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How would the loss of production due to an herbicide have repercussions in the food web of an intertidal mudflat? Sensitivity analysis of an inverse model for Brouage mudflat, Marennes-Oléron Bay, France

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Abstract: The presence of herbicides in the run-off water coming over Brouage mudflat (Marennes-Oléron Bay, France) is suspected to cause a loss of primary production by benthic diatom biofilm. Microphytobenthos being the main primary producer of this ecosystem, it was questioned about what could be the effect of such a modification of primary production on the entire food web that depends on it. The probable impacts were investigated through a sensitivity analysis conducted on the steady-state model of the Brouage mudflat, coupling two seasons and trophic-hydrodynamic flows. The loss of benthic primary production had an effect on compartments at a low trophic level, but was buffered at higher levels because of the compensation of herbivory by other pathways and especially detritivory. The consequences seemed more important on physical flows through resuspension and export by advection, but this should be apprehended through dynamic modeling coupling physics and biology.

Résumé : *Quelles sont les répercussions de la perte de production due à un herbicide sur le réseau trophique d'une vasière intertidale ? Analyse de sensibilité d'un modèle à l'état stationnaire de la vasière de Brouage, Baie de Marennes-Oléron, France.* La présence d'herbicides dans les eaux de drainage de la vasière de Brouage est susceptible de provoquer une baisse de la production primaire benthique au niveau du biofilm de diatomées. Ce microphytobenthos étant le principal producteur primaire de cet écosystème, on peut se demander quel serait alors l'impact d'une telle perte de production sur l'ensemble du réseau trophique qui en dépend. Les conséquences probables ont été étudiées par une analyse de sensibilité d'un modèle de réseau trophique à l'état stationnaire de la vasière de Brouage. Ce modèle couple deux saisons, et les flux physiques et trophiques. La perte de production primaire benthique a de moins en moins d'effet quand le niveau trophique augmente, les flux herbivores étant compensés par des flux principalement détritiques. Les conséquences semblent être plus marquées pour les flux physiques de resuspension et d'exportation par advection. Cependant seul un modèle dynamique couplant phénomènes physiques et biologiques permettrait d'appréhender ces conséquences.

Keywords: Sensitivity analysis; Inverse analysis; Microphytobenthos; Pollution; Intertidal-mudflat food web

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Introduction

Most littoral zones are subject to herbicides run-off from agricultural or urban areas. This pollution may lead to loss of primary production (Dorigo & Leboulanger, 2001) and consequently have repercussion through trophic pathways in the whole biocenosis (Pratt et al., 1997). In France, the contamination is mainly due to atrazine and diuron (IFEN, 2001). Whereas the first is now forbidden and the second is limited, both are still found in important quantities in the environment, and especially in coastal zones where they could impact the food web (Munaron, 2004).

The microphytobenthos, mainly composed of diatoms forming a biofilm at the surface of the sediment (Herlory et al., 2004), is the main primary producer of the intertidal mudflats of many estuaries (Blanchard et al,. 1998; Guarini, 1998; Underwood & Kromkamp, 1999), and is the main food source for benthic invertebrates (Riera, 1995; Riera et al., 1996) and for cultivated bivalves (Riera & Richard, 1996). The effect of atrazine and diuron as inhibitors of the photosynthesis of the microphytobenthos has been demonstrated (Legrand et al., 2006).

The Brouage intertidal mudflat in Marennes-Oléron Bay is an important experimental and observation site, chosen for its high oyster production and primary productivity. Information has been accumulated for more than 20 years and concerns nowadays almost each compartment of the biocoenosis. This allowed the building of a very complete and precise food-web steady-state model aiming at synthesize and confront all the accumulated knowledge. For this synthesis, the optimization method of inverse analysis (Vézina & Platt 1988) has been applied and modified in order to take into account two coupled seasons (Degré et al., 2006). The model coupled benthic and pelagic compartments and added physical flows of deposition and re-suspension to the classical trophic flows. The obtained model was at equilibrium at the annual scale but allowed biomass variation between seasons. Such a model is a useful tool to investigate the effect that benthic primary production modifications could have on the whole food web of an intertidal mudflat.

