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**USE OF AN ECOSYSTEM MODEL FOR THE
ASSESSMENT OF THE INFLUENCE OF
CULTIVATED OYSTERS (*CRASSOSTREA GIGAS*)
ON THE NITROGEN CYCLING IN THE
MARENNES-OLERON BAY.**

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Use of an ecosystem model for the assessment of the influence of cultivated oysters (*Crassostrea gigas*) on the nitrogen cycling in the Marennes-Oléron Bay.

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INTRODUCTION

A model of the growth of cultivated oyster in the Marennes-Oléron bay was developed to assess the influence of the nutrients input and of the amount of oysters on the growth performance (Raillard, 1991).

The ecosystem main characteristics are:

- short residence time of the water,
- high turbidity level, depending on the season, tidal level, bathymetry, currents and wind. The turbidity acts on the primary production through light limitation and on oyster production as a food dilution factor.
- presence of high density cultivated areas on mid-tidal flats. The amount of oysters is ranging between 80 000 and 110 000 tons according to the year.
- spatial variability of the biological and physical features.
- coupling effects of the physic process (transport, sedimentation, resuspension) and the biological relationship between the main compartments.

Consequently, the system could be described as forced by the residual circulation of water, the input of nutrients from the Charente river, and the presence or absence of cultivated oysters. The combined effects of these factors were assessed with a spatial box model (Raillard, 1991) and enabled to show that the Marennes-Oléron bay had a high carrying capacity.

In order to be compared with other cultivated or natural systems, and with flows measurements, further insight was given to the results yielded by the model. Yearly and seasonal nitrogen budget were therefore computed for every spatial box and for the whole bay. Residence time of the nitrogen was computed for each compartment. The introduction of new compartments and process was discussed as well as the part played by the cultivated oysters as a stabilizing or a control factor of the environment.

MATERIAL AND METHODS

The model fundamentals were described by Raillard (1991). The ELISE software (Ménèsguen, 1992) was used. Because of the limiting effect of the nitrogen on the primary production, the nitrogen cycling was computed between the compartments: phytoplankton, zooplankton, nutrients, oysters, detritus in the water column and in the sediment (fig. 1a). The spatial variability of the state variables was coupled to the biological scheme thanks to a spatial box design (fig. 1b). The water and particulate exchanges between the boxes were computed from the

