The uptake and release of suspended and dissolved material by oysters and mussels in Marennes-Oléron Bay

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Abstract

The uptake and release of material by oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) in Marennes-Oléron Bay (SW France) were measured *in situ* using benthic ecosystem tunnels (BEST). There was a large variation in seston concentrations, owing to high sedimentation/erosion dynamics. Organic matter was diluted by resuspended sediment, but had a low C/N ratio, *i.e.* a high quality, owing to resuspension of microphytobenthos. In many cases a significant decrease of chlorophyll concentrations was observed in tunnels with oysters and mussels. Average clearance rates per tidal cycle ranged from 4 to 7, and from 0.9 to 2.7 $l.g^{-1}AFDW.h^{-1}$ throughout the season, for oysters and mussels respectively. Calculation of the filtration pressure (the fraction of the primary production filtered per day), indicated that bivalves in the bay were able to filter much more than the daily pelagic primary production. It seemed obvious that the bivalve stocks depended not only on phytoplankton but also on microphytobenthos. Significant regeneration of nitrogen could be demonstrated from musselbeds on the sediment, at higher rates than direct excretion of ammonium. No significant release of nutrients was observed for the oysters or mussels, when they were put on tables, as practised by the oyster farmers. It seemed likely that biodeposits were flushed away from the tunnels in this case, and mineralization occurred elsewhere. It was concluded that the carrying capacity of the bay for herbivores is extensively exploited by the shellfish. Mineralization of bivalve biodeposits represent a large potential for nitrogen regeneration.

Keywords: Ammonium, biodeposition, bivalves, chlorophyll, filtration.

Le matériel en suspension dissous absorbé et rejeté par les huîtres et les moules dans la baie de Marennes-Oléron.

Résumé

L'absorption et le rejet de matériel particulaire par les huîtres (*Crassostrea gigas*) et les moules (*Mytilus edulis)* dans la baie de Marennes-Oléron ont été mesurés *in situ* en utilisant des tunnels benthiques (BEST). Il y a une grande variation entre les concentrations de seston allant d'une érosion importante à une sédimentation intense. La matière organique diluée par la remise en suspension du sédiment a un faible rapport C/N, c'est-à-dire une bonne qualité permettant la remise en suspension du microphytobenthos. Dans de nombreux cas, une baisse significative des concentrations en chlorophylle est observée dans les tunnels avec les huîtres et les moules. Les taux moyens de filtration par cycle de marée s'étendent de 4 à 7, et de 0,9 à 2,7 $l.g^{-1}.h^{-1}$ de matière sèche quelle que soit la saison pour les huîtres et les moules respectivement. Le calcul de la pression de filtration (la fraction de la production primaire filtrée par jour), indique que les bivalves de la baie sont capables de filtrer plus que la filtration primaire pélagique journalière. Il semble évident que les stocks de bivalves dépendent non seulement du phytoplancton mais aussi du microphytobenthos. Des régénérations significatives d'azote peuvent être mises en évidence provenant du sédiment des zones de culture de moules à des taux plus importants que l'excrétion directe d'ammonium.

Il n'y a pas de rejet significatif de nutriments observé à partir d'huîtres ou de moules, lorsqu'elles sont placées sur des tables comme cela est pratiqué par les ostréiculteurs. Il semble que les biodépôts sont chassés des tunnels dans ce cas, et que la minéralisation s'effectue ailleurs. En conclusion, la capacité de stockage de la baie pour des herbivores est exploitée par les coquillages de façon considérable et la minéralisation des biodépôts des bivalves présentent un large potentiel pour la régénération de l'azote.

Mots-clés : Ammonium, biodépôt, bivalves, chrolophylle, filtration.

INTRODUCTION

In many coastal ecosystems, bivalve suspension feeders such as oysters and mussels occur in high densities and in cultivation areas densities are often further enhanced by farmers. In Marennes-Oléron Bay, SW France, average biomass of oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) is 15 and 1.5 g ash-free dry weight. m^{-2}, respectively (Prou *et al.*, 1994). The farmers regulate the majority of the shellfish densities (Héral, 1993).

