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MODELING JAPANESE OYSTER PHYSIOLOGICAL PROCESSES UNDER NATURAL TIDAL VARIATION IN SUSPENDED PARTICULATE MATTER.

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ABSTRACT.

Feeding and growth of the Japanese oyster *Crassostrea gigas* is simulated by a deterministic model. However, physiological processes, estimated by statistical relationships, have not been tested under extreme environmental conditions such as high level of suspended particulate matter. Ecophysiological experiments were therefore conducted *in situ* in the Bay of Marennes-Oléron during a spring and neap tide cycle in May 1991, to get a better representation of 2 important components of the energy budget of the Japanese oyster : clearance rate and selection efficiency. The relationships previously established by Raillard et al. (1993) are re-evaluated by integrating the action of high seston load, typical of tidal effect within estuaries, on the physiological processes.
For the clearance rate, the re-evaluated parameterization includes:

- a negative effect of turbidity.
- a clogging threshold set to 192 mg/l.

Selection efficiency parameterizations are modified by incorporating :

- a constant inorganic ingestion for increasing seston load, set to 17 % of the inorganic filtered ration.
- an upper selection threshold for the particulate organic matter caused by an overload of particulate material. This threshold was set to 160 mg/l .

The oyster growth model should be enhanced by integrating theses new equations built-up on realistic field conditions, where food availability is regulated by tidal variation.

INTRODUCTION

A mathematical model which simulates feeding and growth of the Japanese oyster *Crassostrea gigas* in the bay of Marennes-Oléron was first studied by Bacher (1991) on the basis of the energetical budget model developed by Bayne et al. (1976) for *Mytilus edulis*. This oyster model was modified by Raillard et al. (1992) who added the effects of food quality and quantity on the physiological processes. Theses authors integrated the preferential ingestion of organic matter. They parameterized the organic / inorganic sorting of particles which occurred during pseudofaeces production. However, the functional relationship used in the model to simulate the organic enrichment was derived from laboratory experiments with a maximum seston concentration of 50 mg/l. Furthermore, simulation of clearance rate included the assumption that there was no effect of particle concentration till a clogging threshold (empirically set to 200 mg/l) from which clearance rate ceased.

In situ experiments were therefore designed to get a better representation of clearance rate and selection efficiency under natural conditions of food availability and composition. The model of the energetics of suspension-feeding oyster should be enhanced by incorporating theses new parameterizations since they integrate short-term changes in food quality and quantity typical of tidal effects within the estuary of Marennes-Oléron. The others components of the energy budget, not presented in this study, have been evaluated simultaneously to avoid building the model with isolated determinations.

MATERIALS AND METHODS

The experiment was set up in Le Chapus in May 1991 during a spring and neap tide cycle. (fig. 1). Physiological responses to tidal variation in food quality and quantity were studied on a population (100 oysters ; total dry weight = 134 g) using a raceway system, and on 6 individuals placed in experimental chambers, (Mean dry weight = 0.6045 ± 0.076). Informations about Suspended Particulate Matter (SPM) and chlorophyll-a and pheopigments, continuously recorded by 2 nephelometers and 2 turbidimeters, were sent to a computer through an acquisition card, Analog connection. In the meantime hourly water samples were collected in order to calibrate both signals and obtain an estimation of the Particulate Organic Matter (POM) and Particulate Inorganic Matter (PIM).

Physiological determinations.

a. Clearance rate

Clearance rate was determined both for the population and the individuals with 2 different methods.
It was determined for the population by directly measuring chlorophyll-a fluxes from the in- and outflow of

the raceway. In Le Chapus, Barillé et al. (1993) have shown that fluorescence is less sensitive to clearance rate underestimation due to retention efficiency since most chlorophyll is within large particles. Clearance rates were then related to SPM.

For the individuals the relationship between clearance rate and SPM was estimated from derivation of the relationship previously established between total filtration rate and SPM. Total filtration rate (mg/h) was estimated indirectly by measuring biodepositions rates. This method is based on the assumption that inorganic matter passes unaltered through the gut. In Marennes-Oléron 90 %, as an average, of the oyster diet is composed of inorganic material. It is therefore reasonable to assume that the ingested inorganic matter is not absorbed.

b. Selection efficiency

Selection efficiency was studied on the individuals for the 2 components of the SPM : PIM and POM. Organic selection was defined as the ratio of organic pseudofecal rate and organic filtration rate. Inorganic selection was defined as the ratio of inorganic pseudofecal rate and inorganic filtration rate. Selection efficiency was quantified this way for the first time by Bayne et al. (1976) in *Mytilus edulis*. Although others formulation of selection efficiency are available (Kiørboe et al. 1985 ;Bayne et al., 1989), selection efficiency calculated in this study was chosen in accordance with the previous relationships used in the oyster model by Raillard et al. (1992).

