

Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France)

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ABSTRACT: We used a carbon-based food web model to investigate the effects of oyster cultivation on the ecosystem of an intertidal mudflat. A previously published food web model of a mudflat in Marennes-Oléron Bay, France, was updated with revised parameters, and a realistic surface area and density of existing oyster cultures on the mudflat. We developed 2 hypothetical scenarios to estimate the impact of oyster cultivation on the food web structure of the ecosystem: one with no oysters, the other with a doubled area devoted to cultivated oysters in the bay. Oysters are direct trophic competitors of other filter feeders, and their presence modifies benthic–pelagic coupling by forcing a shift from pelagic consumers to benthic consumers. Increasing the surface area of cultivated oysters caused secondary production to increase, providing food for top predators (in particular juvenile nekton), reinforcing the nursery role of the mudflat in the ecosystem, and altering the species composition available to the top predators.

KEY WORDS: Carbon flux · Inverse analysis · Food web · Network analysis · Bivalve culture

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INTRODUCTION

The impact of human activity on the functioning of coastal and estuarine ecosystems is central to modern ecology studies (French 1997). Humans impact ecosystems in numerous ways, e.g. by habitat transformation, introduction of organisms, resource depletion, or food web modifications (Botsford et al. 1997). Thus, humans must be considered a component of ecosystems (Boydén 1993), in which they frequently act as predators (Castilla 1999, de Boer & Prins 2002). In studies of exploited marine resources, e.g. the effect of oyster cultivation on the functioning of marine coastal environments, various tools have been used, e.g. the assessment of the carrying capacity of the ecosystem in terms of sustainable marketable production (Héral et al. 1986, Héral 1991, Dame 1996, Bacher et al. 1998).

Some 60 mollusc species are consumed in France, 10 of which are grown commercially. Of the total grounds leased in France for the culture of molluscs (20 000 ha),

72% is for the culture of the oyster *Crassostrea gigas* (Gouletquer & Héral 1997). The Marennes-Oléron Basin (MOB) on the Atlantic coast of France is the major European site for oyster culture and produces 30 000 to 45 000 t of oysters per year (Héral et al. 1989, Bacher et al. 1998). MOB is also one of the few ecosystems in which oysters have, on 2 occasions, been overstocked (Dame & Prins 1998), leading to poor growth, and high mortality (Héral et al. 1989).

Oyster farming impacts the mudflat ecosystem both biologically and mechanically. Biological mechanisms include the oysters' food uptake and release of dissolved material into the water column, competition with indigenous species (Sauriau et al. 1989), depletion of the plankton in the water column (Dame & Prins 1998, Gangnery et al. 2001), and enhancement of phytoplankton productivity through nutrient replenishment (Ball et al. 1997). Mechanical impact occurs by production and deposition of pseudofeces, and the modification of current patterns by oyster racks in the

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cultivation areas (Nugues et al. 1996), which enhance the accumulation of organic biodeposits (Escaravage et al. 1989).

The present study evaluates the impact of oyster cultivation on the functioning of an intertidal mudflat food web. Our goal was to evaluate energy/mass flows on the community scale. Many models can be used to achieve this, e.g. predator–prey (Wiegert 1981, in Héral 1991) or input–output flow (Dame & Patten 1981) models. However, in the modeling of any system, it is important to choose a level of complexity compatible with the available data (Dame & Patten 1981). Predator–prey models require sufficient time-series data and a precise knowledge of the interactions between the various compartments, information that is often incomplete or unavailable for a number of compartments. Inverse analysis (Vézina & Platt 1988) may compensate for inadequate data sets. Its principal advantage is the instantaneous evaluation of trophic exchanges between the various components of an ecosystem, thereby integrating all the existing knowledge on the ecosystem (Vézina & Platt 1988).

We have added recent data from the mudflat ecosystem along the eastern side of the MOB into a previous model of the mudflat created by the inverse analysis method (Leguerrier et al. 2003). As 16% of the MOB area is devoted to oyster culture (O. Lemoine pers. comm.), we used this percent as a basis for constructing a mudflat food web representative of the present-day situation in the MOB. We constructed 2 hypothetical scenarios: one representing a system with no oyster cultivation, the second assuming a system with twice the actual area of oyster cultivation at the same oyster density per m^2 . The results of the 3 scenarios ('no oysters', 'realistic', and 'doubled cultivation') were compared to determine the role of oyster cultivation in the functioning of the MOB mudflat ecosystem.

MATERIALS AND METHODS

Study site. The Marennes-Oléron Bay (Fig. 1), situated between the French Atlantic coast and Oléron Island, covers $116 km^2$, of which $18 km^2$ are used for oyster culture (O. Lemoine pers. comm.). It is a macrotidal system, with a tidal range of up to 6 m during spring tides. Residual currents from inputs from the Charente River (Ravail et al. 1988, Soletchnik et al. 1998) and the Gironde River (Dechambenoy et al. 1977) flow from north to south (Bacher 1989). The MOB contains various types of habitats, including rocky shores and mudflats. The eastern mudflat covers a total area of $40 km^2$ (Gouleau et al. 2000) (Fig. 1). It has a relatively flat bottom (slope 1:1000) and a very large tidal area covered with prominent surface struc-

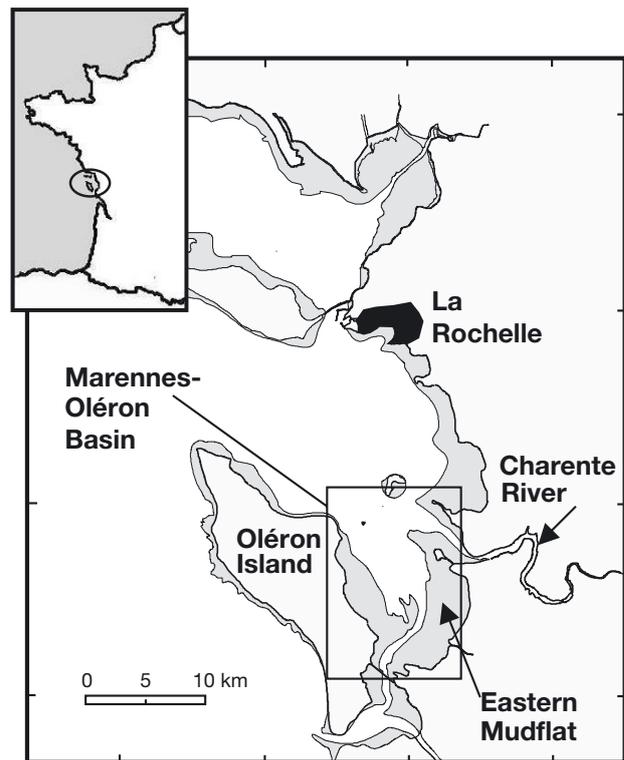


Fig. 1. Study site: Marennes-Oléron Bay, west coast of France. The intertidal mudflats are situated on the eastern side of the bay

tures described as 'ridges and runnels' by Gouleau et al. (2000). Current speeds can vary from 0.2 to $0.6 m s^{-1}$ (Bassoullet et al. 2000, Le Hir et al. 2000). Half of the lower part of this intertidal zone is covered by oysters from an abandoned oyster farm; the other half is still being used for oyster culture.