The aim of the present study was to evaluate the way an inhibition of the microphytobenthic photosynthesis, and consequent loss of primary production, could have repercussions on the organic-carbon budget in the complete food web. A sensitivity analysis was performed on the steady-state C-flow model of the Brouage intertidal mudflat. All the flows of the model were re-evaluated by inverse analysis, for different values of benthic primary production. The values of benthic primary production tested were chosen in a range of possible values. This range covered loss and gain of benthic primary production in order to observe if the consequences were symmetric. It was interpreted as showing the possible effects of a modification of production on the available food for the different consumers of the mudflat and on several emergent properties that characterize the food web as a whole.

Table 1. Compartments in the Brouage-mudflat model (Degré et al. *accepted*).
Tableau 1. Compartiments du modèle de la vasière de Brouage (Degré et al. *accepted*).

Abbreviation	complete name
pphy	**Phytoplankton** (& resuspended microphytobenthos)
bphy	**Microphytobenthos**
pmic	**Microzooplankton** (ciliates, flagellates)
bfor	**Benthic protozoa** (mainly foraminifera)
pmes	**Mesozooplancton** (mainly copepods)
bmei	**Meiofauna** (mainly nematods & a few copepods)
bbiv	**Bivalves**
bgas	**Gastropods** (*Hydrobia ulvae*)
bann	**Annelids & nemerteans**
bart	**Arthropods**
cult	**Cultivated oysters and mussels**
pjuv	**Juvenile fish** (mainly *Solea solea*)
bmul	**Grazing fish** (mainly *Liza ramada*)
limi	**Shorebirds** (limicolus)
pbac	**Pelagic bacteria**
pdoc	**Pelagic DOC** (Dissolved Organic Carbon)
ppoc	**Pelagic POC** (non-living Particulate Organic Carbon)
bbac	**Benthic bacteria**
bdoc	**Benthic DOC**
bpoc	**Benthic POC**

Methods

Study site

The Brouage mudflat (Fig. 1), at the eastern part of the Marennes-Oléron Bay, is a very large intertidal area, characterized by a gradual slope (1:1000). It presents regular prominent structures at its surface, described as ‘ridges and runnels’ (Gouleau et al., 2000). The residual currents from river inputs flow from north to south, hence bringing water from the Charente River to the mudflat area (Bacher, 1989). The bay is the first European production site for oyster but the Brouage mudflat is mainly covered, in its lower part, by abandoned oyster cultures and still used mussel cultures.

Model used

Ecological knowledge on the Brouage mudflat was gathered in a model that was subject to different publications along its evolution (Leguerrier et al., 2003; Leguerrier et al., 2004; Degré et al., 2006). The most recent one, used for

