

Simulations of the population dynamics of *Pectinaria koreni* in a 2-D vertical advection-diffusion model of the Seine estuary

Model
Dispersion
Growth
Development
Pectinaria koreni

Modèle
Dispersion
Croissance
Développement
Pectinaria koreni

François CARLOTTI

Université Paris VI/INSU/CNRS, BP 28, F-06230 Villefranche-sur-Mer,
France.

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ABSTRACT

A mathematical model describing the population dynamics of *Pectinaria koreni*, a benthic annelid species, and the larval dispersion in an idealized two-dimensional model in the along-stream and depth dimensions of the Seine estuary, is presented. The population dynamics model takes into account the several planktonic, meiobenthic and benthic stages with their different physiological and behavioural characteristics. The physical model takes into account the horizontal residual circulation and the vertical and horizontal eddy diffusion. Model applications provide an estimate of the respective roles of development and advective drift on recruitment. A basic simulation reproduces the mean path of the population in the estuarine hydrodynamic structure. Starting from realistic initial conditions of female egg production and density of genitors, the simulation produces realistic abundances of larvae and aulophores. The model predicts an exponential larval growth in good environmental conditions. The simulated grazing rate during the pelagic larval life is $0.46 \text{ g DW m}^{-2} \text{ d}^{-1}$. Complementary simulations show that larvae resting above the recruitment area have the highest probability of recruitment. Anything which promotes larval retention (short development time, limited dispersion) favours the recruitment of juveniles. The model gives a larval biomass of 6 g DW m^{-2} sinking to the bottom, 90 % of which fail to reach the recruitment area.

RÉSUMÉ

Simulations de la dynamique de population de *Pectinaria koreni* dans un modèle 2D de l'estuaire de la Seine.

Un modèle mathématique de la dynamique de population et de la dispersion larvaire de *Pectinaria koreni*, une espèce benthique d'annélide, est présenté dans une structure bidimensionnelle profondeur-distance de l'axe longitudinal de l'estuaire de la Seine. Le modèle de dynamique de population prend en compte les différents stades planctonique, méiobenthique et benthique avec leurs caractéristiques physiologiques et comportementales; le modèle physique prend en compte la circulation résiduelle de marée et la diffusion. L'utilisation du modèle permet d'estimer les rôles respectifs du développement larvaire et de l'advection sur le recrutement. La simulation de base reproduit le trajet moyen de la population dans la structure hydrodynamique estuarienne. A partir de conditions initiales réalistes (production d'œufs par les femelles, nombre de géniteurs), le modèle simule des abondances observées de larves et d'aulophores. Il prédit une croissance larvaire exponentielle dans de bonnes conditions environnementales. Le taux de broutage simulé lors de la vie larvaire pélagique est de $0,46 \text{ g poids sec m}^{-2} \text{ j}^{-1}$. Des simulations complémentaires montrent que des larves se maintenant au-dessus de l'aire des adultes ont les plus fortes probabilités de recrutement. Tout ce qui augmente la rétention larvaire (forts

taux de développement, dispersion limitée) favorise le recrutement de juvéniles. Le modèle calcule une biomasse de larves arrivant sur le fond égale à 6 g poids sec m^{-2} , dont 90 % n'atteindront pas la zone de recrutement.

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INTRODUCTION

Our understanding of the biological and physical mechanisms involved in the persistence of marine holo- and meroplanktonic populations is rapidly improving as a result of research projects developed and co-ordinated by the GLOBEC (GLOBAL Ocean ECosystem Dynamics) programme. An intensive study was conducted within the framework of the French program *Programme national du déterminisme du recrutement* (PNDR) from 1986 to 1991, in order to understand the dynamics of two populations of annelids, *Pectinaria koreni* and *Owenia fusiformis*, in the bay of Seine. This study was supported by an interdisciplinary investigation of the estuary of the Seine and the bay of Seine (Cabioch, 1986). Juveniles and adults of these two species coexist in the mouth of the river. Both species have key developmental stages in the plankton, but of different duration. Investigations into the life cycles and their links with the hydrodynamics of the estuary (Lagadeuc, 1990, 1992a and b; Lambert, 1991; Thiébaud *et al.*, 1992; Thiébaud, 1994) have helped to understand the recruitment of both species.

Like the United States GLOBEC programme (Eckman, 1994), the PNDR programme sustains modelling studies for different projects. In this paper, a numerical model of the life cycle of *Pectinaria koreni* in an idealized 2-dimensional longitudinal section of the Seine estuary is presented. Models designed to describe the population dynamics of holo- and meroplanktonic species in space and time have already been developed by Wroblewski (1982), Davis (1984), Possingham and Roughgarden (1990) and Hill (1990); however, in those models the biological processes are often reduced to stage survival, transfer rate between stages and adult reproduction. There are two reasons for this: firstly, there is a lack of information on the feeding and metabolic rates of planktonic larval stages, especially for meroplanktonic species; and secondly, computer capacities are rapidly exhausted by the requirements of the physical portion of the model.

It is well known that the oceanic physical environment affects population dynamics partially through individuals. Nevertheless, the biological processes at the individual level are not represented in most models. With a number of colleagues, the author elaborated a biological model describing the life cycle of copepods (Carloti and Sciandra, 1989; Carloti and Nival, 1992a) in which the development of organisms through successive stages is controlled by their growth. This approach owed its success to the numerous results of laboratory and field tests on copepods described in the literature, and to the relative ease with which some of the model predictions could be experimentally verified (Carloti and Nival, 1992b).

The primary purpose of the present paper is to synthesize current knowledge of the biological processes of mero-

planktonic larvae in a similar manner and to incorporate the findings into a coupled physical and biological model. For these reasons, the physical model is simple, taking the form of an idealized 2-dimensional model in the along-stream and depth dimension of the Seine estuary (Fig. 1). The population dynamics model takes into account the several planktonic stages with their different physiological and behavioural characteristics. The model simulations are compared with the results of field studies by Lagadeuc (1990), Lambert (1991) and Thiébaud (1994) on the space and time distribution of swarms of pelagic larvae and benthic post-larvae and juveniles in the eastern bay of Seine. The sampling stations of the field studies are presented in Figure 1.

The model

A 2-dimensional model of the Seine estuary

The investigations of polychaete larval dispersal in the bay of Seine benefited from knowledge of the general

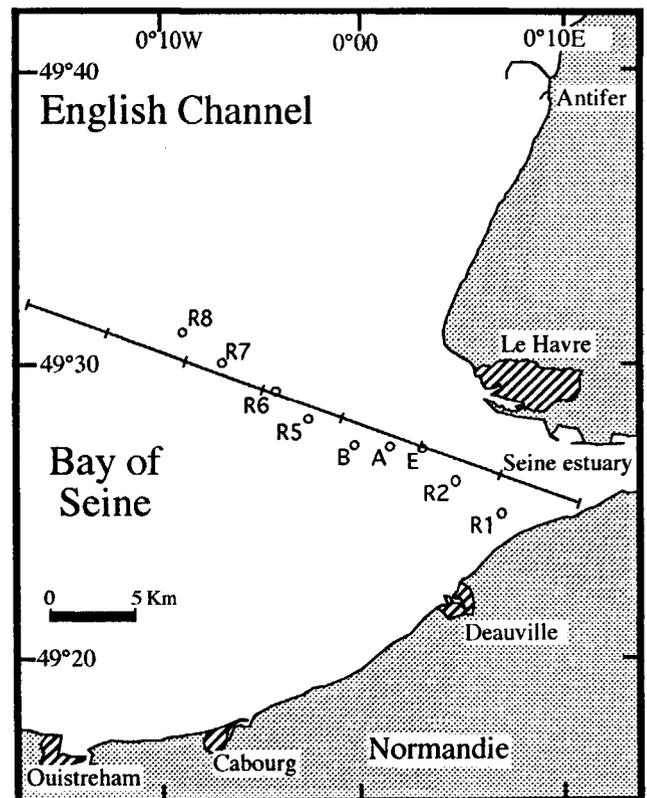


Figure 1

Longitudinal direction of the physical model (straight line) and location of sampling stations in the study area of the bay of Seine (see Lagadeuc, 1992a for details).