Bivalve suspension feeders have the potential to filter considerable quantities of particulate matter from the overlying water, and transport material from the water column to the bottom. In situ measurements in the Oosterschelde estuary have shown that filtration rates of chlorophyll by mussels in the field were comparable with laboratory measurements of clearance rates (Prins and Smaal, 1994). Moreover, in situ measurements have shown high release rates of inorganic nutrients from oyster reefs (Dame *et al.*, 1989) and mussel beds (Prins and Smaal, 1994). These release rates were generally higher than direct excretion rates of nutrients by bivalves, as measured in the laboratory, and the difference is attributed to the mineralization of biodeposits (Smaal and Prins, 1993). It is hypothesized that the nutrients, regenerated from bivalve beds, are available for primary production. Consequently, biofiltration, biodeposition and subsequent mineralization may stimulate phytoplankton turnover (Asmus and Asmus, 1991), and enhance the carrying capacity of the ecosystem for the bivalves (Prins and Smaal, 1994; Dame, 1996).

In situ measurements of uptake and release of material by oysters and mussels were conducted in Marennes-Oléron Bay (S.W. France; Fig. 1) (Zurburg *et al.*, 1994*a*, *b*). In this paper the uptake of chlorophyll and the release of ammonium will be discussed in relation to the carrying capacity of Marennes-Oléron Bay.

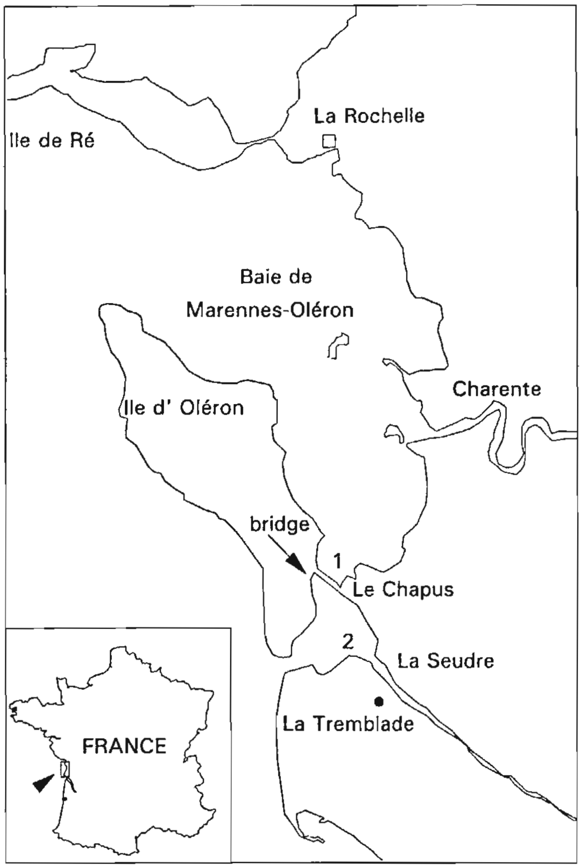


Figure 1. – Location of experimental sites Le Chapus (1) and La Seudre (2) in Marennes-Oléron Bay (SW France).

MATERIALS AND METHODS

Experimental setup

The uptake and release of dissolved and suspended material by oysters and mussels were measured with two benthic ecosystem tunnels (BEST), as originally developed by Dame *et al.* (1984) (Fig. 2). The plexiglass tunnels were 12 m long, 0.8 m wide and had a cross-sectional area of 0.23 m^2. The distance between sampling points within the tunnel was 10 m, and covered 8 m^2 of bottom area. Water is well mixed within the tunnel; current velocities were reduced by ca 20%, and show the same patterns as outside the tunnels; current velocities at inflow and outflow are similar; inflow and outflow samples are taken within short time periods in which a steady state can be assumed (*see* for methodological evaluation: Prins, 1996).

Measurements were executed at two intertidal locations in Marennes-Oléron Bay: in May and October 1991 and February and May 1992 at Le Chapus, and in June and October 1992 at La Seudre (Fig. 1).

