

MODELLING OF THE RECRUITMENT OF MARINE SPECIES

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ABSTRACT. The flux of young adults to the parent stock is controlled by various biological processes. The processes include the trophodynamics of each individual (feeding, excretion, metabolism, growth), as well as phenomena at the population level (predation, death rate). All these processes acting in combination determine the probability of mortality of a given individual in a cohort. The various forcing functions to these processes need to be considered to understand the evolution over time of the probability of mortality and its cumulative effects on the growth rate of the species.

Mathematical models permit one to evaluate the part played by each variable in the total mortality of a cohort, as soon as the basic information on which the theoretical structure is built is pertinent and informative enough.

A model of larval dynamics which takes into account larval age-and-mass budget to estimate the transfer rate from one stage to the other, can simulate some experimental results. It is used to estimate the effect of perturbations in the food concentration. Starvation can reduce the recruitment of larval stage 4 but the phase between hatching of larvae and the perturbation is very important if predation by a selective predators occurs.

The match between hatching, food abundance, and the mismatch with the predators are the conditions which determine the success of a cohort development.

1. INTRODUCTION

Many factors influence the dynamics of the diverse components of the pelagic ecosystem. Some of them are endogenous, others, outside the system, are usually considered as forcing variables.

Models of the system can be simple, complex or detailed. Most models that include physical, chemical and biological processes are based on a very simple picture of the biological variables of the ecosystem. Some models with a rather complicated structure can stimulate observations made at sea (Radach, 1982; Kremer and Nixon, 1978; Wroblewski, 1980; Platt *et al.*, 1981). Others take into account

as many biological details as possible at the present state of our knowledge of the processes. They are designed to simulate a restricted part of the planktonic system (Lehman, 1976; Steele and Frost, 1977).

The mathematical structure, which translates the picture into mathematical relationships, implies that all the relations suspected between variables are known, or, at least, that it is possible to suggest the type of function which gives the known properties.

For different reasons, many models give a very crude representation of biological variables. First, it is not necessary to design a complicated structure for the biological part of a model which is simple in its chemical or physical parts; second, the time-and-space scales of the phenomena which are to be simulated do not need to take into account complicated mechanisms if the input to these mechanisms are constant; and third, the measurements of the variables with which the output of the model are to be compared are highly aggregated variables.

The first and second points can be generally accepted, but the third must be considered carefully. As an example, consider the variable "phytoplankton." Usually the phytoplankton density is measured by chlorophyll concentration or nitrogen content. This easily measured variable integrates a great variety of organisms with different characteristics and behaviors. Depending on the "filter" used to collect particulate matter, a selection of sizes is made. This observation is also valid for such a variable as "zooplankton", which may be based on measurements of total dry weight of organisms collected by a plankton tow. A single relation between a variable "phytoplankton" and a variable "herbivorous zooplankton" can be misleading because the trophic relations are obscured (Figure 1). The importance of the underlying structure of these variables must be carefully evaluated when the relevant structure of a model is set (see also Andersen, 1985). In order to take into account the difference in growth-and-mortality between larval stages and adults of each species, it is necessary to consider the developmental stages of each species (cf. Rothschild 1986:Chapter 8).

As another example, the input of larvae of benthic organisms into the water column often results in a sudden change in the total planktonic population. These larvae, representing new herbivores and also new prey for carnivores, disappear from the pelagic community at the end of their larval development with a suddenness comparable to their appearance. An oversimplified model could not simulate the correct transient behavior of the natural system.

Another reason to take into account the complexity level of developmental stages in models of pelagic ecosystems is the need to estimate the variations in the recruitment of adults in marine species exploitable by man. Moreover the understanding of stability of prey-predator relations which shape the behavior of the whole pelagic ecosystem, might depend strongly on the larval stage dynamic. The variations in time and space of a given species might be influenced by the relation not only of the adult, but also of the different developmental stages to food, predators or physical conditions

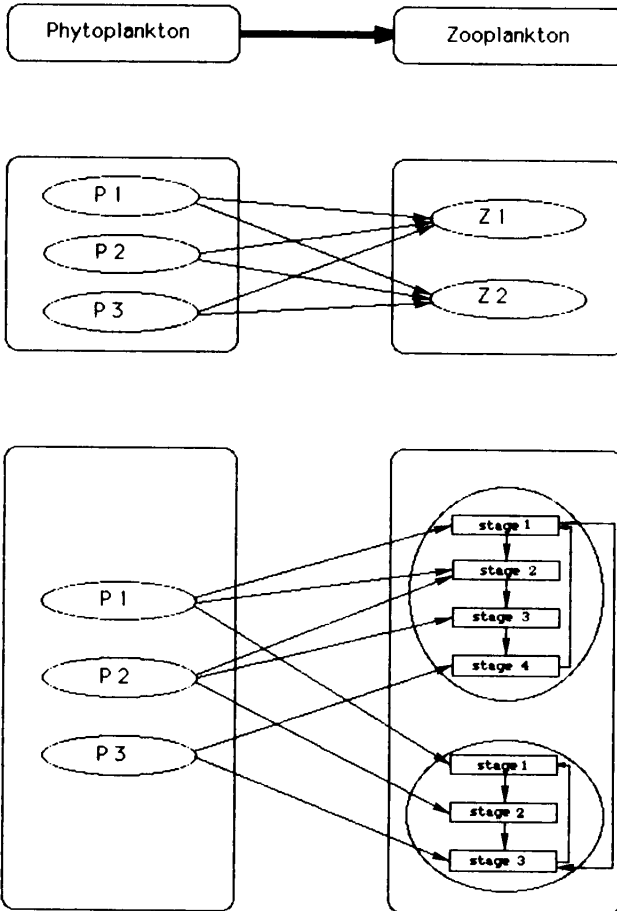


Figure 1. Different representations of two trophic levels in models. (A) Species of phytoplankton and zooplankton are not considered, but only biomass. This is the simplest representation which ignores modifications of the transfer related to the species characteristics. (B) The major species are considered as different state variables. (C) A more complex picture of trophic relations results from introduction of population dynamics of animal species. This last picture is necessary to understand the variation in the recruitment of one species. Some relations between species can be specified only if this level of complexity is taken into account.