Direction longitudinale du modèle physique (ligne droite) et position des stations d'échantillonnage dans l'aire d'étude en baie de Seine (voir Lagadeuc, 1992a)

hydrodynamic conditions in the bay (Salomon, 1986; Le Hir *et al.*, 1986). The circulation of the Seine estuary is a 2-layered system with a net downstream flow of less saline water moving out at the surface and a net upstream non-tidal flow of a more dense ocean water going upstream along the bottom (Salomon, 1986). For the model, an idealized 2-dimensional along-stream section of the Seine estuary in the direction W-NW (*see* Fig. 1) is considered, going through the main location of the benthic adult population of *Pectinaria* (called station A) and with the normal drifting direction of the larvae, without wind (*see* Fig. 3 of Lagadeuc *et al.*, 1990; and Fig. 1 of Thiébaud *et al.*, 1992). The spatial extent of the model (Fig. 2) is large enough to avoid boundary effects. The upstream boundary (0 km) corresponds to the mouth of the Seine, the downstream boundary is 35 km W-NW of this. Observations showed that the larvae rarely drifted beyond 30 km, except in windy conditions, when they are lost to the population (Lagadeuc, 1990; Thiébaud, pers. comm.). The adults' area (around the station A) is located between 10 and 15 km seaward (*see* Fig. 1), and only individuals which settle on this area will develop and survive (*see* Fig. 2). The height of the model water column is constant at 30 m. The model uses a grid size of 1 km in the horizontal direction and 5 m in the vertical direction. This fine spatial resolution is necessary to avoid numerical diffusion of the larvae. At the bottom, an additional benthic layer permits settled individuals to accumulate.

The physical processes take into account horizontal tidal residual circulation, and vertical and horizontal eddy diffusion. Because the pelagic life time of *Pectinaria* is much longer than a tidal period, the effect of tides is not taken into account. In the model, the horizontal advection term is a depth-dependent velocity u . Salomon (1986, Fig. 6) gives a vertical profile of tidal residual currents at station

A (Fig. 2) which is used for the velocity u . This flow profile is assumed to be constant over time and horizontal distance. The larvae, as well as any particles, are randomly dispersed by the process of eddy-diffusion (Okubo, 1971). This process can be important in the cohort dynamics of benthic species (Strathmann, 1974). The coefficient of eddy diffusion depends on the scale of the observation. By using Okubo's log-log graph (1971, his Fig. 4) with the dimension of the grid unit, horizontal and vertical coefficients of eddy diffusion equal to 3.49×10^4 and 86.4×10^1 respectively, are obtained. The advection-diffusion reaction equation is presented in Table 1. The numerical scheme is explained later.

Model of larval development

During its life cycle, *Pectinaria* goes through three different phases: planktonic, meiobenthic and benthic (Fig. 3). In the bay of Seine, larval cohorts of *Pectinaria* are usually observed in May and June. Lagadeuc (1990, 1992b) estimated the larval life to be around 15 days and distinguished two trochophore stages, three metatrochophore stages and one aulophore stage. Trochophore and metatrochophore stages occupy the upper part of the water column (Lagadeuc, 1992a and b). Following an ontogenetic vertical migration towards the sea bottom effected by the aulophore stage (stage 6 in Lagadeuc, 1992a, b), the individuals become meiobenthic post-larvae, seeking a favourable substrate for settlement. The duration of the post-larval stages is estimated to be around two weeks (Lambert, 1991), but varies depending on the substrate and the hydrodynamics above the bottom. The metamorphosis from aulophore to post larvae is a lengthy process, with a progressive building of the sandy tube (Lambert *et al.*, 1996). Aulophores with sandy

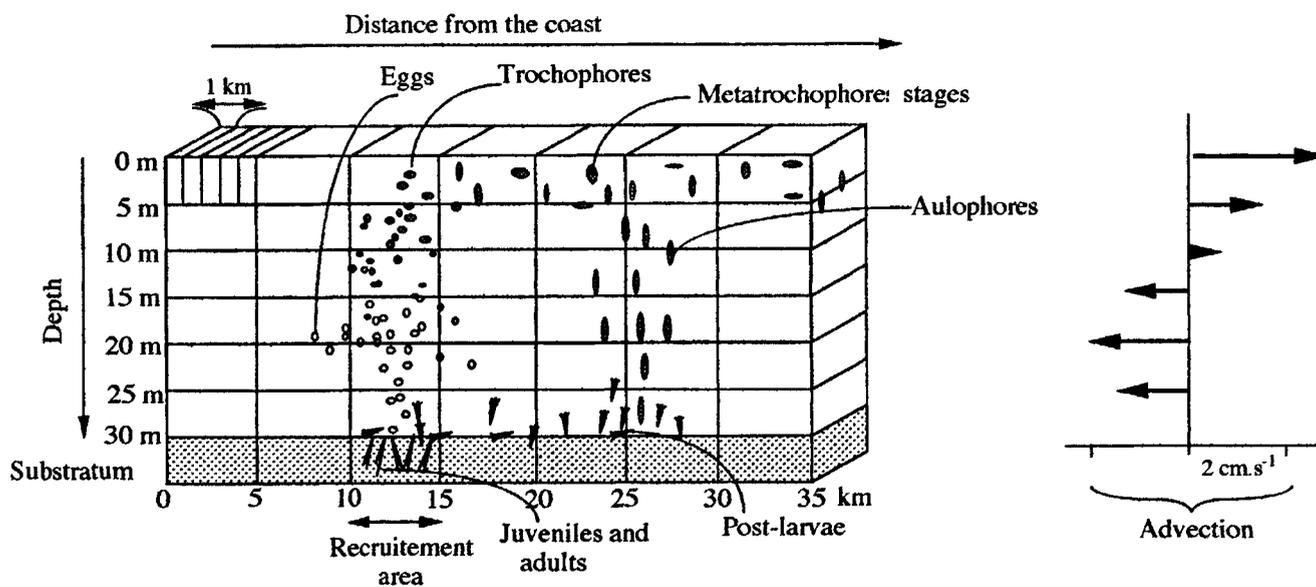


Figure 2

Schematic representation of the 2-dimensional space and of the processes that influence the distribution and abundance of larvae during the pelagic and meiobenthic phases. The vertical profile of residual tidal currents comes from Salomon (1986)

Schéma de l'espace bidimensionnel et des processus qui influencent la distribution et l'abondance des larves durant les phases pélagiques et méio-benthiques. Le profil vertical de courants résiduels de marées provient de Salomon (1986).

Table 1

Differential equations and processes. *i*: stage; *j*: age-class. *F*: food; *Te*: temperature; *W_{i,j}*: weight; *N_{i,j}* = abundance. *P1_i* to *P12_i*: biological parameters (see Table 2). *u*: horizontal advection, *w*: vertical speed of organisms, *K_x*, *K_z*: horizontal and vertical eddy diffusivities.

Differential equations		Formulations
Spatial processes		
All age-classes (<i>j</i>) in stage (<i>i</i>)		$\frac{\partial N_{i,j}}{\partial t} + u \frac{\partial N_{i,j}}{\partial x} + w \frac{\partial N_{i,j}}{\partial z} - K_x \frac{\partial^2 N_{i,j}}{\partial x^2} - K_z \frac{\partial^2 N_{i,j}}{\partial z^2} = S_{i,j}$ (1)
Demographic processes		
Eggs (<i>i</i> = 1)		$S_{1,1} = (L_{6,j} N_{6,j}) - (T_{1,1} + M_{1,j} + C_{1,j}) N_{1,j}$ (2)
St. 2 to 5 (1st age-class)		$S_{i,1} = \left(\sum_{j=1}^n T_{i-1,j} N_{i-1,j} \right) - (T_{i,1} + M_{i,1} + C_{i,j}) N_{i,1}$ (3)
St. 2 à 5 (other age-classes)		$S_{i,j} = - (T_{i,j} + M_{i,j} + C_{i,j}) N_{i,j}$ (4)
Adults (1st age-class)		$S_{6,1} = \left(\sum_{j=1}^n T_{5,j} N_{5,j} \right) - (M_{6,1} + C_{6,1}) N_{6,1}$ (5)
Adults (other age-classes)		$S_{6,j} = - (M_{6,j} + C_{6,j}) N_{6,j}$ (6)
Growth		
Eggs (<i>i</i> = 1)		$\frac{dW_{1,1}}{dt} = 0$ (7)
Other stages (<i>i</i> = 2 to 5)		$\frac{dW_{i,j}}{dt} = B_{i,j}$ (8)
Adults (<i>i</i> = 6)		$\frac{dW_{6,j}}{dt} = B_{6,j} - MR_{6,j}$ (9)
Processes	Units	Formulations
Growth		
Larvae and Post-larvae (<i>i</i> = 2 to 4)		
Ingestion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$I_{i,j} = (P1_i F) P2_i (W_{i,j}^{P3_i})$ (10)
Egestion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$EG_{i,j} = (1 - P4_i) I_{i,j}$ (11)
Excretion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$EX_{i,j} = (P5_i W_{i,j}) + (P6_i I_{i,j})$ (12)
Growth rate	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$B_{i,j} = I_{i,j} - EX_{i,j} - EG_{i,j}$ (13)
Juveniles and adults (<i>i</i> = 5 and 6)		
Ingestion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$I_{i,j}$ function of sediment working and <i>Te</i> (see text)
Egestion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$EG_{i,j} = (1 - P4_i) I_{i,j}$ (14)
Excretion	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$EX_{i,j} = P6_i I_{i,j} 10 \left(\frac{W_{i,j}}{P5_i} \right)$ (15)
Reproduction	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$MR_{6,j} = (P7_6 W_{6,j}) \text{ if } MR_{6,j} > P8_6$ (16)
Growth rate	$\mu\text{g d}^{-1}.\text{ind}^{-1}$	$B_{i,j} = I_{i,j} - EX_{i,j} - EG_{i,j} - MR_{i,j}$ (17)
Specific growth rate	d^{-1}	$SB_{i,j} = \frac{B_{i,j}}{W_{i,j}}$ (18)
Dynamics		
Mortality	d^{-1}	$M_{i,j} = P9_i$ (19)
Stage duration	<i>d</i>	$SD_i = P10_i$ (20)
Transfer	d^{-1}	$T_{i,j} = P11_i \text{ if } \geq SD_i$ (21)
Egg-laying	d^{-1}	$L_{6,j} = \left(\frac{MR_{6,j}}{W_{1,1}} \right)$ (22)

