

SESTON DYNAMICS AND BIVALVE FEEDING IN THE BAY OF MARENNES-OLÉRON (FRANCE) *

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KEYWORDS: seston load; seston quality; oyster; mussel; feeding; chlorophyll; microphytobenthos.

ABSTRACT

Within the framework of an investigation into the carrying capacity of the Bay of Marennes-Oléron (France) for bivalve culture, the *in situ* uptake of suspended particulate material by oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) was determined in experiments with benthic ecosystem tunnels. Very high fluctuations in seston quantity and quality were observed within and between tidal cycles. The percentage of organic carbon was inversely related to seston quantity at low concentrations. Organic carbon was diluted by resuspension of material rich in inorganic matter. At high seston concentrations a constant level of about 2% organic carbon was found. The C/N ratio was relatively constant throughout the seasons and fairly low (6.5 to 8.4). Owing to the presence of bivalves large fluxes of suspended particulate material were observed in the *in situ* measurements. Selective retention of organic carbon or nitrogen could not be demonstrated. Clearance rates based on chlorophyll uptake were within a normal range compared to other studies. A large contribution to the food of the bivalves seemed to be formed by resuspended microphytobenthos. Judged by the low C/N ratio, the food was of good quality. Although its quantity was variable by dilution, it may support largely the carrying capacity of the Bay of Marennes-Oléron for the cultivation of bivalves.

INTRODUCTION

In the Bay of Marennes-Oléron (France) the water column is characterized by high turbidity levels that are influenced by season, lunar cycles (spring, neap tides), bathymetry, currents and wind (HÉRAL *et al.*, 1983; PROU, 1991). High seston loads restrict primary production through light limitation, and moreover affect food availability to suspension feeding organisms, such as bivalves, by its dilution.

The total biomass of oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) which are extensively cultivated in the Bay of Marennes-Oléron, varies around 100,000 tonnes (fresh weight) (BACHER, 1989). In such dense communities,

bivalve species are known for their high filtration capacities and the enhancement of sedimentation processes (SORNIN *et al.*, 1983, 1986; SMAAL *et al.*, 1986; KAUTSKY and EVANS, 1987). SMAAL and PRINS (1993) estimated that the total water volume of the Bay of Marennes-Oléron could be filtered in 3 d by the bivalves present in this area. The quality of the filtered material is therefore of utmost importance for the growth of these organisms.

As part of an investigation into the trophic capacity of the Bay of Marennes-Oléron, the *in situ* uptake of suspended particulate material by oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis*) was studied during various seasons, by applying the Benthic Ecosystem Tunnel developed by DAME

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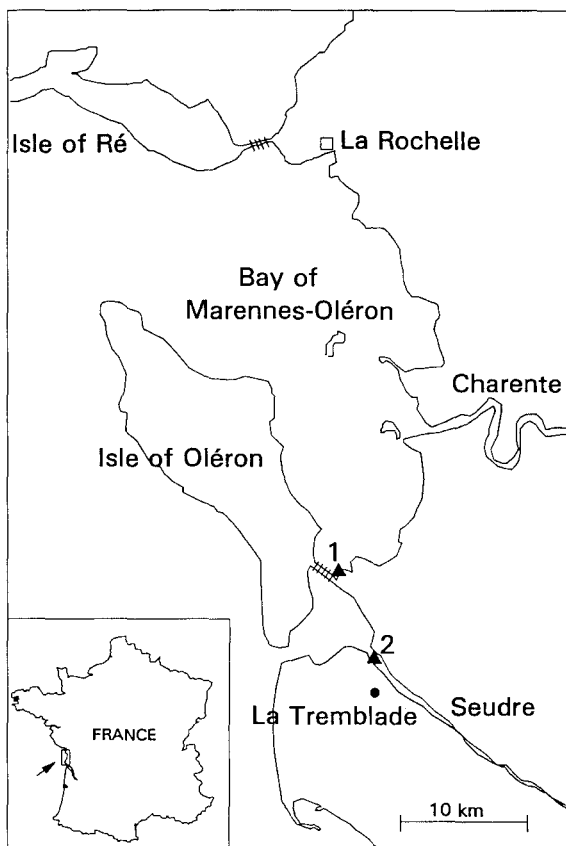


Fig. 1. Location of the experimental sites Le Chapus (1) and Seudre (2) in the Bay of Marennes-Oléron (France).

et al. (1984) and used earlier over mussel and oyster beds in The Netherlands by DAME and DANKERS (1988), DAME *et al.* (1991) and PRINS and SMAAL (1990, 1994). Part of the results on the uptake and release of material by oysters in the Bay of Marennes-Oléron was presented earlier (ZURBURG *et al.*, 1994). In the present paper, the food uptake by oysters and mussels is discussed in relation to the variations in seston quantity and quality in the overlying water.

