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Modelling nitrogen cycle in a small intertidal estuary: respective influence of environmental factors and cultivated oysters.

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Abstract

The Baie des Veys, located on the French coast of the English Channel is an open intertidal estuary (37 km²) with an important oyster farming activity. The main cultivated species is the Pacific oyster, *Crassostrea gigas*, with a standing stock of *ca.* 10 500 tons. This ecosystem is influenced by four rivers which drain an important catchment basin (3 500 km²). Previous results showed that phytoplankton production is mainly influenced by terrestrial nitrogen inputs rather than oceanic nitrogen inputs. In this study, nitrogen dynamics were evaluated by developing an ecosystem box model taking into account all major nitrogen sources. This model simulates the Baie des Veys nutrient-phytoplankton-oyster food web by coupling a primary production model and an oyster ecophysiological model based on the Dynamic Energy Budget theory. The model is split in two compartments, the water column and the sediment. It was validated using *in situ* measurements of chlorophyll *a*, nutrients and biometric data on oyster growth. This coupled model allowed us to study the Baie des Veys nitrogen cycle using two different approaches. First, simulations with average environmental conditions were achieved with and without oyster stock in order to highlight the influence of cultivated oysters (filtration, excretion, biodeposition) on nitrogen dynamics. Second, different scenarios with very contrasted environmental conditions (freshwater and nutrient inputs, meteorology) were tested in order to estimate the influence of the environment on the Baie des Veys nitrogen cycle. Finally, the model results were compared with available data from other cultivated ecosystems using relevant indicators.

Keywords : *Crassostrea gigas*, ecosystem model, nitrogen cycle, environmental factors, indicators

Introduction

The knowledge of the influence of wild and cultivated species on the nutrient cycling is essential to fully understand ecosystem functioning. It allows to define the ecological carrying capacity of an ecosystem (i.e. the stocking or farm density which causes unacceptable ecological impacts (McKindsey et al., 2006)) which is of crucial importance to insure a sustainable development of mollusc farming. Previous results obtained in the Baie des Veys ecosystem highlighted a prevalence of terrestrial nitrogen inputs on the phytoplanktonic production. This indicates that food availability for oysters essentially depends on river inputs more than on oceanic ones. The aim of this study is to determine the respective influence of cultivated oysters and environmental factors (*i.e.* river inputs) on the ecosystem functioning. To this end, different years with very contrasted environmental conditions in terms of river inputs were simulated with and without oysters. Finally, results obtained were compared with the cultivated ecosystem of Tracadie Bay in Canada (Cranford et al., 2007).

Material and Methods

Study area

The Baie des Veys is located on the French coast of the English Channel, in the western part of the Baie de Seine (fig. 1). It is a macrotidal ecosytem with a maximal tidal range around 8 m. The intertidal area is around 37 km². The main cultivated species is the Pacific oyster, *Crassostrea gigas*, with a standing stock of *ca.* 10 500 tons. Other wild benthic suspension feeders were identified close to the oyster farming area, like mussels or cockles but their standing stocks are not known. In its southern part, the bay receives freshwater inputs from four rivers which drain a catchment area of approximately 3 500 km². The total mean discharge is around 53 $m^3 s^{-1}$. The Vire is the main river with 40 % of total inputs.

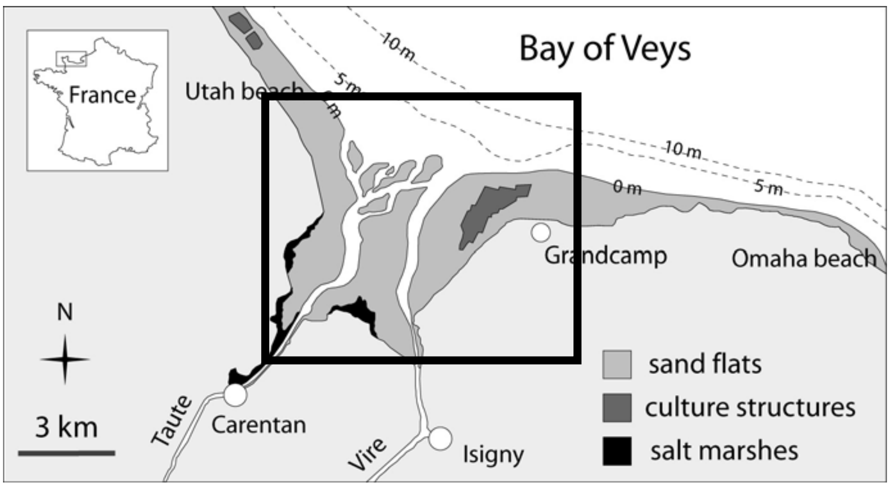

Fig 1: Map of the Baie des Veys estuary (modified after Dubois et al., 2007). The black box corresponds to the geographical area taken into account.

