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Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition

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Abstract

Physiological processes controlling food acquisition by the filter feeding bivalve *Cerastoderma edule* (L.) were quantified under a broad range of seston concentrations and compositions. Experimental diets consisted of suspensions elaborated by adding variable amounts of microalgal cells of different species (or sediment particles in one case) to natural sea-water. Clearance rates exponentially decreased with seston concentration, but the rate of reduction was higher with suspensions of high organic content. Pseudofaeces production appeared as a positive function of the rate of particle filtration; however, for a given filtration rate, more pseudofaeces were rejected when filtered matter had a low organic content. As a consequence, after an initial elevation, ingestion rate remained almost constant across particle concentrations. Pre-ingestive food selection enhanced the rate of particulate organic matter ingestion and this organic enrichment of ingested matter became more pronounced for diets of low food value, where most filtered matter was being rejected as pseudofaeces. Selection of particles at the pre-ingestive level was more efficient in terms of chlorophyll, revealing preferential ingestion of algal particles compared with the whole organic matter. Stronger selection for algae, however, was not evident in terms of preferential nitrogen ingestion, as compared with carbon, which was probably due to similar low values of the C/N ratios in all experimental conditions. Absorption efficiency depended on the organic content of ingested matter according to an exponential, saturating function. In general, feeding processes of cockles appear well adapted to cope with elevations in particle concentration and simultaneous reductions in the food value of available seston that occur when resuspended bottom sediments constitute a significant fraction of particulate materials of the water column. Under these conditions, high rates of seston filtration and pseudofaeces production, together with preferential organic ingestion act to compensate for the dilution of organic matter in suspension and its detrimental effect on the rate of food absorption. However, this compensatory behaviour is not so

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efficient as to make absorption rate independent of the organic value of available particles. The organic content of resuspensible sediments may thus become the main determinant of food acquisition in cockles.

Keywords: Absorption; *Cerastoderma edule*; Elemental budget; Feeding behaviour; Preingestive selection; Sediment resuspension

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1. Introduction

Filter feeding bivalves from littoral areas are usually exposed to broad fluctuations in both availability and nutritional value of suspended particulate matter. Bayne (1993) has identified three different time scales at which those fluctuations occur:

1. Seasonal changes in the phytoplanktonic fraction of total suspended matter, elicited by cycles of primary production. Total particle concentration in suspension also varies according to a seasonal rhythm, due to long-term changes in weather conditions affecting riverine inputs to coastal areas.
2. 'Event-scale' variability, consisting in medium term (7–20 days) variations in the concentration and/or organic content of seston due to short term pulses of phytoplankton abundance or to the spring/neap tidal cycle.
3. Resuspension of bottom material at very short time intervals due to the local action of wind- or tide-induced water currents. Very often, this variability in the characteristics of suspended particulate matter may considerably exceed the seasonal variability recorded as monthly mean values. When resuspension of bottom sediments occurs, the concentration of total suspended particulate matter experiences a considerable increase, but the relative organic fraction of that matter drops due to the high mineral (silt and/or clay) content of bottom materials.

The way in which filter feeding bivalves are affected by these fluctuations in their feeding environment depends on a variety of factors:

1. The size-distribution or granulometry of sediment particles. Small particles are more easily maintained in suspension than bigger ones, their contribution to the total seston being thus higher when fine sediments are brought into suspension. On the other hand, and due to the size-dependence of surface-to-volume ratio, the organic material adsorbed onto particle surfaces represents a higher proportion of total resuspended matter in small than in large particles.
2. The relative contribution of both microphytobenthic algae and organic particles of detrital origin to sedimentary matter. The reduction in the nutritional value of the seston induced by resuspension can be very variable, depending on the organic content of resuspended sediments.
3. Physiological adaptations of bivalves at both feeding and digestive levels, acting to

maximise energy uptake under conditions of high turbidity and concomitant low food value of suspended particles. These adaptations include the capacity for adjusting filtration and pseudofaeces production rates in response to changes in particle concentration and composition, the ability of palial organs for sorting particles of different food value, and the possibility of achieving a positive net food absorption at very low organic contents of ingested matter (Bayne, 1993; Navarro and Iglesias, 1993).