MATERIALS AND METHODS

Uptake of suspended materials was determined *in situ* with two Benthic Ecosystem Tunnels, as described by ZURBURG *et al.* (1994). Both tunnels were used in parallel over oysters (*Crassostrea gigas*) or mussels (*Mytilus edulis*) or over empty oyster shells (control). The tunnels are made of Plexiglass plates, joined together by neoprene strips. The total length between sampling points approx-

imates 10 m, the width 0.80 m and the cross-sectional area 0.23 m². About 8 m² of bottom area with or without animals were covered.

Measurements were carried out in the Bay of Marennes-Oléron (France) at Le Chapus in spring (May 1991 and 1992), autumn (October 1991) and winter (February 1992) and in the Seudre in spring (June 1992) and autumn (October 1992) (Fig. 1). Experiments were performed during 32 different tidal cycles.

Sampling procedure

The tunnels were submersed for 8-10 h during each tidal cycle at spring tide or up to about 11 h at neap tide. From a small boat lying between the tunnels, water samples of 1 l were taken at the inflow and the outflow with battery driven pumps every 20-30 min during the period of submersion. Samples were analyzed for seston, particulate organic carbon (POC) and nitrogen (PON) and chlorophyll-*a*. Details of the analytical methods have been described by PRINS and SMAAL (1990) and DAME *et al.* (1991).

After each experiment samples of the oysters and mussels were taken from three different locations within the tunnel and dried for at least 48 h at 70°C. Subsequently the samples were dried for 4 h at 520°C for the determination of the ash-free dry weight (AFDW). The biomass was between 129 and 236 g AFDW m⁻² (174-312 individuals m⁻²) for oysters and between 436 and 1101 g AFDW m⁻² (1500-7900 individuals m⁻²) for mussels.

Calculation of fluxes and statistical treatment of the results

Water flow through the tunnels was calculated from current velocity data continuously recorded by induction flow meters (Marsh McBirney 201M or NSW Meerestechnik) placed in the centre of the tunnels. Earlier calibration studies were used to correlate the current measured at a single point to water flow (DAME *et al.*, 1984; PRINS and SMAAL, 1990). The fluxes of material were calculated from water flow times and the difference between the inflow and outflow concentrations. Fluxes of control and experimental tunnels were compared by the Mann-Whitney U test.

Fluxes occurring at current speeds lower than 2 cm s⁻¹ were excluded from calculations as vertical mixing of the water within the tunnel probably was not complete (PRINS *et al.*, unpubl. data).

The residence time of the water within the tunnels can be calculated to be less than 8 min at current speeds higher than 2 cm s⁻¹.

Clearance rates

Clearance rates (CR) based on chlorophyll were calculated according to

$$CR_{\text{bed}} = \frac{Q \ln(C_{\text{chl in}}/C_{\text{chl out}})}{A}$$

where CR_{bed} = clearance rate of the mussel or oyster bed ($\text{m}^3 \text{m}^{-2} \text{h}^{-1}$), Q = water flux through the tunnel ($\text{m}^3 \text{h}^{-1}$), $C_{\text{chl in}}$ = concentration of chlorophyll in the sea water at the entrance of the tunnel ($\mu\text{g l}^{-1}$), $C_{\text{chl out}}$ = concentration of chlorophyll at the outlet of the tunnel ($\mu\text{g l}^{-1}$) and A = surface area of the mussel or oyster bed between the sampling points (m^2). Bed clearance rates depend on the individual clearance rates and the density of the oysters or mussels. Clearance rate as a function of body size is expressed by $CR_i = aW_i^b$ with a = clearance rate of a standard animal of 1 g ash-free dry weight and W_i = weight of individual animal, b = weight-exponent. From $CR_{\text{bed}} = a \sum (n_i \cdot W_i^b)$ with n_i = number of animals of sizeclass i , the clearance rate of a standard animal (a) can be calculated.