The physical sub-model

The physical sub-model is a simple one-box model. The box corresponds to the mean features of the area located as indicated on figure 1. The surface is 50 km², the depth is 5 m and the residence time is 5 days (cf. Grangeré et al. poster, ICES CM 2008/H:18). The value used in this study corresponds to an average residence time calculated from different scenarios of environmental conditions (river flows, wind speed and direction). Previous studies never highlighted significant thermal or haline stratification in this ecosystem. Thus, only one vertical layer is taken into account in this model. Variations of state variables in the sediment are simulated using a sediment box. Physical exchanges between water and sediment are mainly diffusion for dissolved variables and erosion/deposition for particulate variables.

The biogeochemical sub-model

The biogeochemical sub-model used in this study was developed by Ménesguen and Hoch (1997) and Guillaud et al. (2000). It is a classical NPZD model (nutrients, phytoplankton, zooplankton and detritus) expressed in nitrogen units. The conceptual structure of the model is presented in figure 2 and state variables are indicated in table 1.

Table 1 : State variables of the Baie des Veys biogeochemical sub-model

State variables	
Water column	
DIN	Dissolved Inorganic Nitrogen
PON	Particulate organic nitrogen
P	Phytoplankton (Diatoms)
H	Oysters
Sediment	
B	Wild benthic filter-feeders
DIN_{sed}	Dissolved Inorganic Nitrogen
PON_{sed}	Particulate organic nitrogen

In the model, dissolved inorganic nitrogen corresponds to nitrate and ammonia. The dominance of diatoms in this ecosystem (Jouenne et al., 2007) led us to consider only this phytoplanktonic group. In the water column, grazing of diatoms by zooplankton and consumption by cultivated oysters are taken into account. The feedback of oysters on the environment (consumption, biodeposition and excretion) is also considered. Growth of the Pacific oyster is modelled using a Dynamic Energy Budget model (Kooijman, 2000). In the benthic trophic layer, wild benthic suspension feeders are taken into account in order to reproduce the existing trophic competition between wild and cultivated filter-feeders.

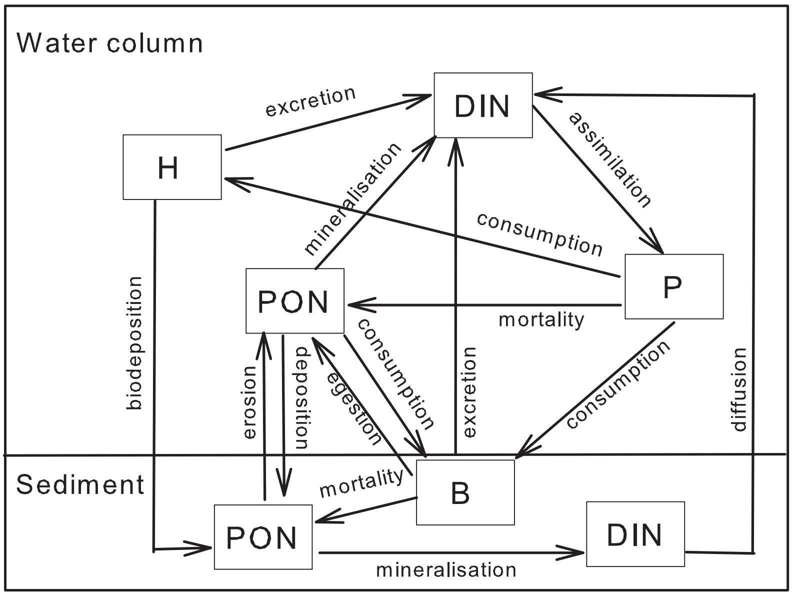

Figure 2 : Conceptual diagram of the biogeochemical model

Further details on equations and parameters are available in Cugier et al. (2005) for the biogeochemical model and in Pouvreau et al. (2006) for the oyster DEB model.