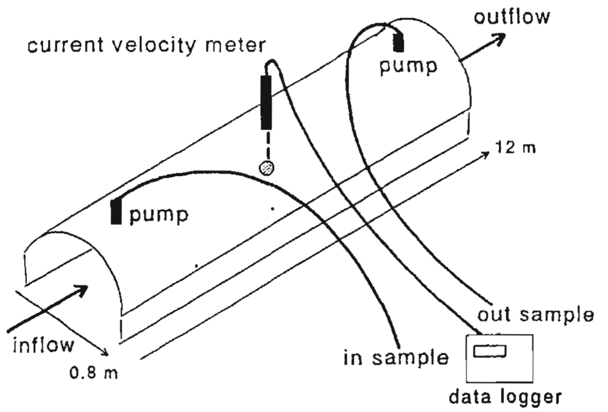


Figure 2. – Schematic representation of the Benthic Ecosystem Tunnel.

In most experiments, oysters or mussels were placed in one tunnel, and in the other tunnel empty shells served as a control. In 1991, experiments were executed with mussels on the sediment and on tables. In these cases there were no control tunnels. The number of oysters in the tunnels were lower than of mussels, owing to the larger size of the oysters (Table 1). At Le Chapus, animals or (control) shells were put in plastic bags and placed on iron framed tables, elevated at 10 cm above the sediment. Tables are used by the local farmers to prevent siltation of the animals, at sites with a very soft substrate. The tables were modified for use in the tunnels. In another series of experiments at Le Chapus, and in all cases at La Seudre, animals were put directly on the sediment (Table 1). In all cases, animals were put in place at least 5 days prior to the measurements, in order to acclimate to the local conditions.

Each experiment lasted for two consecutive tidal cycles, in most cases during spring tide, when tunnels were submersed for 8-10 h per cycle. From a small vessel, lying between the tunnels, samples were taken with battery-driven pumps, every 20 or 30 minutes during submersion (Fig. 2). Water current velocity and direction were measured with a current meter in the centre of each tunnel, and recorded on a data logger. In a number of cases, also water velocity outside the tunnels was recorded. Water flow in the tunnels was reduced by 10 - 20% with animals on the sediment, and 20 - 30% when animals were put on the tables.

Water samples were filtered directly after sampling, stored and later analyzed for suspended particulate matter (SPM), particulate organic carbon and nitrogen (POC, PON), chlorophyll-a and dissolved inorganic nutrients (ammonium, nitrate, nitrite, phosphate, silicate). Details of the analytical procedures are given by Prins and Smaal (1994).

After each experiment animals were subsampled from the tunnels and dried for 48 h at 70 °C, weighed, ashed for 4 h at 520 °C and weighed for determination of ash-free dry weight (AFDW).

Calculations and statistical treatments

Material fluxes across each end of the tunnel were calculated by multiplying the water flow (= current velocity × cross-sectional area) by the inflow or outflow concentration. The net flux is the difference between in- and outflux. Uptake is shown by a positive sign, and release of material by a negative sign. Only data collected at water velocities > 2 $cm.s^{-1}$ were used. Fluxes of control and experimental tunnels were compared by the Wilcoxon signed-rank test. When no control tunnels were used, the inflow was considered as control, and the outflow as treated sample. In that case the Mann-Whitney U-test was used to determine significant differences of the inflow and outflow concentrations. When differences were significant, the fluxes were considered significant. Mean values of

Table 1. – Numbers (N) per m^2, biomass (B in AFDW in $g.m^{-2}$), and mean individual weight (W in mg) of mussels and oysters on tables or on the sediment; with the use of control tunnels indicated.

Period			Control	Substrate	Mussels			Oysters		
					N	B	W	N	N	W
(Le Chapus)										
May	23	1991	–	bottom	3 870	455	118			
Oct.	8-11	1991	+	tables				183	139	760
Oct.	22-25	1991	–	bottom	7 930	899	113			
Feb.	5-6	1992	–	tables	3 700	436	118			
Feb.	11-12	1992	+	tables				236	136	576
May	18-19	1992	+	tables	1 530	470	307			
May	19-20	1992	+	tables				174	129	741
	+ 27/28	1992	+	tables						
(La Seudre)										
June	1-3	1992	+	bottom				312	236	756
Oct.	8-11	1991	+	bottom				183	139	760
Oct.	26-27	1992	+	bottom	1 510	511	338			

fluxes over a tidal cycle were calculated on the basis of all measured fluxes at water velocities > 2 $cm.s^{-1}$.