grains and post-larvae have been found in the water column (Thiébaud, 1994; Lambert *et al.*, 1996; Olivier *et al.*, in press). The time which elapses between egg production by the adults and the settlement of the post-larvae on the same bottom area, is around one month. After final settlement, each animal develops into juvenile and adult forms, both of which have a duration of six months. Precocious organisms mature in the following spring while the others remain until the following year before reproduction.

In the present model, only six stages (*see* Fig. 3) are considered. Trochophore and metatrochophore stages are grouped, the assumption being that morphological differences but not physiological and behavioural ones exist between them. Post-larval forms are grouped in a single stage.

Larval behaviour

The vertical distribution of larval abundances of *Pectinaria* depends on several internal and external factors (Lagadeuc, 1990). The main external factors are turbulence, which is strongly dependent on the wind speed and bottom effects, and salinity, which directly influences the stability of the water column. The larvae are able to regulate their position by active swimming (Chia *et al.*, 1984). Swimming orientation responds to density, salinity, light and gravity (Lagadeuc, 1990). In the model, only speeds of active vertical swimming are taken into account. Eggs and the pelagic larvae swim upwards, the aulophores downwards. Konstantivova (1969, in Chia *et al.*, 1984) gives swimming speeds of trochophores and metatrochophores equal to 0.17 and 0.25 cm s⁻¹. The latter value for the pelagic larvae is used in the present model, which assumes the same vertical speed for the eggs due to buoyancy. The aulophores make an ontogenetic migration to the bottom. The cause of this migration is still unknown and could be simple passive sinking due to higher density from their secreted cone-shaped tube, as suggested by Butman (1989) for *Pectinaria gouldii*. The present model assumes a downward speed of the aulophores equal to 0.25 cm s⁻¹, which is in the range of fall velocities of non-swimming larvae of annelids given by Butman (1989). When aulophores metamorphose into post-larvae, the individuals slowly acquire morphologic characteristics of benthic life by growing mouth tentacles (Lambert, 1991). Nevertheless, because this metamorphosis is slow, young post-larvae are frequently sampled in the water column. Hannan (1984) showed that the resuspension of the annelid *Mediomastus ambiseta* prior to final settlement is an active process. Evidence of similar behaviour in *Pectinaria koreni* has been obtained by sampling with plankton nets above the sea bed, and by collecting individuals with sand grains attached to the anterior ends of their tubes (Olivier *et al.*, in press). The same authors show that passive and active processes are involved in this stratification. The individuals test the substrate, by searching adequate sand grains for their tubes, and are able to move by using fluid flows above the bottom. Olivier *et al.* (in press) have observed the size-frequency distributions of organisms found in the water column: the larger the animals, the less frequent they were in the water column. In the present model, the speed of sinking to the bottom is presumed to increase with the age of the post larvae. Also, for larvae reaching the bottom, the probability of returning into the

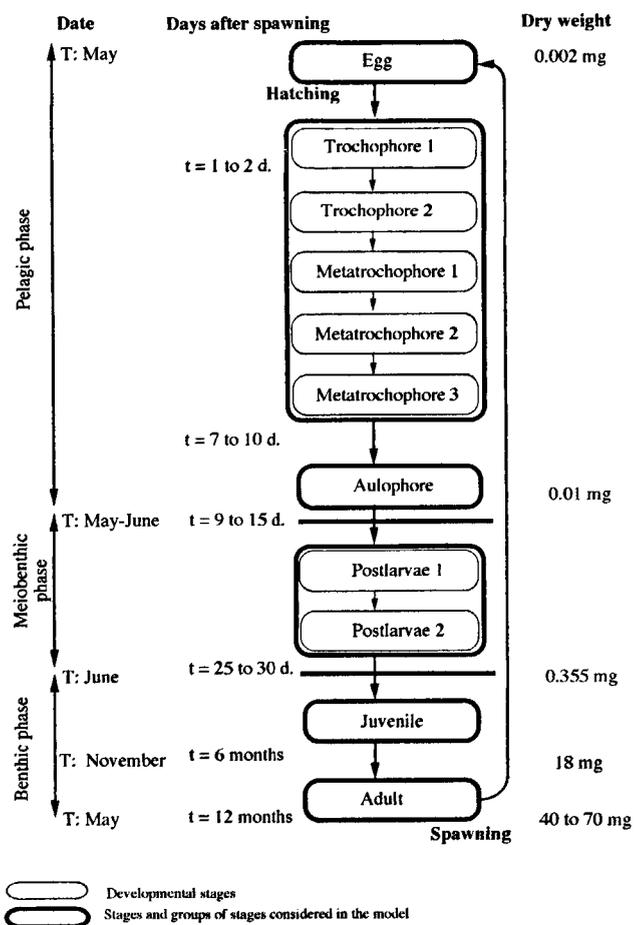


Figure 3

Developmental stages during the life cycle of *Pectinaria koreni*. The different pelagic stages have been described by Lagadeuc (1992b). In the model, the trochophore and metatrochophores stages have been grouped as well as the post-larval stages.

Stades de développement du cycle de *Pectinaria koreni*. Les différents stades pélagiques ont été décrits par Lagadeuc (1992b). Dans le modèle, les stades trochophores et métatrochophores (cercles gras) ont été regroupés ainsi que les stades post-larvaires.

water column decreases with the age of the post-larvae (Fig. 4). The maximal speeds for entering and leaving the sediment are both equal to 0.125 cm s⁻¹. If the individuals enter the right adult area (distance between 10 km and 15 km), they settle on it. Individuals settling elsewhere die.

Demographic processes

The basic structure of the population model is similar to that described by Carlotti and Sciandra (1989) and Carlotti and Nival (1992a) for copepods. The development of organisms can be divided into two nested levels. The first of these corresponds to the different development stages during life. The second corresponds to the age classes within each stage. In each age class, animals have the same age in the stage, the same weight and the same metabolic rates (*see* details in Carlotti and Nival, 1992a).