In MOB, oysters are grown on trestle tables. The oysters are grown in sacks of plastic netting that are secured horizontally to the frames (i.e. the sacks of oysters become the 'table top') $0.5 m$ above the ground (Gouletquer & Héral 1997).

Inverse analysis and application. Inverse analysis method: Inverse methods were developed to solve the problem of the lack of available data when modeling various systems (Parker 1942). In food web modeling, the number of known parameters is generally far less than the number of unknown parameters. Inverse analysis, as developed by Vézina & Platt (1988), seeks to include all existing knowledge about a system in order to achieve the best estimates of food web fluxes. The method requires that the compartments and the possible fluxes linking them be defined (in an *a priori* or conceptual model). Simple mass-balance rules are translated into equations so that the system is in steady state. All available data for the known ecosystem and biological parameters are expressed as linear con-

Table 1. Compartments of the trophic network. The name of each compartment and its respective habitat (B: benthic or P: pelagic) is listed on the left. Non-living compartments are indicated by grey shading

Habitat	Compartment name	Description	Biomass (gC m ⁻²)	Abbreviation	
B	Microphytobenthos	Benthic primary producers	3.13	bphy	
	Benthic bacteria	Free or attached bacteria	0.71	bbac	
	Benthic microfauna	Size range 5 to 100 µm	Unknown	bmic	
	Benthic meiofauna	Size range 100 µm to 1 mm	0.44	bmei	
	Bivalves	Non-cultivated macrofauna (size > 1 mm) classified according to their taxonomic group	1.11	bbiv	
	Gastropods		0.32	bgas	
	Annelids		0.39	bann	
	Arthropods		0.08	bart	
	Cultivated oysters	Biomass of shell (57.6%) + tissue (42.4%) on oyster racks (200 oysters m ⁻²)	67.08	bcoy	
		Benthic particulate organic carbon	Unknown	bpoc	
		Benthic dissolved organic carbon	Unknown	bdoc	
P	Phytoplankton	Phytoplankton, resuspended micophytobenthos, autotrophic protists	1.61	pphy	
	Pelagic bacteria	Free or attached bacteria	0.012	pbac	
	Microzooplankton	Heterotrophic flagellates, dinoflagellates, ciliates <100 µm ; metazoa <100 µm	Unknown	pmic	
	Mesozooplankton	Heterotrophic plankton 100 µm–5 mm	0.073	pmes	
	Juvenile nekton	Mainly juvenile soles (carnivorous)	Unknown	pjuv	
	Adult nekton	Mainly adult mullets (benthic feeders)	Unknown	pnek	
		Pelagic particulate organic carbon	11.86	ppoc	
		Pelagic dissolved organic carbon	Unknown	pdoc	
		Birds	Shorebirds + common shellduck	0.0016	bird

straints on the flows or combinations of flows with minimal and maximal values. These may include biomass — which, along with production/biomass (P/B), respiration/biomass (R/B), or other flux/biomass (F/B) values, leads to equations on fluxes — and growth and assimilation efficiencies, or biological rates; these data may be determined in the field or taken from the literature. Application of constraints reduces the possible solutions but does not result in a unique solution. To arrive at 1 solution (the solution vector), the inverse technique uses the principle of parsimony in that the least-square solution (that with the smallest Euclidian norm) is the 'best' solution.

Mudflat model: In Leguerrier et al. (2003), we constructed a carbon-based food web for an average square meter in an average year in the eastern mudflat. The *a priori* model was composed of 16 compartments: 2 non-living (benthic and suspended detritus) and 14 living (Table 1). The present study is based on a modified version of this model for the simulations of the 3 scenarios.

Adaptation of the *a priori* model: The *a priori* model was derived from a previous model (Leguerrier et al. 2003) with the following modifications: The treatment of recycling mechanisms was improved by dividing benthic and pelagic detritus into particulate and dissolved organic carbon compartments (POC and DOC). Macrofauna were sorted into their respective taxo-

nomic groups (bivalves, annelids [mainly polychaetes], arthropods, and gastropods). The composition of their diets was also defined by constraints on their ingestion flows to share them out between their favourite items. Experiments have shown that, despite their small size, bacteria constitute a food source for bivalves (Amouroux 1986, Prieur et al. 1990), but they result in a lower assimilation efficiency (McHenry & Birkbeck 1985 in Prieur et al 1990, Amouroux 1986), and thus their ingestion by macrofauna has been included in the conceptual food web model. Benthic microfauna were added to properly characterize the exchanges with microzooplankton, which is deposited with the pseudofeces. Nekton were divided into juveniles — mainly carnivorous fishes such as juvenile sea bass *Dicentrarchus labrax* (Laffaille et al. 2000) and flatfish *Solea solea* (Lagardère 1987) — and adults — principally adult mullets *Liza ramada*, which are benthic grazers (P. Richard & X. Fizzala pers. comm.). Details on the macrofauna groups are given in Appendix 1¹.

Some general assumptions about biological rates, based on data from recent studies, were incorporated into the model, and new boundaries (constraints) were added because of the modifications made to the *a priori* model (see Appendix 2¹). The new biological para-

¹Available as MEPS Supplementary Material at: www.int-res.com/journals/suppl/leguerrier_appendices.pdf

meters used were: (1) An estimated ratio of 5 for egestion/excretion of mesozooplankton (Anderson & Ducklow 2001), which was applied to any organism >1 mm. (2) For DOC excretion of microorganisms, we assumed 10% of their ingestion as lower limit and 100% of their respiration as upper limit (Vézina & Platt 1988). (3) DOC excretion of primary producers was taken from Vézina & Platt (1988). (4) Growth and assimilation efficiencies were derived from data of Savenkoff et al. (2001). (5) Data on pelagic bacteria were refined with countings from Héral & Prou (1980). Additional data on the biology of oysters in MOB were also included (Appendix 3¹).

Oyster cultivation: Oysters can absorb dissolved molecules such as amino acids, carbohydrates and fatty acids, and they can filter particulate matter through their gills. Filtered particles are usually between 5 and 100 μ in diameter (Dupuy et al. 1999), and consist of bacteria attached to detritus ('attached bacteria'), detritus, 'phytoplankton' (including suspended microphytobenthos) and microzooplankton (Le Gall et al. 1997). We assumed that oyster consumption of the 3 live compartments was non-selective, and thus consumption was proportional to the compartments' biomass in the water column. However, the oysters were assumed to ingest live carbon preferentially over detritus (Pastoureaud et al. 1996, Lefebvre et al. 2000).