Clearances rates (CR) were calculated on the basis of chlorophyll concentrations, for the shellfish bed (CR_{bed}) and for a standard animals of 1 g AFDW (CR_{ind}): see Table 2.

Table 2. – Calculation of clearance rate of oysters and mussels in tunnels, per m^2, and of standard individuals of 1 g AFDW.

CR_{bed}	$= (Q \ln (C_{in}/C_{out}))/A$
CR_{bed}	= clearance rate of mussel or oyster bed ($m^3.m^{-2}.h^{-1}$)
Q	= water flow through the tunnel ($m^3.h^{-1}$)
C_{in}	= chlorophyll concentration in the inflow ($mg.m^{-3}$)
C_{out}	= chlorophyll concentration at the outflow ($mg.m^{-3}$)
A	= surface between sampling points (m^2)
CR_{ind}	$= CR_{bed}/B_m$
B_m	$= \Sigma (n_i.W_i b)$ ($g.m^{-2}$)
n_i	= number of animals of size class *i*
W_i	= individual AFDW of animals of size class *i* (g)
b	= allometric weight exponent: b = 0.5 for mussels (Smaal *et al.*, in press) and 0.439 for oysters (Bougrier *et al.*, 1995)

RESULTS

Seston characteristics during the measurements

SPM concentrations in the inflow of the tunnels were highly variable, with maximum values up to 330 $g.m^{-3}$. POC concentration varied from 0.5 - 3.0 $g.m^{-3}$ in February and October respectively. The C/N ratio of seston averaged over the tidal cycles in the range 6.5 - 8.4, without any seasonal trend. Chlorophyll concentrations varied during a tidal cycle corresponding with season, with minimum values in February (0.1 - 1.0 $mg.m^{-3}$), and maxima in May (1.5 - 19.2 $mg.m^{-3}$).

Fluxes of chlorophyll

Chlorophyll fluxes in oyster tunnels are presented in Figure 3a, in comparison with fluxes in the control tunnels. High uptake rates of chlorophyll were observed in October 1991 and May 1992 at Le Chapus. In February (Le Chapus) and October 1992 (La Seudre), observed fluxes were very small, due to low chlorophyll concentrations (0.2 - 1.3 $mg.m^{-3}$). In June 1992 (La Seudre) lower fluxes were observed than at Le Chapus in May 1992; in this period, chlorophyll concentrations ranged from 0.9 to 4.5 $mg.m^{-3}$.

In most cases uptake rates in the oyster tunnel were higher than in the control, despite sedimentation of chlorophyll in both tunnels, as measured in the control tunnel. In some cases, however, fluxes were negative, probably due to resuspension of benthic chlorophyll. There was a large variation in the fluxes and consequently only in a few cases were differences significant.

Uptake rates of chlorophyll were similar for mussels laid on tables or on the sediment, and in all but one case, significantly different from the control (Fig. 3*b*). At Le Chapus no control tunnel was applied during the measurements with mussels; in these cases in- and outflows were significantly different.

Uptake rates of chlorophyll were comparable for oysters and mussels: low rates in February, high average rates per tidal cycle in May, up to 21 and 15 $mg.m^{-2}.h^{-1}$, and moderate rates in October 1991 up to 6.4 and 3.8 $mg.m^{-2}.h^{-1}$ for mussels and oysters respectively. In October 1992 (La Seudre), uptake rates for oysters were lower than for mussels.

To account for different densities of oysters and mussels, clearance rates per standard animal of 1 g AFDW are compared, calculated on the basis of chlorophyll fluxes. Table 3 shows higher individual clearance rates for oysters than for mussels of 1 g AFDW. As shown in Table 2, however, total numbers and biomass of oysters were lower in the tunnels due to space limitation, which corresponded with the lower chlorophyll fluxes.