The original copepod model (Carlotti and Sciandra, 1989) couples demographic processes (mortality, transfer) to the processes involved in the energy budget. The linkage rela-

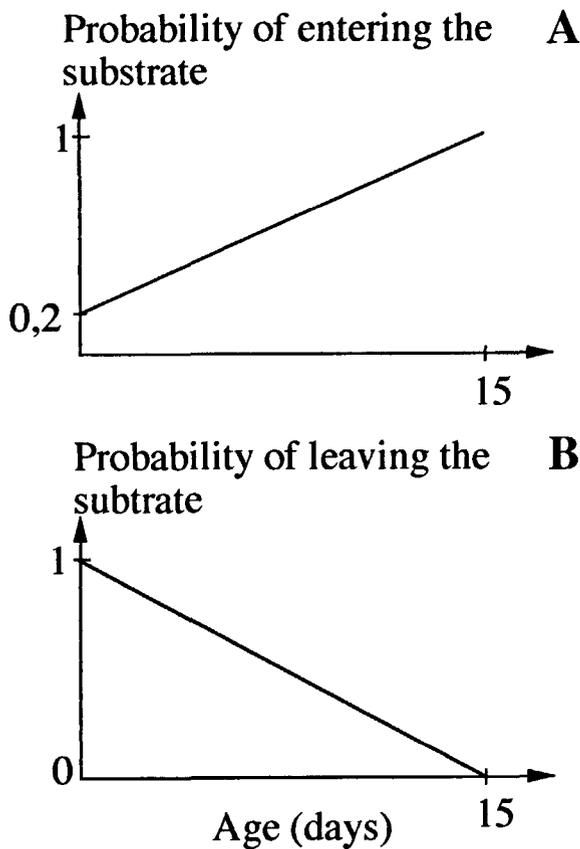


Figure 4
 Age-dependent settlement processes. The probability of a postlarva entering or leaving the substrate is a combination of two simple linear functions (A and B) which depend on the age of individuals.

Processus de fixation dépendant de l'âge. La probabilité de rester ou de quitter le substrat est la combinaison de deux fonctions linéaires simples (A et B) qui dépendent de l'âge des individus.

tionships are based on experimental features described in the literature, and can be tested only if there is a good knowledge on the parameter values of the physiological functions, and available data sets on the development of cultiva-

ted populations in a controlled environment. There also exist some empirical rules relating to copepod development, *i.e.* equi-proportional development (McLaren, 1986). We lacks however, sufficient information on the larval stages of annelids to test the assumptions of such a model. In the present model, growth and stage development are uncoupled (Fig. 5), except for egg production which depends on the material invested for the oogenesis, and on the external forcing variables (temperature, food and predators).

The processes taken into account in the model and the differential equations are presented in Table 1. The equations give the variations in number of individuals, $N_{i,j}$, in an age-class (j) of a stage (i), in a given spatial position (x,z), and in the dry weight $W_{i,j}$ of the individuals.

The phytoplankton concentration is assumed to be 18 mg Chla m^{-3} , a concentration observed in the bay of Seine (Thiébaud, 1994). The temperature function is a sinusoidal fit to average temperatures in the bay of Seine from RNO (1981). Temperatures vary between 5 °C in February and 17 °C in August.

Table 2 gives the values of parameters of demographic processes. The natural mortality is considered stage-dependent and not density-dependent. A rate of 0.06 d^{-1} for the eggs and pelagic stages is used by comparison with mortality rates of other pelagic zooplankton organisms (Strathmann, 1985, for review; Hansen, 1993). For the aulophores and post-larvae, the present model assumes that the mortality rate is 0.23 d^{-1} , a mean value of mortality rates calculated at the sampling stations A, B, E and R7 during the first weeks of life on the substrate (Lambert, 1991). The mortality rates of juveniles and adults are taken from field estimations (Irlinger *et al.*, 1991). The changes of stage occur after a given duration. Age durations could be related to the food and the temperature, following Behleradek's functions (Anger *et al.*, 1986), but as in the presented simulations food is constant and optimal everywhere, and temperature is nearly constant during the larval life, the stage durations are constant. The total number of eggs produced is equal to the reproductive matter invested by a mature female, divided by the egg weight. The present model assumes

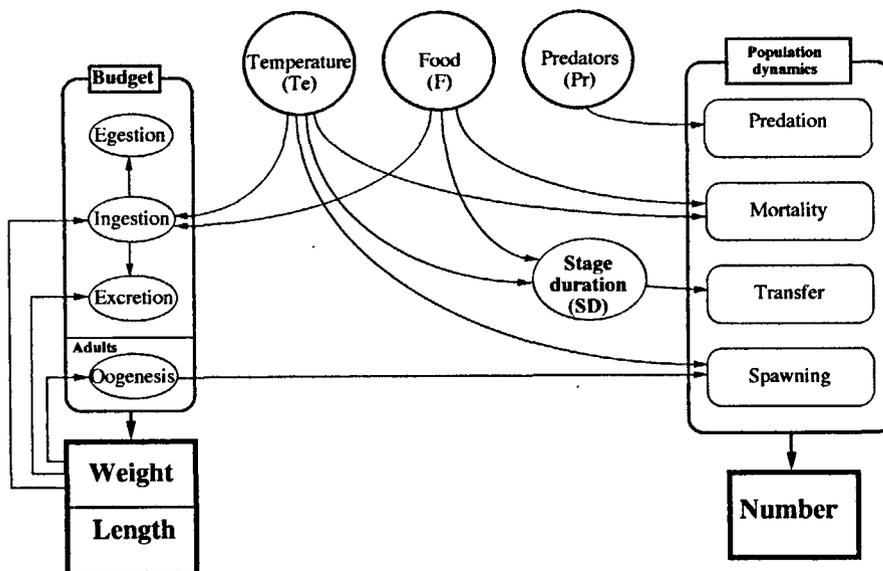


Figure 5
 Conceptual diagram of the model. Processes and variables (symbols in brackets) are connected by arrows denoting relationships detailed in Table 1 and in the text.

Diagramme conceptuel du modèle. Processus et variables sont connectés par des flèches représentant des relations fonctionnelles expliquées dans le tableau 1 et dans le texte.

Table 2

Definitions and values of parameters used in the model.

Parameters	Unit's Definitions	Eggs	Pelagic larvae.	Aulophores	Post-Larvae	Juveniles	Adults	
Stage number		1	2	3	4	5	6	
Ingestion								
P1	d ⁻¹	Maximum ingestion rate		0.4	3	3	*	*
P2	sd	Coefficient of temp. function		1	1	1	*	*
P3	sd	Allometric exponent		0.42	0.7	0.7	*	*
Egestion								
P4	sd	Assimilation rate		0.7	0.7	0.7	0.225	0.225
Excretion								
P5	d ⁻¹	Basal excretion rate		0.04	0.04	0.04		
P5	mg DW	Weight of reference					30	30
P6	sd	Coefficient of proportionality		0.36	0.23	0.23	0.01	0.01
Reproduction								
P7	sd	% of weight invested in eggs						50
P8	mg DW	Critical spawning weight						40
Mortality								
P9	d ⁻¹	Mortality rate	0.06	0.06	0.23	0.23	0.03	0.005
Transfer								
P10	d	Stage duration at 9 °C	0.75	7.5	3	12.5	160	
P11	sd	Maximum transfer rate	2	2	2	2	2	
Velocities								
w	cm.s ⁻¹	Vertical velocity	0.25	0.25	-0.25	**	-0.25	

sd: without dimension

*: special functions for juveniles and adults (see text)

**: age-dependent function (see text)

that egg production only occurs above a certain temperature minimum. Spawning is probably caused by a thermic stimulus, although this is not yet fully understood (Irlinger *et al.*, 1991).

Bioenergetic processes

At each time step, the model calculates the individual energy budget (ingestion, egestion, excretion, and for adults, reproduction) in each age-class of each stage, as well as the probabilities of natural mortality, predation and transfer to the next stage. Definitions and values of parameters are given in Table 2. The eggs ($i = 1$) have a constant weight of 0.002 mg. The other stages feed and have metabolic wastes. Trochophores and metatrochophores of *Pectinaria* (grouped in the model as pelagic larvae, $i = 2$) are planktotrophic (Strathmann, 1987). Little is known about the other processes linked to growth (Dobbs and Scholly, 1986). In the model, ingestion is assumed to be a linear function of the food concentration and an allometric function of weight. This relationship has been described for numerous planktonic organisms (Moloney and Field, 1989). Although filtration by trochophore larvae differs from that of plutei (Strathmann *et al.*, 1972), the model uses the exponent 0.42 obtained for plutei by McEdward and Strathmann (1987). As the larval duration is short, temperature conditions are assumed to be optimal for the larval feeding. The assimilation rate is set at 70 %. Metabolic wastes are separated into two terms: the routine metabolism proportional to weight, and the active metabolism proportional to the ingestion rate (around a third of the ingested material). There appears to be nothing in the literature concerning the values of these processes; the model uses values estimated for the nauplii of

copepods as explained in Carlotti and Sciandra (1989). With these parameter values, the model simulates a weight of 0.01 mg DW for young aulophore larvae, which is realistic. The functions for the metabolic process of aulophores and post-larvae are similar to those of larvae, with some adjustment to provide realistic post-larval weights. Estimates of weights are obtained from the relationship of dry weight to cephalic width established by Nicolaidou (1983). The smaller values of cephalic width measured for post-larvae are 0.3 mm, and the larger ones around 1 mm (Vovelle, 1973).