Cerastoderma edule (L.) is an infaunal, filter-feeding bivalve, inhabiting highly variable media as regards the characteristics of particulate matter in both the bottom sediments and the water column. In this species, physiological parameters controlling energy gain exhibit a considerable flexibility when exposed to large changes in seston quality at moderate concentrations of suspended particulate matter (from 1 to 10 mg l^{-1}) (Iglesias et al., 1992; Navarro et al., 1994). Capacity of cockles for adjusting feeding rates, together with a marked ability to sort and selectively reject particles of low or no food value, constitute the basic mechanisms by which rates of food acquisition are maximised when suspended matter presents high proportions of mineral particles.

This study was designed to provide a set of functional relationships in which the above mentioned physiological parameters may be expressed as a function of the characteristics of the food environment, according to a theoretical framework that has been discussed elsewhere (Iglesias et al., 1992; Navarro and Iglesias, 1993; Navarro et al., 1994). More specifically, this research aimed to define basic physiological relationships governing the trophic associations between bivalves and the environment at the bay of Marennes-Oléron (France), in order to build a model to predict the sustainable shellfish production in the bay. In this respect, rates of food acquisition and processing by cockles were determined under a range of seston concentrations and qualities that covered the broad environmental variability recorded in the bay. Rates of seston processing by cockles were established in terms of total mass, considering the organic and inorganic fractions separately; in addition, carbon and nitrogen contents were determined in order to assess the possibility of a differential elemental processing. By using statistical relationships fitted to experimental data, we have evaluated the energetic implications derived from varying organic richness of the resuspensible fraction of sediments which, at different time and/or space scales, may become the main source of variability in the organic richness of suspended matter.

2. Material and methods

2.1. Collection and maintenance of cockles

Experiments were performed at the LABEIM-UREA (IFREMER, La Tremblade, France), during September 1991 and September 1992. Cockles used in both experiments were collected from a natural population sited at Ronce les Bains (Bay of Marennes Oleron) and transported to the laboratory, where they experienced a 2 wk accommodation period prior to experimentation. During this period, cockles were maintained in an open system with circulating natural sea-water enriched with artificial blooms of the diatom *Skeletonema costatum* (Grev. Cleve) grown in an outdoor culture tank. Temperature varied between 20 and 24°C.

After the accommodation period, between four and nine cockles (depending on the experimental condition) were placed in individual trays where sea-water directly pumped from the bay was passed through. According to the specific dietary requirements of each condition, different kind of particles (microalgae or natural silt) were dosed to the feeding trays. Dosing rates and the proportion of each particle type in the mixture were adjusted to produce a wide range of dietary conditions where both concentration and quality of suspended matter varied. As concentration and organic content of particulate matter suspended in the sea-water directly pumped from the bay were unpredictable, dietary characteristics could not be pre-established, but they were measured a posteriori. Dietary composition for each feeding condition was as follows:

Diet AD: Natural sea-water enriched with artificial blooms of *Skeletonema costatum*, (September 1991).

Diet B: Natural sea-water, (September 1991).

Diet C: Natural sea-water plus resuspended natural silt particles collected from the surface of bottom sediments from the bay, (September 1991).

Diet D: Natural sea-water enriched with indoor cultures of *Tetraselmis suecica* (Kylin. Butch) and *Thalassiosira pseudonana* (Hasle and Heimdal), (September 1991).

Diet E: Artificial blooms of *Skeletonema costatum* enriched with indoor cultures of *Chaetoceros calcitrans* (Takano) and *Isochrysis galbana* (Parke), (September 1992).