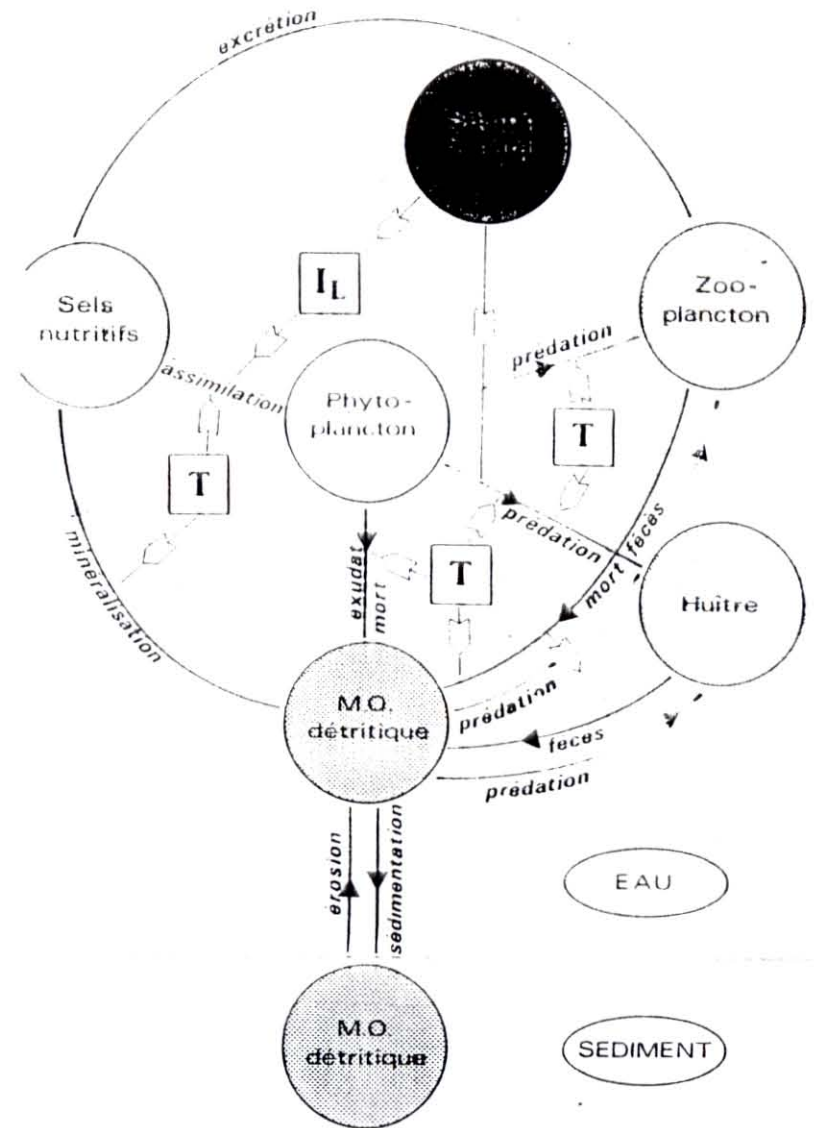
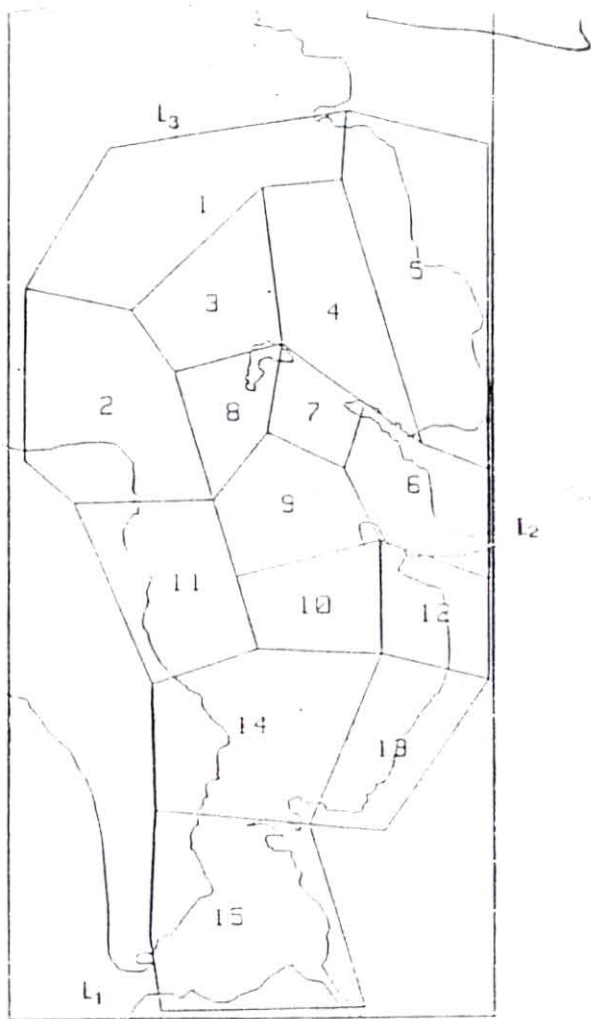


Figure 1. Spatial box design (a) and biological scheme (b) used in the Marennes-Oléron Bay model (Raillard, 1991).

T température de l'eau
 I_L Intensité lumineuse disponible dans la colonne d'eau

residual flows yielded by a hydrodynamical model. The source code was modified to allow the storage of the daily biological flows and exchange flows at the boundaries. Taking into account the box volumes, mean depth and areas, seasonal and yearly flows were derived from these results and expressed in $\text{g N/m}^2/\text{year}$ (total surface was equal to 149 km^2 , and the average depth was 4.9 m). By the same way, the average concentrations of the compartments were estimated and multiplied by the water depth to obtain biomass (g N/m^2). Therefore, pelagic compartments could be compared to benthic ones.