Population behaviour was compared to the individual response by standardazing the clearance rate to a common dry weight of 1 g using the formula:

$$Ys = (1/We)^b\, Ye$$

Ys is the standardized clearance rate. We the experimental weight, Ye the uncorrected parameter and b is the allometric power coefficient. b = 0.4 (Fiala-Medioni & Copello, 1984).

RESULTS-DISCUSSION

The evolution of SPM, strongly related to the forthnightly cycle showed fluctuations from 30 mg/l under neap tide conditions to as much as 350 mg/l during the spring tide. (fig. 1). The organic content, POM%, which is one of the parameters used to assess food quality, appeared related to SPM by an inverse relationship, (fig. 2),

$$POM\% = a + b/SPM$$

The coefficients of this model are derived from the following relationship established between POM and SPM:

$$POM\ (mg/l) = a\ SPM + b\ ,\quad a = 0.087975 \quad b = 3.958 \quad (r^2 = 0.88\ ;\ n = 90)$$

A single model describing the evolution of organic content .versus. SPM was used since no significant differences were found between the 2 following relationships calculated for the spring and neap tide:

Spring tide POM = 0.0836 SPM + 4.578 ($r^2 = 0.94$; n = 43)

Neap tide POM = 0.0938 SPM + 3.749 ($r^2 = 0.83$; n = 47)

The 2 subsequent models describing the organic content variations to SPM concentrations are shown in figure 3.

Such an inverse relationship as been reported by Preston & Prodduturu (1992) in the Mersey estuary between particulate organic carbon and SPM, and arises from the dilution of organic matter by resuspended inorganics sediments. In Le Chapus, inorganics sediments can be either locally resuspended under the action of current speed or transported from an other part of the bay after wind-induced resuspension on the tidal front.

It is likely that in the absence of phytoplanctonic blooms, the detection of marked variations in food quality, which is a necessity for the modelling to cover the wider range of variation for the parameters and their interaction, will only be possible through seasonal fluctuations.

Effect of turbidity on clearance rate.

a. population

The evolution of the clearance rate was established for 6 h continuously during a spring tide cycle with a calculation every minute. This clearance signal was then compared to the evolution of SPM recorded by the nephelometer. (fig 4a). A linear regression calculated between these 2 parameters reveals the negative effect of SPM, in the range 50-192 mg/l, on the standardized clearance rate (l/h/g dry weight):

CRpop = - a SPM + b with a = 0.0102 b = 4.213

n = 303 ; $r^2 = 0.81$

The intercept value, 4.213 l/h/g DW, gives us an estimation of the higher level of clearance within the range of SPM encountered.

It is to be noticed that such a relationship did not occured on the whole semi-diurnal cycle.

b. individuals.

Clearance rate was indirectly estimated from the total filtration rate.

Total filtration rate (mg/h) was expressed as a multilinear function of SPM that can be written as following:

TFR = - a SPM^2 + b SPM with a = 0.00931 and b = 4.1966

n = 17 ; $r^2 = 0.96$

The model fitted from the observations (Fig. 4b) was derived to get an estimation of clearance rate:

CRind = TFR/SPM = - a SPM + b (figure 4c)

This clearance rate calculated for individuals was standardized to the weight of an oyster of 1 g. The standardized relation can be expressed as follows:

CRind (l/h/g DW) = -0.01137 SPM + 5.12

The representation of both relationships (individual and population) in figure 4d. shows a similar evolution of CR .versus. SPM, although the level of feeding was higher for the individuals. This can be attributed to the activity of the population since Razet et al. (1990) have shown that only 90 % of the oysters were active in the raceway.

From these results a new approach for parameterization of SPM effect on clearance rate was considered based on individual behaviour.