Diet F: Artificial blooms of *Skeletonema costatum* diluted with filtered natural sea-water and enriched with indoor cultures of *Tetraselmis suecica* and *Isochrysis galbana*, (September 1992).

Diet G: Artificial blooms of *Skeletonema costatum* diluted with filtered natural sea-water and enriched with indoor cultures of *Chaetoceros calcitrans* and *Pavlova lutheri* (Droop. Green), (September 1992).

Diet H: Artificial blooms of *Skeletonema costatum* diluted with filtered natural sea-water and enriched with indoor cultures of *Pavlova lutheri* and *Tetraselmis suecica*, (September 1992).

It is important to point out that different algal species were not used in order to know the specific effect of each algal combination on the feeding behaviour of cockles, but to achieve a wide range of organic contents in the particle assemblage offered as food and mimic species-diversity of natural phytoplankton.

3. Measurements

3.1. A) Collection and treatment of samples for suspended matter analysis

In the course of experiments, water samples were frequently (ca. every 90 min) collected from the outflow of an empty (control) tray and divided into four samples. A first sample was used to measure the packed volume of suspended particles (*VOL*: mm^3 l^{-1}) with a Coulter Multisizer equipped with a 100 μm aperture tube. A second aliquot was filtered onto ashed and pre-weighed 25 mm GFC filters (Whatman), rinsed with sea water–isotonic ammonium formate, dried in an oven (110°C for 24 h), weighed, and then ashed in a muffle furnace (450°C for 6 h) before final weighing. In this way, total suspended particulate matter concentration (*TPM*: mg l^{-1}) and particulate inorganic matter concentration (*PIM*: mg l^{-1}) were measured. The particulate organic matter concentration (*POM*: mg l^{-1}) was estimated by subtracting *PIM* from *TPM*. The organic content of suspended matter was computed as: $f = POM/TPM$ and the volumetric quality as $q = POM/VOL$ (q: mg *POM* mm^{-3}) (Bayne et al., 1987).

In order to determine chlorophyll *a* concentration (Chl *a*: μg l^{-1}), the third aliquot was filtered through 25 mm GFC filters (Whatman) and filters covered with a magnesium carbonate solution (1%) to prevent chlorophyll acidification and degradation to phaeopigments. Filters were introduced into glass tubes protected from the light and stored at −20°C until spectrophotometric determinations of chlorophyll *a* were performed according to Lorenzen (1967).

The fourth aliquot was used to establish the carbon and nitrogen content of suspended matter. Samples were filtered onto 25 mm preashed-GFC filters (Whatman), which were maintained at −30°C until analysis in a Perkin Elmer CHN elemental analyser. Acetanilide was used as standard.

3.2. B) Collection of biodeposits and physiological determinations

Faeces and pseudofaeces produced by individual cockles were collected separately for 12 h at different intervals. The number of biodeposit samples collected for each experimental condition was variable. Since dietary characteristics were found to be highly variable among collections, successive collections could not be taken as replicates but were considered as individual cases (samples).

Faeces and pseudofaeces were separately filtered onto preashed glass fibre filters GF/C (Whatman) that were treated as described for sea-water samples in order to determine total, inorganic and organic weight of biodeposits. When possible, two aliquots of biodeposits were separated for the determination of chlorophyll *a* content (pseudofaeces) and carbon and nitrogen contents (faeces and pseudofaeces) as described before. The following physiological rates were then determined:

- Rejection rates, as pseudofaeces, of total (*RR*: mg h^{-1}), organic (*ORR*: mg h^{-1}) and inorganic (*IRR*: mg h^{-1}) particulate matter.
- Egestion rates, as true faeces, of total (*ER*: mg h^{-1}), organic (*OER*: mg h^{-1}) and inorganic (*IER*: mg h^{-1}) particulate matter.