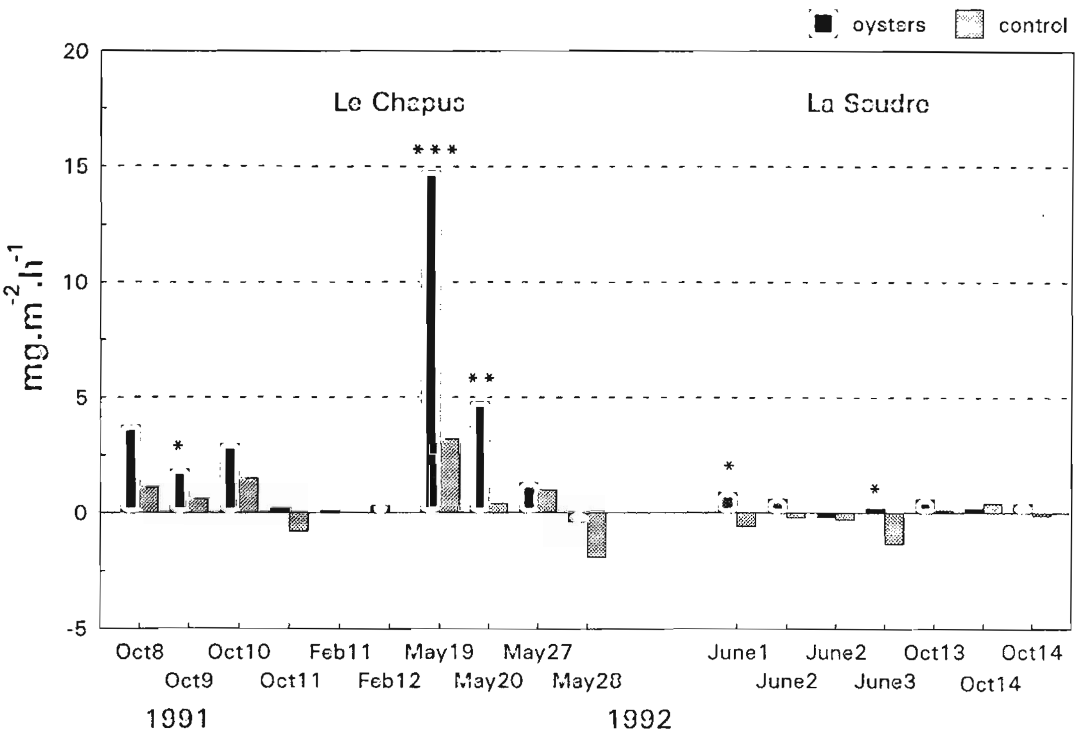
Table 3. – Clearance rates of mussels and oysters, based on chlorophyll-a fluxes, corrected for the control, expressed per standard animals of 1 g ash- free dry weight, in $l.h^{-1}$; mean value with min/max. (in the calculation negative fluxes were adjusted to zero). n.d. = no data.

Period	Mussels	Oysters
Oct. 1991	1.2 (0.12/6.2)	4.2 (0/13.4)
Feb. 1992	1.8 (0/6.2)	2.4 (0/7.4)
May 1992	2.4 (0/5.2)	6.6 (0/18.8)
June 1992	n.d.	3.8 (0/19.3)
Oct. 1992	3.5 (0/8.7)	n.d.