- From 0 to 50 mg/l; previous studies (Deslous-Paoli et al., 1987 & 1992) have shown that clearance rate, within this range of SPM, was independent of concentration. The basic level of clearance was set to 5.12 l/h/g DW, which corresponds to the optimal clearance in the case of individual.

- From 50 to 600 mg/l; the evolution of clearance rate is described by the following equation:

CR (l/h/g DW) = (-0.01137 SPM − 5.12)*(Exp(0.07(Min[0;192 - SPM])))

This equation integrates:

(i) the negative effect of SPM on CR in the range 50-192 mg/l.

(ii) a clogging threshold set to 192 mg/l that have been observed on 6 individuals submitted for 2 hours to a mean SPM concentration of 192 mg/l.

The re-evaluated relationship is given in figure 4e.

Selection efficiency (SE).

A graphical representation of POM/SPM ratio in the pseudofaeces versus POM/SPM ratio in the food, (figure 5a), shows that POM is being preferentially ingested since all points are located below the y = x straight line, for which there is no selection. However, POM selection seems inefficient for high level of particulate matter represented by 3 triangles indicating samples collected above 160 mg/l. The oyster is responding like if above 160 mg/l, the selective mechanism was not operative, likely cause by an overload of particulate matter.

Non linear relationships were fitted to the evolution of organic and inorganic selection versus concentration.

$SEi = 0.83\ (1-\mathrm{Exp}(-0.0716(SPM-5)))$ $n = 243$; $r^2 = 0.42$

$SEo = 0.53\ (1-\mathrm{Exp}(-0.0311(SPM-5)))$ $n = 238$; $r^2 = 0.51$

As SPM ranged from 30 to 192 mg/l, for the individual samples, the equations were forced to begin from a SPM threshold of 5 mg/l that have been described by Deslous-Paoli et al., (1992). It corresponds to the threshold of pseudofaeces production for *Crassostrea gigas*.
The value for which the curve levels off in the case of PIM, 0.83, is similar to the result obtained by Raillard et al. (1992) represented in figure 5b. It reveals that for increasing SPM concentration up to 150 mg/l, 17 % of the inorganic filtered matter is still being ingested. In the meantime, 47 % of POM filtered is being ingested.
A re-evaluation of selection efficiency is proposed. It takes into account :

(i) a constant PIM ingestion for increasing SPM level set to 17 % of the filtered ration. This appears more realistic than the previous parameterizations (Raillard et al., 1992), which assumed, in the model, that all PIM filtered was rejected, above 50 mg/l, through pseudofaeces production.

(ii) an upper selection threshold for POM set to 160 mg/l. Above this threshold POM is treated like the inorganic component of the particulate matter which had not been submitted to preferential selection. The curve which represents organic selection, figure 5c, reaches, above 160 mg/l, the level of inorganic selection previoulsly estimated. The selection model is thus simulating an 83% of rejection of the organic filtered ration

The mathematical formulation of SEo model is thus modified into:

$(0.53(1-\mathrm{Exp}(0.031(\mathrm{Min}[0;5-SPM]))))+0.3(1-\mathrm{Exp}(0.1(\mathrm{Min}[0;160-SPM])))$

CONCLUSION

Resuspended sediments plays a major role in the estuarine complex of Marennes-Oleron. The knowledge of spatial and temporal variability of suspended particulate matter permits to build up hydrodynamic models which can predict evolution of seston concentrations. Primary production and oyster growth models show strong influence of suspended particulate matter on physiological functions (Raillard, 1991).
However, suspended particulate matter is insufficient to characterize food supply for oysters. Barillé et *al.* (1993) showed the importance of cross effects of loads and particle size distributions on filtration processes. Morever, further studies will define precisely feeding parameters that best qualify the organic fraction of the

water column. The relative importance of microphytobenthos and pelagic phytoplankton blooms, their temporal and spatial variability, cell sizes, species composition and pigments characterization will lead to a better accuracy in the oyster growth model.

The elaboration of new relationships based on field experiments that fall within the range of estuarine environmental conditions is essential for a realistic modeling of oyster growth. To understand the oyster feeding response to natural food fluctuations (high levels of seston load in the present study), the evolution of clearance rate and selection efficiency that are 2 important components of the energy budget of *Crassostrea gigas*, have to be considered simultaneously, even though the statistical relationships which simulate their variation have been established independently. As an example, 17 % of PIM ingestion, calculated from the inorganic selection equation, would lead at high SPM concentration to unrealistic inorganic ingestion. However, this will never be the case since the clogging threshold will intervene by limiting the inorganic filtered ration.