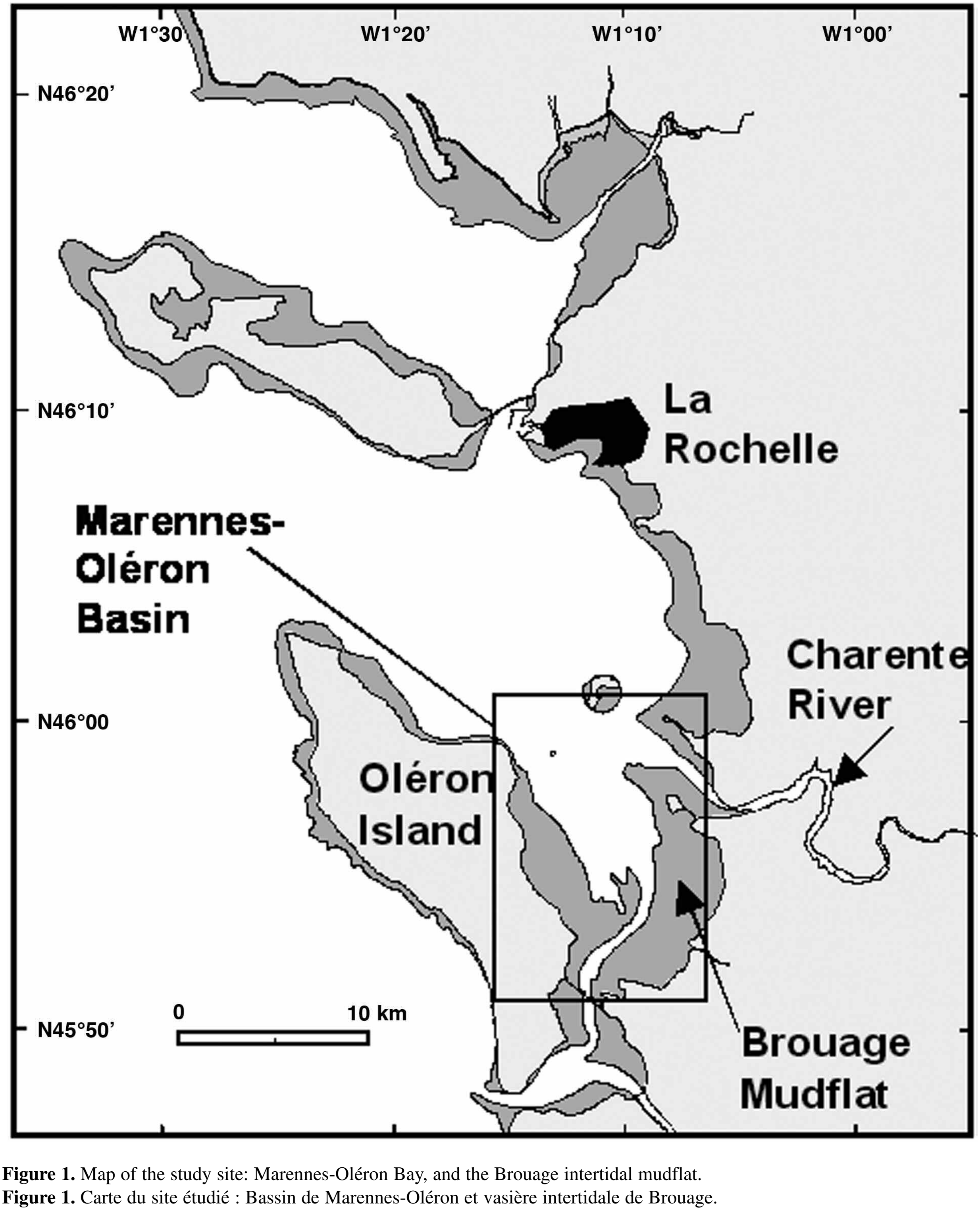


Figure 1. Map of the study site: Marennes-Oléron Bay, and the Brouage intertidal mudflat.
Figure 1. Carte du site étudié : Bassin de Marennes-Oléron et vasière intertidale de Brouage.

the present study, represented 20 compartments (Table 1), living or non-living, and benthic or pelagic, linked by 160 flows, either trophic or physical (deposition, resuspension). The model coupled two seasons: s1 is from mid-March to mid-October (7 months) and s2 is the complementary cold season (5 months).

The method used was derived from inverse analysis applied to food webs (Vézina & Platt, 1988), modified for coupling two seasons (Degré et al., 2006). The mass of each compartment was considered as constant for the year as a whole (equilibrium steady-state on the annual basis), but could vary from one season to the other (non equilibrium steady-state on a seasonal basis). The biological or ecological knowledge was used either as linear equations of flows or as inequalities, giving a range of probable values. These equations and inequalities were either defined for one season or at the annual level.

