Particle selection in the oyster *Crassostrea gigas* (Thunberg) studied by pigment HPLC analysis under natural food conditions

Chloropigments
Crassostrea gigas
Selective feeding
Biodeposits
Marennes-Oléron

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ABSTRACT

Selective feeding in the adult oyster *Crassostrea gigas* was studied using natural particle assemblages in the estuarine environment of the Bassin de Marennes-Oléron (France). Oysters were exposed to natural variations of suspended particulate matter by direct pumping of sea water from the bay during various tidal cycles. Experiments were conducted during the spring over both spring tides and neap tides, so as to obtain a maximum range of variation in seston characteristics, spring tide being characterized by very strong currents with high loads of resuspended materials (sediment, microphytobenthos and detritus). Particles were analysed for their chloropigment content by HPLC. The native pigments consisted exclusively of chlorophyll *a* and *c*, from both benthic and pelagic diatoms. Phaeophorbides were the main degradation products both in oyster faeces and in particles present in resuspended material, mainly composed of biodeposits. Comparisons between the composition of water-column particulate matter and pseudofaeces showed a negative selection against these detritus types by the oyster. This selective capacity was either not effective or was undetected at very high seston loads. Implications for the nutrition of *Crassostrea gigas* living in estuarine environments are discussed.

RÉSUMÉ

Étude de la capacité de tri particulaire de l'huître *Crassostrea gigas* (Thunberg) dans des conditions naturelles d'alimentation par l'analyse en HPLC des pigments.

La capacité de tri du matériel particulaire de l'huître *Crassostrea gigas* a été étudiée dans les conditions naturelles du Bassin de Marennes-Oléron (France). Les huîtres ont été exposées aux variations du matériel en suspension pendant différents cycles de marée. Les expériences se sont déroulées au printemps, en vives-eaux et mortes-eaux afin de tester les conditions extrêmes de charges sestoniques rencontrées par les huîtres dans leur milieu d'élevage, les marées de vives-eaux étant caractérisées par des courants importants qui provoquent la remise en suspension de matériel benthique (sédiment, microphytobenthos et détritus). L'analyse du contenu en chloropigments de ces particules a été effectuée par HPLC.

Les pigments non dégradés sont les chlorophylles *a* et *c* provenant des diatomées pélagiques et benthiques. Les phéophorbides sont les principaux produits de dégradation détectés dans les fécès d'huîtres et dans le matériel remis en suspension qui est probablement principalement constitué de biodépots. La comparaison entre la composition pigmentaire du matériel particulaire dans l'eau de mer et des pseudofécès a montré une selection négative vis-à-vis de ces détritus dans les conditions de faible charge sestonique. Cette capacité de selection était non effective ou indétectable aux fortes charges sestoniques (> 100 $mg.l^{-1}$). Les conséquences pour la nutrition de *Crassostrea gigas* dans son environnement sont discutées.

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INTRODUCTION

In nature, suspension-feeding bivalves are exposed to a food supply extremely variable in both quantity and quality. They present various strategies for controlling the ingestion of particulate matter, including the capture of particles on the gills, their transport to the labial palps and mouth, and selection before ingestion. Regulation of feeding duration and clearance rate primarily affects the amount of food ingested (Foster-Smith, 1975; Bayne and Newell, 1983). Both quality and amount of the ingested food are also controlled by changes in retention efficiency or differential clearance rates (Shumway *et al.*, 1985; Newell *et al.*, 1989; Barillé *et al.*, 1993) as well as by production of pseudofaeces above a certain threshold of seston concentration.

Various investigations have shown that many bivalves can reduce the concentration of either the organic matter or the chlorophyll a voided in pseudofaeces (Kiørboe *et al.*, 1980; Kiørboe and Møhlenberg, 1981; Newell and Jordan, 1983; Bricelj and Malouf, 1984; Razet *et al.*, 1990; Prins *et al.*, 1991; Deslous-Paoli *et al.*, 1992; Bayne *et al.*, 1993). These mechanisms are usually presumed to enhance the quality of particles consumed by rejecting those particles lower in nutritive value, but they also result in elimination of material that exceed the animal's ingestive or handling capacity (Beninger *et al.*, 1992). This is considered as an adaptation for living in turbid waters.

Direct observations by video endoscopy on several suspension-feeding bivalves have greatly improved the knowledge of particle transport (Beninger *et al.*, 1992; Ward *et al.*, 1993; Ward *et al.*, 1994), these observations, together with histological studies have demonstrated the role of mucus in these mechanisms (Beninger *et al.*, 1991; 1993). Nevertheless, the mode of particle selection prior to ingestion remains unanswered and the complexity of the composition of the particulate matter in coastal zones usually used for bivalve culture renders understanding of these mechanisms dificult. Moreover, there have been few studies made in natural environments which take into account the effect of short-term variations in both quality and quantity of potential food on the feeding behaviour of suspension-feeding bivalves. Stenton-Dozey and Brown (1992 and 1994) have demonstrated the importance of this natural constraint on the feeding behaviour of *Venerupis corrugatus*, and MacDonald and Ward (1994) on *Placopecten magellanicus*. Razet *et al.* (1990) studied food selection by *Crassostrea gigas* under natural food conditions in the Bassin de Marennes-Oléron (France) and demonstrated that selection efficiency depends on the seston load.