(Boucher, 1984; 1988). As it is easier to identify and count adults of marine species than larvae, the data on larval distribution at sea are scarce, in spite of the great number of experimental works done on larvae.

2. THE MODEL

The model we have designed to represent the pelagic phase, in the life cycle of a marine species is based on differential equations (at least one for each life stage) giving the variation rate of individuals. The structure is similar to the models of Sciandra (1982, 1986) and Davis (1984) who have improved the model of Wroblewski (1980). Some of the processes are represented in the same way as Andersen and Nival (1986). In a simple model, the dynamics of each stage would be represented by one equation that has a term of transfer from the preceding stage and a term of transfer to the following. In this case, a certain number of larvae reaching stage I at time t , would be transferred to stage I+1 at time $t+dt$, depending on the rates of transfer (dt being the integration step). This is not what is usually observed. Larvae stay some time in each stage before moulting and transferring to the next stage. Some models designed for insects include delays to minimize complicated formulations (Manly, 1974; Blythe *et al.*, 1982). In this case it is difficult to take into account the modifications of the larvae related to changes in the environment during the delay. We preferred, like Sciandra (1982) and Davis (1984), to consider the age of individuals in each stage. It is therefore possible to define a probability of transfer from one stage to the next depending on age, or eventually on other processes which may become influential as the larvae got older. Anger and Spindler (1987) have shown that the transition to the next stage (Zoea I to Zoea II of *Menippe mercenaria*) does not occur before the concentration of a hormone reaches a threshold value. However, the probability of transfer from one stage to the other is not a step function in terms of the whole population. The data from Nival and Nival (1983) show that the probability of transfer from stage copepodite C4 to C5 of the copepod *Temora stylifera* is zero during the first 12 h and increases afterwards.

We are mostly interested in the behavior of a single cohort of larvae because most experiments yield such data and because many marine species are semelparous so that their larvae belong approximately to the same cohort.

Blythe *et al.* (1985) and Gurney and Nisbet (1985) give examples of sophisticated models of population dynamics used to study the stability and dynamics of discrete generations. Neither the simplifications they adopt, nor their use of lag time are convenient for our purpose, which is to estimate the effect of variable environment on recruitment.

The model we have designed, has two types of differential equations. One set gives the variation per unit time of the numbers of larvae in each age class and each stage. The other one gives the variation per unit time of the weight of the larvae. Each stage is divided into 11 age classes (Figure 2). The 11th age class corresponds to larvae which do not proceed to a next stage. The numerical integration of the equations using the method of Runge Kutta

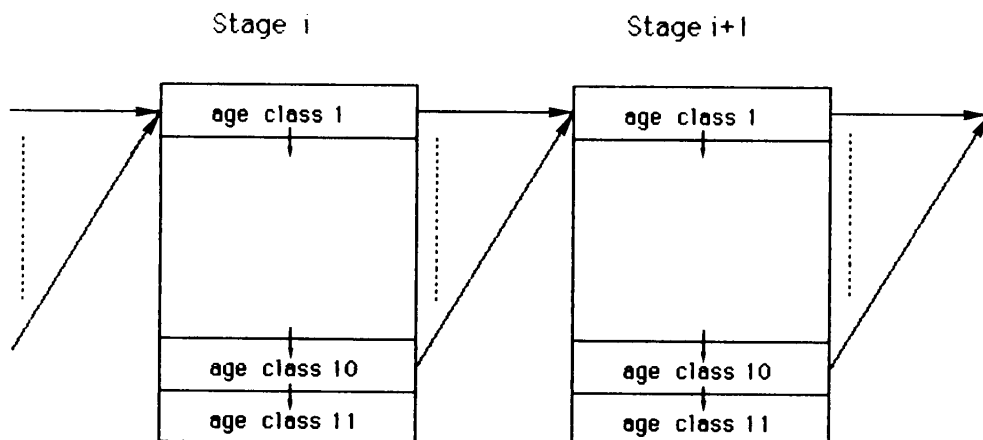


Figure 2. Conceptual framework of the model: two of the four stages of the model are represented. Early stage is divided into 11 age classes. Every day, the larvae in one age class are shifted into the next. At any time a proportion of larvae of an age class can reach the age class of next stage. All the larvae of age class which have not been transferred to the next larval stage are assumed to be in bad condition and are stored in the 11th age class.

gives the time variation of weight and numbers for the different stages.

Tables 1 and 2 respectively, give the processes and equations of the model. Details of the model structure can be found in Carlotti (1986, 1987). Figure 3 shows the connection of the different processes which modify transfer rate and mortality rate. We consider that the number of individuals transferred from one stage to the other depends on food, predators, mortality and growth rate. We consider that an individual at any stage of its development has some probability of dying, changing stage or being eaten by a predator.

1. The probability of dying (M) depends on the amount of food ingested and available for growth. From a high value when the animal is starved, it declines to relatively low constant value when it is well fed.
2. The probability of being eaten by a predator (P) depends on the abundance of predators and on the efficiency with which such predators catch each larval stage. For instance, Pennington and Chia (1984) show that the ability of the trochophore larvae of *Sabellaria cementarium* to expand larval setae can reduce the predation of some species on this development stage, compared to the previous one which has no setae.

Table 1. Mathematical formulation of the biological processes considered in the model.