Boundary conditions

Two boundaries are considered, the northern one receives marine inputs from the Baie de Seine, whereas the southern one receives terrestrial inputs from the rivers (fig. 1). Marine boundary conditions come from outputs of the three-dimensional model of the Baie de Seine developed by Cugier et al. (2005). River boundary conditions are derived from measurements carried out in the four tributaries. River discharges were measured every day by the "DIrection Régional de l'ENvironnement (DIREN)". Dissolved nutrient measurements (inorganic nitrogen and silicon), organic nitrogen and temperature were performed monthly by the "Agence de l'eau Seine-Normandie". Initial conditions for pelagic variables were determined using field measurements. Concerning benthic variables, because of the lack of available data, initial conditions for benthic stocks (nutrients and detrital matter) were fixed equal to zero. Meteorological forcing was provided by Météo-France at the Englesqueville-la-Percée station (north-east of the bay).

Simulated scenarios

All standing stocks are annual averages expressed in tons of nitrogen (t N) and all fluxes are integrated over the year and expressed in tons of nitrogen per year (t N y^{-1}). Preliminary results showed that the influence of zooplankton on the Baie des Veys nitrogen cycle is lower comparison to fluxes associated with other state variables. Consequently, fluxes associated with this compartment are not taken into account in this study. River inputs are primarily DIN and PON. Phytoplankton from river fluxes is not taken into account. Oceanic exchanges are estimated using results of the Baie de Seine model (Cugier et al., 2005) as previously explained. Values indicated correspond to net difference between inputs and outputs.

Several scenarios with different environmental conditions were performed. Three years with contrasted environmental conditions in terms of river inputs were simulated: 2003, 2002 and 2001. River nitrogen inputs represent *ca.* 3000, 5000 and 7400 t N y^{-1} for these three years respectively. As a whole, these river discharges are rather important. Thus, we tested two additional scenarios with lower river discharge in order to fully understand the influence of the environment on the Baie des Veys nitrogen cycle. Furthermore, two simulations were achieved for each scenario to estimate the influence of cultivated oysters: the first one with oysters and the second one without oysters.

Results and Discussion

Influence of cultivated oysters on the Baie des Veys nitrogen cycle

The influence of oysters in terms of nitrogen fluxes is only presented for the year 2002. This scenario has been chosen because environmental conditions in terms of river inputs and meteorology (luminosity and temperature) correspond to an average year for this ecosystem. The influence of the year-to-year variability of the environment on the nitrogen cycle will be discussed in the next section.