The ingestion rate used in the actual oyster model will be modified according to the equations provided in this study. Finally, the model will be completed by the parameterization of absorption efficiency.

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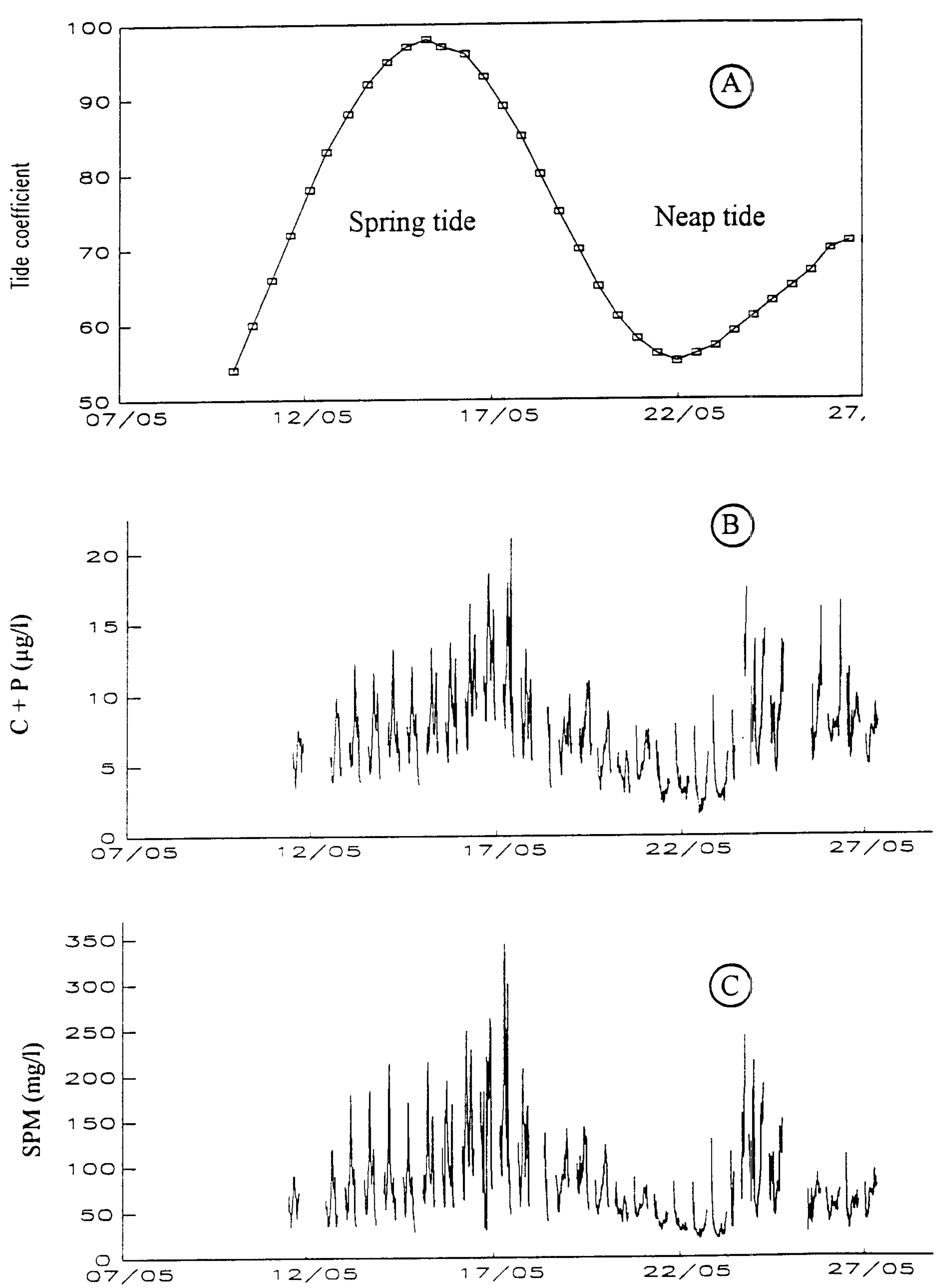

Figure 1. **A**. Evolution of the tide coefficient in May 1991 at Le Chapus. **B**. Tidal variation in the sum Chlorophyll-a + Pheopigments (C+P). C. Tidal variation in Suspended Particulate Matter (SPM).