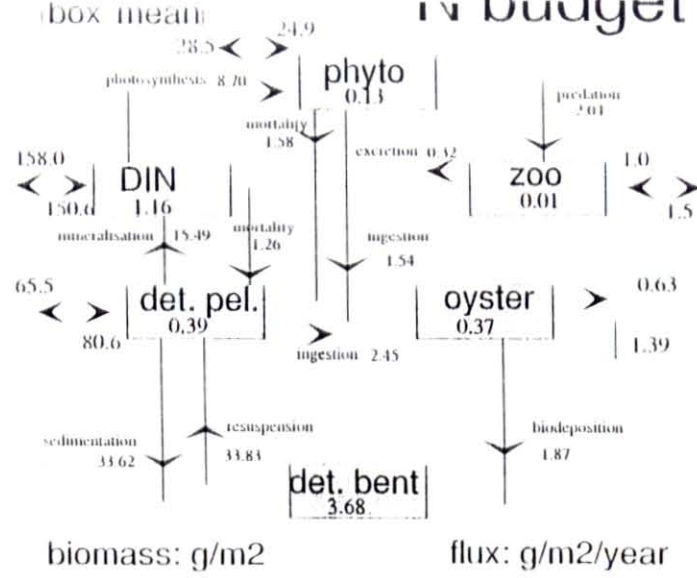
An algorithm was written to assess the residence time of one mass unit of nitrogen according to its compartment. It was based on the fact that the annual budget was conservative because of the seasonal periodicity of the process. Therefore the outflows of nitrogen from each compartment were converted into probability to flow into another compartment or to exit the system. The residence time was defined as the mean time for the nitrogen to exit the system. Matricial computation enabled to assess the mean residence time of nitrogen in the system as well as the residence time of nitrogen issued from each compartment.

Flows and biomass computations were compared to data obtained by Feuillet et al. (1988) on a central location of the Bay that was corresponding to the box no. 14. Annual flows measurements concerned the impact of oyster cultivation on the sedimentation/resuspension process, and the use of particulate organic matter by the oyster population through consumption, assimilation and biodeposition. Though the spatial scale used in the experimental measurements was not consistent with the box model scale, it was thought that useful indications could be derived from the experiments to validate the relevance of the model as a diagnostic tool.

RESULTS

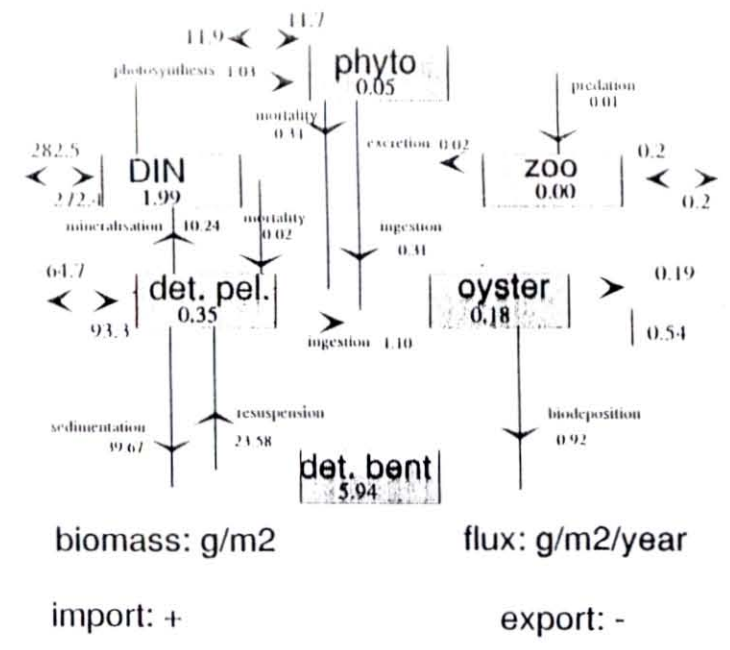
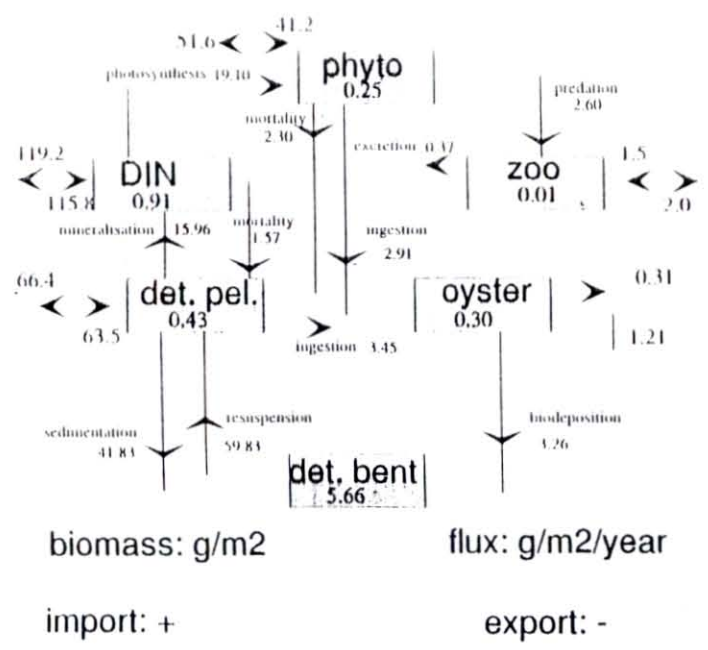
Annual flows and biomass are displayed on figure 2a. The first evidence depicted on the graph was related to the input and output of exogeneous nitrogen compounds. For instance, the bay was importing $151 \text{ gN/m}^2/\text{year}$ of inorganic dissolved nitrogen (DIN) and exporting $158 \text{ gN/m}^2/\text{year}$, thus resulting in a net export of nutrients. Phytoplankton and detritus in the water column import and export were a little lesser, with an order of magnitude of 25 (phytoplankton) and 65-80 $\text{gN/m}^2/\text{year}$ (detritus). Comparatively, the zooplankton inflow and outflow were almost negligible. The oyster compartment export was estimated to $0.63 \text{ gN/m}^2/\text{year}$. This flow included mortality, spawning and the second age class renewal at the end of the year.