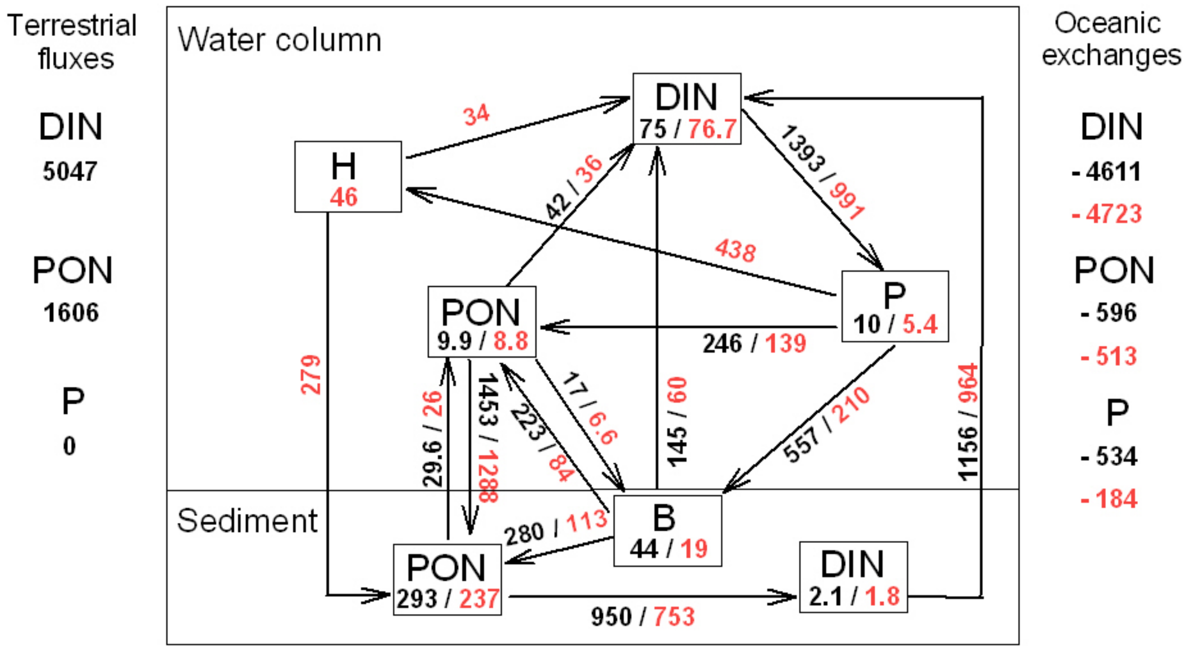

Figure 3 : Average stocks (t N) and integrated fluxes (t N y^{-1}) for the Baie des Veys box model for the year 2002. Black values correspond to results of the simulation without oysters and red ones represent simulation with oysters.

Generally, results showed that all state variables were not affected in the same way by the presence of oysters. DIN average stock in the water column and in the sediment and PON average stock in the water column did not display a significant difference between simulations with and without oysters. In contrast, the PON stock in the sediment decreased of 20 % when oysters are present. The highest effect of oysters was observed for phytoplankton and wild suspension feeders stocks with a reduction of 45 and 57 % respectively in the scenario with oysters.

Whatever the scenario studied (with or without oysters) net fluxes from freshwater and offshore sources were positive for DIN and PON indicating an importation into the Baie des Veys. However, these two compartments were not affected in the same way by the presence of oysters. PON imports were higher in the simulation with oysters than in the simulation without oysters whereas DIN imports were lower in the presence of oysters. The net flux for phytoplankton was always negative indicating an exportation of microalgae to the adjacent sea. Nevertheless, when oysters were present exportation of phytoplankton was reduced by approximately 65 %.

Within the ecosystem, all fluxes were reduced in the presence of oysters. Annual phytoplankton production (DIN → P) and phytoplankton consumption by wild filter-feeders (P → B) were reduced by 29 % and 62 % respectively. The addition of oysters led to a higher total grazing pressure of 14 % on phytoplankton (P → B + P → H). Thus, the decrease in phytoplankton production and the increase in total grazing could explain the high reduction of the annual average stock of phytoplankton as its exportation to the adjacent sea. In the presence of cultivated oysters, a trophic competition occurred with wild filter-feeders which could explain the strong reduction in the annual average stock and in the grazing flux of wild filter-feeders. In parallel, the decrease in phytoplankton and wild filter-feeders stocks led to a decrease of phytoplankton mortality rate (P → PON) ca. 43 % and of wild filter-feeders egestion rate (B → PON) ca. 60 %. Surprisingly, that did not induce a significant decrease in PON average stock in the water column. This could be explained by the fact that the strong reduction of fluxes within the system in the presence of oysters was compensated by a diminution in PON exportation to the adjacent sea.

Influence of the year-to-year variability in environmental conditions on the Baie des Veys nitrogen cycle

In order to illustrate the influence of the year-to-year variability in environmental conditions on the nitrogen cycle, results were presented for the assimilation rate of phytoplankton (figure 4) and the grazing rate by both wild filter-feeders and cultivated oysters (figure 5). The later point also allowed to discuss the existing trophic competition between the two groups of suspension feeders. Year-to-year variations in assimilation and grazing rate were presented as a function of DIN river fluxes.