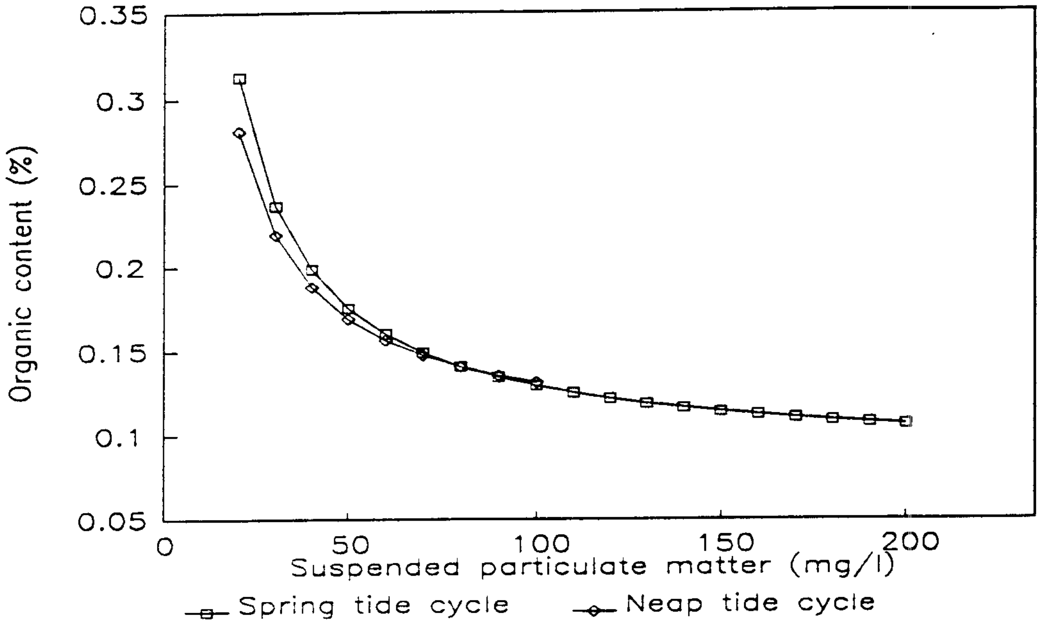

Figure 2. Organic content models for the spring and neap tide in May 1991 at Le Chapus.

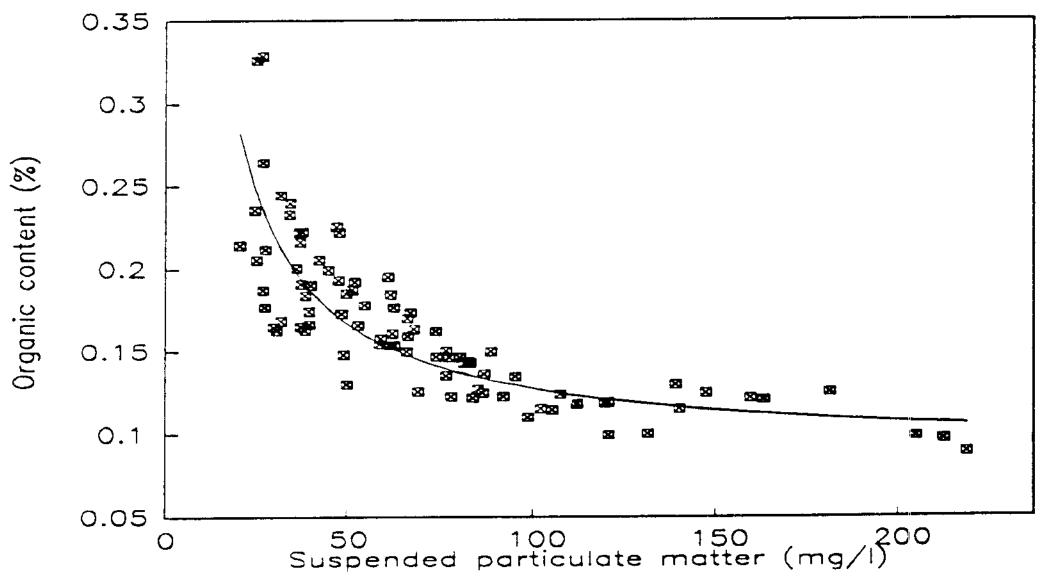

Figure. 3 Organic content model in May 1991 at Le Chapus.