<i>Process Represented in Model</i>		<i>Construct</i>
L	Biomass of larvae	
B	Mass budget	$B = I - E_g - E_x$
I	Ingestion rate	$I = b \cdot B_p \cdot W^{0.75}$
b	Filtrated volume	
B_p	Biomass of phytoplankton	
W	Weight	
E_g	Egestion rate	$E_g = 0.3 \cdot I$
E_x	Excretion rate	$E_x = 0.1 \cdot W$
P	Predation rate	$P = Pr \cdot I_p \cdot E/L$
Pr	Biomass of predators	
I_p	Predator ingestion rate	$I_p = I_{pmax} \cdot (L - L_{min}) / (K_1 + (L - L_{min}))$ $I_p = 0$ if $L < L_{min}$
I_{pmax}	Maximum ingestion rate	
L_{min}	Threshold of larval biomass	
K_1	Half saturation constant	
E_c	Capture efficacy	
M	Mortality rate	$M = M_{max}$ if $B < B_{min}$ $M = M_{min} + a_m / (B - b_m)$ if $B > B_{min}$
M_{max}	Maximum mortality rate	
M_{min}	Minimum mortality rate	
B_{min}	Threshold of mass budget	
a_m, b_m	Shape factors	
T	Transfer rate	$T = T_m \cdot f(S_b) \cdot g(W)$
T_m	Maximum transfer rate	
$f(S_b)$	Function of mass budget	$f(S_b) = S_b / (S_b + C_b)$
S_b	Mean mass budget over the last 5 hours	
C_b	Half saturation constant	
$g(W)$	Function of weight	$g(W) = W^k / (W^k + C_w k)$
W	Weight	
k	Shape factor	
C_w	Specific weight for half maximum transfer rate	

3. The probability of changing stage (transfer rate T) depends first on the mass budget of the animal, that is, to some extent, on the ingestion rate but also on the respiration or excretion rate, and on the weight which depends on the growth. Figure 4 shows how varies T in the space of mass budget and weight. We assume that this probability varies at two different time scales:

- the scale of hours (effect of short term variations in food abundance). This effect should be damped to take

Table 2. Equations giving the rates of variation in number (L) and weight (W). M: mortality rate; T: transfer rate; P: predation rate; Bp: phytoplankton concentration.

Equations for abundance:

$$\frac{dL(1,1)}{dt} = (-T(1,1)-M(1,1)-P(1,1)) \cdot L(1,1)$$

$$\frac{dL(1,J)}{dt} = (-T(1,J)-M(1,J)-P(1,J)) \cdot L(1,J) + \sum_{i=1}^{10} T(1,J-1) \cdot L(1,J-1)$$

$$\frac{dL(I,J)}{dt} = (-T(I,J)-M(I,J)) \cdot L(I,J)$$

$$\frac{dL(11,J)}{dt} = (-M(I,J)-P(I,J)) \cdot L(I,J)$$

Equations for weight:

$$\frac{dW(I,J)}{dt} = ((0.7) \cdot b \cdot B_p \cdot W(I,J)^{0.75}) - ((0.1) \cdot W(I,J))$$

I: age classes (1 to 11)

J: stages (1 to 4)

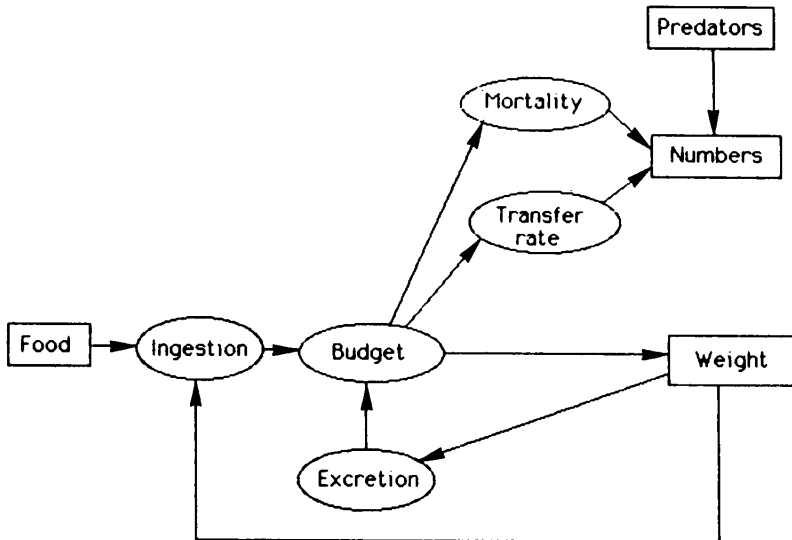


Figure 3. Relationship between processes. Food concentration affects numbers of organisms and their weight through series of steps, each one of them depending on others.

into account food storage in larvae that can smooth the variability of resources.

the scale of a few days to a week to take into account the cumulative effect of growth, or the building up of some substances (hormones) that trigger morphological changes.

Table 3 gives the coefficient used in the reference simulation (Figure 5.A). Figure 5.B, 5.C and 5.D show some simulations of cohort evolution for different values of the coefficients C_b , C_w and k which shape the transfer rate T . When C_b increases (Figure 5.B1 to 5.B2) the duration of stages is longer; k affects the shape of the abundance curve in its early part: when k is high the slope is steeper (Figure 5.C1 to 5.C2). C_w translates the position of the curves (Figure 5.D1 to 5.D2).

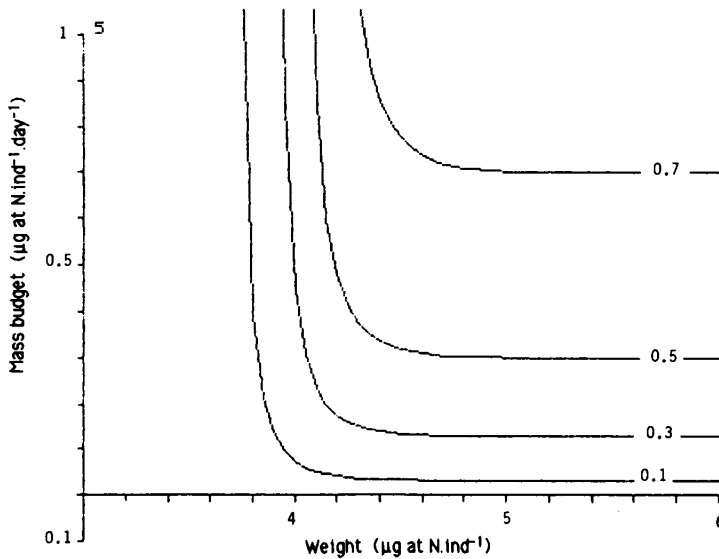


Figure 4. Isolines of transfer rate in the space of energy budget and weight for a given larval stage. (Here stage 1)

3. RESULTS

We have used the model to simulate experimental conditions reconstituted by different authors, mainly working on crustaceans. The molting of crustacean larvae provides a conspicuous marker for changes in stage and permits simple experiments.

Table 3. Set of coefficient values used for reference simulation (Figure 5a).