Sensitivity analysis on the benthic primary production

In the steady-state model of carbon flows, the primary production by microphytobenthos was estimated to fit in an interval of probable values ranged between 0.9 and 1.2 $gC.m^{-2}.d^{-1}$ in s1 (warm season) and between 0.7 and 1 $gC.m^{-2}.d^{-1}$ in s2 (cold season). The average value of 1.15 $gC.m^{-2}.d^{-1}$ in s1 and 0.85 $gC.m^{-2}.d^{-1}$ in s2 was considered as the most probable and used as a biological constraint in the building of the general model (Degré et al., 2006). In the present study, we explored the sensitivity of the result when this value was modified from the lowest to the highest values of these two intervals. For s1, the realized simulations corresponded to a production of microphytobenthos - 3%, - 6%, - 9%, - 11%, - 14%. These values could be assimilated to a production loss due to an herbicide. We also tested the values + 3%, + 6%, + 9%, + 11%, + 14 %, in order to observe if the consequences were symmetric. For s2 the tested values were the average – or + 4, 7, 11, 14 and 18%, in order to fit in the interval. This production being computed in order to fit biomass changes during daytime emersion, it was considered as a gross primary production minus 25% of respiration, grazing and extracellular release. This percentage was modified to 50% for the gastropod grazing, considered as occurring only at emersion, when biofilms are formed (Haubois, 2003; Degré et al., 2006).

Table 2. Values of the reference model for throughputs and overall indices whose variations are presented in Fig. 1 and 2. GPP = gross primary production, Bio-exports = export out of the system by biotic vectors (fishes and birds), Phy-exports = exports by advection in the water column, Ben = benthic, D/H = detritivory / herbivory ratio.

Tableau 2. Valeurs des activités (somme des flux entrant dans chaque compartiment) et des indices globaux du modèle de référence. Leurs variations dans les simulations sont présentées en figures 1 et 2. GPP = production primaire brute, Bio-exports = exportations du système par les vecteurs biotiques (poissons et oiseaux), Phy-export = exportation par advection dans la colonne d'eau, Ben = benthique, D/H = rapport des régimes détritivores / herbivores.

Index	Value in s1	Value in s2
Throughputs in $mgC.m^{-2}.d^{-1}$		
Bphy	1299	1022
Bmei	273	234
Bfor	470	270
Bmul	69	335
Bann	125	0
Bdoc	1574	1349
Bpoc	1518	2479
Overall indices in $mgC.m^{-2}.d^{-1}$		
GPP	1343	1034
Bio-exports	35	257
Phy-exports	7440	8980
Respiration	2489	1973
Burial	747	1753
Resuspension	830	218
Deposition	1387	1081
Ben-detritivory	623	528
Ben-herbivory	505	381
Overall index (no unit)		
Ben-D/H	5.76	9.18

Indices used for characterizing food-web properties

As the model was composed of numerous flows, simple synthetic indices were computed, in order to characterize the compartment behavior, or the overall behavior of the food web. The *throughput* of each compartment is the sum of all entering flows into the compartment. The exports were separated in those made by biotic vectors (*bio-export*), and those by advection (*phy-export*) in the water column. The total *respiration*, *resuspension* and *deposition*, *burial* in the sediment, benthic and pelagic *detritivory* and *herbivory* were calculated.