This bay, which supports an important production of cultivated oysters *Crassostrea gigas* (110 000 tons), is characterized by very strong tides and currents, together with high loads of suspended materials. In previous studies of this site, Héral *et al.*, (1989) and Soletchnik *et al.*, (1991), by continuously monitoring current velocity, turbidity and *in vivo* fluorescence over several successive days, described how resuspension of sediment associated with benthic plant material (microphytobenthos) and detritus (including biodeposits) gave rise to very marked temporal variability in the quality and amount of suspended particulate matter over and between tidal cycles.

The object of our study was to characterize these particles by their chlorophyll pigment content and to evaluate, in the context of these short-term variations in both quantity and quality of food, the capacity of *Crassostrea gigas* to select among the different types of organic matter present in different forms of plant materials. Using HPLC analysis, we compared chlorophyll pigments in water-column particulate matter with the composition in pseudofaeces and faeces. The HPLC technique for algal photopigments was first developed by Mantoura and Llewellyn (1983), and permits the unambiguous measurement of algal chlorophyll pigments and of the different degradation products that classical methods fail to distinguish and to quantify accurately. This method has provided important information in studies of both grazing activity and digestive processes in molluscs and zooplankton (Burkill *et al.*, 1987; Bianchi *et al.*, 1988; Hawkins *et al.*, 1986; Robinson *et al.*, 1989; Roy *et al.*, 1989).

Two *in situ* experiments were conducted during the spring time in the estuarine environment of Marennes-Oléron over both spring tide and neap tide cycles so as to obtain a maximum range of variation in seston characteristics.

MATERIAL AND METHODS

Experimental procedure

Experiments were performed in a temporary field laboratory located at a central point of the Marennes-Oléron bay (Le Chapus). Individual oysters were exposed, under flow-

through conditions, to natural seston by direct pumping of sea-water from about 0.5 m above the bottom which is the situation of cultured oysters on their iron tables. Experiments were carried out in spring during five days:

Exp. 90: 27 April = Spring tide 90, 2 May = Neap tide 90, 8 May = Inter 90: as intermediate tidal situation,

Exp. 91: 14 May = Spring tide 91, 22 May = Neap tide 91.

Each experiment lasted 6 to 11 hours according to the tidal cycle, with different emersion times.

Water samples were taken hourly for HPLC pigment analysis at the inflow of the experimental tank: between 150 to 300 ml of prefiltered sea-water (200 μm) were passed through 47 mm Whatman GF/C filters (nominal pore size = 1.2 μm) in triplicate. During Exp. 90, water samples were taken every two hours for microscopic examination. Turbidity was monitored continuously as described by Razet *et al.*, 1990 and Soletchnik *et al.*, 1991 and total seston was determinated after drying of precalcinated and weighed filters at 60 °C until constant weight.

Experimental adult animals were collected near the experimental site; tissue dry weights ranged from 0.9 to 1.5 g. They were cleaned of epibionts and kept in experimental tanks for 24 h before sampling. Four oysters were used for each day in Exp. 90 and 5 in Exp. 91.

Pseudofaeces and faeces were collected separately and hourly:

– in Exp. 90, biodeposits were sampled non-quantitatively by pipette just after their release to avoid any subsequent degradation of pigments ;

– in Exp. 91, biodeposits were sampled using a special tank where oysters were arranged in such a way that faeces and pseudofaeces fell into separate funnels. Biodeposits were collected during a quarter of an hour after the water sampling.

Each sample was immediately frozen and kept in the dark, in liquid nitrogen or dry ice, just after collection.

Pigment analysis

Extractions were carried out into 5 ml 90% acetone, by crushing and stirring the filters with a glass rod. Vials were then stored for 2 hours in the dark at 4 °C before analysis. The HPLC system consisted of two pumps (Kontron, model 414), an injection valve (Altex model 210) and a fluorescence detector (Kontron spectrofluometer SFM 25, excitation at 430 nm, emission at 663 nm). The gradient control and data acquisition were performed using an HPLC computer (Kontron model 450). The column (100 × 4.6 mm) was filled with 3 μm ODS Hypersil. Chlorophyll type pigments were analysed by reverse-phase ion-pairing HPLC using the method of Knight and Mantoura (1985). The flow rate was 1.5 ml/min and the solvent programme was the following: start from 100% A (80:10:10, methanol: water: ion-pairing reagent) to 100% B (60:40, methanol: acetone) for 5 min, then hold in 100% B for 5 min and return to initial conditions in five minutes.

Chloropigments were quantified using solutions of purified pigments. Chlorophyll *a* was purchased from Sigma-Chimie, chlorophyll *c* was isolated from a culture of the diatom Phaeodactylum tricornutum Bohlin. Chlorophyllide *a* was obtained from this alga according to the protocol of Barret and Jeffrey (1971).