Since respiration increases with temperature, the range of the respiration rate was calculated according to the minimum and maximum temperatures observed each season in MOB (Blanchard et al. 1996, 1997).

In situ oyster mortalities are common at MOB each year (Soletchnik et al. 1999). The shells of dead oysters represent unusable carbon, whether they are physically removed from the trestle tables or become buried in the sediments; therefore, shell carbon was added to the export term. The soft tissues of dead oysters decompose completely, and these were therefore added to the feces in the flux to the benthic carbon.

The fate of feces differed from that of pseudofeces (PSF). Feces are decomposed by digestion and were thus assigned to the detrital pool. Conversely, PSF are assumed not to have been digested, as active primary production has been measured in sampled PSF (Barillé & Cognie 2000). As it is surrounded with mucus, the living part of PSF (microalgae, bacteria, microfauna) may be less available or have a less activity than 'free' material. For example, dead or moribund crustaceans surrounded with mucus are found in mussel PSF (Davenport et al. 2000). In the present model, both phytoplankton and bacteria were considered alive and active in PSF. Also, although PSF particles sink, they are easily resuspended in the water column (Razet et al. 1990, Pastoureaud et al. 1996) by the

strong tidal currents on the mudflats (Bassoullet et al. 2000, Le Hir et al. 2000). As no data were available to quantify *in situ* sedimentation and resuspension under the oyster tables, PSF sedimentation was arbitrarily set at 50% of the total PSF, and the remainder was considered to return unchanged to the water column. The composition of organic material in PSF was identical to that of organic seston (Barillé & Cognie 2000). Thus, PSF were represented as fluxes from the pelagic live compartments to the corresponding benthic compartments (phytoplankton to microphytobenthos, microzooplankton to benthic microfauna, and pelagic bacteria to benthic ones), bypassing the oyster compartment.

Sedimentation of POC from PSF is not a trophic flux and was not included in the inverse analysis because too few data were available to calculate the natural sedimentation of POC (which cannot be distinguished from the PSF in the inverse analysis calculation). This decision was reinforced by the results of the sensitivity analyses (see 'Results of the sensitivity analyses'). As the aim of the study was to estimate the impact of oysters on trophic fluxes, we chose to focus on biological, rather than physical, fluxes. Since its components have not been digested, PSF sedimentation can be considered a physical flux. As its live component has a direct impact on biological fluxes, this was taken into account in the inverse analysis calculation.

Simulations: In the following, Simulation A refers to the 'no oysters' model, Simulation B to the Simulation with 16% of the area covered by oyster cultivation (present situation), and Simulation C to the Simulation with twice the present cultivation (32% of the area). The 'no oysters' simulation (A) is a hypothetical model, in which the benthic community occupying the surfaces of the oyster tables has been replaced by the community outside the tables. The macrofauna and meiofauna biomass underneath and surrounding the oyster tables was inferred from the data of Sauriau et al. (1989) and Castel et al. (1989) (Appendix 4¹). To our knowledge, there is no data in the literature on other benthic compartments (microphytobenthos, microfauna, bacteria) underneath and surrounding the oyster tables, so we used the same production rates in all the simulations.

Each simulation was based on a weighted average of the oyster, macrofauna and meiofauna biomass. The linked constraints are adapted to those changes, maintaining the ranges of productivity, respiratory, and other rates.

Network analysis. Network analysis indices synthesize the main characteristics of a network. We used the Netwrk 4.2[®] Program (Ulanowicz 2002: Robert Ulanowicz homepage: <http://cbl.umces.edu/~ulan/>; link to download program:

umces.edu/~ulan/ntwk/network.htm) to calculate indices for the network obtained by inverse analysis. The individual activity (or throughput, A_i) of a compartment (i) is the total material passing through this compartment. Since the system is in equilibrium, A_i represents the sum of all inputs to, or the sum of all exports from, the compartment in question. The total system throughput (TST) is the sum of all fluxes in the system (Hannon 1973, Baird & Ulanowicz 1989, Ulanowicz 1997), and is an indicator of the biocenosis activity that is used to normalize most of the indices discussed below.

The cycling coefficient (C_{c_i}) of each compartment (i) represents the fraction of its activity that returns to the specific compartment due to cycling within the whole system. The cycling activity (Ac_i) of a compartment (i) equals the cycling coefficient multiplied by its activity A_i , and represents the total amount of material that cycles through the compartment. The Finn Cycling Index (FCI) (Finn 1976, Baird & Ulanowicz 1989) is the sum of all those cycling activities (total system cycling throughput) normalised by the TST. It represents the proportion of the carbon fluxes involved in cycling for the whole system.

Sensitivity analyses. The result of Simulation B was used as the reference for the sensitivity analyses. We tested individually the following inputs: (1) primary production; (2) nekton consumption; (3) pelagic bacterial biomass; (4) pelagic microzooplankton biomass; (5) macrofauna distribution by taxonomic group; and (6) all the data related to cultivated oysters. We tested the inputs of the simulation individually. For each tested datum, a constraint was changed from Simulation B. A new value was assigned to the datum, imposing a value to the constraint successively from the minimum to the maximum (or further in the case of nekton grazing, where we removed the constraints). Then, an inverse analysis was run with the new set of equations and constraints. Finally, the result of this simulation was compared to the unaltered Simulation B. This comparison highlighted which fluxes were the most strongly linked to the input datum tested and how they were correlated to the values tested. We then assessed (1) the robustness of our conclusions, (2) the impact of some fluxes on the system behaviour, and (3) poorly constrained results that may require further investigation in the ecosystem.

RESULTS

Inverse solution for Models A, B, and C are given in Table 2. The fluxes for Simulation B are represented in Fig. 2.

Food web simulations

The total inputs of matter to the system increased from Simulation A through C. While the microphytobenthic production value did not change, the relative contribution of this compartment decreased from 59 % of the total inputs in Simulation A to 56 % in Simulation B and 50 % in Simulation C. The contribution of phytoplankton remained around 17 %. Inputs showing the greatest relative changes were pelagic particulate carbon (+45 % from Simulation A to B) and phytoplankton and particulate carbon inputs (+25 % from Simulation B to C).

Total outputs from the system were mainly dissipative (through respiration pathways). They were more than 96 % of the total in each of the 3 models. Total respiration was mostly attributed to benthic bacteria (>50 % of the total).

From Simulation A to Simulation B (introduction of oysters), 28 % of the 174 fluxes decreased (e.g. micro- and mesozooplankton-related fluxes), 36 % increased (e.g. consumption of primary producers deposited as PSF), and 37 % remained the same. Some fluxes disappeared (e.g. export of phytoplankton from the system, ingestion of phytoplankton by adult and juvenile nekton, of mesozooplankton by adult nekton, and of annelids by birds). Other fluxes appeared in Simulation B that were initially zero in Simulation A (e.g. grazing of microphytobenthos by annelids and arthropods, predation of nektonic juveniles on benthic macrofauna, benthic macrofauna and bivalve POC consumption, and resuspension of benthic POC).