Since the net inflow/outflow budget was equal to $9 \text{ gN/m}^2/\text{year}$, the bay could be considered as slightly productive. The nitrogen uptake due to



STRONG

WEAK



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Figure 2. Computation of the nitrogen budget (flows in gN/m²/y, biomass in gN/m²) derived from the annual simulation and averaged on one year (a), on spring (b) or winter (c). Import to the bay and export from the bay were also reported.

phytoplankton photosynthesis equalled 8.7 gN/year/m^2 and represented around 25% of the total phytoplankton inflow, the remaining 75% being explained by the exogeneous import. Predation by the oysters had the same order of magnitude as predation by zooplankton (1.5 versus 2.0 gN/year/m^2). The oysters food ration consisted on detritus and phytoplankton. The detritus ingestion was almost twice the phytoplankton ingestion (resp 2.5 , 1.5 gN/year/m^2). An important part of that food was rejected as feces. Nearly 50% outflowed from the oyster compartment as biodeposition. Another 30% fraction vanished through respiration which was derived from conversion coefficients between energy loss, dry weight and nitrogen content of the flesh. The most important biological flows corresponded to the sedimentation and resuspension process. On the whole, resuspension balanced sedimentation, resulting in a net inflow to the benthic detritic compartment due to the biodeposition. Therefore, the mass budget of this compartment was not conservative, and the biomass slightly increased from year to year. A strong link related the DIN and pelagic detritus compartments. The mineralisation transformed particulate matter (detritus) into dissolved inorganic compounds pooling ammonium, nitrates and nitrites, and reached 15.5 gN/year/m^2 . However this flow explained only 10% of the inflows to the DIN compartment, the remaining 90% being imported. The particular case of the benthic detritus apart, the DIN compartment had the most important biomass (1.2 gN/m^2). In a decreasing order of importance, we found pelagic detritus (0.39 gN/m^2), oyster (0.37 gN/m^2), phytoplankton (0.13 gN/m^2) and zooplankton (0.01 gN/m^2).