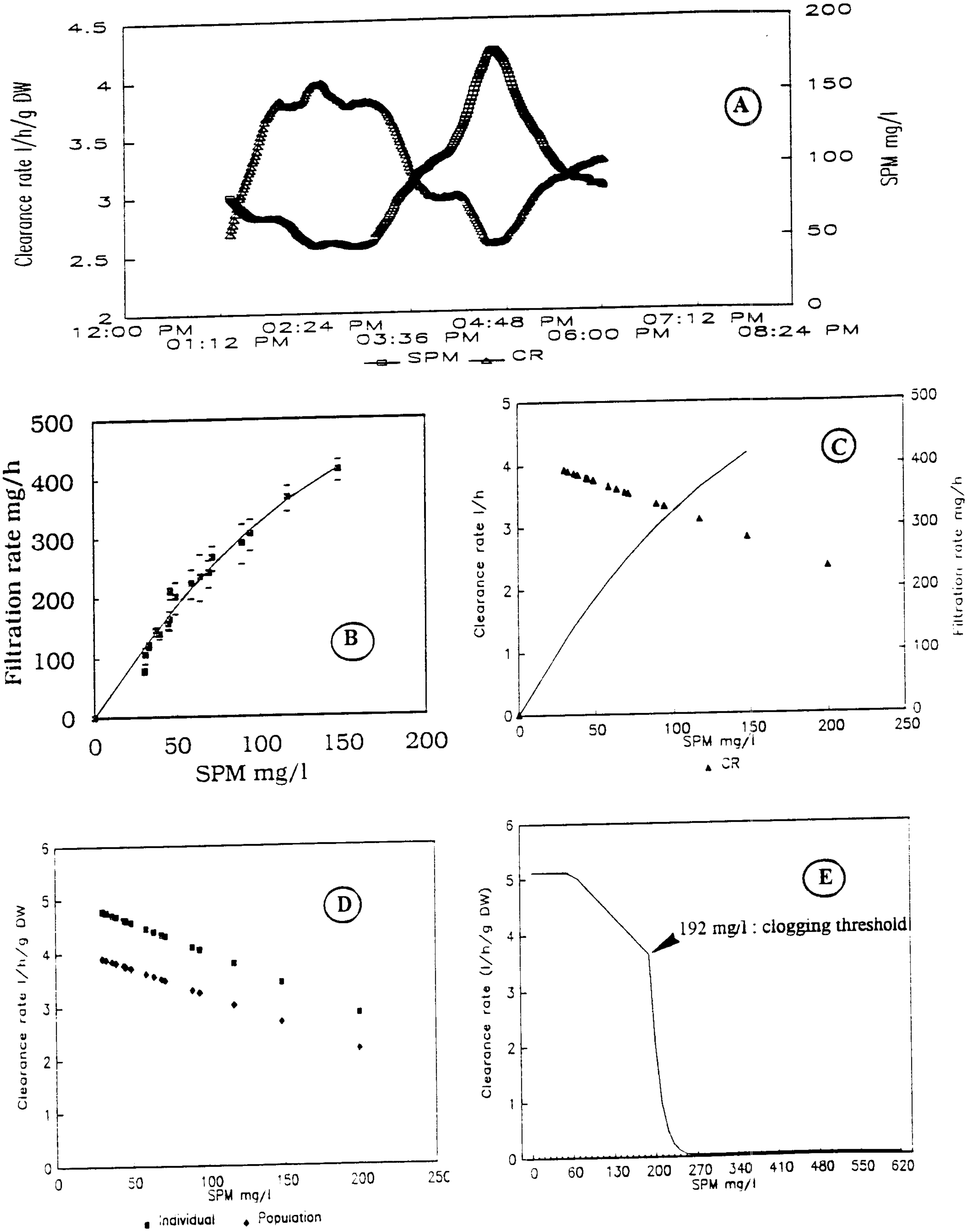

Figure 4 :

A Simultaneous evolution of Suspended Particulate Matter and standardized Clearance Rate during a spring tidal cycle.
B Relation between Filtration Rate and SPM calculated on individuals during spring and neap tidal cycles.
C Clearance Rate of individuals derived from filtration rate model.
D Comparison of clearance rate estimated from individuals and from the population.
E Clearance rate model versus Supended Particulate Matter.

