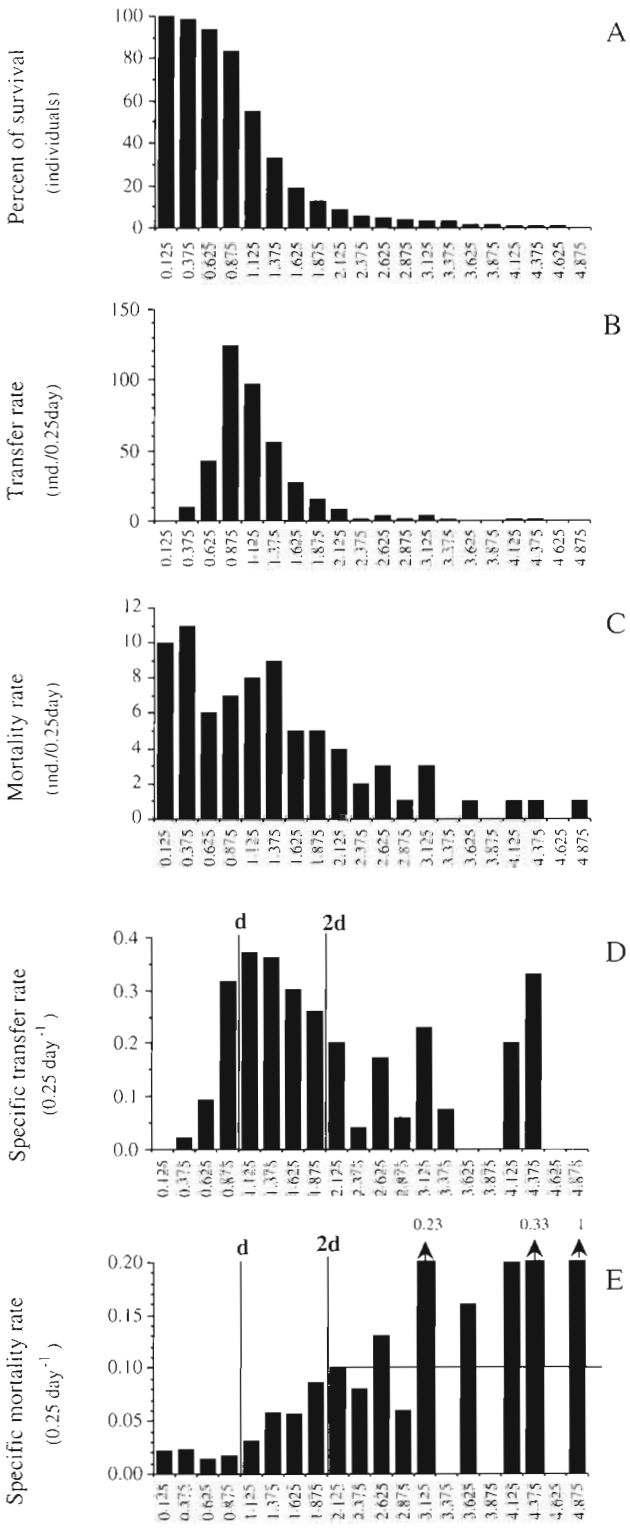

Fig. 3. *Centropages typicus*. (A) Survival curves in a copepodite stage (mean of survival curves from the 5 copepodite stages). (B & C) Mean distribution of transfer rate and mortality rate for individuals of all copepodite stages. (D & E) Specific transfer rate and specific mortality rate (per 0.25 d) obtained by the ratios of graphs B and C, respectively, to the absolute abundance. The life duration unit, indicated by 'd' in panels D & E, corresponds to the mode of the duration of copepodite stages in Fig. 1 (after normalization). The maximum transfer rate occurs at this value. For the specific rates, there is a strong variability at the end of the curves, due to the individuals which progressively disappeared (for instance, at 4.875 duration units, the death of the last individual induces a mortality rate of 100 %). Individuals which stay within a stage longer than 2 × d reach a maximum mortality rate (horizontal line)

lishing laws linking processes which vary simultaneously, e.g. growth rate and mortality rate, which cannot be controlled. It is impossible to discriminate the effect of deterministic fluctuations of processes from those generated by individual variability. It is easier to observe life durations in stages and survival as functions of variables which can be controlled: food level, temperature, etc. However, when interpreting results obtained by such an approach, we must bear in mind that not all the functional steps have been taken into account.

The use of a physiological model (Carlotti & Sciandra 1989, Carlotti & Nival 1992) is probably another means of obtaining information for interpreting the population dynamics of planktivorous animals. There may be processes or variables to which the experimenter has no access, because fluctuations are hidden by other processes or even by individual variability (see function f4 of the model; Carlotti & Sciandra 1989, Carlotti & Nival 1992). That is why processes and variables are ignored in conceptual schemes established with experimental data. The model, however, is capable of representing the patterns of functional relations which underlie developmental and growth phenomena, as well as testing them. The results presented here constitute an experimental check of the simulations of a physiological model. Therefore we discuss below the hypotheses suggested by the model: how do the physiological processes involved in growth and development influence the pattern of moulting and mortality rate during the moulting cycle?

Moulting rate

The probability of moulting depends on age within stage, and thus is not constant. An individual which has just moulted cannot immediately moult to the following stage; it must acquire the capacity to do so. Consequently, it must stay in a stage for a minimum length of time. In the model, the transfer rate is controlled by weight and by the mean growth rate over the preceding hours (for details see the hypotheses in Carlotti & Nival 1992). The distribution of individual durations in a copepodite stage (Fig. 3B) falls into 2 distinct parts, like the distributions obtained by simulation (Fig 7 in Carlotti & Nival 1992), suggesting that at least 2 biological factors play a role. In the model, the weight function influences the first part. The hypothesis that the critical moulting weight is the same for all the individuals in a stage, i.e. that it is a specific characteristic of growth, means there is a rapid increase in moulting probability when the individuals come close to that weight. Individual variability in growth rate is the only factor which can generate a spreading of the moulting age in the population. With this type of model, the variability in development of copepods bred from a synchronous cohort no longer appears to be a purely random phenomenon, but seems to be determined by the diversity of physiological conditions displayed by different members of the same population.