The value of b taken was 0.67 for mussels (JONES *et al.*, 1992). For oysters the value of 0.439 was taken as found by FIALA-MEDIONI *et al.* (1984) and by S. BOUGRIER (pers. comm.) for the population of *Crassostrea gigas* under study. Corrections were made for chlorophyll uptake or release in the control tunnel. Computing averages over tidal cycles, negative values found for clearance rates were considered to be zero.

RESULTS

Characteristics of seston

From the water samples taken at the entrance of the benthic ecosystem tunnels some characteristics of the water column become evident. The variation in seston quantities in the water column of the Bay of Marennes-Oléron is presented in Table 1 for the two locations used in our experiments. The concentrations varied from 7 to $>300 \text{ mg l}^{-1}$. Particulate organic carbon (POC) concentrations increased linearly with seston concentrations as shown in Fig. 2 for the October 1991 and 1992 experiments. The percentage of organic carbon (Fig. 3) remained constant at high seston concentrations (around 2%), but was inversely related to seston at low concentrations. In the other experimental periods similar patterns were observed (not shown). Chlorophyll concentrations varied largely over the

Table 1. Mean concentrations of seston (mg l^{-1}), chlorophyll ($\mu\text{g l}^{-1}$) and C/N ratios in the water entering the tunnels at two locations in the Bay of Marennes-Oléron during six experimental periods. Between brackets: minimum and maximum values. n is number of tidal cycles in each period.

	n	Seston	Chlorophyll	C/N
LE CHAPUS				
May 1991	2	110 (28/246)	5.6 (2.5/19.2)	8.14 (5.30/17.25)
Oct 1991	8	114 (23/331)	2.1 (0.3/ 5.6)	8.35 (4.01/13.25)
Feb 1992	6	40 (10/332)	0.2 (0.1/ 1.0)	6.96 (3.69/13.91)
May 1992	6	62 (26/146)	7.3 (1.5/14.3)	6.50 (3.35/ 9.60)
SEUDRE				
Jun 1992	4	19 (7/ 38)	2.4 (0.9/ 4.5)	7.18 (4.09/14.86)
Oct 1992	8	43 (8/201)	1.5 (0.3/15.9)	8.35 (4.69/14.78)

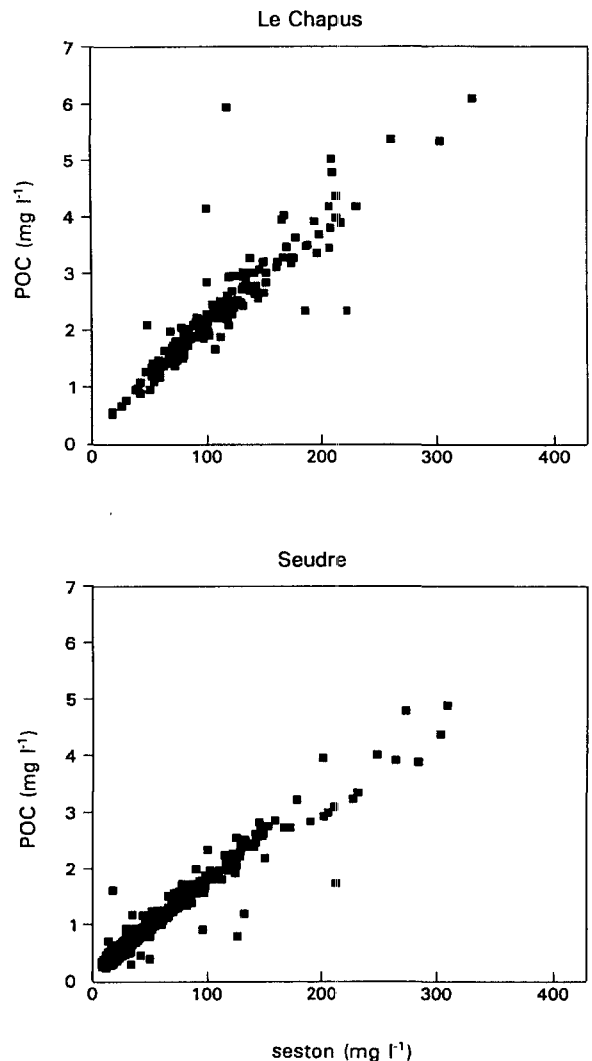


Fig. 2. Relation between POC concentrations (mg l^{-1}) and seston concentrations (mg l^{-1}) at Le Chapus (October 1991, 8 tidal cycles) and in the Seudre (October 1992, 8 tidal cycles).