The benthic phase of *Pectinaria* is better known, and there is a great deal of information on other deposit feeders (Fauchald and Jumars, 1979). Some mathematical models of particle selection have been developed (Jumars *et al.*, 1982). In this paper, a similar approach is followed, but it is incorporated in a more complete representation of energy budget. The ingestion function for juveniles and adults depends on food availability, individual weight and temperature. Dobbs and Scholly (1986) related the rate of sediment working (RSW, in g of sediment per hour) to the cephalic width (CW, in mm) by

$$RSW = 10^{(0.556 CW - 0.933)}$$

Using Nicolaidou's allometric relationship (1983) between dry weight (W in mg) and cephalic width,

$$W = 0.3554 CW^{2.6588}$$

it is possible to relate the rate of sediment working to the dry weight. This calculation gives a rate around 1 kg per month, which is in agreement with direct estimates

(Nichols, 1974). Gordon (1966) demonstrated that the ingestion rate is proportional to the rate of sediment working and the concentration of organic matter (COM).

Nicolaidou (1983) showed that the activity needed for working the sediment is temperature-dependent. In this model, the author use a beta function:

$$f(T) = \left[\left(\frac{T}{T_0} \right) \left(\frac{T_s - T}{T_s - T_0} \right) \left(\frac{T_s - T_0}{T_0} \right) \right]^a$$

The function reaches a maximum at the optimal temperature T_0 , taken as 17 °C. Above this value, the curve shows a sharp decrease, and activity stops at 22 °C. Below 17 °C, activity increases exponentially with temperature. The exponent of the function fixes the threshold for the feeding activity and adjusts the rate of increase.

Deposit feeders ingest sediment, but a large fraction is lost through the pseudo-defecation. Dobbs and Whitlatch (1982) estimate that 77.5 % of worked sediment is not ingested. There is no information on the metabolic wastes of *Pectinaria*. Metabolism is considered dependent on ingestion and weight. The relationship linking metabolism and weight defines a proportionate metabolic loss which increases with weight. Individuals increasing their weight from 20 to 40 mg DW, will increase their losses from 4.6 % to 20 % of the ingestion rate. Mature females ready for spawning have a cephalic width greater than 5.5 mm (Nicolaidou, 1983; Elkaim and Irlinger, 1987). Following Nicolaidou's relationship, this cephalic width corresponds to organisms heavier than 40 mg DW. In the model females exceeding this weight are able to spawn. The number of oocytes in the thoracic cavity has been calculated at between 5000 and 15000 per female (Irlinger *et al.*, 1991). Grémare *et al.* (1989) estimated the weight specific reproductive output to be 35 % for *Capitella capitata*. The author suppose that this quantity represents 50 % of the total weight of a female.

Numerical scheme

The mathematical model calculates in a first step the dispersion of organisms and in a second step the bioenergetic and demographic processes. The advection-diffusion equations of the concentration $N_{i,j}(x,z)$ (for each age-class j of stage i) of larvae at the position (x,z) are solved numerically by a finite difference method with an upwind scheme for the advection terms and a centred scheme for the diffusion terms with a time step of 5 min. At the surface, there is no sinking or mixing across the upper boundary; at the bottom there is no mixing, but larvae sink or swim out of the sediment boxes. The horizontal boundaries, close to the mouth of the Seine and seawards, are far enough from the adult habitat for the loss of larvae at this boundary to be small. The model uses an artificial absorption of larvae at these boundaries (Possingham and Roughgarden, 1990).

For each spatial box of the model, a new average individual weight $W_{i,j}(x,z)$ (for each age-class j of stage i) is calculated from values of larval transfer and larval weights. For the biological part, the system of equations for the stage dynamics and growth equations is solved by a fourth-order Runge-Kutta numerical integration.

RESULTS

The baseline case

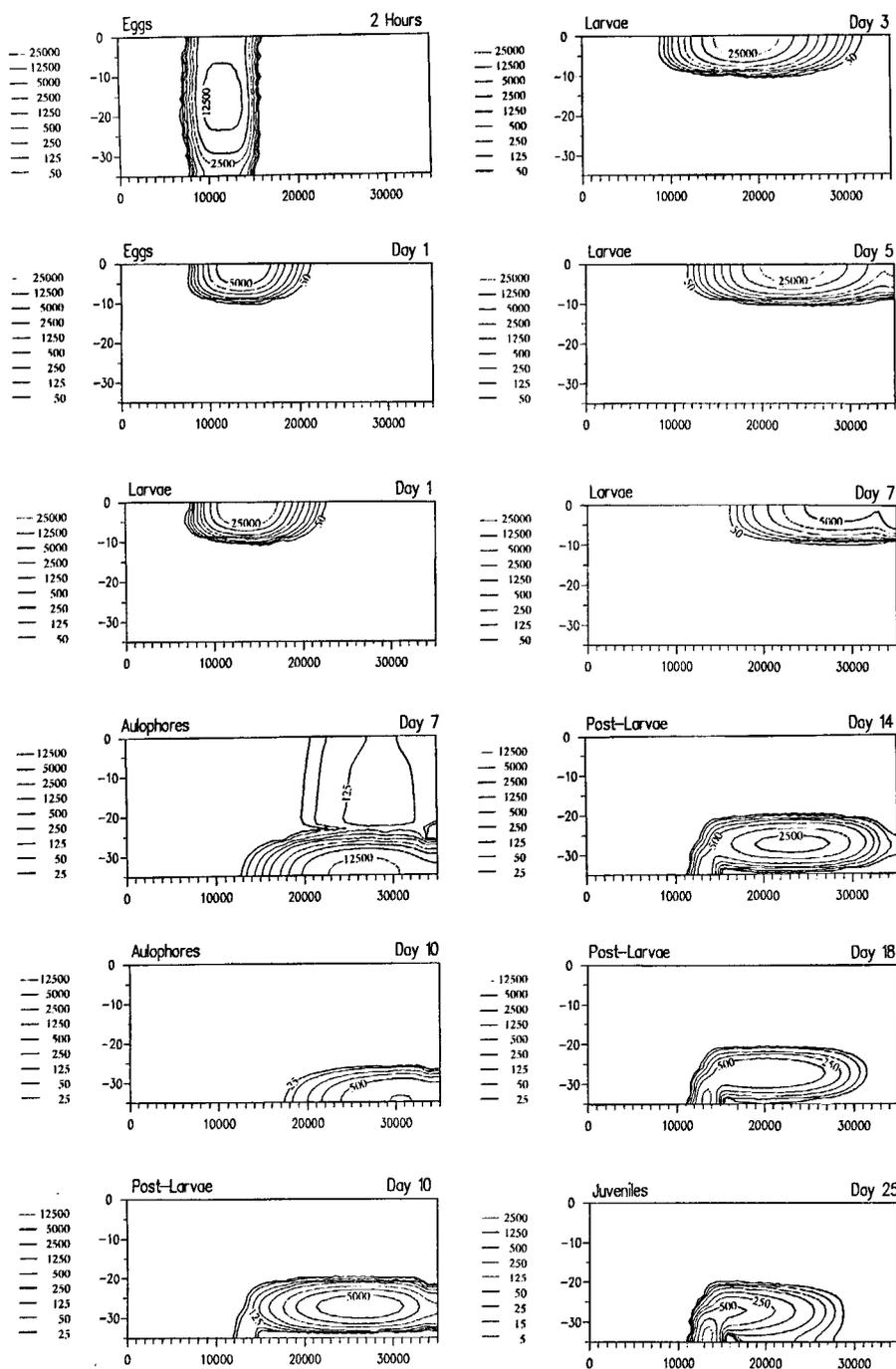
Figure 6 illustrates the simulated spread of individuals during the first 25 days of their pelagic life. The simulations begin with $5 \cdot 10^5$ eggs m^{-2} , the production of an average density of 50 females m^{-2} , as observed on the substrate of the Seine estuary (Gentil *et al.*, 1986; Lagadeuc, 1990; Lambert, 1991; Thiébaud, 1994). Egg release is instantaneous and occurs on 23 May, the date of the second spawning period in 1987. Afterwards, the buoyant eggs quickly spread into the water column overlying the adult area. Hatching of larvae occurs mainly at depth, and larvae and non-hatched eggs are located in the surface layers after one day. Simulated distribution patterns of larvae show a surface seaward displacement from day 1 to day 7, until their metamorphosis in aulophore between day 7 and day 10. In Figure 7 the simulated larval densities are compared with Lagadeuc's data (1992a, b) for stations R5 and R8 situated near the 17th and 26th km of the transect (*see* Fig. 1). Lagadeuc used fixed sampling stations to study the vertical distribution of larvae (Lagadeuc, 1992a), and horizontal transects in the bay of Seine to follow the larval transport (Lagadeuc, 1992b). The larval production originated from a spawning occurred between 23 May and 27 May 1987. From Lagadeuc (1992a, his Fig. 3), the peak values of observed larval densities at the depth 5 m, for the stations R5 and R8 are used in the model; from Lagadeuc (1992b, his Figs. 4, 9, 12), the observed values at the nearest position of station R8 are used. Despite the simplicity of the physics in the model (no wind, no tide), the simulated larval densities are in the range of observed values over the first days. Lagadeuc (1992a) observed that the larval patch mainly stayed above 10 m depth. The vertical distribution predicted by the model is consistent with these observations.