Mortality rate

The experimental results (Fig. 3C) show that the intrinsic mortality rate in a stage is not constant, but varies with age. It increases when the copepods live longer than the mean life duration and reaches a maximum when this duration doubles. This observation is due to a decay in the physiological state of the organism as a function of age. The model (Carlotti & Sciandra 1989, Carlotti & Nival 1992) proposes a relation between mortality rate and growth rate. We have seen that the tails of the distribution of the individuals in a stage were influenced by an increasingly lower growth rate of the organisms. It follows that these low growth rates are the cause of a higher probability of death.

The natural mortality rate of the copepod *Centropages typicus*, i.e. the mortality caused by physiological decay, varies from 0.01 to 0.1 d^{-1} among copepodite stages. This is generally the range of mortality rates observed in cultures and sometimes *in situ* under favourable conditions (Fager 1973, Landry 1978, Parslow et al. 1979, Uye 1982, Yassen 1984, Strathmann 1985, Tande 1988). The difference between the lowest and highest mortality rates is attributable to the ageing of organisms in a given stage and to their failure to prepare for moulting.

Actually, it is almost certain that, *in situ*, the portion of natural mortality that has a physiological cause is represented by the minimum mortality rate (see Fig. 3), since the individuals which live longer than normal die more easily due to physiological deficiency, and are also more easily caught by predators.

It would be interesting to repeat this experiment in order to determine the minimum mortality rate at different temperatures, and compare the results with those obtained by Tande (1988). Since the mortality rate in the model (Carlotti & Nival 1992) depends on the growth rate, and as it is relatively easy to obtain the growth rates at different temperatures (see e.g. Miller et al. 1977), the accuracy of the function used to predict mortality can be checked.

Conceptual model of moulting and mortality rates during the moulting cycle

Miller et al. (1984) attempted to establish whether moulting rate was inversely related to stage duration, using numerous examples. They observed this some-

times, but not always. Their formulation was based on the assumption that copepods are uniformly distributed within a given stage (Fig. 4A). This is possible if: (1) recruitment is constant at the start (when the copepods enter the first stage); (2) there is no physiologically caused mortality during development (no loss of animals); (3) the copepods moult as soon as they reach the end of the stage duration time; (4) there is no mortality of copepods which have moulted (this would lead to an incorrect interpretation of results). Fig. 4B shows the distribution obtained in a particular case of constant recruitment (see Fig. 10 in Carlotti & Nival 1992) with the time course of transfer and mortality rates proceeding as a function of the moulting cycle, established by the model and the experiment (see Fig. 3). At first, due to a minimum physiological mortality (1 to 2 %), some individuals disappear, thus inducing a slight decrease in the abundance. The animals then moult according to the transfer rate rule or, if they stay in the stage, they disappear because of an increasing probability of death.

The distribution can then spread more or less widely, according to the shapes of the curves for the transfer and mortality rates. If the transfer rate function is very densely clustered around its mode, the population disappears rapidly. This phenomenon will occur only when food and temperature conditions are the most favourable for development of the organisms (see Fig. 11 in Carlotti & Sciandra 1989). Under favourable conditions, the minimum mortality rate will be a few per cent and the distribution of individuals in the stage, will be almost uniform, as long as recruitment is continuous. Under unfavourable conditions, there would be a broader spreading of the transfer and mortality curves, and recruitment into the stage would presumably be discontinuous.

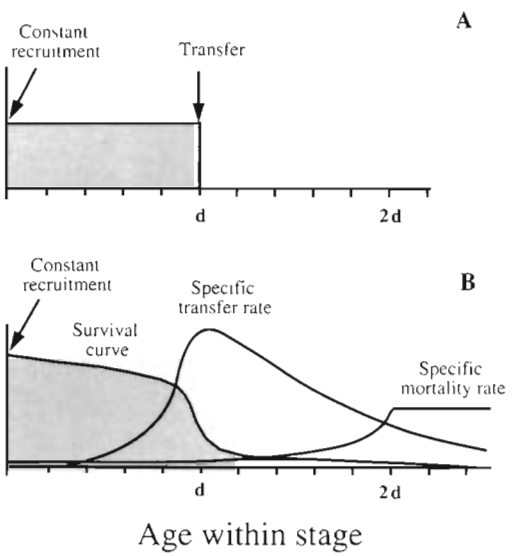

Fig. 4. (A) Uniform distribution of age within stage. Such a distribution would require constant recruitment, no mortality and a typical moulting age. (B) Distribution obtained with realistic rates of moulting and mortality related with age. Only with constant recruitment, and optimal environmental conditions, can a nearly uniform distribution be obtained

When following the growth of individuals of the same population under identical conditions, a similar mean pattern with some individual variability is observed. The growth of an individual of a given species can then be assumed to go through characteristic ontogenic phases, and the time spent in the different compulsory phases depends on the growth rate. Thus, the relation between transfer rate and age within stage is a consequence of biological phenomena. What really matters, therefore, is the discovery of suitable biological criteria. Any essentially analytical biological model should be free from functions related simply to age or time. In our model, we suggest the existence of a critical moulting weight, which can possibly decrease with temperature (see discussion in Carlotti & Sciandra 1989). To validate this approach, it would be necessary to explore it experimentally, for instance by following the development of the progeny of 1 female under different temperature conditions.

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