Assuming that absorption of inorganic matter through the digestive system is negligible, the sum of *IRR* and *IER* was considered to represent the rate of inorganic matter filtration (*IFR*: mg h^{-1}) and, hence, clearance rates (*CR*: l h^{-1}) were estimated as $CR = IFR/PIM$ (see Urrutia et al., 1996 for details concerning the methodological validation of this procedure). Filtration rate of total particulate matter (*FR*: mg h^{-1}) was computed as $FR = CR \times TPM$ and filtration rate of particulate organic matter (OFR: mg h^{-1}) as $OFR = CR \times POM$. Ingestion rates of total (IR: mg h^{-1}), and organic (OIR: mg h^{-1}) particulate matter were estimated as $IR = FR - RR$ and $OIR = OFR - ORR$, respectively. The rate of food absorption (AR: mg h^{-1}) was computed as $AR = OIR - OER$, and absorption efficiency (AE) as $AE = AR/OIR$.

Preingestive selection efficiencies for both total filtered organic matter (SE_o) and filtered algal matter (SE_a) were also estimated as: $SE_o = 1 - (p/f)$, (Navarro et al., 1992) and $SE_a = 1 - (cp/cf)$, where p is the organic content of the pseudofaeces ($p = ORR/RR$), f is, as defined above, the organic content of suspended matter ($f = POM/TPM$), cp is the chlorophyll a content in the pseudofaeces (μg Chl a mg^{-1}) and cf is the chlorophyll a content in the filtered matter (μg Chl a mg^{-1}). In several samples, selection and absorption efficiencies for carbon and nitrogen were separately estimated on the basis of measured C and N contents of food and biodeposits and estimated C and N contents of the ingested matter.

3.3. Size standardisation of physiological rates

Once the physiological measurements were completed, soft tissues from each cockle were excised, dried at 80°C for 48 h and weighed. Rates were assumed to scale with body size and, consequently, measurements were standardised to an equivalent 0.5 g. dry tissue cockle by using the formula $Y_s = Y_e \times (500/W_e)^b$, where Y_s = rate of the standard-sized cockle; Y_e = uncorrected physiological rate; W_e = measured weight of experimental animal and b = the weight power established for clearance rate of cockles ($b = 0.57$; unpublished results), which has been assumed to represent the size dependence for rates of food processing in general.

3.4. Statistical procedures

In order to obtain functional relationships between physiological parameters and the characteristics of food suspensions, a set of regression equations was fitted to experimental data, following standard least squares procedures. Regression analyses were performed by simple linear, polynomial, multiple linear and non-linear procedures, depending on the most appropriate function to be fitted in each case. The specific function fitted and the procedure followed for each physiological parameter will be presented with the Results.

4. Results

4.1. Ration conditions

Dietary characteristics are presented in Table 1. Diets A, B and D are similar in both *TPM* and organic content. Differences in composition among them are based on the addition of algal cultures in diets A and D. This did not result in a significant increment of organic content, indicating that added phytoplankton represented a minor fraction of

Table 1
Characteristics of experimental diets

DIET	*TPM* (mg l^{-1})	*POM* (mg l^{-1})	f (=*POM*/*TPM*)	*VOL* (mm^3 l^{-1})	q (mg *POM* mm^{-3})	Chl a (μg l^{-1})	C/N
A	6.959±2.473	2.294±0.690	0.339±0.064	5.992±2.082	0.391±0.071	21.6± 1.2	6.338±0.755
B	5.447±0.965	1.527±0.254	0.281±0.035	3.275±0.516	0.505±0.097	4.9± 1.9	7.398±1.281
C	21.420±2.764	3.220±0.376	0.151±0.012	6.340±1.133	0.515±0.049	3.8± 0.9	7.212±0.429
D	7.873±0.786	2.245±0.161	0.286±0.018	5.750±0.651	0.394±0.036	21.7± 1.9	6.209±0.438
E	12.834±0.640	7.027±0.382	0.548±0.026	42.100±1.730	0.162±0.018	136.2± 6.8	5.588±0.118
F	11.339±0.966	7.846±0.531	0.647±0.075	38.725±7.186	0.210±0.038	148.7±15.3	5.465±0.232
G	8.645±0.966	5.950±0.591	0.689±0.013	23.170±0.600	0.257±0.030	271.9± 3.6	5.614±0.119
H	16.990±1.240	12.668±0.966	0.746±0.006	52.715±2.500	0.233±0.009	271.9± 3.6	6.054±0.277