Table 2. Fluxes of seston, POC, PON ($\text{g m}^{-2} \text{h}^{-1}$) and chlorophyll-*a* ($\text{mg m}^{-2} \text{h}^{-1}$) in experimental (oyster or mussel) and control tunnels (mean over one tidal cycle, minimum and maximum values). – = release, no sign = uptake. n is number of samples taken during one tidal cycle. Significant differences between experimental and control tunnels are indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (Mann-Whitney U test).

OYSTERS		n	Seston	POC	PON	Chlorophyll
<i>Le Chapus</i>						
Oct 8, 1991	Oysters	11	116 (-414/279) *	2.2 (-6.9/5.3) **	0.37 (-1.04/0.92) **	3.8 (-2.3/17.0)
	Control	11	56 (-34/177)	0.6 (-2.9/2.4)	0.11 (-0.12/0.31)	1.1 (-2.9/ 9.1)
Oct 9, 1991	Oysters	12	140 (-91/379) **	2.0 (-2.9/7.1) *	0.32 (-0.11/0.95) *	1.9 (-2.4/5.6) *
	Control	12	18 (-137/154)	0.2 (-3.0/3.4)	0.05 (-0.48/0.50)	0.6 (-0.3/1.8)
May 19, 1992 (night)	Oysters	14	97 (-8/232)	1.0 (-1.4/3.9)	0.21 (-0.92/0.97)	14.8 (3.1/27.7) ***
	Control	14	87 (-11/215)	0.7 (-0.4/2.9)	0.21 (-0.13/1.09)	3.2 (-3.7/15.6)
May 20, 1992	Oysters	15	40 (-3/139)	0.2 (-1.2/2.1)	-0.07 (-1.07/0.53) *	4.8 (-23.2/18.0) **
	Control	13	57 (0/145)	0.7 (-0.2/2.3)	0.34 (-0.22/1.12)	0.4 (-16.6/ 7.5)
<i>Seudre</i>						
Oct 13, 1992	Oysters	14	24 (-14/87) **	0.3 (-0.4/1.4) *	0.11 (-0.11/0.79) *	0.6 (-1.8/7.1)
	Control	14	-30 (-340/17)	-0.1 (-1.2/0.4)	-0.04 (-0.14/0.11)	0.1 (-0.7/1.1)
MUSSELS						
<i>Le Chapus</i>						
May 18, 1992	Mussels	15	150 (-202/820)	0.8 (-7.5/4.3)	1.14 (-0.13/7.62) *	10.6 (-69.3/33.7) **
	Control	15	60 (-125/445)	0.9 (-3.7/6.3)	-0.01 (-2.11/1.48)	4.4 (-5.1/15.6)
May 19, 1992 (day)	Mussels	15	135 (-244/360) *	3.0 (-3.3/8.6) **	0.52 (-1.48/5.25)	9.7 (-22.4/23.1) ***
	Control	15	82 (-9/182)	1.5 (-0.8/3.3)	0.05 (-1.08/1.41)	1.0 (-6.3/ 9.3)
<i>Seudre</i>						
Oct 26, 1992	Mussels	16	236 (-131/537) ***	3.5 (-2.7/11.6) *	0.60 (-0.41/2.00) *	3.6 (-3.6/12.9)
	Control	15	11 (-142/148)	0.3 (-2.7/ 3.1)	0.02 (-0.90/0.49)	1.3 (-1.8/10.4)