From Simulation B to Simulation C (increase in the surface devoted to oyster culture), fluxes that disappeared included consumption of benthic bacteria by annelids and arthropods. No new fluxes appeared. The export of nekton increased.

Figs. 3, 4 & 5 show the contribution of each compartment to the diets of macrofauna, oysters and nekton in Simulations A, B and C. As the surface area of oyster culture was increased in the simulations, the total consumption of bivalves and arthropods decreased due to their reduced biomass, whereas consumption by nekton increased. The diets of nekton and bivalves contained less planktonic and more benthic material.

Indices of network analysis

The TST increased from 2.3 kg C m⁻² yr⁻² in Simulation A, to 2.5 kg C m⁻² yr⁻² and 2.9 kg C m⁻² yr⁻² in Simulations B and C, respectively. The FCI varied slightly: it increased from 37 % (A) to 40 % (B) and 41 % (C).

The activities (A_i) of benthic bacteria and DOC were the same in the 3 simulations, and also remained the

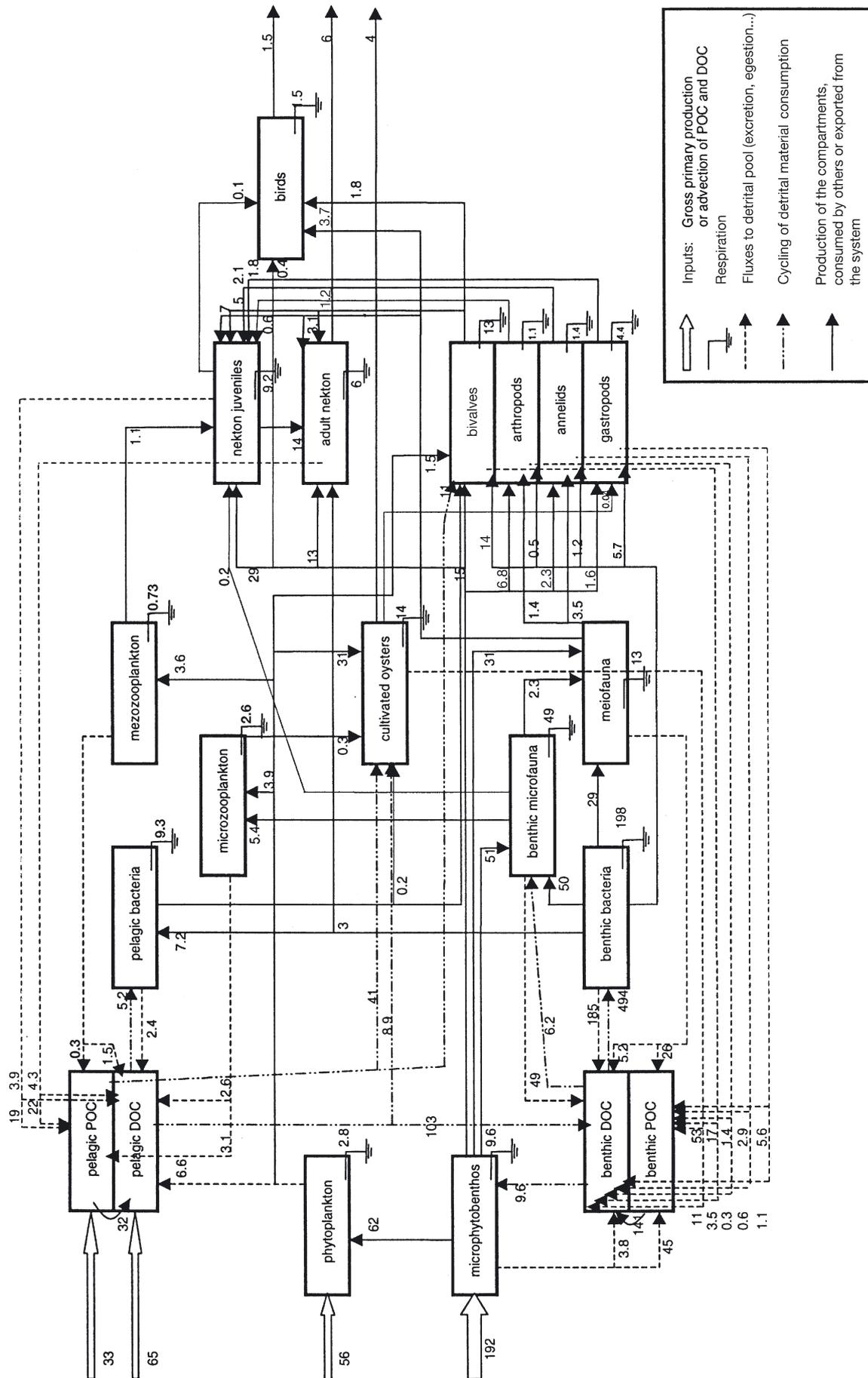


Fig. 2. Food web model, for an average square meter over an average year, of an intertidal mudflat with 16% of the area devoted to oyster cultivation on tables. Fluxes are given in $g\ C\ m^{-2}\ yr^{-1}$, between the 20 compartments. Dashed lines represent the flows linked to detrital carbon

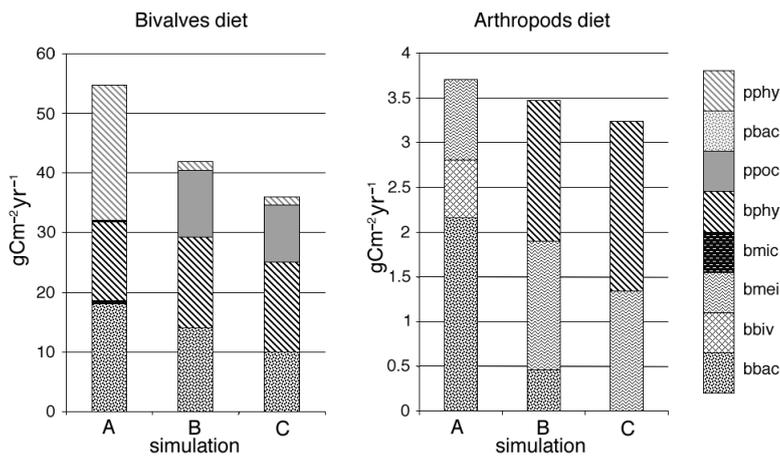


Fig. 3. Bivalve and arthropod diets in Simulations A (without oyster cultivation), B (with 16% of area devoted to oyster cultivation) and C (with a doubled population of oysters). Food ingestion is given in $\text{gC m}^{-2} \text{yr}^{-1}$