These values, as well as flows values, were also examined for some boxes and for each season. Because of the great amount of results, viewing all the results would be cumbersome. Since the system was very sensitive to the oceanic and river boundaries and the presence of oysters, the boxes number 9, 14 were selected to give further details. The first one contained no cultivated oysters. For the other compartments, the related flows were generally lower in box 9 than in the box 14. The photosynthesis was almost twice in the former case, and the mineralisation 5-fold. The sediment/resuspension budget was positive in box 9, negative in box 14. In that box however, the net outflow of detritus from the sediment was compensated by the biodeposition due to the oysters. Compared to the mean values, the two boxes gave an idea of opposite behaviours. Flows and biomasses of the box 9 were generally higher than the mean values previously described. On the contrary, the box 14 had lower levels of biomass and flows, except for the flows involving the oyster compartment. Because of the location of the cultivation area, the oyster biomass was higher in box 14 than in the whole bay. The ratio between the ingestion or biodeposition flows on one side, the biomass on the other side, was

nearly constant when compared from the average values to the box 14. The local biomass was 4 fold the average one, and the resulting flows obeyed therefore the same multiplicative relationship.

The computation of seasonal flows also revealed further details on the nitrogen import/export and the relative importance of the biological flows. First, the net nitrogen budget was negative in spring (fig. 2b), positive in winter (fig. 2c). Consequently, nitrogen was imported in winter, and exported in spring. The spring inflow was comparatively more concerned by the phytoplanktonic compartment than the winter. On the contrary, the DIN inflow was approximatively two-fold in winter than in spring. Besides the intensity of the inflows and the outflows, the net contribution of each compartment to the budget was quite different according to the season. DIN and detritus were mainly exported in winter, as phytoplankton was exported in spring. The seasonal variation of the biological flows was even more pronounced than the inflows/outflows. The primary production and the predation by zooplankton were multiplied by almost a factor 20 between autumn and spring. Phytoplanktonic ingestion by the oysters was equal to 2.9 gN/m²/year in spring, instead of 0.3 in winter. The difference was not so acute for the ingestion of detritus, ranging from 1.1 in winter to 3.5 in spring. Mineralisation slightly increased from 10.2 in winter to 16.0 in spring. Last, the net sedimentation/resuspension budget deeply differed. Sedimentation was dominated by resuspension in spring, and was responsible for the net nitrogen input to the sediment in winter. In no case was the net budget compensated by the biodeposition by oysters. Due to the fact that both biological inputs and outputs were highly variable, the biomasses did not vary so deeply. Phytoplanktonic biomass increased from 0.05 to 0.25 gN/m², and DIN and oyster nitrogen contents were multiplied by a factor 2. Pelagic and benthic detritus were more or less constant. In summer, two facts were outlined. First, the DIN inflow and outflow dramatically decreased by a factor 6. Second, all the biomass decreased from spring to summer but zooplankton and oyster.