Purification of these pigments was performed on a preparative column [Merck Lichroprep RP-8 (40-63 μm) size A (240-10)]. Phaeophytin and phaeophorbide *a* were prepared by acidification of, respectively, chlorophyll *a* (Chl *a*) and chlorophyllide *a*. Phaeophorbide a obtained in this way produced only one peak on the chromatogram, but we used it to quantify all peaks assumed to be phaeophorbide *a*-like pigments (PhideL), according to Hawkins *et al.*(1986); Vernet and Lorenzen (1987).

Data analysis

In order to test differences in composition in sea-water and pseudofaeces over the four tidal cycles, a covariance analysis was performed on phaeophorbide concentrations. Chlorophyll *a* concentration was used as covariate.

The model used was defined as :

$$\mathbf{P_{ik}} = (\alpha + \alpha_i)\, \mathbf{C_{ik}} + (\beta + \beta_i) + \mathbf{e_{ik}} \qquad (1)$$

P_{ik} and C_{ik} are the phaeophorbide and chlorophyll *a* concentrations for the ith factor (pseudofaeces and sea water) and the kth sample.

Selection of phaeophorbide in pseudofaeces is tested by comparaison with the restricted model :

$$\mathbf{P_k} = \alpha \mathbf{C_k} + \beta + \mathbf{e_{ik}} \quad (\alpha_i = \beta_i = \phi) \qquad (2)$$

$$F = \frac{(RSS2 - RSS1) / (2p - 2)}{RSS1 / (n - 2p)}$$

where p = 2 is the number of factors and RSS1 and RSS2 are respectively the residual sum of squares of the two models.

The F statistic is compared with the Fisher-Snedecor distribution at p = 0.05 level.

From all results we calculated a selection coefficient derived from the selection efficiency used by authors which compared the composition of pseudofaeces to food (Kiørboe and Møhlenberg, 1981; Urban and Kirchman, 1992; Bayne *et al.*, 1993).

Selection coefficient = P/S where P is the phaeophorbide/chl *a* ratio in pseudofaeces and S this ratio in sea-water at the same time. In case of non-selective ingestion of non-degraded forms, the coefficient is 1, if a preferential rejection of degraded form occurs, the coefficient is higher than 1.

RESULTS

The native pigments were chlorophylls *a* and *c*, corresponding to the diatom populations observed by microscopy. Figure 1 shows typical chromatograms of pigments from sea water and faeces obtained by fluorescence. The main breakdown products of chlorophyll *a* were phaeophorbides. Other compounds, (chlorophyllide *a*, allomerized