The larvae are supposed to feed on phytoplankton and not to be food-limited. They develop over a period of about 25 days through pelagic larvae, aulophores and post-larvae before settling in the area of the adult population as juveniles. The main patch of sinking aulophores is located between 25th and 32nd km at day 7, which represents a mean distance of 16 km from the adult area. The average distance of larval transport observed without strong wind stress is between 5 and 10 miles (Lagadeuc, 1992b). The simulated aulophore densities in the water column and above the substrate respectively are in the order of 125 individuals m^{-3} and 5,000 individuals m^{-3} , which is comparable to Thiébaud's observations (1994, Fig. 40). These aulophore larvae, which gradually metamorphose into post-larvae, are driven towards the mouth of the estuary by the bottom current. By day 10, the first post-larvae reach the adult area and settle on the substrate, although the centre of the post-larval patch is still located 14.5 km distant from the recruitment area. Post-larval densities simulated on day 18 near the bottom are above 500 individuals m^{-3} , whereas Thiébaud (1994) observed 800 individuals m^{-3} . Highest densities are found above the substrate due to the post-larvae's ability to return into the water column, in agreement with the observation by Olivier *et al.* (in press). In the model,

Figure 6

Simulated dispersion and development of the larval cohort resulting from the release of 5×10^5 eggs m^{-2} by the adults fixed in the suitable habitat (between 10th and 15th km).

Simulation de la dispersion et du développement de la cohorte larvaire résultant de l'émission de 5×10^5 œufs m^{-2} par les adultes fixés sur leur habitat (entre les kilomètres 10 et 15).



post-larvae metamorphose into juveniles, either on the bottom or in the water column. Juveniles have a higher sinking velocity than post-larvae due to their higher weight, and they settle in high numbers. On day 19, the densities of the recruited, newly metamorphosed juveniles are 13,500 individuals m^{-2} and reach 28,000 individuals m^{-2} by day 25. Lambert (1991, Fig. 39) gives a maximum density of 25,000 individuals m^{-2} in 1987. Post-larvae and juveniles settled on unfavourable bottom, outside the adult area die.

The temporal change of stage abundances of a group of individuals produced by 1 m^2 of adult genitors, is shown in Figure 8. Although the eggs were spawned simultaneously, the model simulates a variability in the stage development, which induces temporal overlaps between stages. About 4 %

of the initial egg production develop into the juvenile stage, and only half of these juveniles arrive in the recruitment area.

The same simulation delivers the mean individual growth in the successive stages (Fig. 9). As not all the individuals transfer simultaneously into the next stage, there are temporal overlaps between the growth curves. Laggards in a stage have lower growth rates than individuals which quickly develop into the following stage. The results suggest that the average individual growth is exponential during the larval life.

The simulated weight for post-larvae is initially 0.025 mg DW at day 8, and reaches 0.25 mg DW at day 20. Following Nicolaidou's allometric relationship (1988), these weights correspond to individual cephalic diameters varying from 350 μm to 900 μm . Lambert *et al.* (1996,

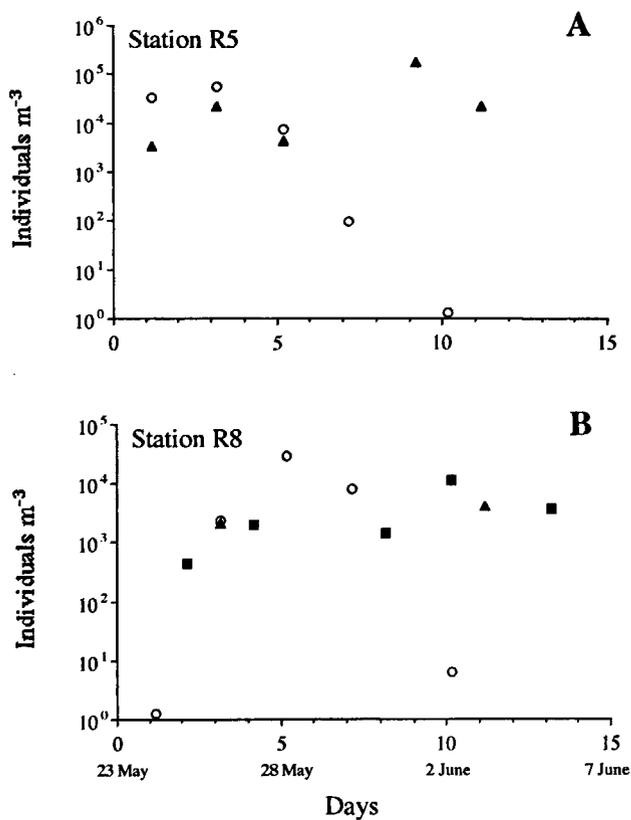


Figure 7

Comparisons of simulated (circles) and observed (triangles and squares) larval densities at 5 m deep at the stations R5 (A) and R8 (B) located near of the 17th and 26h km of the transect considered in the model. Data from Lagadeuc (1992a and b) were obtained from fixed station samplings (triangles) and a horizontal transect (squares) in the bay near of station R8.

Comparaison des densités larvaires simulées (cercles) et observées (triangles et carrés pleins) à la profondeur 5 m aux stations R5 (A) et R8 (B) proche des positions 17 km et 26 km du modèle. Les données de Lagadeuc (1992a and b) ont été obtenues lors d'échantillonnage en station (triangles pleins) et lors d'échantillonnage de surface en continu (carrés pleins) proche de la station R8.

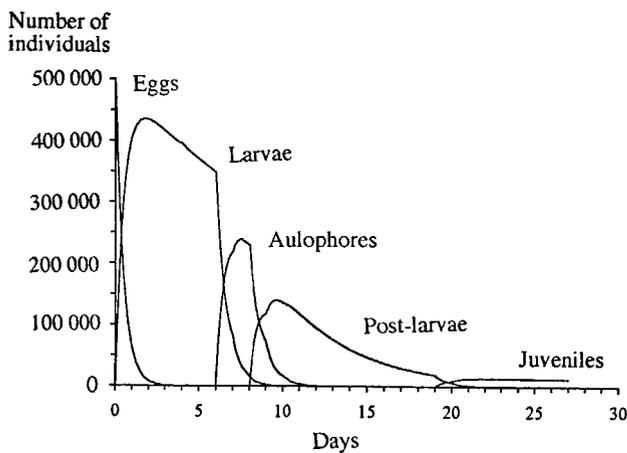


Figure 8

Simulated survival and development of individuals produced by 1 m² of genitors.

Survie et développement simulés des individus produits par 1 m² de géniteurs.

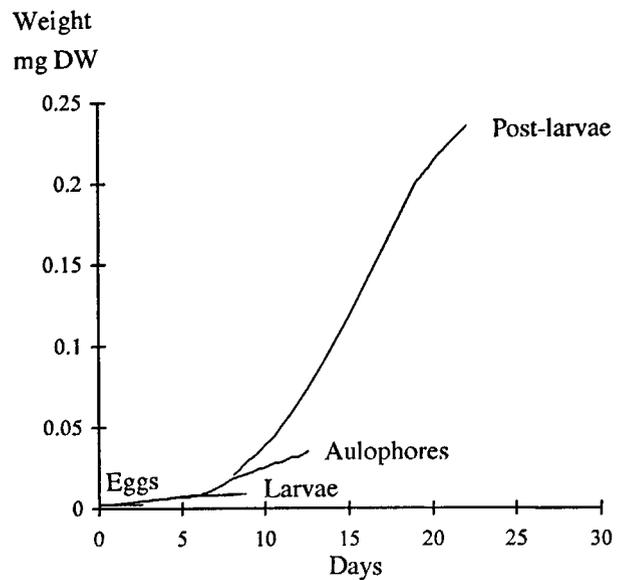


Figure 9

Growth curves of larval stages simulated by the model. The curves are stopped when stage abundances represent less than 0.5 % of the total population.