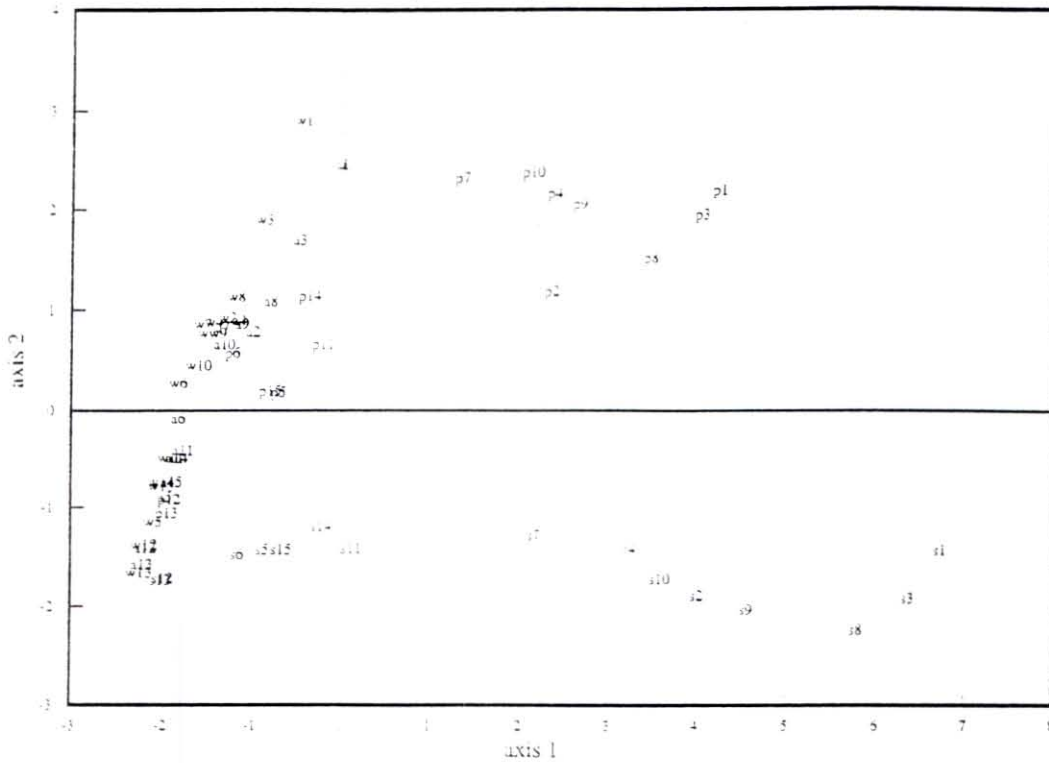
Seasonal and spatial results of the main flows were synthetized with a principal component analysis. In this analysis, the variable were the flows between the biological compartments. The observations were the combinations of the season and box values of the flows. Since only six boxes were concerned with oysters, the flows involving the oyster compartment were not included in the analysis, reducing the number of variables to 9: primary production, predation egestion and excretion by zooplankton, phyto- and zoo-plankton mortalities, mineralisation, sedimentation and erosion. Therefore, PCA is a way to compare the spatial and seasonal variability of the nitrogen represented in the model. The three first axes represented 97 % of the variance, with respectively 67%, 23% and 7%. Three groups of variables

were distinguished : the sedimentation and erosion flows were mainly correlated with the second axis, the primary production and mineralization were correlated with the first and second axes (with opposite signs on the second axis), and the other variables were related to the first axis. The observations were projected on the first plane (axes 1 and 2) (fig. 3a), and the second plane (axes 1 and 3) (fig. 3b). The first axis opposed the seasons spring and summer on one side, to the winter and autumn on the other side. For the first two seasons, the spatial variability had two components along the first axis: in the northern part of the bay, a north to south gradient appeared (boxes 1, 3, 8, 9, 10). Besides, the boxes 5, 6, 11, 12, 13, 14, 15 were opposed to the other ones. This difference between the boxes resulted from the low values of all the flows inside the water column in the last group. For the winter and the autumn, the spatial variability was lesser and concentrated on the axes 2 and 3. On the latter, boxes of the north-western part of the bay (boxes 1, 2, 3, 8, 9) were opposed to the others, due to higher values of erosion and sedimentation flows.

Residence times were computed for each box on the mean annual basis, because of the mass conservation requirements (see annex). This concept was related to the time spent in the bay by a nitrogen elementary quantity, as a function of the initial spatial box and biological compartment. The computation took into account the different paths nitrogen could follow due to the yearly averaged flows and weighted by the biomass. Very high values were obtained for the benthic detritus compartment, with residence times laying between 40 and 600 days. On the opposite, the residence time for the nitrogen coming from the phytoplankton and nutrients compartments commonly ranged between 1 and 70 days (table 1). These results highlighted the buffering capacity of the sediment (as represented in the model), and the north to south residence time gradient due to the horizontal transport. Except for the boxes 4 and 5 (north-eastern part of the bay), the nutrients residence time was far lower than phytoplankton. For the former, the residence times were closed to the residence times for water particles (not shown), due to the fact that, even when depleted, the major part of the nutrients crossed the bay with the water flow.