Symbol of Coefficient	Units	General Process	Coefficient			
			Specific Process 1	Specific Process 2	Specific Process 3	Specific Process 4
B_p	$\mu\text{g at N}\cdot\text{l}^{-1}$	8				
P_r	$\text{ind}\cdot\text{l}^{-1}$	50				
b	$1\cdot\mu\text{g at N}^{-1}\cdot\text{j}^{-1}$		0.035	0.042	0.050	0.065
E_c			0.	1.	0.	0.
T_m	j^{-1}		1.	1.	1.	1.
C_b	$\mu\text{g at N}\cdot\text{j}^{-1}$		0.3	0.5	0.5	-
C_w	$\mu\text{g at N}$	30	4.	5.5	8.	-
$I_{p\text{max}}$	j^{-1}	0.3				
L_{min}	$\text{ind}\cdot\text{l}^{-1}$	5				
K_1	$\text{ind}\cdot\text{l}^{-1}$	10				
B_{min}	$\mu\text{g at N}\cdot\text{l}^{-1}$	0				
M_{max}	j^{-1}	0.08				
M_{min}	j^{-1}	0.04				
a_m	$\mu\text{g at N}\cdot\text{j}^{-1}\cdot\text{ind}^{-1}$	0.06				
b_m	$\mu\text{g at N}\cdot\text{j}^{-1}\cdot\text{ind}^{-1}$	-1.5				

3.1 Summation of experimental results.

3.1.1. *Test of the transfer function.* It is possible to simulate for one larval stage the input of individuals coming from the previous stage and the output to the next stage. Figure 6 gives an example of the evolution with time of the number of larvae arriving at and leaving stage 2 during 7 hours. The maximum of these curves occurs at the inflexion points on the abundance curve, and output is equal to input at the maximum of the abundance curve. The difference in the maximum of the input and output curves depends on the mortality rate and on the difference in the coefficients of the transfer function from one stage to the other. The input curve influences the shape of the beginning of abundance curve, and the output one shapes the end of abundance curve. The data of Sciandra (1982) show such curves with a tail of late individuals that his model is unable to simulate because it has a too simple transfer function. Parslow *et al.* (1979) assume that the transfer function is a Gaussian curve.

Sulkin and Van Heukelem (1986) give results of this kind for the blue crab (*Callinectes sapidus*). Each day, they collected the megalopae which had appeared in a culture of zoeae and gave the evolution in time of the input in the megalopa stage. Figure 7 gives an example of the fit one can get by adjusting the duration of stage 2 in the model to the 30 days series of the experiment. In this case,

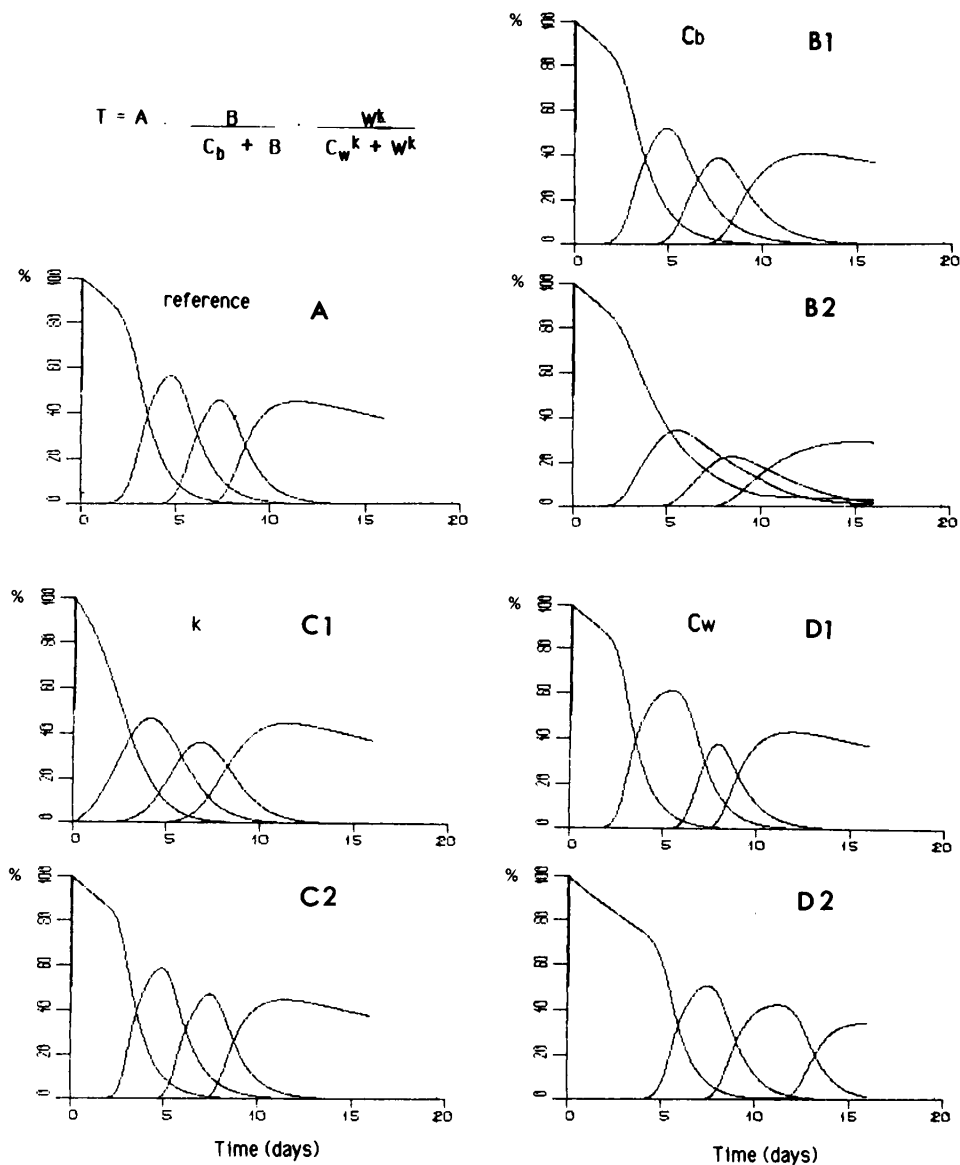


Figure 5. Effect of changes on the coefficient of the transfer rate formulation on the shape of abundance curve of each larval stage. (A) Reference simulation. Each simulation starts with 100 larvae, each one weighing $3 \mu\text{g}$ at N . (B) Effect of C_b [B1: $C_b(1)=1$, $C_b(2)=2$, $C_b(3)=3$; B2: $C_b(1)=5$, $C_b(2)=6.5$, $C_b(3)=8$]. (C) Effect of k [C1: $k=10$; C2: $k=40$]. (D) Effect of C_w [D1: $C_w(1)=4$, $C_w(2)=6.2$, $C_w(3)=8$; d2: $C_w(1)=5$, $C_w(2)=7$, $C_w(3)=12$].