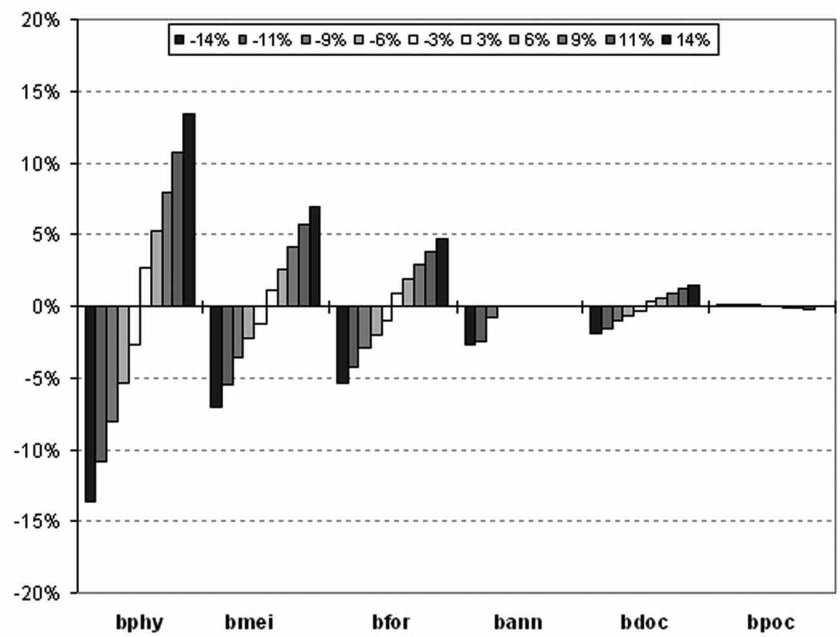
Results

The results of this sensitivity analysis are presented partially, with synthetic indices. Those were expressed as percentage of variation of the reference state corresponding to the published model (Degré et al., 2006, reference values presented in Table 2).

Compartmental analysis

Variations in the benthic primary production had consequences on the throughput of 6 compartments in s1: the microphytobenthos itself (bphy), the benthic nematods (bmei), foraminifers (bfor), annelids (bann), DOC (bdoc), and non-living POC (bpoc) and of 5 compartments in s2: microphytobenthos (bphy), the benthic foraminifers (bfor), mullets (bmul), DOC (bdoc) and POC (bpoc) (Fig. 2).

a)



b)

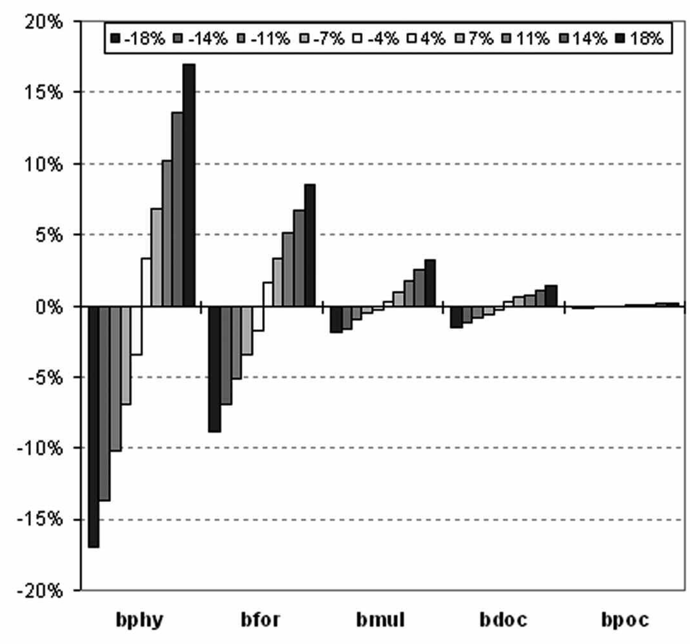


Figure 2. Sensitivity of the compartment throughput to primary production modifications. The main impacted living compartments are selected for each season: a) in warm season s1 and b) in cold season s2. The modification is expressed in percentage of the reference state. Abbreviations are explained in Table 1. The variations are observed after simulation of a decrease or increase of primary production at regular intervals. No value indicates no variation.

Figure 2. Sensibilité des activités (somme des flux entrants dans chaque compartiment) des compartiments aux modifications de la production primaire. Les compartiments les plus sensibles sont sélectionnés pour chaque saison : a) en saison chaude ou s1, b) en saison froide ou s2. L'ordonnée indique la variation d'activité, exprimée en pourcentage de la valeur du modèle de référence. Les abréviations sont explicitées en table 1. Les variations d'activité sont observées après simulation d'une baisse ou d'une hausse de la production primaire, à intervalles réguliers. Une absence de valeurs exprime une absence de variation.