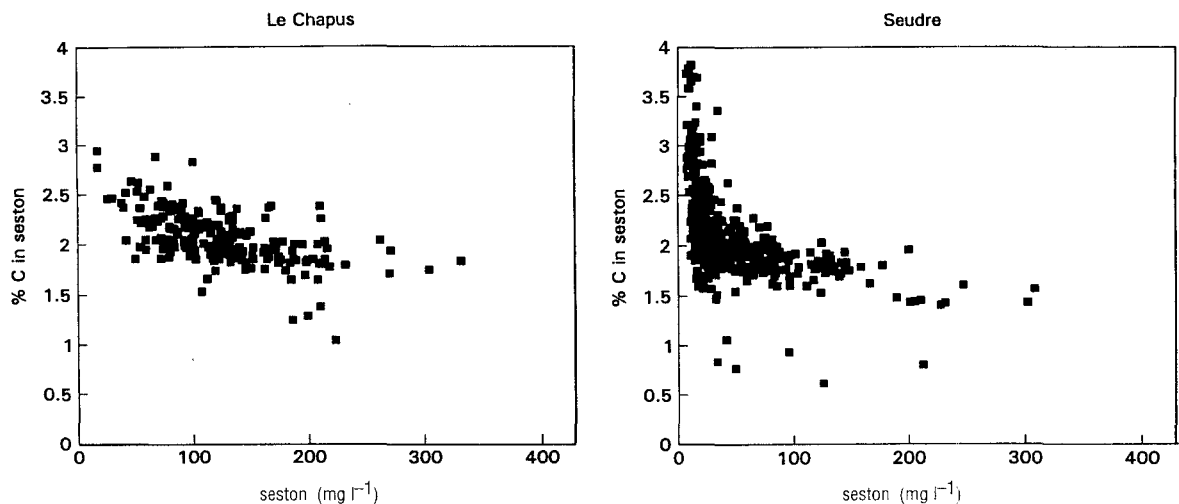


Fig. 3. Fraction of organic carbon (%) in total seston plotted against seston concentrations (mg l^{-1}) at Le Chapus (October 1991) and in the Seudre (October 1992).

seasons (Table 1). In spring (May), phytoplankton blooms occurred resulting in high maximum values which occurred also in October 1992. In winter (February), concentrations were very low.

The C/N ratio (POC/PON) in the suspended particulate matter was fairly constant during the year

with a relatively low mean between 6.5 and 8.4 (Table 1).

Uptake of suspended particulate material

In the experiments with the Benthic Ecosystem Tunnels uptake of suspended particulate

material by oysters or mussels was demonstrated. In Table 2 fluxes of seston, POC, PON and chlorophyll are given for several experiments. In control experiments with oyster shells also fluxes were observed due to sedimentation or, if negative, by resuspension of particulate material. A general pattern of uptake of material was observed which was enhanced by the presence of oysters or mussels. Chlorophyll uptake was evident in all the presented experiments, although not statistically significant in three cases. Based on the chlorophyll uptake (Table 2), clearance rates were calculated for the oysters and mussels in the May 1992 experiment which are shown in Table 3.

DISCUSSION

The variation in seston concentrations between 7 and more than 300 mg l⁻¹ (Table 1) has been found in other investigations on the Bay of Marennes-Oléron (HÉRAL *et al.*, 1983; DESLOUS-PAOLI and HÉRAL, 1984; PROU, 1991). An inverse relation-

Table 3. Mean, minimum and maximum clearance rates (in l h⁻¹ per standard animal of 1 g AFDW) over one tidal cycle of mussels and oysters based on chlorophyll uptake.

	Date	Clearance rate mean (min/max)
Mussels	May 18 1992	2.47 (0/ 4.77)
	May 19 1992	2.36 (0/ 5.22)
Oysters	May 19 1992	7.66 (0/18.76)
	May 20 1992	5.50 (0/16.78)

ship between the percentage of carbon and seston concentrations (Fig. 3) has been reported earlier by RAZET *et al.* (1990) and BARILLÉ and PROU (pers. comm.) for the Bay of Marennes-Oléron, but also for other areas, *e.g.* the Mersey estuary (UK) (PRESTON and PRODDUTURU, 1992). Organic material is diluted by resuspended sediments which consist for about 98% of inorganic matter. The origin of this material may be variable. Local action of currents could cause resuspension, but the material could be transported also from other parts of the bay after wind-induced resuspension on the tidal front.