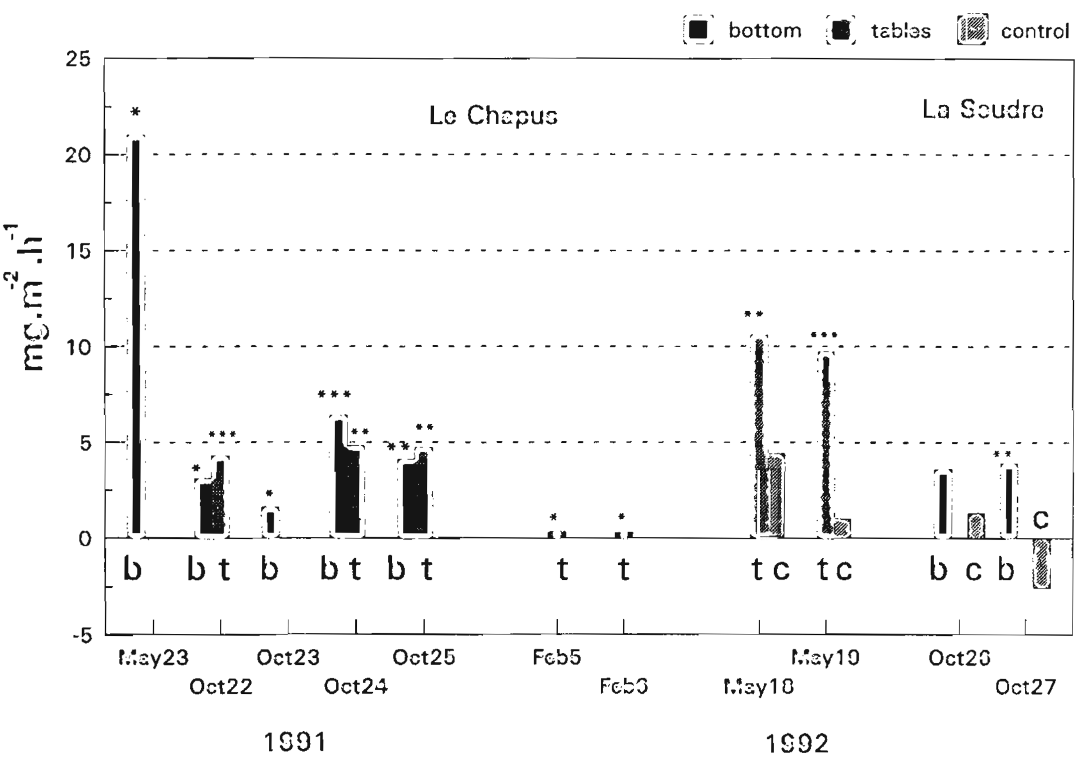
Fluxes of dissolved inorganic nitrogen

Fluxes of dissolved inorganic nitrogen, predominantly ammonium, from tunnels with oysters, on tables or on the sediment, were in almost all cases not significantly different from the control tunnels.

Significant ammonium release rates were observed from tunnels with mussels. Release rates of ammonium, from mussels laid on the sediment, were significantly higher than from mussels on tables, and from controls except in one case (Oct. 26, 1992) (Fig. 4). Ammonium fluxes of mussels on tables were not significantly different from the control (Fig. 4). For nitrate and nitrite no significant fluxes were observed in all but one case.



(a)



(b)

Figure 3. – Uptake fluxes of chlorophyll ($mg.m^{-2}.h^{-1}$) by oysters (3*a*) and mussels (3*b*), placed on the bottom (b) or on tables (t), for the oysters and for the mussels only in 1992 in comparison to control tunnels (c).
* $p<0.05$; ** $p<0.01$; *** $p<0.001$.