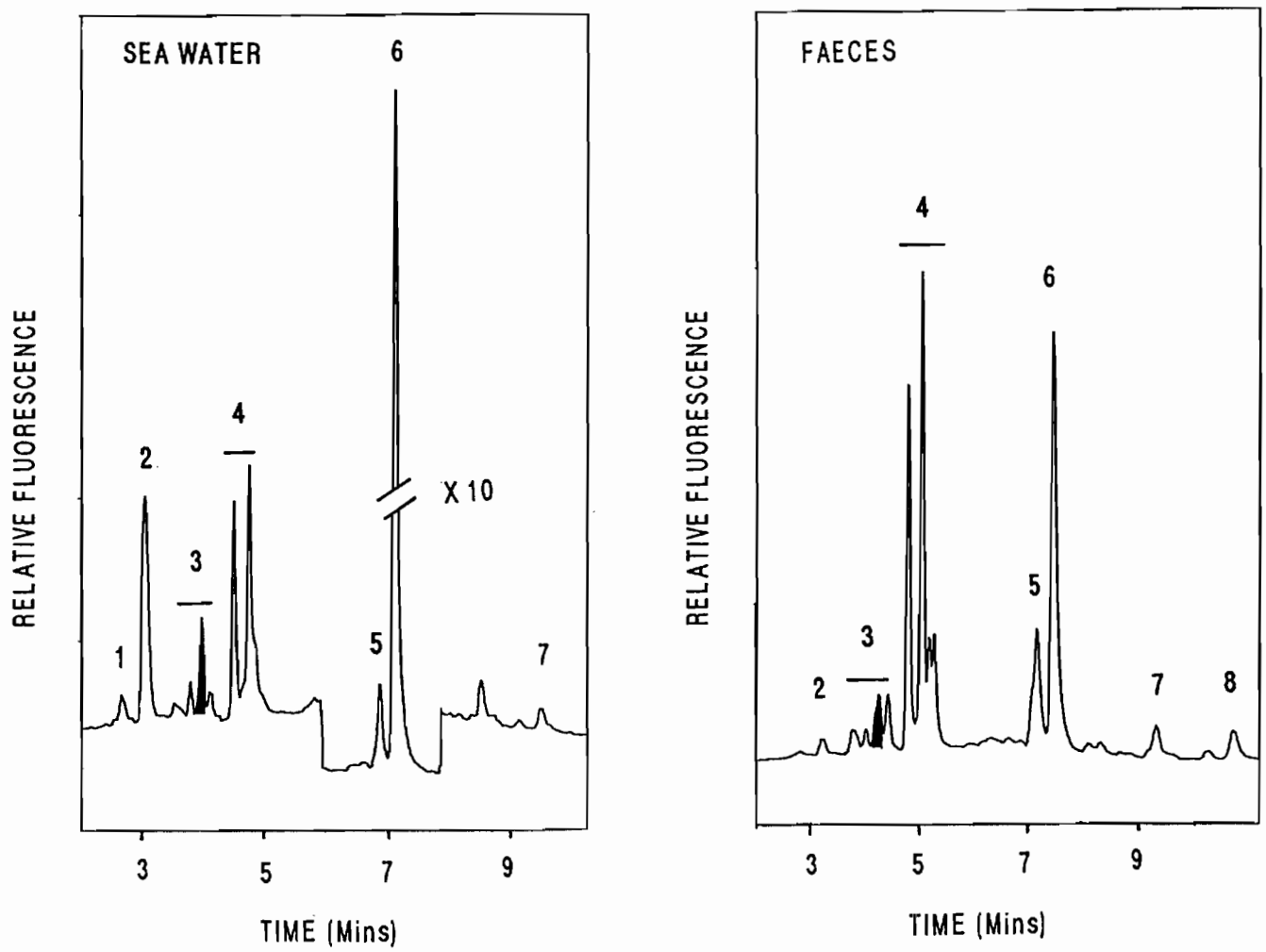

Figure 1

Typical chromatograms of chlolorophyll; type pigments in sea water and faeces. 1. chlorophyllide a; *2. chlorophyll* c; *3. first group of phaeophorbides* a; *4. second group of phaeophorbides* a *(phaeophorbide* a*-like); 5. allomerized chlorophyll* a; *6. Chlorophyll* a; *7, 8. phaeophytins* a.

chlorophyll *a* and phaeophytine *a*) always constitued less than 10% of the total pigments. Six to eight phaeorphobides of different polarity were observed. They could be separated into two groups. In the first one, more polar, the shaded peak in Figure 1 corresponded to the compound obtained from *Phaeodactylum*. The second group, less polar, was always quantitatively the most important: it constituted between 55 and 85% of all the degraded forms (weight/weight). The first group was often close to the threshold of detection or below, so data presented as phaeophorbide *a*-like (PhideL) were those of the second group.

Spring tides were characterized by high resuspension rates, by rapid changes in seston load and by concomitant changes in total pigment concentration (Fig. 2). Neap tides showed lower seston and pigment concentrations, these variations being not always simultaneous. Changes in chlorophyll *a* and phaeophorbide *a*-like concentrations were also given in Figure 2 as the main conponent of the total pigments. During spring tide and the intermediate tidal situation, variations of phaeophorbide *a*-like concentrations were linked with seston load, in association with resuspension.

During each tidal cycle, a change in the ratio of degraded forms versus chlorophyll *a*, calculated on a molar basis was observed (PhideL/Chl *a*). Figure 3 shows the typical changes occurring during two tidal cycles in seston concentration and in the PhideL/chl *a* molar ratio in sea water and pseudofaeces. This ratio can be interpreted as an indicator of the relative abundances of living algae (low values) and plant detrital material mainly composed of biodeposits (high values). It clearly appears that the ratio PhideL/chl *a* in sea water was linked with seston concentration, indicating a resuspension of detrital matter. Under spring tide conditions, important changes in seston characteristics were observed, the variations over neap tide cycles being less pronounced. The mean PhideL/Chl *a* ratio in pseudofaeces was above the correspondent value in sea water showing a selective rejection of degraded matter but the differences were more or less important according to the seston load.

This dependence of the selective coefficient on the seston load is illustrated in Figure 4: below approximately 50 mg l^{-1}, values of the selective coefficient were usually above 2 and often higher than 4; between 60 and 90 mg l^{-1}, values ranged between 1 and 4, and above 90 mg l^{-1} close to 1. During the spring tide 90 cycle, irrespective of the ses-