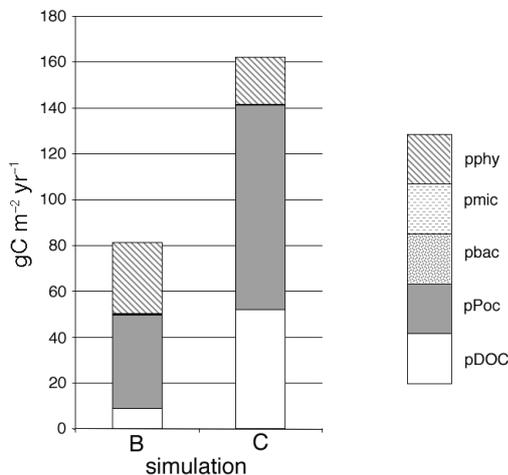


Fig. 4. Oysters' diet in Simulations B and C

most important ones in the system. The introduction and intensification of oyster cultivation changed the order of compartments according to their activities (A_i) (Fig. 6). Most activities increased, except for the activities of benthic non-cultivated macrofauna and mesozooplankton, where production approached its maximum limit in Simulation A, and stayed at its lower limit in Simulations B and C. Pelagic DOC and microzooplankton activities decreased from Simulation A to Simulation B and increased from Simulation B to Simulation C.

The total benthic activity (sum of the fluxes linking benthic compartments, e.g. consumption by deposit feeders) increased with the cultivated surface area, while the total pelagic activity (sum of the fluxes

linking pelagic compartments, e.g. zooplankton grazing on phytoplankton) was slightly lower (Fig. 7). In Simulation A, transfers from the pelagic to the benthic layer were more important than transfers from the benthic to the pelagic layer, but the situation was reversed after the introduction of oysters (Simulations B and C). Exchange between the benthic and pelagic sectors is due to resuspension and deposition processes (e.g. the resuspension of microphytobenthos), and consumption of the pelagic component by benthic organisms (e.g. by filter feeders) and viceversa (e.g. mullets grazing on microphytobenthos).

Sensitivity analyses

Sensitivity analyses were conducted on microphyto-benthic and phytoplanktonic production. Microphyto-benthos net primary production was raised from the minimal boundary ($188 \text{ gC m}^{-2} \text{yr}^{-1}$, reached in the inverse analysis result) to the maximal boundary ($306 \text{ gC m}^{-2} \text{yr}^{-1}$), and similarly phytoplankton net production was raised from 46 to $60 \text{ gC m}^{-2} \text{yr}^{-1}$. The results showed that microphytobenthos production had a higher impact on the system. New export fluxes appeared when microphytobenthos production increased, whereas an increase in phytoplankton production only increased its own export. Each of these primary productions influenced bivalve diet and predation of nektonic juveniles on benthic microfauna.

Adult nekton grazing was tested too. It has been imposed its minimal value ($3 \text{ gC m}^{-2} \text{yr}^{-1}$), and the constraint has been removed. In the second case, the result

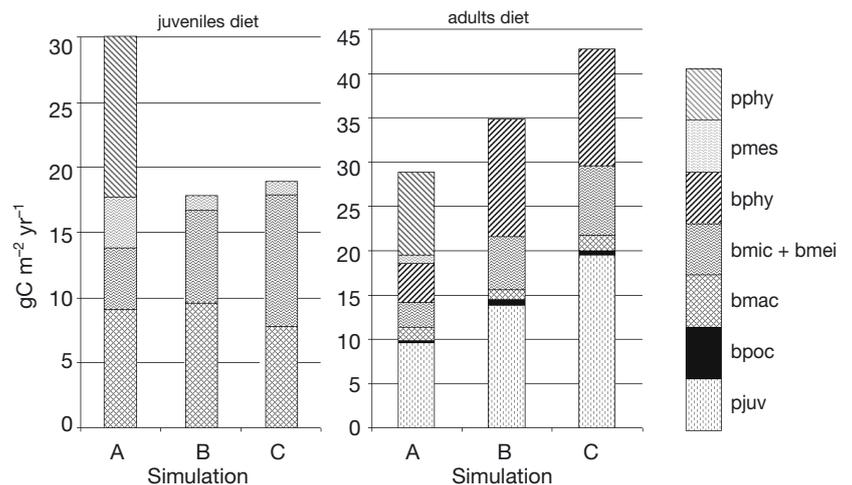


Fig. 5. Juvenile and adult nekton diets in simulations A (without oyster cultivation), B (with 16% of area devoted to oyster cultivation), and C (with a doubled population of oysters). Food ingestion is given in $\text{gC m}^{-2} \text{yr}^{-1}$

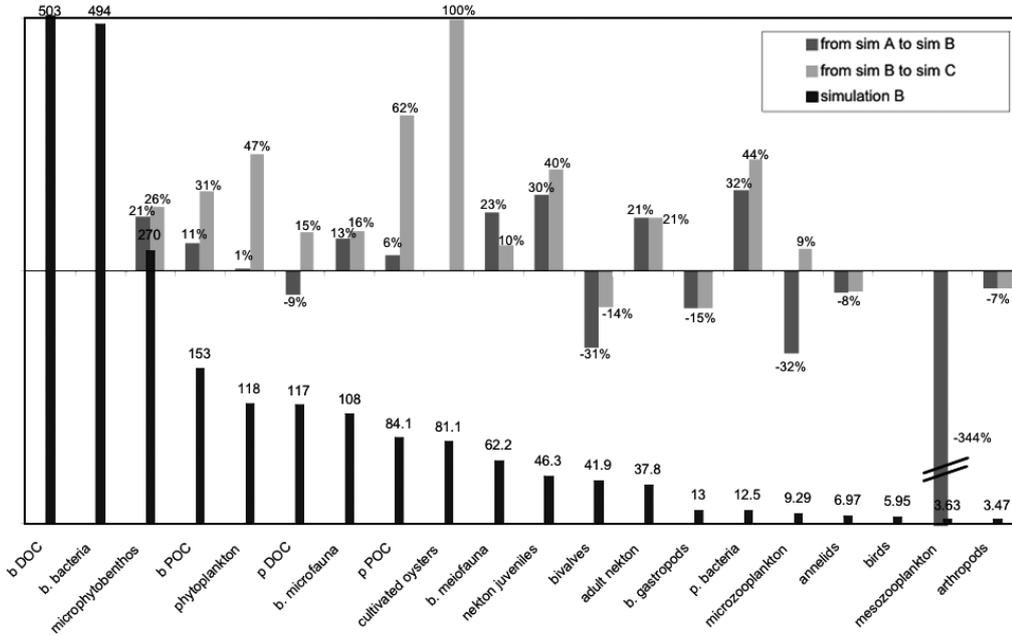


Fig. 6. Compartment activities, in $\text{gC m}^{-2} \text{yr}^{-1}$. Compartments are classified by decreasing activity in Simulation (sim) B (16% of area devoted to oyster cultivation, black histograms). The dark and light grey histograms represent the variation of activity of each compartment between sim A (without oysters) and sim B, and between sim B and sim C (with a doubled population of oysters), respectively. b: benthic; p: pelagic

for this flux was $19.6 \text{ gC m}^{-2} \text{yr}^{-1}$, which is 48 % higher than in Simulation B ($12 \text{ gC m}^{-2} \text{yr}^{-1}$, the maximal boundary). It influenced all nekton, benthic macrofauna and meiofauna diets. This compartment is poorly understood and must be studied further. The mathematical result of $19.6 \text{ gC m}^{-2} \text{yr}^{-1}$ should be realistic.