Courbes de croissance dans les stades larvaires simulées par le modèle. Les courbes sont arrêtées lorsque les abondances des stades représentent moins que 0,5 % de la population totale.

Fig. 7) present a growth curve for post-larvae based on cephalic diameter, for recruited individuals at the station A in 1987, which vary from 288 μ m to 828 μ m over 24 days, from 3 to 27 June. Thus the simulation produced a growth rate which is twice the natural growth.

Mean weights are of little relevance to the recruitment of benthic species because the variability is almost always as large as the mean itself (Lambert *et al.*, 1996, Fig. 8). The present model is able to calculate the weight distributions of the stages in successive age-classes (Fig. 10). For several reasons, the simulated results cannot be compared directly to the observations. First, Lambert *et al.* (1996) use cephalic diameters instead of weight. In addition, the simulation was initiated with a massive egg production, and homogeneous conditions of temperature and food were assumed.

Budget of the meroplanktonic larvae

The model takes into account trophic and demographic processes and thus permits estimation of the exchanges of matter between the studied population and its environment. The fluxes of matter through the simulated larval cohort of *Pectinaria koreni* (Figs. 8, 9) have been accumulated over time and space and the mass balance is presented in Figure 11. The biomass of the larval population increases until the post-larval stage, and then decreases during this stage because mortality is not compensated for by the growth of survivors. The maximum value is 6 g DW m⁻² and occurs at day 12 when all the individuals have just metamorphosed into post-larvae. When the population reaches the juvenile stage, the biomass decreases

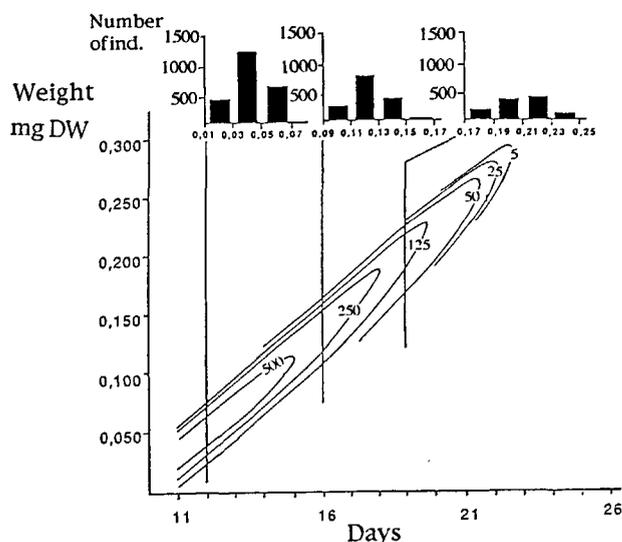


Figure 10

Weight distribution histograms during the post-larval development calculated from the simulated isolines of densities in weight-time space.

Histogrammes des distributions de poids lors du développement post-larvaire, calculés à partir des isolignes de densités simulées dans l'espace poids-temps.

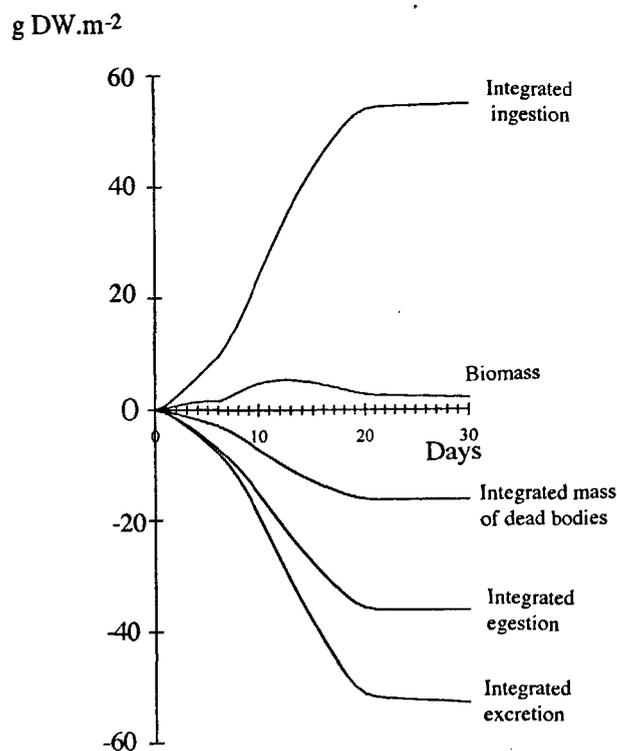


Figure 11

Balance of matter going through the larval population released by genitors on 1 m^2 . Ingestion, excretion, egestion and mass of dead bodies are accumulated over time and depth over the complete larval development. The biomass results from the difference between gains and losses.

Bilan de matière traversant la population larvaire issue des géniteurs vivant sur 1 m^2 . L'ingestion, l'excrétion, l'égestion et la masse de cadavres sont cumulés dans le temps et l'espace durant tout le développement larvaire. La biomasse provient de la différence des gains et des pertes.

very slowly. Ingestion seems extremely low for juveniles, as well as their metabolic wastes (all the cumulative curves are horizontal). The total material grazed by this population during its pelagic life (until day 8) is around 10 g DW m^{-2} .

Recruitment probabilities vs. drifting

Depending on its direction, wind stress can reinforce the transport of larvae away from the coast or help to maintain larvae above the recruitment area. What are the chances of recruitment for groups of pelagic larvae placed at different positions on the transect? Simulations for groups of 100 old pelagic larvae (age: 7 days), with the same weight, and ready to metamorphose into aulophores show that the larvae above the recruitment area have the highest probability to be recruited, and the probability decreases exponentially with the distance (Fig. 12). The individuals which have the highest chance of recruitment are those staying nearest to the adult area, although the majority of the population follows a mean trajectory using the hydrodynamics of the estuary. Based on the simulated densities on day 7 along the transect (cf. Fig. 6) and these probabilities of recruitment, it is calculated that 75% and 99.2% of recruited post larvae will not drift to distances greater than 10 and 15 km respectively from the recruitment area.

DISCUSSION

In the present model, all steps influencing the recruitment are represented: the larval supply, the larval transport mechanisms, the trophic conditions for survival and the settlement success. Several parts of the model, physical and biological, are very simple and need to be discussed, but the results presented in this paper already show interesting points. In the present study, a substantial effort has been made to synthesize the physiological data from the existing literature. Starting from realistic initial conditions of female egg production and genitor density, the basic simulation produces realistic abundances of larvae and aulophores (see Fig. 11). The model predicts an exponential larval growth, using physiological functions originating in part from studies on other species. An exponential growth has already been shown for polychaete larvae (Day and Simon, 1984; Anger *et al.*, 1987; Hansen, 1993), and the simulated weight at the end of the post-larval life is within the range of the observed weights (Reculé, 1986). The model shows that growth, development and behaviour in the successive stages are of primary importance in the interactions of the population dynamics with the physical processes.

One interesting aspect of the model is the synthesis between demographic patterns and individual growth patterns, which permits estimation of the flow of energy and an assessment of the ecological role of the simulated population. In the middle of the larval patch at day 5 (see Fig. 6) there are around 15×10^4 larvae m^{-2} . The model predicts that the grazing rate is around $0.46 \text{ g DW m}^{-2} \text{ d}^{-1}$, i.e. $0.184 \text{ g C m}^{-2} \text{ d}^{-1}$, if the author suppose a carbon-dry weight ratio equal to 0.40. At the time of the phytoplankton peak in the Chesapeake bay, White and Roman (1992) found a total grazing by the zooplankton community of $231 \text{ mg C m}^{-2} \text{ d}^{-1}$, of

which 81 % was due to polychaete larvae. The total material grazed by the larval population produced by 1 m⁻² of genitors has been calculated by the model as being equal to 10 g DW m⁻² for the whole pelagic life (see Fig. 12). Simulations made with a comparable model for the copepod *Calanus finmarchicus* in the North Sea (Carlotti and Radach, 1996) give around 40 g C m⁻² from 20 April to 8 June. Thus, the phytoplankton locally grazed by a cohort of meroplanktonic larvae, could reach 10 % of the grazing pressure of the major herbivore of the pelagic ecosystem. The results of the model suggest that a larval cohort of *Pectinaria* could have a high grazing rate, but we need to know more about the feeding preferences of *Pectinaria* to estimate the consequences for the ecosystem. The post-larvae could also have an important impact on the substrate, because their calculated cumulated ingestion is around 40 g DW m⁻².