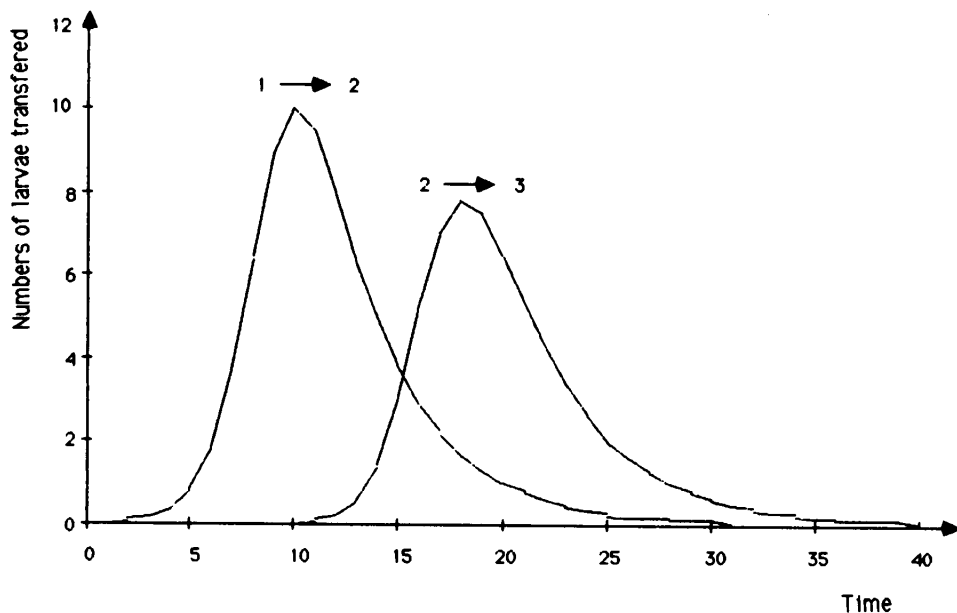


Figure 6. Variation in time of the transfer rate from 1st to 2nd stage (input to stage 2) and from 2nd to 3rd stage (output from stage 2). We have considered the number of larvae transferred during successive 7 hour intervals. The unit of time is 7 hours. These curves are skewed to the left. The leading tail simulate the late individual which grow slowly.

the model can reproduce the shape of transfer rate evolution. (The unit of time is 1/29th of the stage duration taken when input of larvae 2 is 1% of larvae initially present.)

3.1.2. *Test of the effect of starvation.* An experiment from Anger et al. (1981) provides an opportunity to test the model output. These authors wanted to estimate the effect of a starvation period during the stage Zoae I of a crab (*Menippe mercenaria*) on the following stage Zoae II. If the starvation period occurs early in the stage, the mortality is high and the duration of the stage is long; if the starvation period occurs later on, the effect on the mortality of starved stage is the same but the following stage is less affected (Figure 8).

We simulated the same experiment with the model which can reproduce the shape of the experimental results but the mean duration of the first and second stage are larger in the model than for *Menippe* (Figure 9). Some exceptions appear in Figure 9.A. The first two feeding regimes give larger values for development duration than measured in the experiment. This discrepancy is related to the

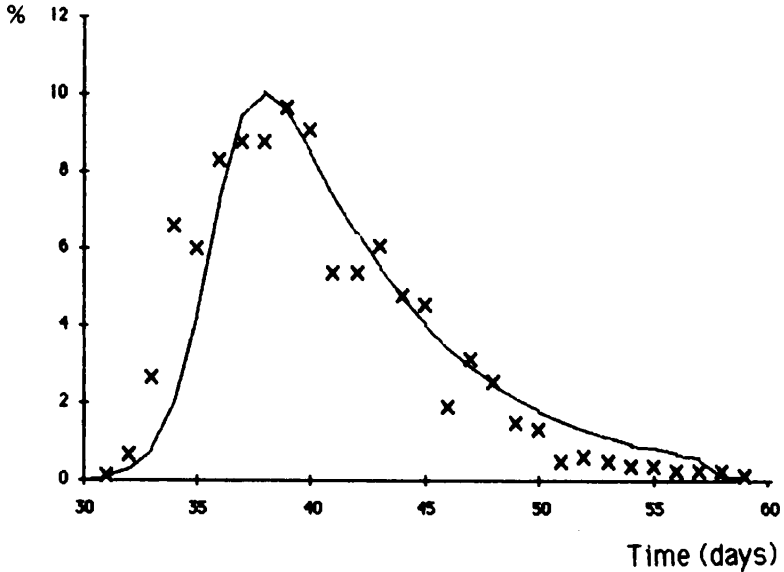


Figure 7. Comparison of the time variation of the transfer rate (numbers of individuals per day during 29 days) from one stage to the other (continuous line) with data from Sulkin and Van Heukelem (1986): transfer rate from the zoea stage to the megalopa stage in the *Callinectes sapidus* (+: % of total number of megalopae collected during the experiment, data from Sulkin and Van Heukelem (1986); -: model simulation).

criterion adopted to estimate the development duration from a population which shows individual variability. The determination of the duration of a stage is complicated if the larvae develop asynchronously. We first assumed that the duration is the difference in time of the maximum of abundance curve (Figure 9.A), second that it is the difference in time of the 50% of abundance of the same stage (Figure 9.B). We can see that the results of the model with the second criterion are better fitted to the results of Anger *et al.* (1981) than with the first criterion.