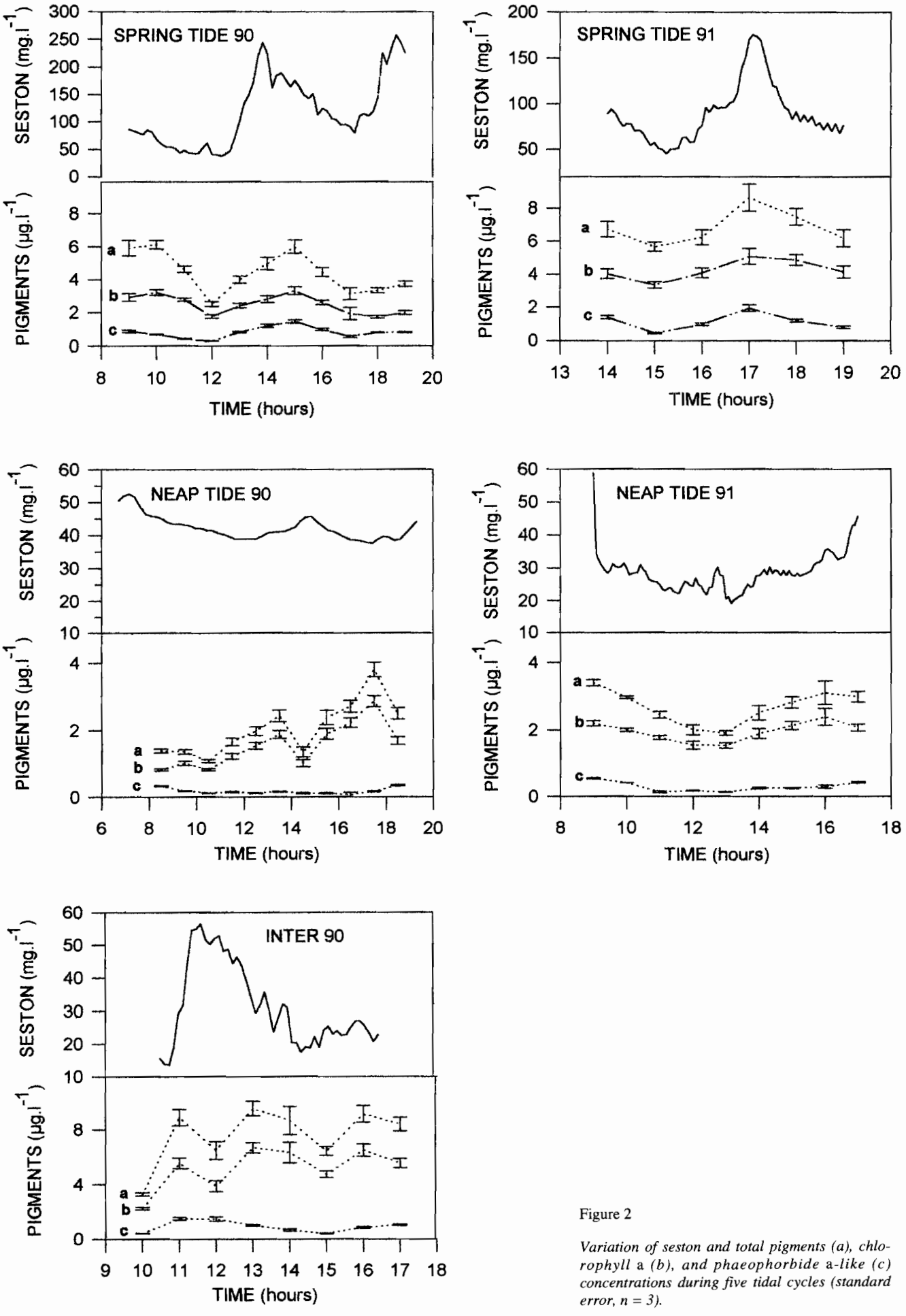

Figure 2

Variation of seston and total pigments (a), chlorophyll a *(b), and phaeophorbide* a*-like (c) concentrations during five tidal cycles (standard error, n = 3).*

Table 1

Results of ANCOVA based on linear model PhideL = f(Chl a*) calculated for sea-water and pseudofaeces over 5 tidal cycles.*

Date	Number	Regression coefficients PhideL/Chl *a* Sea water			Regression coefficients PhideL/Chl *a* Pseudofaeces			F test	Significance at 95%
		Slope	Intercept	R^2	Slope	Intercept	R^2		
Spring tide 27-04-90	24	0.46	0.10	0.29	0.44	- 0.02	0.76	0.21	NO F(2;20) = 3.49
Neap tide 02-05-90	28	0	0.35	0	0.37	0.09	0.79	11	YES F(2;24) = 3.40
Spring tide 14-05-91	34	0.98	- 2.77	0.66	0.74	0.26	0.89	28	YES F(2;30) = 3.32
Neap tide 22-05-91	52	0.50	- 0.60	0.44	0.63	0.09	0.89	75	YES F(2;48) = 3.19
Inter 90	39	-0.08	1.90	0	0.89	0.32	0.84	42	YES F(2.35) = 3.28

ton load, the selective coefficient was close to 1 in relation with very high seston load during the whole tidal cycle (Fig. 2). Data analysis (Tab. 1) confirmed these observations: no statistical difference was observed between water and pseudofaeces composition on spring tide 90.

Under neap tide conditions, *i.e.* at seston loads < 40 mg/l, the differences between pseudofaeces and sea water were always important and statistically significant.

In faeces, the range of the PhideL/chl *a* ratio was 1 to 30. Significative changes were absent over tidal cycles but significant variations did occur between the different experiments (Tab. 2).