Mean biomass and flows values were estimated from field measurements by Feuillet et al. (1988). Since the measurements concerned a cultivated oyster population, the results obtained by these authors on the impact of oysters had to be corrected by a factor equal to the ratio between the local nitrogen oyster biomass and the mean biomass averaged over the bay. Due to the central location of the box 14, the results yielded for that box were compared to the measurements. Therefore the observed biodeposition flow corrected for the

Principal components analysis



Principal components analysis

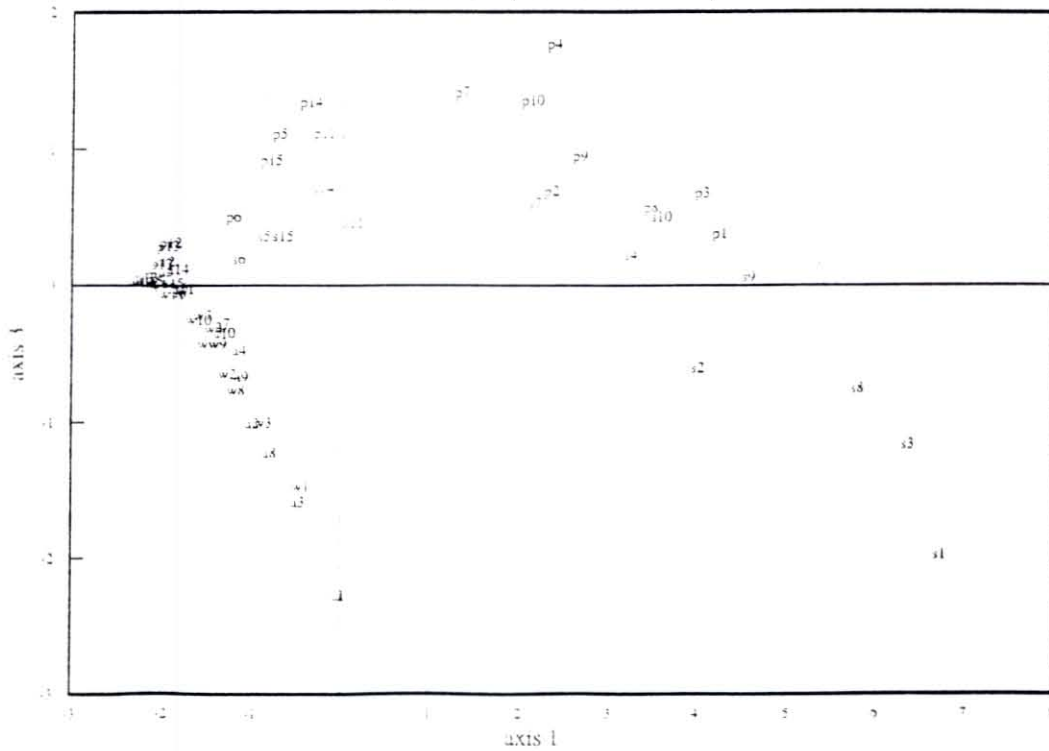


Figure 3. Principal components analysis of the mean seasonal biological flows computed in each spatial box. The boxes were referred to with their number (from 1 to 15), and the seasons were denoted by w (winter), p (spring), s (summer) and a (autumn). The observations were projected on the axes 1 and 2 (a) and the axes 1 and 3 (b). The three first axes explained 67%, 23 % and 7% of the total variance.

Table 1. Nitrogen residence time (days) according to the initial box and initial compartment.

box	phytoplankton	benthic detritus	nutrients
1	6	40	3
2	2	33	2
3	15	82	6
4	32	128	18
5	71	318	68
6	56	319	7
7	27	166	7
8	14	113	4
9	29	106	6
10	21	92	4
11	45	168	5
12	49	612	4
13	51	475	2
14	16	57	4
15	5	44	1

biomass was equal to 170 gN/m²/year, which was 20 times greater than the simulated flow. The corrected ingestion flow was 5 times greater than the result yielded by the model. Observed measurements showed that the sedimentation had two components, the first related to natural sinking velocity of the particles, the second due to the influence of the tables supporting the oysters on the turbulence of the water. This latter term was almost ten times higher than the former one, resulting in a total sedimentation under cultivated oysters of nearly 2700 gN/m²/year. The model took into account only the natural sedimentation term which was equal to 26 gN/m²/year for the box 14. Therefore, one order of magnitude made the observed and computed natural sedimentations different. These great differences between the model results and the reality make the model unrealistic, even if, fortunately, the net budget of the benthic detritus was balanced both in the field and the model representation. However, the model results were consistent with the annual variability of the phytoplankton biomass and the oyster growth (Raillard, 1991). This is the main reason why further insight in the vertical process will be developed.