3.1.3. *Test of a time series.* The data from Blaszkowski and Moreira (1986) can be used to compare the shape of the simulated curves and data from a culture. Figure 10 shows that the timing and the amplitude of abundance curves are well reproduced. This result is obtained after minor changes from the reference set of coefficients: a decrease in the mortality rate and a modification in the constant C_b in the transfer function.

This set of data obtained in constant food conditions cannot allow a complete test of the ability of the model to simulate

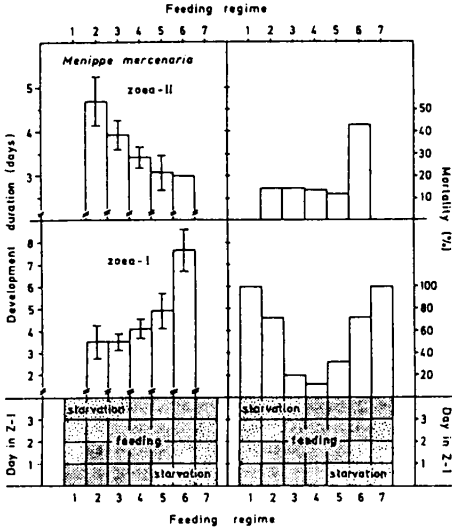


Figure 8. Effect of different feeding regimes in the development time and mortality rate for two successive stages of the larvae of the crab *Mennippe mercenaria* from Anger et al. (1981).

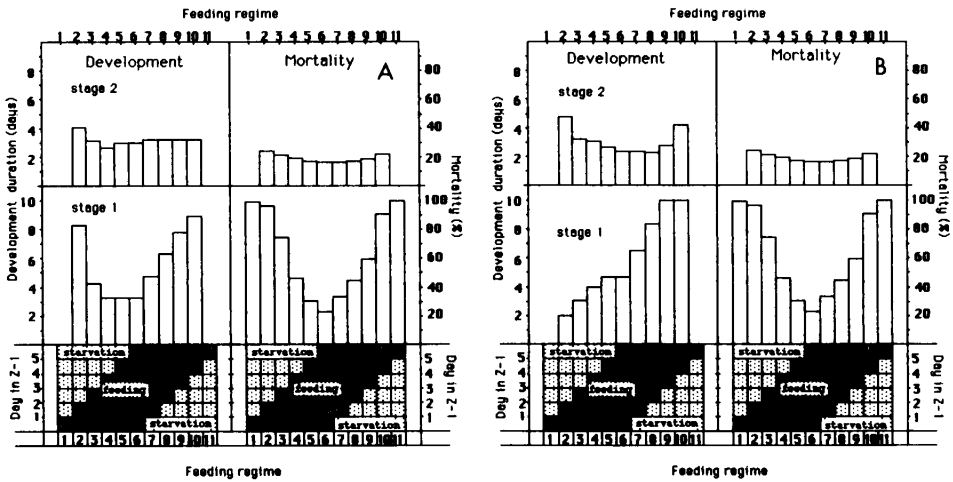


Figure 9. Results of simulations from the model for similar patterns of feeding regime. (A) Development time calculated from time interval between the maximums of abundance of stages 1 and 2, (B) Development time calculated from time interval between 50% of maximum abundance for stage 2. In this case, the output of the model is similar to the experimental results depicted by Figure 8.

population dynamics. It is necessary to rear larvae in variable food conditions. We should compare the effect of a period of starvation on the recruitment of a species reared in the laboratory and simulated by the model. Because of the complicated output which is expected, such experimental design are rarely set up.

3.2. Simulation of perturbations on larvae environment.

The preceding tests show that the model is able to reproduce some properties of larval growth, but specific experiments should be designed to verify the usefulness of all of its functions. Nevertheless, we can use this theoretical structure to investigate some situations relevant to the effect of the environment of the larvae in simple situations.

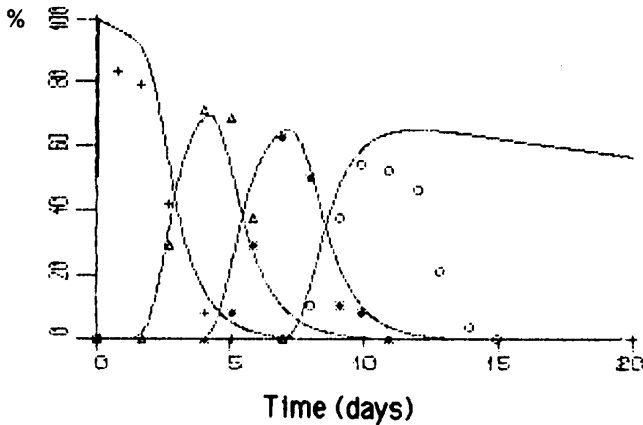


Figure 10. A simulation (solid lines) which fit the data of Blaskowski and Moreira (1986) on *Pagurus criniticornis* (Dana) for the first three stages (crosses, triangles and stars, respectively). In the present state of the model, the 4th stage accumulates larvae from third stage which explains the deviation why the simulation deviates from the real data (squares).

3.2.1. *Effect of food on recruitment.* Food affects the cohort evolution in a complicated way. It affects the ingestion rate which determines the budget and consequently the transfer rate. It is a three stage process, and each step is controlled by other processes. If we simulate a laboratory experiment with constant food, the food must exceed a threshold to allow the transfer from stage 1 to stage 2 (Table 4).

Table 4. Effect of food level on recruitment of stage larvae.

Food	5	6	7	8	$\mu\text{g at N}\cdot\text{l}^{-1}$
Recruits	0.05	25.6	37.2	44.7	%
Time to reach stage 4	>20	17.7	13.62	11.42	days

Figure 11.A shows the modifications of the cohort evolution when a period of two days of starvation is translated from day 1 after hatching to day 7. Starvation reduces the transfer between two stages, so the stage following the one which is affected by the starvation appears later. The lengthening of development duration increases the loss of individuals by mortality, so the recruitment declines, but it does not change much with the period of starvation (Table 5). The main feature is the increase of the period of presence of the affected stage, allowing a predator selecting stage 2, for instance, to catch a large amount of them.