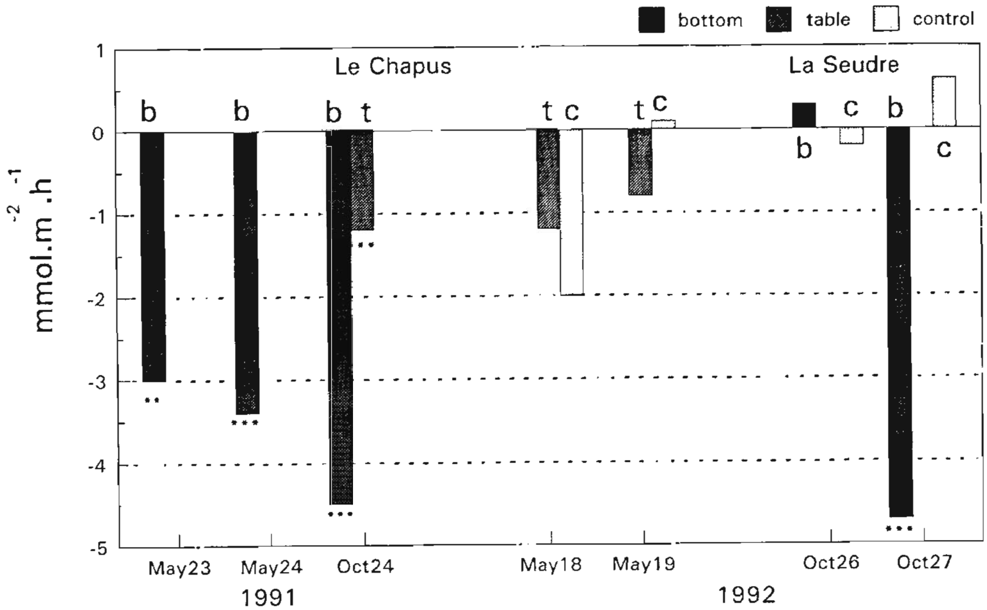


Figure 4. – Release of ammonium (mmol.m $^{-2}$.h $^{-1}$) from tunnels with mussels on tables or on the sediment, in 1992 compared with the control. * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

DISCUSSION

There is a large tidal variability in total seston concentration in Marennes-Oléron Bay, owing to resuspension and sedimentation of bottom material (Prou, 1994). An inverse relationship was found of seston concentrations and percentage of carbon: organic material was diluted by resuspended sediments, which had a low organic matter content (Zurburg *et al.*, 1994*b*). However, the quality of this material was high, considering the low C/N ratios. As shown by Zurburg *et al.* (1994*b*), a significant correlation between SPM and chlorophyll concentrations was observed in February, at both neap and spring tides. In May, this correlation was significant at spring tide only. Resuspension of benthic diatoms was observed in winter, when pelagic algae are diminished, and at high current velocities (spring tide) in other periods. Indeed, Prou *et al.* (1994) observed that in May 1990, benthic diatoms accounted for 50% of the total water column abundance at spring tide, and only 10% at neap tide. It was concluded that microphytobenthos contributed considerably to the plankton.

The fluxes in the control tunnels revealed high erosion/sedimentation dynamics of seston. In many cases both uptake and release of material was observed. In tunnels with oysters or mussels seston fluxes were in many cases higher than in control tunnels, although the differences were not significant in most cases, due to the large variability. Sedimentation of seston was enhanced by the bivalves (Zurburg *et al.*, 1994*b*). In contrast to *in situ* measurements of bivalve activity in other areas, which showed higher retention of POC and PON than of total SPM (Smaal and Prins, 1993; Prins *et al.*, 1996), in our study no selective retention of POC and PON was observed. Only for chlorophyll, uptake rates were significant. This indicates selective retention of chlorophyll by both oysters and mussels, which is explained by filtration and selective ingestion of chlorophyll, while the other seston fractions were rejected as pseudofaeces, which were subsequently resuspended. Chlorophyll uptake rates were in the same range as observed in the German and Dutch Wadden Sea (Smaal and Prins, 1993).

In situ clearance rates of 5-7 and 2.5 l.h^{-1} expressed per standard oyster and mussel respectively, were well within ranges found by other authors, especially regarding field conditions (*see* Bayne and Newell, 1983, for review; Deslous-Paoli *et al.*, 1987; Bougrier *et al.*, 1995; Smaal *et al.*, in press). It is noted that in February and October clearance rates of oysters, in particular, were low. There was no relation between clearance rates and current velocities. Consequently, filtration rates were determined by seston and chlorophyll concentrations (Zurburg, 1994*a*).

The release of nutrients from the oysters was in most cases not significantly different from control tunnels. Also the nutrient fluxes from mussels on tables were not significant, except in one case for ammonium. Only the release of ammonium from mussels laid on the sediment was in a number of cases significantly different from the control, or from the influx.

The observed release of ammonium from musselbeds was higher than direct excretion rates, which

Table 4. – Average clearance rates (CR), potential clearance time (time to filter the total volume of the Bay CT), phytoplankton filtration, and potential filtration pressure (daily phytoplankton filtration as a fraction of primary production FP) by oysters and mussels in Marennes-Oléron Bay (SW France). (C-chlorophyll ratio = 30).