Table 2

Molar ratio of phaeophorbide a*-like to chlorophyll* a *in oyster faeces. (Average, standard deviation and number of samples).*

	Molar ratio Phide.L. Chl a^{-1}		
Spring tide 90	2.03	s:0.87	(n:13)
Spring tide 91	4.22	s:2.10	(n:28)
Neap tide 90	2.86	s:2.49	(n:19)
Neap tide 91	17.22	s:5.96	(n:37)
Inter 90	11.18	s:6.87	(n:29)

DISCUSSION

The dominance of diatoms in the water column of the experimental site has already been reported (Héral *et al.*, 1983). This is why pigment analysis could not show any difference between phytoplankton and resuspended microphytobenthos. The dominance of diatoms in microphytobenthic communities has been well established (Colijn and de Jonge, 1984; Riaux-Gobin *et al.*, 1987; Barlow *et al.*, 1990). Nevertheless, the concomitant rise in total pigments and seston already described at this site by Héral *et al.* (1989); Razet *et al.* (1990) and Solechtnik *et al.* (1991) led us to believe that benthic populations could be resuspended along with detritus and biodeposits.

It is not surprising that the main breakdown product present in the particulate matter of the water column is phaeophorbide, this compound being present in large amounts in oyster faeces (this work, Fig. 1), and also in zooplankton and mussel biodeposits (Shuman and Lorenzen, 1975; Hawkins *et al.*, 1986; Vernet and Lorenzen, 1987; Plante-Cuny *et al.*, 1993). The concomitant rise in Phide/chl *a* ratio with seston indicates the importance of resuspended biodeposits in the detrital pool. The large biomass of bivalves present in the Bassin produces abundant biodeposits (Sornin *et al.*, 1983; Deslous-Paoli *et al.*, 1987). This leads to an accumulation of degraded material on the bottom, which is then resuspended by strong currents and wave action. This results in the availability of these biodeposits to oysters.

The difference between PhideL/chl *a* ratios in pseudofaeces and those in sea-water can be interpreted as negative selection by the oysters against detritus which is likely to consist of biodeposits. Systematic experimental error caused by degradation occurring between the moment of rejection by the oyster and that of collection is unlikely because of the precautions taken in sampling, especially in Exp. 90.

Another possible error concerns particle size. The particulate matter analysed as potential food should normally be restricted to the specific size range retained by the oysters. We analysed particles ranging from 1.2 (nominal pore size of the GF/C filters) to 200 μm, yet Héral (1985) showed that *Crassostrea gigas* retained particles with 100% efficiency over the size range 6 to 10 μm, with lower retention efficiencies for small particles, especially at increasing seston loads. Thus, our conclusions about selectivity would be wrong if, during our experiments, blooms of pico- or nanoplankton had occurred, leading to a great biomass of living algae (*i.e.* particles of high content of chlorophyll *a*) smaller than 6 μm, and which would not have been retained by oysters.

The fact that microscopical observations showed a dominance of diatoms larger than 6 μm does not eliminate the possibility that other small cells could have been present