3.2.2. *Effect of predation mortality on the recruitment.* If the predator grows slowly (abundance nearly constant) and is able to collect all stages with the same efficiency, the result is an increase of the overall mortality and a reduction of the recruits.

We can first investigate the effect of a predator which is able to collect only stage 2. The stage specific predation is known for copepods (Mullin, 1979; Bailey and Yen, 1983) and for a variety of other planktonic invertebrate larvae (Rumrill *et al.*, 1985; Pennington *et al.*, 1986).

If we consider a predator which captures larvae when their concentration is over five per liter and has a maximum predation rate of 10 preys per day, the potential amount of larvae captured is maximal when the starvation begins on day 5 (Table 5). This increase of predation on stage 2 has an effect on the recruitment of stage 4.

Simulations considering the combination of a starvation period and the presence of a predator selecting stage 2 give results shown on Figure 11.B. The effect of the predation is more important when the concentration of larvae tends to be high during a long period of time (Figure 11.A. and 11.B. at 5-7).

The effect of starvation and predation on the recruitment depends on the duration of the starvation period and on the abundance of predators, but this simulation shows that the outcome is not simple.

3.2.3. *Effect of timing of maximum food concentration and maximum predator concentration.* There is considerable literature on the value of different food species to the rearing success of larval stages for marine animals (Hines, 1986). Sulkin (1975) shows that the survival of *Callinectes sapidus* larvae depends strongly on food species. Measurement of available food by particulate carbon or chlorophyll is certainly not correct if a specific item is needed. The species composition changes when the spring bloom develops (Robinson *et al.*, 1986) so the short advantageous food species and the most efficient

Table 5. Effect of a starvation period of two days on the recruitment of larvae stage 4 (L4). Potential predation is the number of larvae which can be eaten by a predator selecting stage 2 during the total development time. Starvation influences the recruitment, but its timing has only a slight effect. On the contrary, when a selected predation on stage 2 is added, the number of recruits becomes highly variable.

	<i>Without Predation</i>			<i>With Predation</i>	
	Recruitment (%)	Time for max L4 (days)	Potential Predation (ind/pred)	Recruitment (%)	Time for max L4 (days)
Without starvation	44.7	11.4	35	19.7	11.4
Starvation Period (days)					
dates					
1-3	32.2	15.1	28	12.5	15.0
3-5	32.4	15.0	53	8.7	15.0
5-7	33.5	14.7	69	6.7	14.9
7-9	34.9	14.5	43	15.2	14.5

predator can be occurring in a sequence, relative to the hatching of larvae, which might not correspond to the sequence of the total phytoplankton and total zooplankton.

If we assume that the predator's maximum and the food maximum are not linked, it could be possible to find the occurrence of predators before the occurrence of food. The model can be used to determine the variation in recruitment for different lags of predator and food maximum relative to the hatching date.

Figure 12 shows that when the food species occurs early, the recruitment depends very much on the lag of the predator bloom. It confirms the intuition that when the predator bloom is late much of the development of the larvae has been completed and the recruitment is successful. If the food species blooms late, the development is lengthened and the natural mortality is higher. The recruitment is reduced, but the predators are less effective. This simulation put the emphasis on the fact that a successful recruitment requires an abundance of food with larval development and a mismatch in the advent of the predator.

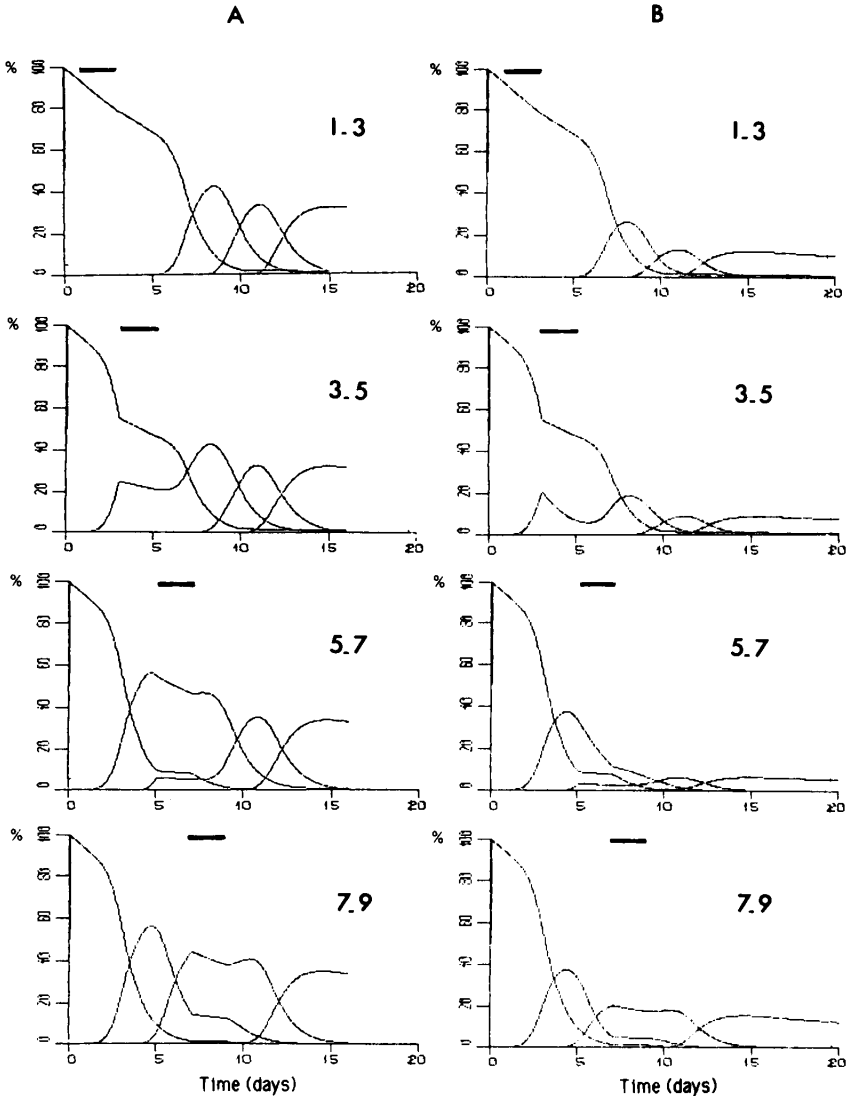


Figure 11. Effect of a starvation period of two days assumed to originate from a physical perturbation (mixing) of the food distribution on larval development and recruitment of stage 4. Food at a constant concentration except during the perturbation where it declines to zero. (A) No predator. Depending on the timing of the perturbation (---), stage 2 is delayed or extended. Table 5 gives the recruitment efficiency for the four situations. (B) Presence of a predator which feeds specifically on the stage 2 (1-3; 3-5; etc.: post hatching days subjected to the perturbation).