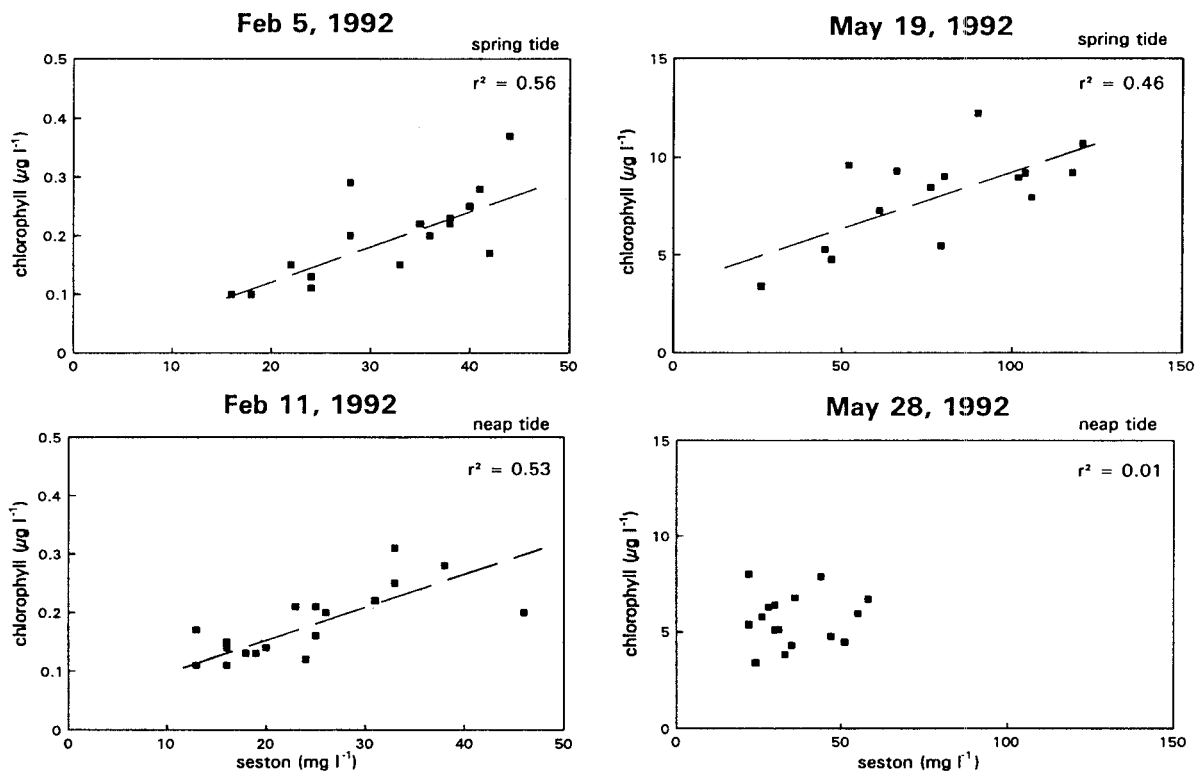


Fig. 4. Relation between chlorophyll concentrations ($\mu\text{g l}^{-1}$) and seston concentrations (mg l^{-1}) at Le Chapus in February and May 1992 during spring tide and neap tide.

Resuspension processes may also be involved in the origin of chlorophyll in the water column. In winter chlorophyll concentrations were very low (Table 1). At this time pelagic phytoplankton is supposed to be absent. Resuspension of microphytobenthos could then explain the amount of chlorophyll found in the water column. To investigate further the origin of chlorophyll, concentrations of this pigment were plotted against seston concentrations (Fig. 4). In February both at spring and neap tide, a linear relationship between chlorophyll and seston concentrations was found. In May this was only observed at spring tide.

In the experimental area, at neap tides current velocities are usually much lower than at spring tides (PROU, 1991). So at neaps, resuspension of sediment is much less important (sedimentation of particles is dominant), which is evident from the lower seston concentrations at neap tide in May. Here chlorophyll originated from pelagic phytoplankton, whereas at spring tide a mixture from resuspended microphytobenthos and pelagic phytoplankton was present. In May 1990 PROU (1991) demonstrated that at spring tide benthic species formed about 50% of the diatoms in the water column, whereas at neap tide only about 10% could be found.

It was calculated that in winter (February), resuspended microphytobenthos may account for all the chlorophyll in the water column. Assuming that microphytobenthos is present in the top centimetre of the sediment only, a bottom chlorophyll concentration of 100 mg m^{-2} (data from IFREMER) or $10 \text{ } \mu\text{g cm}^{-2}$ is equivalent to $10 \text{ } \mu\text{g cm}^{-3}$. With a sediment density of 1.8 g cm^{-3} this gives $10/1.8 = 5.5 \text{ } \mu\text{g}$ chlorophyll per g of sediment. This value is in good agreement with that of $6.25 \text{ } \mu\text{g}$ chlorophyll g^{-1} seston derived from Fig. 4 (February, spring tide, $0.25 \text{ } \mu\text{g}$ chlorophyll in 40 mg seston). It is concluded that resuspension of the top layer of the sediment can explain the amount of chlorophyll in the water column in winter.