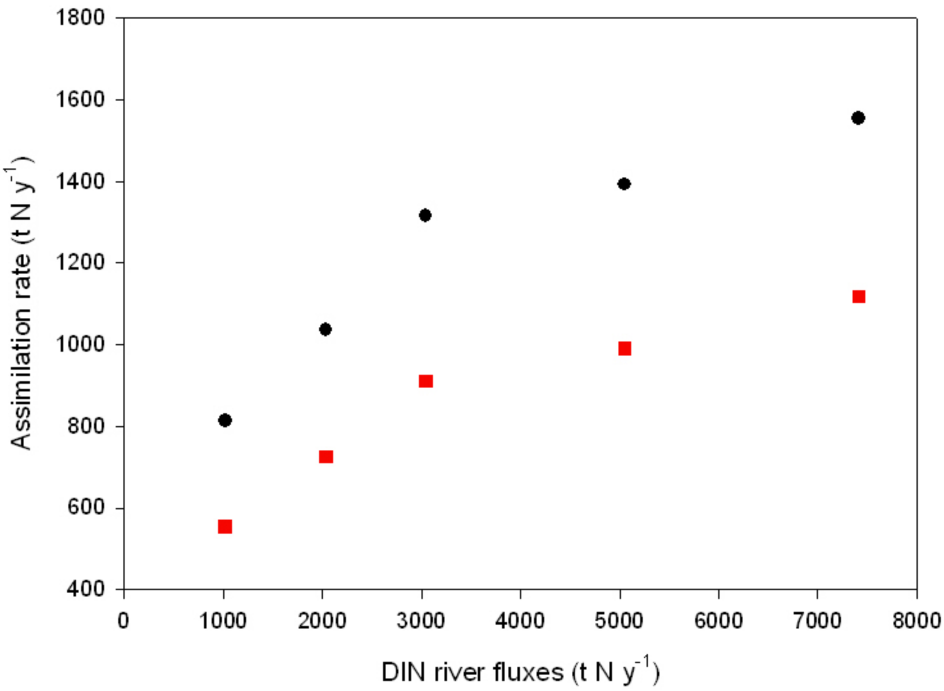

Figure 4 : Year-to-year variability in the phytoplankton assimilation rate. Black dots correspond to the simulation without oysters and red ones to the simulation with oysters.

The increase of DIN river fluxes induced an increase of the phytoplankton assimilation rate (figure 4). For the lowest contributions (< 3000 t N y^{-1}) and whatever the scenario studied (with or without oysters) a linear increase was observed. When river fluxes were higher than 3 000 t N y^{-1}, the increase was lower. A strong difference was also observed between scenarios with and without oysters for all environmental conditions simulated. As a whole, these results indicated that for river fluxes lower than 3000 t N y^{-1}, the influence of oysters was similar to the influence of the environment. More precisely, the presence of oysters resulted in a decrease of *ca.* 200 t N y^{-1} in the phytoplankton assimilation rate. In the same way, the effect related to river fluxes also corresponded to a variation of ca. 200 t N y^{-1} in the phytoplankton assimilation rate. Beyond the threshold value of 3 000 t N y^{-1}of DIN river inputs the influence of oysters was always much more important than that of the environment.