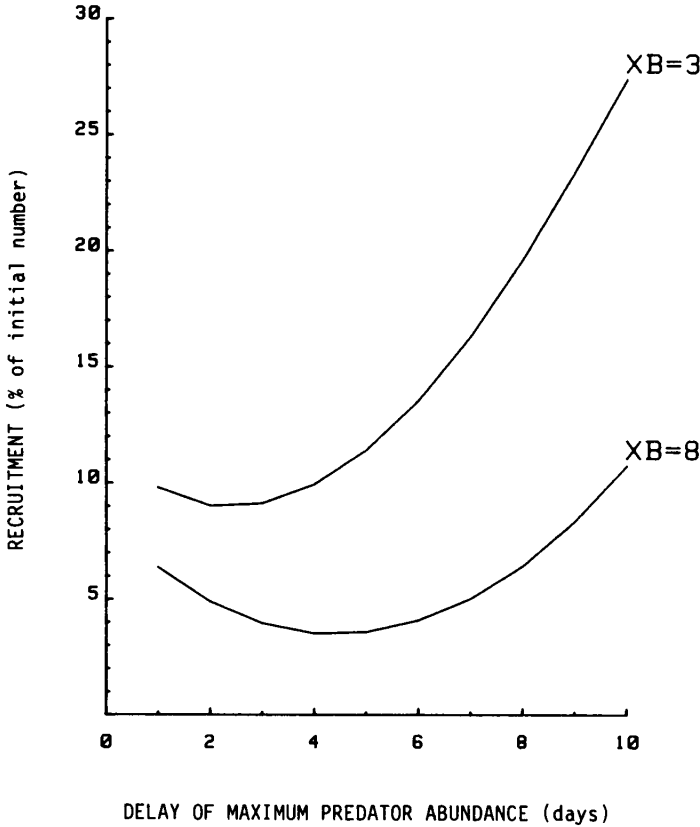


Figure 12. Effect of the maximum predator concentration (XP) relative to egg hatching, on the recruitment of stage 4 for two different delays of maximum food concentration (XB). The predator can collect every stage with the same efficiency. When the food supply is maxima early in development, the effect of a delay in the advent of predators is conspicuous.

4. DISCUSSION

This model includes two kinds of processes that control the transfer rate and ultimately the amount of larvae reaching a defined stage in their life cycle. The first type is related to the physiology: ingestion, excretion, etc. It is sensitive to rapid variations of available food through mass budget. The second, based on the larval weight, is cumulative and takes into account the different events affecting the mass budget since hatching. We have kept our representation of the mass budget very simple, and we have assumed that the temperature is constant; this holds for species with a rapid

development. Ingestion does not take into account the regulation by digestion rate and stomach volume (Lehman, 1976). It also ignores different capture efficiencies for the different food species the larvae can encounter, but there is less information in the literature for larvae than for copepods and it seems more complicated (Strathmann, 1971). Capture and growth efficiencies are important parameters which determine the fit of the larval development to the available food. They must be considered but we need better experimental evidence. The present model assumes that the food does not change in type during the larval development.

Another important control, which is not included in the model, is related to storage which damps the fluctuations of the food. This control is necessary to simulate the evolution of larvae hatching from telolecith eggs, or larvae which can accumulate stored reserves (e.g. crustaceans).

Models connecting biological and physical process usually simplify the biological coupling (Walsh, 1976; Klein and Steele, 1985). At the present time it is certainly the only thing to do because the knowledge of the connections or interactions of the processes at different time scales is not sufficient. Nevertheless, it is urgent to construct some models with processes working at different time scales because the structures which exist at different space scales should be the consequence of these processes. Jackson (1986) estimated the influence of physical process like transport on the settlement of planktonic larvae. Its conclusions depend largely on the biological process considered. The length of the pelagic period and the ability for larvae to attain competence for settling are not simple functions of time.

The quantitative estimation of the recruitment at a defined stage in the life cycle of a species must be based on a good understanding of the process controlling the different causes of mortality. However, a model will not be realistic if there is not enough knowledge of the basic processes and of the way they interact. An experimental approach well connected with a theoretical approach is necessary to focus the design of experiments on badly known aspects of biology or on processes to which the model is most sensitive. The model presented here shows that laboratory experiments on feeding and growth of specific larvae, are necessary to know the functions and values of their coefficients; however, experiments made in mesocosms are also very important because some processes are not easy to isolate from others and we only observe the results of their interactions. This is the situation when interaction of the biology and the environment is to be studied.

Models are also important for understanding the behavior of the biological variables to perturbation of their interactions by physical events. Wind stress, inducing a mixing with, for instance, changes the food concentration in the vicinity of the larvae, is not constant but has a characteristic frequency spectrum. This model shows that the effect of a perturbation in the food concentration on the outcome of the larval development is not simple because it modifies the relations of the larvae not only with their food but with their

predators. This shows that it is important to identify the trophic structure appropriate for the type of larvae studied. A second important fact shown by the model is the phase between hatching (start of the chain of events in the growth of the larvae) and perturbation.

Models can allow one to test hypotheses about recruitment success if their structure takes into account the most important biological processes and the food web to which the larva belongs. A model is necessary to understand the behavior of complex systems, especially to answer the question: Is the recruitment depending mainly on food or on predators? We suggest here that the question is not so simple and cannot be answered by observations at sea only. More experimental studies of biological process and their modifications by physical processes are needed in order to determine the shapes of each element of the puzzle of interactions which determine the recruitment success. Such studies should help to improve the model structure.

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