This impact mainly corresponded to a modification in the available food. During the warm season, the consumption of benthic diatoms by foraminifers and meiofauna appeared as correlated to the benthic primary production value, as well as the consumption of protozoa of the benthos assimilated to the foraminifer compartment by foraminifers themselves and meiofauna. The meiofauna, which was the most constrained component, lowered its total ingestion in proportion to the benthic primary production. The foraminifers, on the contrary, which role in the food web was less documented, compensated the lack of benthic diatoms by a higher consumption of detrital POC. The annelids, which did not consume any benthic primary production in the reference model, were impacted by a loss of available meiofauna, for the 3 simulations with the smallest benthic primary production. During the cold season, the meiofauna had a lower ingestion level and was not affected by the benthic primary production loss. The foraminifers presented, when benthic primary production was low, a diet less composed of benthic diatoms and detrital POC, but with more bacteria and other protozoa. The mullets, whose activity was higher in s2 than in s1, had less meiofauna and POC available as a food source when the benthic primary production was low.

During s1, the impact also influenced the non living carbon compartments bdoc and bpoc. The benthic DOC was produced in quantity proportional to the benthic production, as defined in our constraints. As a consequence, it was also less available as a food source for the foraminifers. The loss of DOC exudation by the diatoms was, in the simulations, compensated by an increase in POC formation and its oxidation into DOC, and an increase of direct DOC formation by bacteria mediated by the viral lyses. This was due to the demand in DOC, especially by bacteria, which remained high. In s2, the same phenomenon was observed for the DOC but remained negligible as far as the POC was concerned.

Overall indices

The sensitivity of the model to primary production can also be characterized for the food web as a whole (Fig. 3). As the model is at equilibrium on an annual level, the total sum of inputs is equal to the outputs. Among the inputs, only the benthic primary production was modified here. The pelagic primary production and inputs by advection were constant. The most sensitive outputs to the benthic PP modification, with a positive correlation, are the loss of organic matter by burial and the carbon dissipation by respiration. The loss of primary production also caused a loss in the resuspension of benthic diatoms and consequently on the level of export by advection.

The amount of herbivore and detritivore flows showed that the loss of benthic primary production which lowered the benthic herbivory, was only slightly compensated by consumption of non-living material (benthic detritivory). Hence, the modification of the ratio detritivory/herbivory was mainly due to the modification in herbivory flows.

Discussion

The effect of Atrazine and Diuron has been shown on the primary productivity of benthic diatoms from intertidal mudflats (Legrand et al., 2006). These two herbicides are both present in the Charente River and in small channels between adjacent salt marshes and the Brouage mudflat (Munaron, 2004). Values inferior to 100 $mg.L^{-1}$, often encountered in the Charente River, did not show a significant impact but some peaks of herbicides concentration can be observed (Munaron, 2004). The potential effect of herbicides on benthic primary production, then could be either punctual or correspond to a long-term increase of the run-off. This Charente run-off has potential impact on the Brouage mudflat functioning as the hydrodynamic model shows that the plume of the Charente is often directed to the South, on the Brouage mudflat location (Munaron, 2004).

The sensitivity analysis gave indices for considering the effect on the entire food-web. This was a preliminary view, and not a real simulation, as the initial constraints of the model were not modified, i.e. supposing that the communities remained unchanged and that no drastic change in species metabolism occurred. Physiological rates remained in usually observed ranges. However, the probable trend of modification was given in case of an enhancement of the herbicide run-off.

The present view is a food web with numerous compartments at a quite low trophic level, with a strong consumption of either microphytobenthos or detritus and associated bacteria (Degré et al., 2006). Even if the benthic primary production was high, the detritus remained a consequent resource. This could be seen by the high level of detritivory/herbivory which was especially strong in winter when the benthic primary production was reduced. Detritivore flows then reached almost 10 fold herbivore flows (Table 2). Consequently to a loss of benthic primary production, two behaviors could be observed, according to the constraints used, in the low level animals that are foraminifers, meiofauna (mainly nematodes) and mullets. Either the ingestion was lowered or was maintained the same, with a shift in their diet in order to compensate the diatoms by detritus and associated bacteria. Then the detritivory and recycling became more important. In the two situations, the impact was totally buffered at the following trophic level and top predators were not at all impacted.