Meiofauna biomass was also tested: it was not enhanced under the oyster tables, more predation

occurred within the macrofauna compartment and the consumption of microfauna and bacteria increased. Nekton, birds, and juveniles consumed less meiofauna and macrofauna under these conditions. This showed that the meiofauna enhancement by the oyster cultures played a key role in carbon transfer.

The uncertainties of fluxes linked to the oyster data were tested. Respiration, feces, production and mortal-

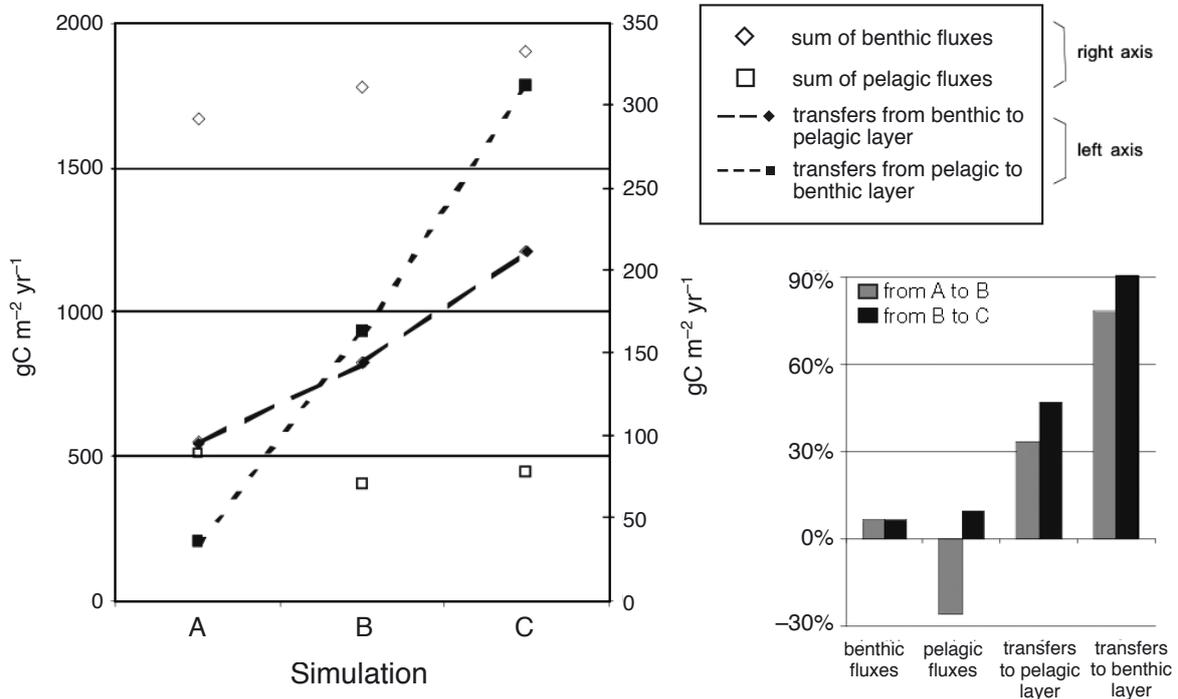


Fig. 7. Evolution of benthic and pelagic fluxes and exchanges. Left: total carbon fluxes transferred between or exchanged within the pelagic and benthic layers. Right: relative variations of those quantities

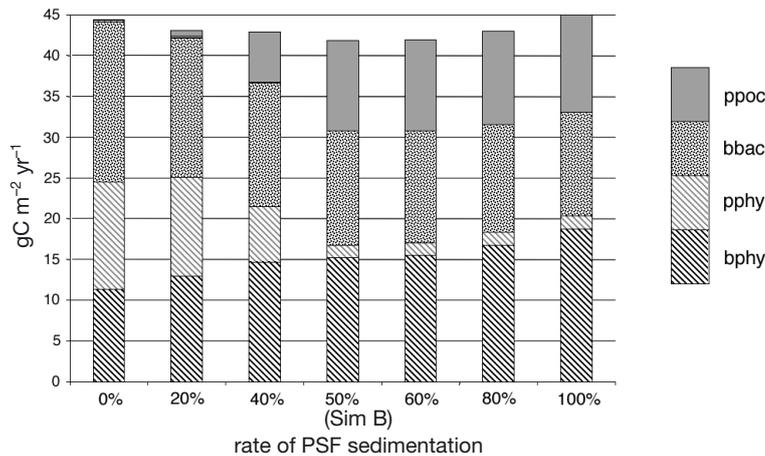


Fig. 8. Result of the sensitivity analysis: effect of the fraction of pseudo feces (PSF) sedimenting on bivalves' diet. The fraction was raised from 0 to 100% of total living PSF, the mean value (50%) being the one imposed for Simulation B

ity rates have been imposed successively their minimal or maximal possible values (the bounds of the constraints), and intermediate values.

Increased or decreased oyster production (by imposing a P/B of $\pm 24\%$ of the imposed mean value) led to variations of less than 10%. The consumption of microfauna by nekton juveniles was most affected, and was inversely correlated with the oyster production rate. The mortality was set to its minimal value in the result of inverse analysis (8%). We have imposed a raise to its upper limit: 18% of oyster production. In general, doubling the mortality rate led to a less than 1% variation in flows, except for the 8% increase in the consumption of benthic macrofauna by juvenile nekton and the 2% increase of DOC assimilation by oysters. Hence, although an increase in the amount of oysters should diminish their production and increase their mortality rate (Héral et al. 1986, Fréchette et al. 1996), we maintained oyster mortality between the same limits in both Simulations B and C.

The egestion and respiration fluxes reached their minima in the result of inverse analysis. Their maximal values were progressively imposed in the sensitivity analyses. Apart from the flows directly linked to oysters, the most impacted flows were: juvenile nekton consumption of benthic microfauna, resuspension of POC, ingestion of bacteria by arthropods, and consumption of bivalves by adult nekton. The microfauna compartments (benthic and pelagic), poorly known and hence poorly constrained, were the most easily impacted. Additional data on these compartments would greatly improve the model.

Sensitivity analyses were also conducted on the sedimentation rate of PSF (i.e. PSF production). The rate

was varied from 0% (no PSF production/sedimentation) to 100% (all production sedimented, or elevated PSF production). PSF production/resuspension had an impact on benthic macrofaunal diets and on the total consumption or production rates of bivalves. Fig. 8 shows the variations of bivalve consumption and diet at increased PSF sedimentation rate. Increase in PSF production reduced the fraction of bacteria and phytoplankton consumed by macrofauna, and increased consumption of microphytobenthos. Under these conditions, bivalves consumed no benthic POC (bPOC), less phytoplankton and more pelagic POC (pPOC), in addition to the microphytobenthos.