CONCLUSION

Raillard and Menesguen (submitted) already outlined the role played by the cultivated oysters in the control of the available food in the Bay. The carrying capacity was assessed with the model from the sensitivity of the oyster growth to its stock level. These authors concluded that the oyster population did not exert a strong control on the phytoplankton biomass, because the low residence time of water resulted in a great renewal of the potential food. Further calculations showed that the residence time of the nitrogen was however deeply modified by the biological process. More precisely, the exchanges between the benthic (oyster, detritus) and the pelagic compartments increased the nitrogen residence time. Héral (comm. pers.) estimated that only few days were necessary for the oyster population to filter the water volume of the bay. Therefore, the greatest part of the particulate matter would have a chance to be caught before exiting the bay. However, the model predicted that up to 60 % of the biodeposition was directly rejected as pseudofeces in the water column without any change, resulting in a lower grazing pressure.

For the moment, global characteristics of the bay computed from the model simulations, as the residence time and the comparison between the spatial and the temporal variability, should be handled with care and only on a qualitative level. They are tools for exploring the major properties of the ecosystem and allowing further comparisons with other systems. Two concluding remarks will result in model improvements. First, the place of the benthos in such systems is very important (see

buffering capacity expressed as the residence time) and requires a more realistic description of the water column / sediment interface. This will be achieved by both taking into account the vertical physical process (sedimentation, erosion) and the biological process on the sediment (phytobenthic production) in a realistic manner, with the use of a fine spatial quantification of these process. Second, the system can be characterized as a low productive/high turnover system. Due to high turbidity level, the primary production is not important. The carrying capacity of the bay is then inversely correlated with the water residence time: the food renewal is mainly due to the ability of the bay to transport very quickly the phytoplankton locally produced or imported. Therefore, the model developments should also emphasize the system sensitivity to dramatic disturbances due to interannual climatic variability (nutrients input at bloom period, low temperature in winter) than can affect the physiological state of the oyster population.

ANNEX: residence time computation

Transition probabilities between compartments were derived from the nitrogen flows. If F_{kl} was denoting the flow between the compartments k and l , and B_k the biomass in compartment k , the probability to outflow from k to l was equal to:

$$P_{kl} = F_{kl} / B_k$$

P_{kk} represented the probability of remaining inside the compartment k . The summation of the P_{kl} terms was generally equal to 1, except for the compartments a part of which was directly exiting.

These values were grouped in a vector U :

$$U = (P_{10}, \dots, P_{n0}),$$

where P_{k0} represented the flow from the compartment k outside the system.

If $U^h = (u_k^h)$ describes the distribution of the biomasses in the compartments k at time h , the probability to flow outside the compartment at time h was written:

$$p(t=h) = \sum P_{k0} \cdot u_k^h \quad (1)$$

The vector U^h was the iterative product of the P matrix during h time steps:

$$U^h = P^h \cdot U_0, \quad (2)$$

where U_0 was the initial distribution of the biomasses.

Then, the residence time was equal to the average residence time, with the density function $p(t=h)$. Therefore:

$$T = \sum p(h-1) \cdot h$$

(1) and (2) yielded:

$$T = U \cdot (\sum P^{h-1} \cdot h) \cdot U_0,$$

or

$$T = U \cdot Q \cdot U_0 \quad (3)$$

with

$$Q = \sum P^{h-1} \cdot h,$$

or

$$Q = I + \dots + P^{h-1} \cdot h + \dots,$$

where I is the identity matrix.

The expression within parentheses was the derivative of the function of P :

$$f(P) = \sum P^h,$$

which was also written :

$$f(P) = (I - P)^{-1}.$$

Obviously, $f'(P) = (I - P)^{-2}$, so

$$Q = (I - P)^{-2}$$

U_0 was written as the initial distribution of the biomasses in the system :

$$U_0 = (U_{0k}), k = 1 \dots, n$$

with $U_{0k} = B_k / \sum B_k$

Accordingly, it may be seen from (3) that the residence time of the nitrogen in the compartments was simply given by the terms of the vector : $U \cdot Q$.