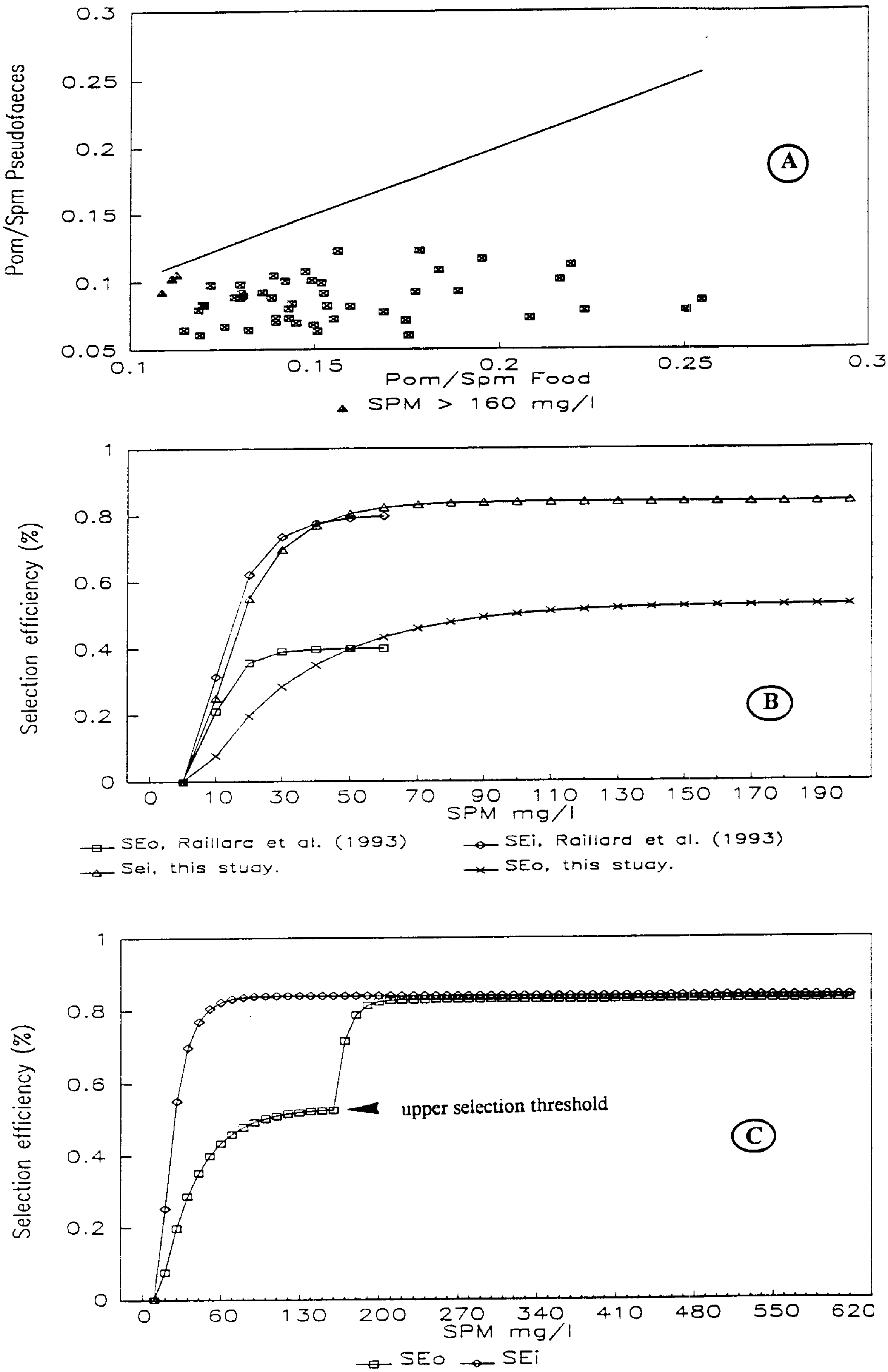

Figure 5.

A Selection of Particulate Organic Matter through pseudofaeces production.
B Selection efficiency models for Particulate Organic Matter and Particulate Inorganic Matter.
C Selection efficiency model including an upper selection threshold for POM.