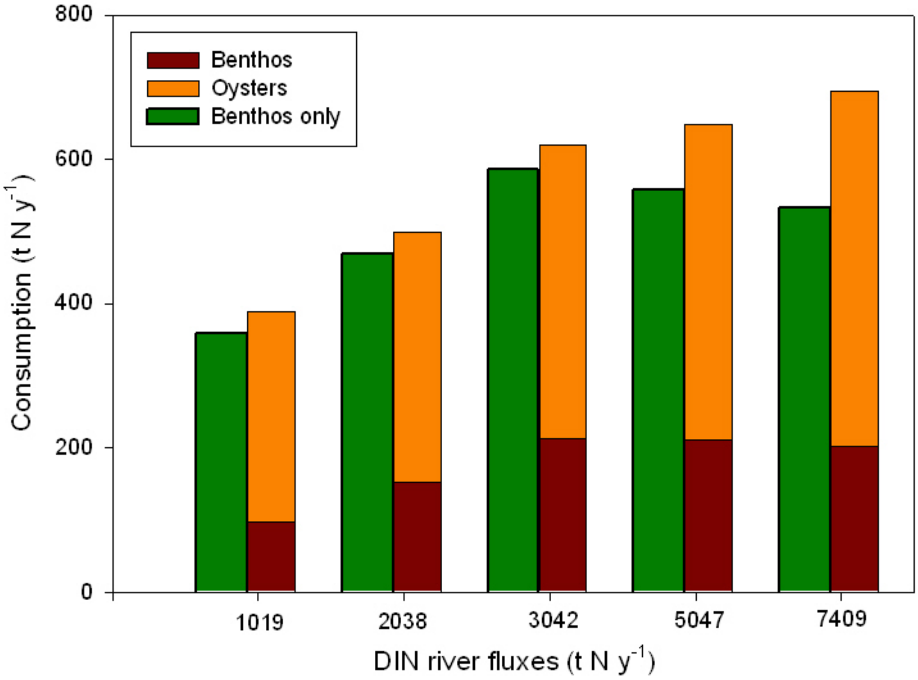

Figure 5 : Year-to-year variability in phytoplankton consumption rate. For each simulation, the first bar corresponds to consumption rate by wild filter-feeders in the scenario without oysters and the second one corresponds to the respective consumption of wild filter-feeders and cultivated oysters.

In the simulations without oysters, a regular increase in the consumption rate of wild filter-feeders was observed until the threshold value of 3 000 t N y^{-1}. Then, a regular decrease occurred when river fluxes were higher than 3 000 t N y^{-1} (figure 5). In the simulations with oysters, the consumption rate increased continuously with the increase of river inputs. However, as for the phytoplankton assimilation rate, the increase was more important before the threshold value of 3 000 t N y^{-1}. The additional introduction of oysters allowed to compare the respective influence of the two compartments of filter-feeders (wild *vs.* cultivated) on the ecosystem functioning. The presence of oysters in the ecosystem tended to inhibit the development of wild filter-feeders making the consumption rate of this group always lower than that of cultivated oysters. When river fluxes exceeded 3 000 t N y^{-1} the consumption rate of wild filter-feeders reached a plateau, whereas, it further increased for the oysters. In contrast, below 3 000 t N y^{-1} of river inputs the total consumption rate was similar between the simulations with and without oysters. Beyond 3 000 t N y^{-1} of river inputs the total consumption rate still increased in the presence of oysters whereas it decreased without oysters. This could be explained by an inhibition in the development of the wild filter-feeders due to a density-dependent limitation. A high density of wild filter-feeders implied a decrease in the consumption rate in order to limit the development of the population. In the presence of oysters, the stock of wild filter-feeders was not high enough to allow this process.

Comparison with another cultivated ecosystem : Tracadie Bay, Prince Edward Island, Canada.

Another interesting aspect in the study of the nitrogen cycle in an ecosystem was a possible comparison with other ecosystems. The figure 7 displayed the same fluxes estimated for the Baie des Veys (simulation with oysters presented on figure 3) and Tracadie Bay (Cranford et al., 2007). All variables indicated in figure 7 are identical to those presented in table 1 and are common for both ecosystems. The only difference is the species in culture : the Pacific oyster in the Baie des Veys and the Blue mussel in Tracadie Bay. Because of different physical characteristics (size, depth, water residence time…) between systems, it was difficult to compare directly the different fluxes. Thus, all fluxes were standardised as a function of DIN river inputs. Due to higher river inputs in the Baie des Veys, standardization led to lower values for the Baie des Veys. Thus, standardized fluxes for Tracadie Bay were divide by a factor 10 to compare results at the same scale.