	Standing stock	CR	CT	Phyto-C/ filtration	PP	FP
	10^6 g	$m^3.m^{-2}.d^{-1}$	d	$gC.m^{-2}.d^{-1}$	$gC.m^{-2}.d^{-1}$	Phyto-C/PP
Oysters	2 000	1.26	4	0.58		2.64
Mussels	200	0.13		0.06		0.27
Rest	650	0.4	1.3	0.19		0.86
Tot/av	2 850	1.8	2.7	0.83	0.22	3.77

is estimated as 1.2 μmol NH_4-N.g^{-1}AFDW.h^{-1} (Bayne and Scullard, 1977; Smaal *et al.*, in press).

Based on the mussel biomass in the tunnel, this is 1 mmol NH_4-N.m^{-2}.h^{-1}, which is 22 - 33% of the *in situ* releases. Prins and Smaal (1994) measured both in situ fluxes and individual excretion rates of mussels in the Oosterschelde estuary and reported ammonium excretion equal to 13 - 80% of *in situ* rates.

The higher *in situ* release rates might be explained by sedimentation and subsequent mineralization of biodeposition, which could occur on musselbeds, and not when animals were put on tables. It seemed likely that, in comparison with tunnels with animals on the sediment, a considerable amount of biodeposits was exported from tunnels with animals on tables. The absence of a significant release of nutrients from oysters on the bottom at the location La Seudre, might be explained by the low activity, *i.e.* the relatively low clearance rates in that period, in combination with relatively low oyster densities.

By using another approach, Sornin *et al.* (1983) have been able to estimate the amount of biodeposits produced by oysters in the bay, which varied from 480 - 6 600 g SPM $m^{-2}.d^{-1}$, with 1.5 - 7.7% C, and a C/N ratio of 6.6 - 12.4. These values are comparable with other areas, and may have a large potential for mineralization and nutrient regeneration (Smaal and Prins, 1993).

The potential impact of oysters and mussels on the ecosystem of Marennes-Oléron Bay consists of the filtration of large quantities of seston, including chlorophyll. The total standing stock of bivalves in Marennes-Oléron Bay is estimated as 2 850 tons AFDW, of which 2 000 tons are oysters and 200 tons are mussels (Prou *et al.*, 1994). The average clearance rate per day of all bivalves is estimated as 1.8 $m^3m^{2-}d^{-1}$, which means that, with an average depth of 5 m, the bivalves have the potential to filter the total bay volume within 2.8 days. With a residence time of the water mass of 7 days, it can be expected that the bivalve community has a large impact on particulate matter in the bay.

Assuming a pelagic primary production of 0.22 $gC.m^{-2}.d^{-1}$ (C. Bacher, pers. commun.), it is quite obvious that the filtration pressure is far greater than the daily pelagic production (Table 4). The filtration pressure for Marennes-Oléron Bay (3.77) is much higher than estimated values for the Dutch Wadden Sea (0.17), the Oosterschelde estuary (0.59) and the Ria de Arosa (0.55) (Smaal and Prins, 1993). As argued previously, it seems likely that microphytobenthos contributes to the quantity and quality of organic matter in the water column; hence it is an important food source for bivalves. The residence time of the water mass is only 7 days, and import of organic matter may as well contribute to food availability for bivalves in the bay.

The regeneration of nutrients from musselbeds shows values comparable with *in situ* estimations of other bivalve beds (Smaal and Prins, 1993). Yet, the total standing stock of mussels is relatively small, and hence their impact is of limited importance. If we assume that biodeposition, produced by bivalves on tables, is mineralized in the bay, then the total stock of bivalves would have a large potential for nutrient regeneration, through filtration, biodeposition and subsequent mineralization. This is particularly relevant for the productivity of the system during periods of nitrogen limitation.

CONCLUSION

The carrying capacity of Marennes-Oléron Bay for herbivores is extensively exploited by the shellfish stocks. Pelagic primary production does not sustain the uptake rates by oysters and mussels, and benthic diatoms should presumably be considered as a major food source. The measured regeneration of ammonium was significant from mussel beds only, and observed release rates of ammonium were higher than literature estimates of direct excretion rates. Yet, the extensive stock of bivalves in the Bay produces a large amount of biodeposits, which has a considerable potential of nitrogen remineralization.

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