On an overall point of view, the consequences mainly concerned exchanges with the adjacent oceanic ecosystem. As a consequence of the buffer effect in the food web, the

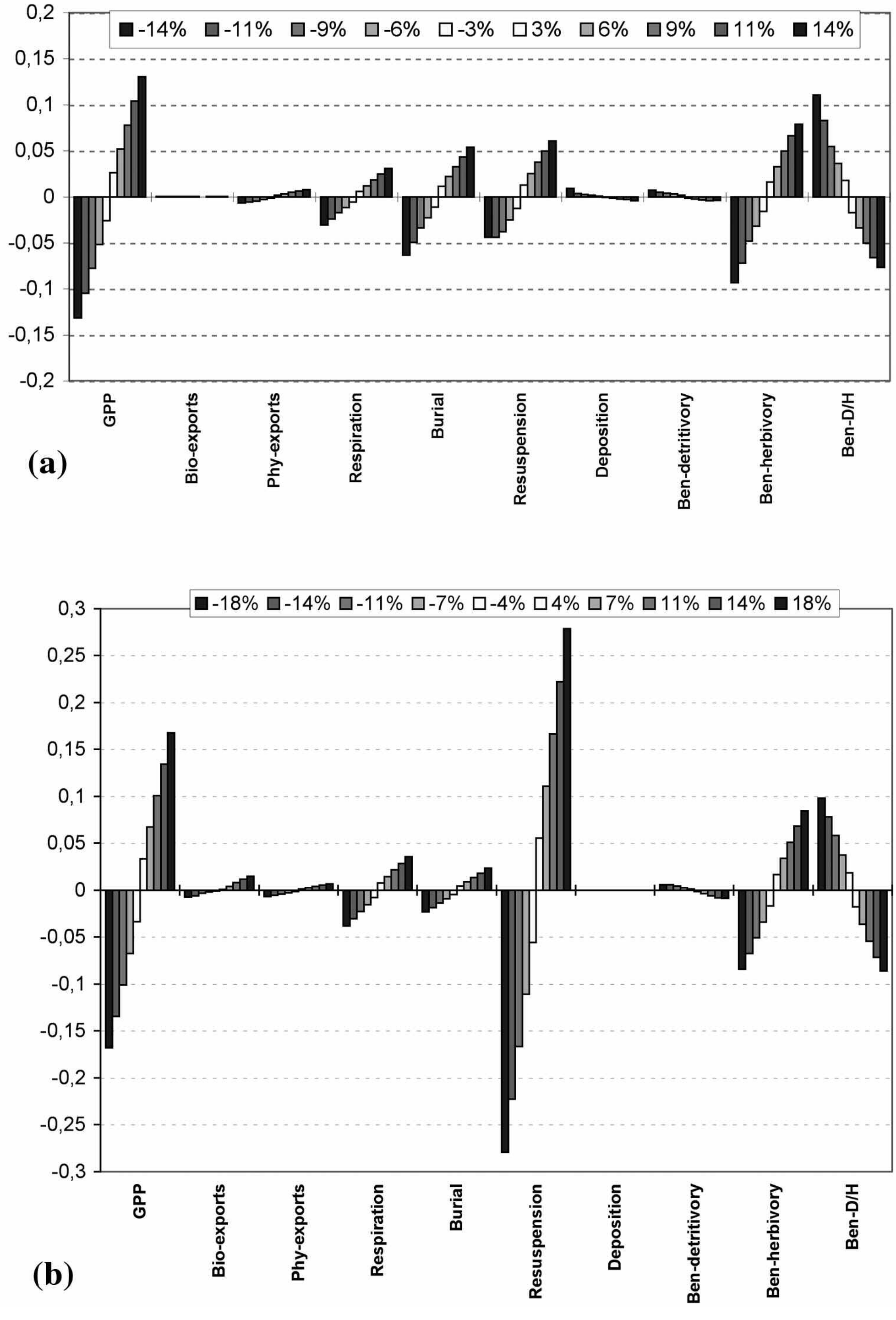


Figure 3. Sensitivity of the overall indices to primary production modifications, a) in warm season s1 and b) in cold season s2. The modification is expressed in percentage of the reference state. The variations are observed after simulation of a decrease or increase of primary production at regular intervals. GPP = gross primary production, Bio-exports = export out of the system by biotic vectors (fishes and birds), Phy-exports = exports by advection in the water column, Ben = benthic, D/H = detritivory/herbivory ratio.

Figure 3. Sensibilité des indices globaux aux modifications de la production primaire : a) en saison chaude ou s1, b) en saison froide ou s2. La modification (en ordonnée) est exprimée en pourcentage de la valeur du modèle de référence. Les variations d'activité sont observées après simulation d'une baisse ou d'une hausse de la production primaire, à intervalles réguliers. GPP = production primaire brute, Bio-exports = exportations du système par les vecteurs biotiques (poissons et oiseaux), Phy-export = exportation par advection dans la colonne d'eau, Ben = benthique, D/H = rapport des régimes détritivores/herbivores.

export by biotic vectors was not significantly modified by the loss of benthic primary production. The main biotic vector affected was the mullet compartment, mainly active in the cold season. The other biotic vectors were at too high a trophic level to show an impact. The sensitivity analysis showed an important impact on the resuspension of diatoms, on the burial of detritic material and on the overall respiration. However the resuspension remains a poorly described phenomenon and should demand extra physical studies. The resuspension modification was associated with a modification of the flux of organic carbon exportation through advection in the water column. Even if it appeared low in percentage (0.7% of modification max), this represented a high value as the reference flow is high. The flow was modified of 57 to 61 $mgC.m^{-2}.d^{-1}$ according to the season. This flow was more important that the totality of exports by biotic vectors.