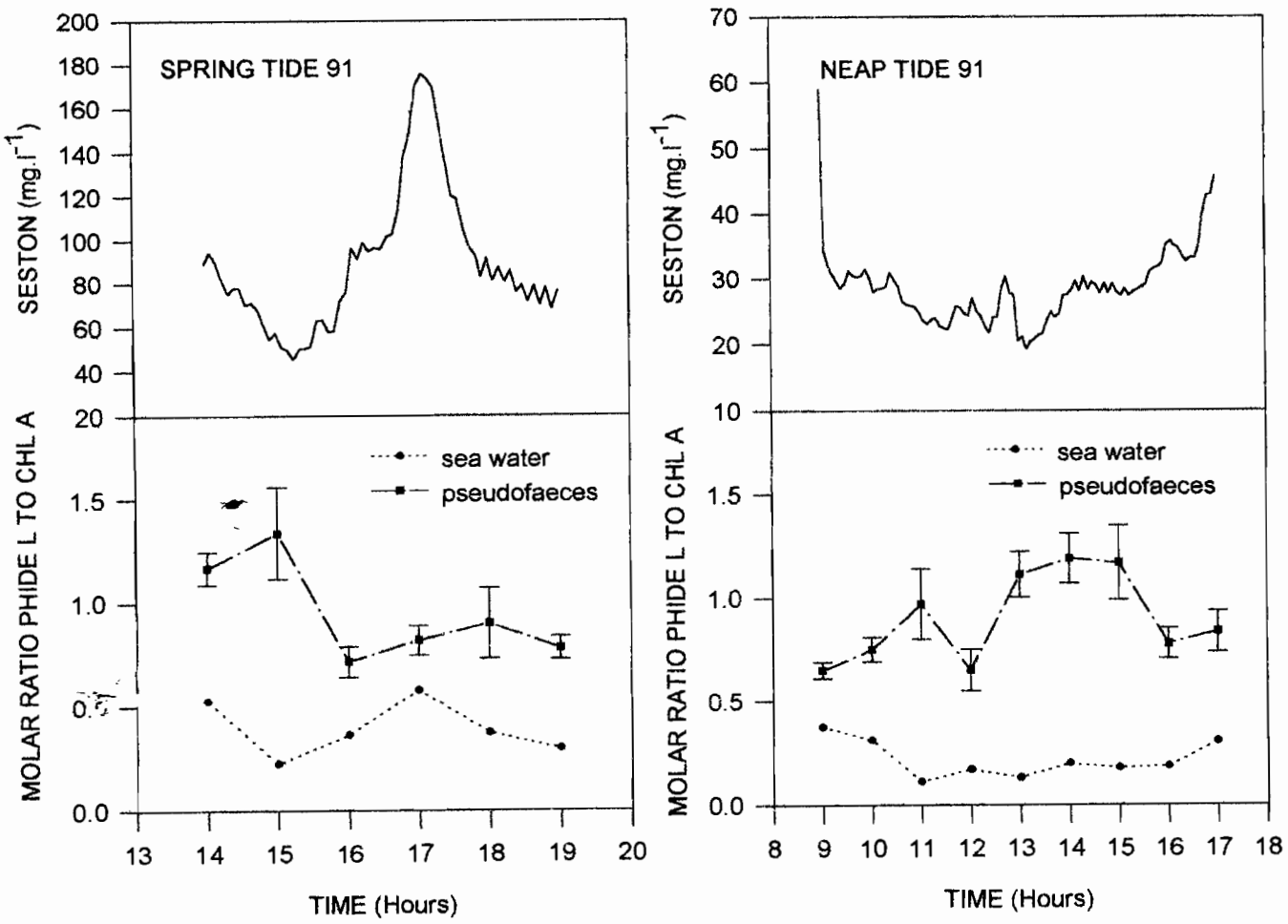

Figure 3

Variation of seston concentration and of the molar ratio of phaeophorbide a-*like to chlorophyll* a *in sea water and in pseudofaeces during two tidal cycles (standard error, n = 5).*

but destroyed by fixation. However, it seems improbable that they would have represented a large proportion of the biomass and of the chlorophyll *a*. There are no data available on picoplankton occurrence in the Bassin, but the minor importance of such organisms in temperate estuarine waters has been reported by Iriarte and Purdie (1994). Moreover, during Exp. 91, a parallel experiment performed by Soletchnik *et al.* (1991), in which the filtration rate of *Crassostrea gigas* was estimated by continuous monitoring of turbidity and *in vivo* fluorescence, showed that the clearance rate, calculated from measures of turbidity created by the total seston, was only half that calculated from the fluorescence signal. These results confirm that the unretained particles were mainly inorganic. Finally and most important, Barillé *et al.* (1993) showed that retention efficiency of small particles was higher at low seston loads, which is when we, too, observed the higher selectivity.

Our results show that *Crassostrea gigas* distinguishes living phytoplankton from degraded plant material. This result is slightly different from previous studies where chlorophyll *a* was considered as a marker of living microalgae, since faeces (*i.e.* dead microalgae) still contain chlorophyll *a*. Above a particulate matter concentration of approximately 50 $mg.l^{-1}$ (Fig. 4) the decrease in selection efficiency is probably due to the saturation of the animal's ingestive or handling capacity. This point has been made clear by Beninger *et al.* (1992) who described the ejection of captured particles at high particle concentration in *Placopecten magellanicus* and showed that selection can only be observed when these capacities were not exceeded, the time of exposure to low or medium seston concentration leading to the same effect. The differences in selectivity obtained during the two spring tides, despite the overlap in seston concentration (Fig. 2), also suggest that factors such as duration in high seston load exposure could have an important effect on selective capacity in oysters: in the case of a short increase in seston load (Fig. 3), the oysters seem able quickly to resume their selection capacity. This result can be explained by a reduction of clearance rates during exposure to high seston concentrations. Soletchnik *et al.* (1991) in their parallel experiment previously cited, observed during spring tide 91 a slight reduction of clearance rate from 3 l. h^{-1} to 2.5 $l.h^{-1}$ (mean for 100 oysters). This reduction probably prevented the saturation of ingestion and sorting capacity. The observations of Ward *et al.* (1994) on the feeding behaviour of *Crassostrea virginica* also suggested that oysters were capable of discontinuous ingestion, as particles can be removed from suspension and pseudofaeces can be produced without ingestion taking place. Many bivalve species living in turbid environments thus control their ingestion by either production of pseudofaeces or reduction of clearance rates (Foster-Smith, 1975;

Kiørboe *et al.*, 1980; Møhlenberg and Kiørboe, 1981; Bricelj and Malouf, 1983) or both. MacDonald and Ward (1994) found that in *Placopecten magellanicus* living at low seston concentration (< 15 mg.l^{-1}), qualitative characteristics of suspended particles, based on chlorophyll *a* content, were more important in regulating clearance and pseudofaeces production than quantitative factors. In our experiment, no such conclusion can be made since this parameter showed only small variations and remained low (0.01 to 0.07 μg Chl *a*. mg seston^{-1}), except for the intermediate tidal situation (0.07 to 0.27) when no increase in selection efficiency was observed (Fig. 4). The model of suspension-feeding zooplankters proposed by Sierszen and Frost (1992) shows that high variability in the value of available food would favour selective feeding but emphasizes the advantages for a species to adjust its degree of selectivity in order to overcome the costs of this operation. Although the costs of selectivity for bivalves are unknown, it seems that *Crassostrea gigas* is able to adapt its feeding strategies to live in high variable food conditions.