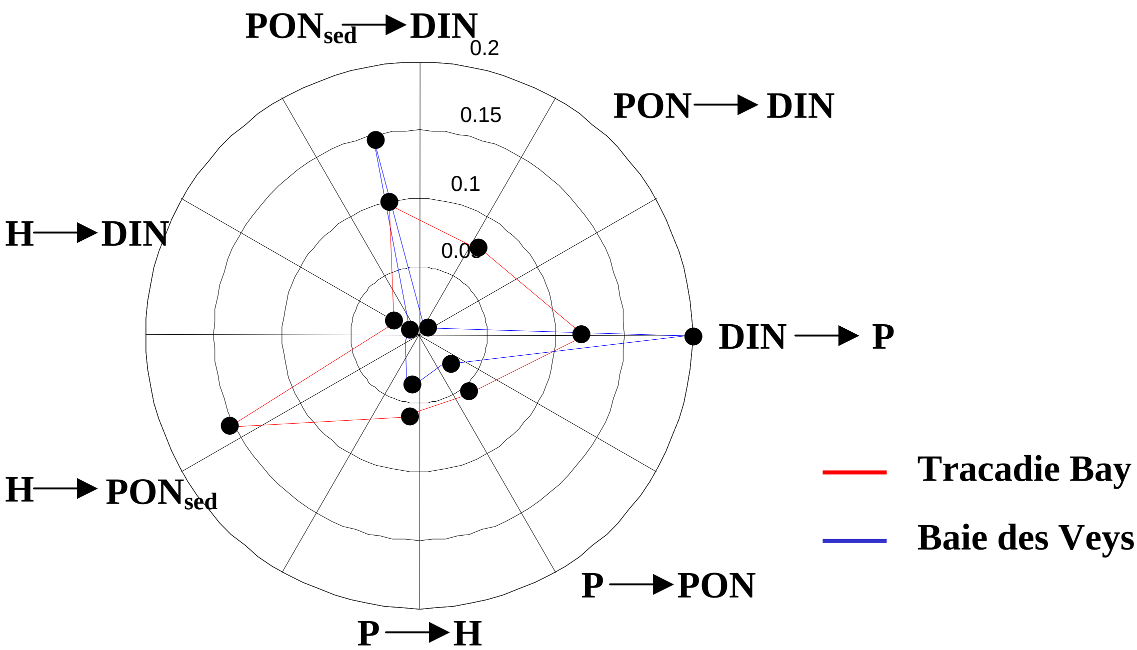

Figure 7 : Comparison between fluxes estimated in the Baie des Veys (with oysters) and in Tracadie Bay (with mussels). All fluxes were standardized as a function of DIN river inputs. In order to use the same scale, results obtained for Tracadie bay were divided by a factor 10. Symbols are explained in table1. H symbol corresponds to oysters in the Baie des Veys and mussels in Tracadie Bay.

Results showed that only 3 fluxes were similar between these two ecosystems: phytoplankton mortality (P → PON), excretion (H → DIN) and ingestion by cultivated filter-feeders (P → H). Two fluxes were more important in the Baie des Veys ecosystem: phytoplankton assimilation (DIN → P) and remineralisation of organic matter from the sediment (PON_{sed} → DIN). In contrast, remineralisation in the water column (PON → DIN) and biodeposition by filter-feeders (*i.e.* faeces deposition, H → PON_{sed}) were much more important in Tracadie bay. This comparison highlighted the different functioning of these cultivated areas. In the Baie des Veys, the remineralisation process was more important in the sediment. In Tracadie Bay, this process was more pronounced in the water column. The influence of faeces deposition was essential in the nitrogen cycle of Tracadie Bay, whereas, it was negligible in Baie des Veys. Surprisingly, the ingestion by cultivated filter-feeders was lower in the Baie des Veys, whereas phytoplankton production was higher. This difference could be explained by the fact that in contrast with the baie des Veys, filter-feeders from Tracadie Bay fed on phytoplankton but also on organic matter (Cranford et al., 2007). Furthermore, the existing trophic competition with wild filter-feeders highlighted in the Baie des Veys tended to reduce the phytoplankton availability.

As a conclusion, results of this study highlighted that the main variables influenced by the presence of oysters in the Baie des Veys ecosystem were phytoplankton and wild suspension feeders. The higher grazing pressure on phytoplankton induced by the addition of cultivated oysters as well as the trophic competition existing between wild filter-feeders and cultivated oysters explained the strong decrease in phytoplankton and wild filter-feeders stocks. The analysis of the year-to-year variability in river inputs indicated that the main fluxes of this ecosystem tended to increase with the increase of external inputs. However, the influence of cultivated oysters seemed to be more important than that of the environment beyond a threshold value of river inputs around 3000 t N y^{-1}. In the Baie des Veys, river inputs were seldom lower than 3000 t N y^{-1}, so, the nitrogen cycle in the Baie des Veys was influenced more by the cultivated oysters than by the environment. Finally, the comparison of fluxes between different ecosystems allowed to improve the knowledge on the influence of cultivated species on their environment. However, the comparison was difficult due to the numerous differences existing in the structure and the functioning of these cultivated areas.

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