Another modification that could be added to the one simulated here would be also a loss of planktonic primary production and of phytoplankton inputs into the ecosystem. It is likely that these flows are also impacted by the herbicides which action of phytoplankton has been demonstrated (Arzul & Durand, 1999). However, the flow of planktonic primary production, estimated from modeling (Struski pers. com., Struski, 2005) appears to be very low in the water recovering the Brouage mudflat (44 and 12 $mgC.m^{-2}.d^{-1}$ in s1 and s2 respectively).

This approach presents a weak point as far as cultivated oysters are concerned. In the reference model (Degré et al., 2006), the oyster production, consumption and respiration were constrained, but their diet remained unconstrained. As a result, the oyster's diet relied strictly on detritivory, whereas their consumption of living material has been shown in the Marennes-Oléron Bay, and especially of planktonic diatoms directly coming from the microphytobenthos resuspension (Riera, 1995). Consequently, the buffering effect of the different trophic levels, on the primary production variations, should be reconsidered as far as cultivated bivalves are concerned. One may suppose that the oysters could also shift from herbivory (microphytobenthos consumption) to detritivory, but the consequences on their metabolism should be apprehended, with experimental designs.

The sensitivity analysis applied in this study gave clues to a strong buffering of the benthic primary production loss in the food web and suggested to focus mainly on exports flows out of the system, but this implies further studies on the resuspension process and of coupling in a model physics and biology flows.

The buffering effect, which appears as the main characteristic of this food-web model, relies on the strong complexity of the food web and the strong omnivory, allowing the animal compartments to shift from herbivory to detritivory. However, all this simulation is realized in constant conditions, especially of community composition. One could suppose that the diet shift that could buffer the primary production variation would be associated to a community modification, but only experimentation could then analyze this change and its ecological consequences.

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