The relatively low C/N ratio found during all experimental periods is similar to that of marine phytoplankton (FENCHEL and JØRGENSEN, 1976), which implies that the organic matter consists mainly of pelagic plankton or/and resuspended microphytobenthos. Consequently, the feeding quality of the (re)suspended particulate material is high. The quantity, however, is relatively low by dilution with inorganic material.

The fluxes of suspended particulate material caused by oysters or mussels (Table 2) imply that sedimentation is greatly enhanced. A flux of 100 g

$\text{m}^{-2} \text{ h}^{-1}$ results in deposition of a layer of about 0.5 cm on the bottom during one tidal cycle.

Bivalves, in general, are capable of selective retention and ingestion of material from offered food (KJØRBOE and MØHLENBERG, 1981; NEWELL and JORDAN, 1983). From our results no selective retention within the tunnels can be deduced. The POC fluxes did not account for more than 2% of the seston fluxes (Table 2), the same percentage as found for organic carbon in seston (Fig. 3). In other areas of Europe, selective retention could be demonstrated *in situ* (SMAAL and PRINS, 1993), but seston concentrations in the water column were generally much lower (around 20 mg l^{-1}) than in the Bay of Marennes-Oléron. RAZET *et al.* (1990) could not find sorting out of organic carbon by the oyster *Crassostrea gigas* when seston concentrations were over 40 mg l^{-1} . As our experiments were performed mostly at high seston loads (Table 1), our findings confirm those of RAZET *et al.* Similarly, no selective retention *in situ* of nitrogen over carbon nor of chlorophyll could be demonstrated.

The seston concentrations found during our experiments were all higher than the threshold concentration for pseudofaeces formation being around 5 mg l^{-1} for the mussel (BAYNE and NEWELL, 1983) and 4.6 mg l^{-1} for the oyster (DESLOUS-PAOLI *et al.*, 1992). Therefore, large amounts of pseudofaeces must have been formed by the bivalves in the tunnel experiments. From the limited nutrient release in the benthic ecosystem tunnel experiments (ZURBURG *et al.*, 1994) we conclude that the biodeposits formed by the bivalves were resuspended and lost to the environment.

Filtration of suspended particulate material by the bivalves concomitant with processes of sedimentation and resuspension, however, leads to very variable fluxes during one tidal cycle (Table 2). Selective retention of one component over another may have been masked by this high variability.

The clearance rates calculated for oysters and mussels in May 1992 (Table 3) of $5\text{--}7$ and 2.5 l h^{-1} per standard animal, respectively, fall within the range found for these species by DESLOUS-PAOLI *et al.* (1987) and BAYNE (1993). The weight-exponent b we used for the oyster (0.439), is lower than the theoretical value of 0.67 for bivalves (JONES *et al.*, 1992) or the value of 0.72 for *Crassostrea virginica* (RIISGÅRD, 1988), but is based on experiments with the same population of *Crassostrea gigas* (BOUGRIER, personal communication). For the mean size of animals used ($0.75\text{--}0.80 \text{ g AFDW}$), an exponent of 0.7 would give clearance rates that are only 10–15% higher than listed in Table 3.

Compared to laboratory experiments cited by JØRGENSEN (1990), the clearance rates we found are low for mussels (2.5 vs. 7.5 l h⁻¹). This difference may be explained by the longer period of observation (one tidal cycle) in the benthic ecosystem tunnels for which a mean clearance rate was calculated. The activity of the animals will not have been at its maximum during the whole tidal cycle. Moreover, high seston concentrations have been shown to reduce clearance rates of mussels and cockles (PRINS *et al.*, 1991). Compared to observations on different populations of mussels (BAYNE, 1993) the rates presented in Table 3, lie within a normal range.

Although high seston loads in the water column do not appear ideal for growth, the relatively good quality of the food (indicated by the C/N ratio) may contribute largely to the carrying capacity of the Bay of Marennes-Oléron for the cultivation of bivalves.

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