A new simulation including the sedimentation of pPOC due to PSF was run: since POC constitutes 88% of the PSF, we imposed a value of $509 \text{ gC m}^{-2} \text{ yr}^{-1}$ for pPOC-bPOC. The result, compared with the result of Simulation B (results not presented here) was that (1) benthic grazing on microphytobenthos was reduced (-39% on average) to the benefit of detritus consumption in the benthic layer (bPOC consumption increased 50), (2) resuspension of bPOC increased (38% of the sedimented POC was resuspended), (3) less detritus was produced by live organisms (-41% on average), and (4) the other affected fluxes were linked to poorly known compartments, such as benthic microfauna, the production of which increased. The inverse analysis method (and in particular the parsimony principle: Leguerrier et al. 2003) forced a redistribution of bPOC throughout the food web. Instead of simply an increase of accumulation in the benthic layer, organisms that are supposed to select qualitative food seem to ingest more detritus. Further study of the actual flux of sedimented POC, accumulation of bPOC after consumption by organisms, and bPOC integration into the microbial loop will be required to model this flux. The addition of such a physical flow strongly impacts the trophic web, but only through a mathematical bias.

DISCUSSION

General properties of the ecosystem (Simulation B)

Simulation B synthesised the current state of knowledge about the eastern mudflat of the Marennes-Oléron Basin. Differences between the current and the earlier version of the model (Leguerrier et al. 2003) increased the TST. This is partly linked to the different level of aggregation (Kay et al. 1989), but can also be due to enhanced recycling, as shown by the high FCI value (Ulanowicz 1997). The FCI attained 40%

(whereas it was 21% in the former model), because oyster PSF and assimilation of DOC by many organisms were taken into account. Baird et al. (1991) and Monaco & Ulanowicz (1997) found similar or lower values in other estuaries or bays (48% in Narragansett Bay, 44% in Swarctops Estuary, 37% in Delaware Bay, 30% in Chesapeake Bay, 28% in the Ems Estuary, and 23% in the Baltic Sea).

Microphytobenthic production was the most important carbon input and had the strongest impact on the functioning of the system. Imports of both DOC and POC were observed; as these were not constrained, they were also considered non-limiting. DOC and POC could enter the system via pelagic imports, demonstrating the system's demand for extra carbon. Microphytobenthic production is a key process for benthic pelagic coupling in the Marennes-Oléron mudflat system (Guarini et al. in press). Resuspended microphytobenthos organisms are food to many filter feeders, such as cockles and oysters (Swanberg 1991, Riera & Richard 1996, Urrutia et al. 1996, Riera 1998, Cognie et al. 2001), while phytoplankton production is limited by high turbidity in the water column (Cloern 1987).

Meiofauna was an important compartment in the system. Meiofaunal activity ($62.2 \text{ gC m}^{-2} \text{ yr}^{-1}$) was comparable to the total activity of macrofauna ($65.34 \text{ gC m}^{-2} \text{ yr}^{-1}$), although meiofauna biomass was 3 times lower. Hence, meiofauna had a P/B ratio of 30 yr^{-1} , whereas the macrofauna P/B ratio was 7.8 yr^{-1} , which is consistent with observations from other tidal flats (Kuipers et al. 1981 in Giere 1993). According to Schmid-Araya et al. (2002), the meiofauna also has a key position in the food web, as it increases the complexity of the web and represents an important intermediate step in trophic patterns.

The non-dissipative exports of the system in Simulation B were largely due to the export of carbon to the nekton (52%) and birds (13%), as well as to oyster production (35%). Nekton production was reduced in the present model (using an estimate of consumption by mullet, P. Richard pers. comm.), and accounted for the lowered total production of the system ($11.5 \text{ gC m}^{-2} \text{ yr}^{-1}$, instead of $51 \text{ gC m}^{-2} \text{ yr}^{-1}$ in the Leguerrier 2003 model). However, nekton production remained an important export from the system, suggesting that fishes exert important pressure on the ecosystem. Fishes also export matter from salt marshes to marine waters (Lafaille et al. 1998, Lefeuvre et al. 1999), and predation by sole juveniles may regulate the meiofauna in lagoons and coastal marshes (Castel & Lasserre 1982).

Predation by birds may have been underestimated, as they had consumption efficiencies of 6.3% and 3.9% of the meiofauna and macrofauna production, respectively. These efficiencies are low in comparison to other estu-

aries. For example, Baird & Milne (1981) found an efficiency of 54% in the Ythan Estuary, and Moreira (1997) found 12% in the Tagus Estuary. It is also low in comparison to the nekton, whose consumption efficiency was 18% of the meiofauna and 23% of the macrofauna. These differences suggest there is competition for food resources between fishes and birds in the mudflat ecosystem. Studies on food resources and consumption by birds on the mudflat in the coming winters (P. Bocher pers. comm.) may clarify this point in the future.

Variations between the scenarios

Feedback effects between oyster cultivation and adjacent ecosystems have been reviewed by Prins et al. (1998) and Dame (1996). Oyster culture may modify the cycling of nutrients and cause food depletion (a negative impact on the growth of other bivalves), through top-down control of phytoplankton biomass and growth, change in phytoplankton composition, and changes in carrying capacity. Not all of these effects destabilize the system; suspension feeders may also stabilize the ecosystem, since it is the balance between positive and negative feedbacks that determines overall productivity (Dame 1996). The functional and structural sustainability of ecosystems can be enhanced through the nutrient cycling mechanism. Hence, bivalve cultivation may affect phytoplankton biomass both negatively (Cloern 1982) and positively through nutrient cycling (Dame 1996), and deplete other ecological components (Davenport et al. 2000). These phenomena should only have limited impacts on the ecosystems (Spencer et al. 1998). When aquaculture causes serious organic pollution of an ecosystem (Kusuki 1977, Dählback & Gunnarsson 1981), the benthic macrofauna and biogeochemistry of the sediment may reach an unstable equilibrium that is easily disrupted (Karakassis et al. 1999). In the simulations presented and discussed here, oyster culture indirectly impacted the diets of many ecosystem components and the overall properties of the system. The system remained stable, suggesting that oyster culture has a small impact on the stability of the ecosystem, or, rather, that the ecosystem has long been adapted to oyster culture.