Another interesting comparison concerns the estimates of the energy transfer through the water-sediment interface. Bhaud (1981) sampled larvae of three polychaetous annelid species (*Lanice conchilega*, *Poecilochaetus serpens* and *Chaetopterus variopedatus*) in a large area off the French Catalan coast and estimated a transfer to the bottom equal to 7.5 g DW m⁻² year⁻¹. As most of the larvae were not on suitable sediments, they were lost for the recruitment. The results of the presented model give a biomass of 6 g DW m⁻² of larvae sinking to the bottom, 90 % of which did not reach the recruitment area. Thus 5.4 g DW m⁻² of larvae of *Pectinaria* are a potential food for benthos.

In the present state, the model only delivers rather theoretical results, and should be refined for use as a predictive tool. The improvements concern both the physical part of the model and the biological part. The physical part of the model should take into account the change of depth with the along-stream distance, the tide, the stratification and the wind stress. In the simulations presented, a constant depth-dependent advection is assumed for the whole horizontal distance. Depth and advection vary along the transect. Moreover, the Seine estuary is very much influenced by tide (see Simpson *et al.*, 1993). Thus, tidal shear should be added to the model. It has been shown that the degree of stratification of the water column might influence the aggregation of larvae (Thiébaud *et al.*, 1992) and also their metabolism and growth (Raby *et al.*, 1994). Even with these potential modifications, it would still be possible to keep the model 2-dimensional. The introduction of wind

stress, however, would make it necessary to change the dimensionality of the physical model. There is evidence that wind-forced transport of *Pectinaria* larvae could change the recruitment considerably (Lagadeuc, 1990). A 3-dimensional model would be needed because winds vary not only in intensity but also in direction, thereby modifying the sea surface currents (Salomon and Breton, 1993). When such wind stress occurs, the larvae can drift further and may be lost for recruitment (Lagadeuc, 1990). This idea could be tested with a more realistic model. It is important to point out that the adding of new physical processes would make it necessary to represent with more details of the swimming of larvae, because they are able to change their vertical position according to the physical regime (Thiébaud *et al.*, 1992; Lagadeuc, 1992a).

The second kind of improvement concerns basic knowledge of the biology of larval and post-larval stages. There is very little known about the effect of food and temperature on the larval stage durations of polychaetes. A complete validation of the model remains difficult, as long as the field studies for sampling the larvae (which already represent an enormous effort) are not accompanied by physiological studies on the organisms and the measurement of environmental parameters (temperature, chlorophyll, detritus). For gastropod larvae an inverse relationship exists between rates of larval growth and length of larval life (Pechenik and Lima, 1984). As regards the naupliar development of copepods living in cultures with different temperatures, a difference of one degree changes the duration of the naupliar development by one to two days (Haq, 1972). The same mechanisms occur for the trochophore and metatrochophore of annelids (Bhaud, 1988). This could have a marked effect on the drift of the organisms before their ontogenetic migration at the aulophore stage. The model results suggest that slower-growing larvae are advected further in the open sea than faster-growing larvae. As a result, the faster growing larvae also have a better chance of being recruited to the adults' area (see Fig. 13). This may have important evolutionary consequences.

Survival, growth and behaviour of the post-larvae of *Pectinaria* are still largely unknown. Settlement can be more or less active (Reculé, 1986), but the model results show that large-scale distributions must be mainly due to passive sinking and transport. The functions of settling and of active resuspension in the bottom current proposed in the model are hypothetical, but represent a phenomenon observed for

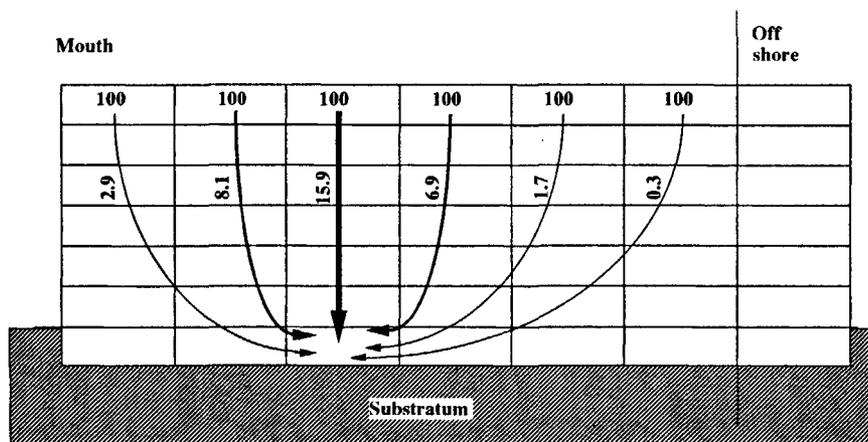


Figure 12

Probability of recruitment for newly molted aulophores following their position in the upper surface layer. The simulations begin with 100 larvae of same age, weight and growth rate, in each initial position.

Probabilité de fixation des larves pélagiques en fonction de leur position sur la radiale. Les simulations démarrent avec 100 larves de même âge (proche du passage en aulophore), de même poids et de même taux de croissance, dans chaque position initiale.

Table 3

Simulated and observed dry weights, in mg, of *Pectinaria koreni* during the benthic phase. The simulation begins on 15 April for comparison with the data.

Model Bay of Seine		Elkaim and Irlinger (1987) Bay of Seine		Nicolaidou (1983) Bay of Colwyn (Wales)		Kirkegaard (1978) Isefjord (Denmark)	
Date	Weight	Date End of March	Weight Spawning	Date	Weight*	Date	Weight*
15 April	Spawning			April-May	Spawning		
15 May	0.31						
15 June	0.53	21 June	1.52	5 June	0.01	15 June	Recruitment
15 July	0.79	22 July	1.58	28 July	3.88		
15 August	1.71					15 August	0.26
15 September	3.20	30 September	6.03	2 September	8.45	15 September	4.71
15 October	5.04	22 October	5.05	10 October	14.59	15 October	8.63
15 November	8.62	29 November	6.63	11 November	20.83	15 November	9.32
15 December	13.56			8 December	20.23	15 December	9.39
15 January	19.00	6 January	6.75	15 January	18.39	15 January	9.48
15 February	21.72	9 February	5.62	16 February	16.53	15 February	9.56
15 March	39.44	9 March	6.83	15 March	20.76	15 March	9.63
15 April	39.44	15 April	14.08			15 April	9.72
		25 May	15.59			15 May	9.80
		8 June	16.71			15 June	9.88

* : From the relationship dry weight-wet weight: $DW = 0.1408 W^{0.8993}$ (Nicolaidou, 1983)

Pectinaria (Butman, 1989). In the model, this behavioural ability is related to the age of the post-larvae. Knowledge of the mechanisms of resuspension in the water column and drifting (Lambert *et al.*, 1996; Olivier *et al.*, in press) would permit more detailed representation. Several other aspects of post larval settlement should be taken into account: the competition for the substrate with other individuals (adults and other post-larvae of *Pectinaria*, other species), gregariousness (Gotelli, 1990) and predation.

The population dynamics of juveniles and adults has been treated simply in this study. Nevertheless it is interesting to note that the weight increase obtained from the ingestion, based on the rate of sediment working is within the range of weights for different populations of *Pectinaria* (Tab. 3).

CONCLUSION

Recruitment of larvae to an adult population is the most important natural process controlling population size in many species of invertebrates (Roughgarden *et al.*, 1988). However, recruitment is difficult to measure. The determining factors for recruitment, still unknown, could be the trophic conditions for growth and development during the diffe-

rent stages (Cushing and Dickson, 1976), or the physical factors influencing the larval dispersion (Sinclair, 1988). Recruitment variability is assumed to result from variable survival during larval and post-larval stages, and advective losses of larvae (Butman, 1987). Many authors have speculated on the importance of the estuarine hydrodynamics in the transport of larvae during their pelagic life and in recruitment. With quantitative results on the larval distribution and physiological parameters, the present model is a useful tool for gaining new insights concerning this problem. Such work, based on the dynamics of *Owenia fusiformis* in the bay of Seine, is already in progress (Thiébaud, 1994).

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