Like some other suspension-feeding bivalves, *Crassostrea gigas* can be considered to be more a herbivorous than a detritivorous species. But detritical organic matters have different origins and do not always contain pigments. The relatively high concentrations of detritus found in the Bassin de Marennes-Oléron probably also contribute to the growth obtained (Héral, 1985); Velimorov (1991), in a literature review of detritus studies, discussed the difficulty in precisely characterizing detrital matter, and emphasized that most definitions are based on methods used to quantify detritus which have often been developed in view of the dominant types of detrital matter founded in particular areas. The potential value of the detrital complex as food for estuarine organisms is well recognized (Newell *et al.*, 1982; Mann, 1988), but most works on suspension-feeding bivalves have focused on macrophyte debris with their associated bacteria, because of its quantitative importance in many areas supporting bivalve culture, and have shown that bacterial colonization of detritus improves its food value (Griffiths, 1980; Stuart *et al.*, 1982; Cranford and Grant, 1990; Crosby *et al.*, 1990; Langdon and Newell, 1990). In the estuarine bay of Marennes-Oléron, Feuillet-Girard *et al.* (1994) found that 84% of the particulate organic carbon is of detrital origin, and, using the isotopic composition of this material, concluded that only 20% of this material is of terrestrial origin even during the maximum input in winter. In our study, during spring, the part of the detrital pool characterized by its pigment composition can be attributed mainly to biodeposits, probably recently egested. The rate of degradation of pigments in this material has not been studied yet, but Roy and Poulet (1990) found the content of chlorophyll pigments in aged copepod fecal material to decrease with time, although a non-negligible content could still remain after up to 11 days at 15 °C. As bacterial colonization acts quickly on both the physical and the biochemical features of faeces (Stuart *et al.*, 1982; Fabiano *et al.* 1994), this material could have a nutritive value for oysters. Thus, despite the low seston quality encountered by oysters in the Bay, this material could be used since « selection is rarely an all (100%) or nothing (0%) response » (MacDonald and Ward, 1994). Results of

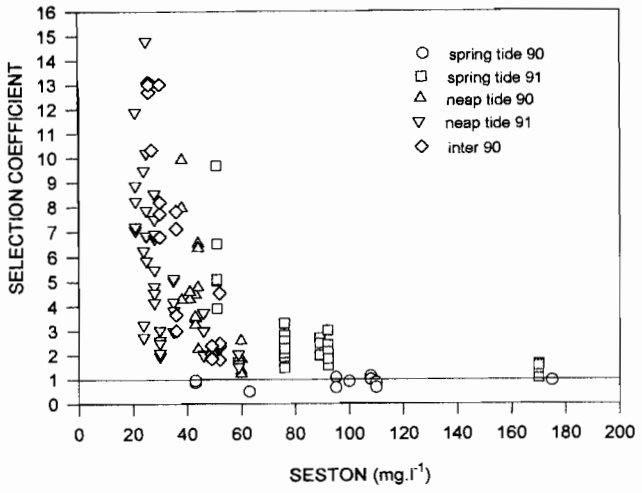

Figure 4

Influence of seston load on the selection coefficient (= P/S where P is the molar ratio of phaeophorbide a-like to chlorophyll a *in pseudofaeces and S this ratio in sea water at the same time).*

Riera and Richard (1995) confirm this suggestion: using isotopic analysis, they found that *Crassostrea gigas* is able to grow on different type of foods (including detritus) according to its situation along an estuarine trophic gradient.

The different values of the molar ratio PhideL/Chl *a* in oysters faeces observed between days cannot be explained easily, and it may be the result of two processes not previously studied in *Crassostrea gigas*. One is the acid and enzymatic degradation of chlorophyll *a* during digestion, leading to its transformation into phaeophorbide and perhaps also into residues that cannot be detected fluorometrically (Klein *et al.*, 1986; Gieskes *et al.*, 1991). The second process is the differential absorption of the different chlorophyll-derived pigments during the passage through the digestive tract (Hawkins *et al.*, 1986; Robinson *et al.*, 1989). Also, different algal species compositions could lead to different levels of degradation of pigments, as well as temperature effect.

Further studies under controlled conditions, on the degradation of the photosynthetic and accessory pigments, such as carotenoids, are required to provide more information about digestive processes and nutrition in *Crassostrea gigas* living in estuarine environments. This might permit pigments to be used as biomarkers of biodeposits and their behaviour in the ecosystem. The persistence of chlorophyll *a* in dead algae in biodeposits has to be evaluated because of the important use made of this parameter in estimating living biomass when resuspension occurs.

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