Considering all 3 Simulations A, B and C, TST and the FCI increased, and the detritus compartments also increased in importance to the system. The benthic layer became more important relative to the pelagic one after the introduction of oyster cultivation. Decreased pelagic activity resulted from food source depletion in the water column. The rise in the TST from Simulation A to Simulation B ($+130\%$, $[\text{TST(B)} - \text{TST(A)}] / \text{TST(A)}$) and from Simulation B to Simulation

C (+98%), was due to flows linked directly to oysters (consumption + production + respiration + PSF production). The activities of 7 compartments were lowered between Simulation A and Simulation B (macrofauna, pelagic DOC and micro- and mesozooplankton activities), and the activities of 9 compartments increased (primary producers, benthic and pelagic POC, benthic microfauna and nekton) (Fig. 6). These changes in the compartment activities illustrate how severely the macrofauna and zooplankton were negatively impacted by the introduction of oyster cultivation into the system, whereas bacteria, microfauna, and meiofauna were positively impacted. Primary production was also raised by the introduction and intensification of oyster cultivation in the model.

Food quality and competition in the pelagic layer

The disappearance of phytoplankton export between Simulations A and B suggests that oysters filter all of the resuspended microphytobenthos and phytoplankton from the water column. Oysters generally consume phytoplankton, microzooplankton, pelagic bacteria, and pelagic POC (Prieur et al. 1990, Pastoureaud et al. 1996, Dupuy et al. 1999). Water column filtration by the oysters (total ingestion + sedimented live PSF) could exceed the total primary production of the system (it represented 65% of the total primary production in Simulation B and 121% in Simulation C). The evolution of the oysters' diet between Simulations B and C (Fig. 4) suggests that an increase in oyster cultivation area will decrease the quantity of food available to the oysters. However, microphytobenthic production might have been underestimated (it reached the imposed minimum in Simulation A). The increase in primary production is a mathematical result of the model: it results from a higher demand, which can be fulfilled within the boundaries imposed. However, other studies have described a positive feedback of bivalve culture on primary production, as well as a reduction of the biomass of primary producers (Rodhouse & Roden 1987, Dame & Libes 1993, Prins et al. 1998). On the other hand, oyster cultivation increases water turbidity, which may lower pelagic primary production by reducing the penetration of light (Cloern 1987). However, no excess food is left for export when oysters are added: a part of the phytoplankton sinks with the PSF, and the low supply of valuable food is completed by a high demand for detritus.

Oysters compete with other species, in particular with other filter feeders, and with filter-feeding juveniles and plankton-feeding adult nekton (Fréchette & Bourget 1985). Benthic filter feeders *sensu strictu* are very rare on the mudflat of Marennes-Oléron, to the

benefit of more opportunistic feeders (Sauriau et al. 1989) such as *Macoma balthica* and *Scrobicularia plana* (both facultative suspension feeders). In the model these benthic animals adapted their trophic behaviour: 42% of the food they ingested came from the pelagic layer in Simulation A, and only 30% in Simulations B and C. Hence, trophic competition was not as dramatic as expected, given the amount of material removed from the water column by the oysters. However, doubling the oyster population would increase competition for food resources.

Availability of food to the benthos and to biotic vectors

By concentrating and modifying organic matter from the water column, oyster cultivation may result in increased flux of organic matter to the benthic layer, increased biomass of meiofauna, and more active trophic fluxes towards biotic vectors (birds and nektonic fishes) (Marchand 1991 in Amara & Bodin 1995). The presence of oysters raises the turbidity through increased sedimentation (production of PSF and the presence of the oyster tables which reduce the current speeds) and increased turbulence (also due to the tables). The higher turbidity may also enhance the nursery role of estuaries by improving the survival of early life history stages through reduced predation (Chesney et al. 2000, Jones et al. 2002). The negative influence of oyster culture on macrofauna is mainly due to geochemical changes in the sediment (Castel et al. 1989, Hayakawa et al. 2001). The biodeposits in the model provided food to benthic layer organisms, removing food from the water column. Hence, the presence of oysters provided more organic matter for all deposit feeders or benthic grazers, including nekton and birds. Bivalve facultative filter feeder diets shifted towards deposit feeding. The strong influence of biodeposits on sediment structure and trophic resources also augmented meiofauna biomass (Castel et al. 1989).

The diets of biotic vectors were unconstrained in the model. Phytoplankton consumption by juvenile and adult nekton was allowed, but was possibly overestimated in Simulation A, as it also represented an exit for overproduction by phytoplankton (Leguerrier et al. 2003). This consumption disappeared when the oysters were introduced in Simulations B and C, while consumption rose in other compartments, in particular the consumption of meiofauna and macrofauna by juveniles and the consumption of microphytobenthos, benthic bacteria and juveniles by adult nekton.

Sensitivity analyses showed that the oysters' positive influence on meiofauna biomass resulted in a positive impact on the food supply to the 2 biotic vectors: birds

and fishes. Meiofauna consumption by birds may have been overestimated, as birds prefer small macrofauna (Zwarts & Blomert 1992); this preference is not accounted for in the present approach. Preferential uptake by birds of polychaetes (*Nereis diversicolor*, *Nephtys hombergii*) and molluscs (*Macoma balthica*, *Scrobicularia plana*, *Hydrobia ulvae* and *Corophium* sp.) has been observed on the MOB eastern mudflat (Boileau et al. 2002). Fishes also adapt to food availability (Roblin & Bruslé 1984, Dauvin 1988), and meiofauna is a potential food source for juvenile and adult nekton (Marinelli & Coull 1987). The function of the eastern intertidal mudflat of MOB as a nursery for various nekton species (*Solea solea*, *Merlangius merlangus*, *Dicentrarchus labrax*, *Mullus barbatus*; Guérault & Desaunay 2001) is consistent with the availability of meiofauna (Roblin & Bruslé 1984). Hence, in terms of organic matter fluxes, oyster tables could increase the food supply for top predators (Baird & Milne 1981, Moreira 1997, Lafaille et al. 1998).

Oyster cultivation can also represent an obstacle to birds. The presence of trestle tables and of other structures may divide the mudflat into areas preferred by fishes (under the tables) and areas preferred by birds (the upper part of the mudflat). However, changes in foraging area for birds are thought to be rapidly adapted to (Dumbauld et al. 2001). Moreover, the biological rhythms of bird and fish species divide the mean equilibrated year into 2 main seasons. Birds are more numerous on the mudflats in winter (Deceunink 1998), and juvenile fish growth stops in early autumn, in spite of favourable temperatures (P. Laffargue pers. comm.), but there is no evidence that food availability is the forcing factor.

CONCLUSIONS

On the MOB mudflats, where oyster cultivation is extensive and tidal exchange is high, 3 modeling scenarios show that primary production can be enhanced by the introduction and intensification of oyster cultivation. Oysters compete directly with other filter feeders on the mudflat, depleting the water column of food, by ingestion and PSF production. The high densities of oysters in aquaculture installations modify benthic pelagic coupling, inducing a shift from pelagic to benthic consumers. However, additional information is needed on the fluxes and feedbacks between the benthic and pelagic compartments.

Doubling the surface area of oyster culture caused secondary production to increase, providing food for top predators (in particular juvenile nekton), reinforcing the nursery role of the mudflat and altering the species composition available to top predators.

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