TPM: total particulate matter; *POM*: particulate organic matter; f: organic content of suspended matter; *VOL*: packed volume of suspended matter; q: food quality (in volumetric terms); Chl a: chlorophyll a concentration; C/N: carbon/nitrogen ratio (in mass terms). Values are means±S.D. $n=8$ for diets A, B, C and D and $n=4$ for diets E, F, G and H. See Section 2.1 for details on the specific composition of the diets suspended matter. In diet C, the organic fraction of natural sea-water was 'diluted' with bottom sediments and so presented the lowest organic content. In diets E, F, G and H, the particulate complex in natural sea-water was substituted by artificial *Skeletonema* blooms, which led to higher organic contents in the food suspensions. The lower f value in diet E reflects a high proportion of inorganic particles from the outdoor *Skeletonema* culture, which was supplied to the feeding trays without having been diluted with filtered sea-water. In diets F, G and H, the organic content appeared as a positive function of total particulate matter in suspension, which reflects variable amounts of algal particles mixed with a constant amount of inorganic matter supplied with the *Skeletonema* bloom.

4.2. Clearance and filtration rates.

In cockles, clearance rate (*CR*: $\mathrm{l\ h^{-1}}$) usually appears as an exponential negative function of the concentration of particulate matter in suspension, but that dependence is itself variable according to the organic richness of the diet (Iglesias et al., 1992, Navarro et al., 1994). In order to account for both simultaneous effects, we have followed a procedure similar to that previously used for this same species (Navarro et al., 1994), where *CR* was expressed as a simultaneous exponential function of the concentration of particulate matter in suspension measured in terms of volume (*VOL*: $\mathrm{mm^3\ l^{-1}}$), and the volumetric quality (q: mg *POM* $\mathrm{mm^{-3}}$), including also an interaction term ($VOL \times q$) between both independent variables. However, since all other food processing rates (pseudofaeces production and ingestion) measured in experiments from this work were not established in volumetric terms, the equation was fitted using gravimetric terms instead of volumetric terms. Therefore, clearance rate was expressed as a function of particle concentration (*TPM*: $\mathrm{mg\ l^{-1}}$) and dietary organic richness (f: *POM*/*TPM*). The equation, fitted by non-linear regression was

$$CR = e^{(0.3968\ (\pm 0.0860) - 0.2118\ (\pm 0.0339)\ TPM \times f)}, \quad \text{d.f.} = 112,\ r^2 = 0.498 \qquad (1)$$

This model indicates that clearance rate exponentially declines with increasing concentrations of suspended matter, the reduction being positively dependent on the organic content of the suspension. Thus, rising food qualities lead to higher degrees of dependence (negative) between clearance rate and particle concentration. These effects are clearly shown in Fig. 1 where the degree of dependence of *CR* on *TPM* and f has been presented in two ways: the upper panel shows experimental mean *CR* values obtained for each feeding condition together with the line representing the decrease in *CR* related to the increase in the interaction term predicted by Eq. (1). The bottom panel displays the response surface defined by the function, for the range of *TPM* and f values representative of the conditions tested in this study. Exponential decrease of *CR* with either *TPM* or organic content is clearly seen, resulting in the highest clearance rate corresponding to the condition which combines the lowest seston concentration and lowest organic content.

This result does not exactly match previously reported relationships (Navarro et al., 1994) for wide ranges of seston concentration and quality, but one important interpretative limitation of the present model derives from having been fitted to data obtained at

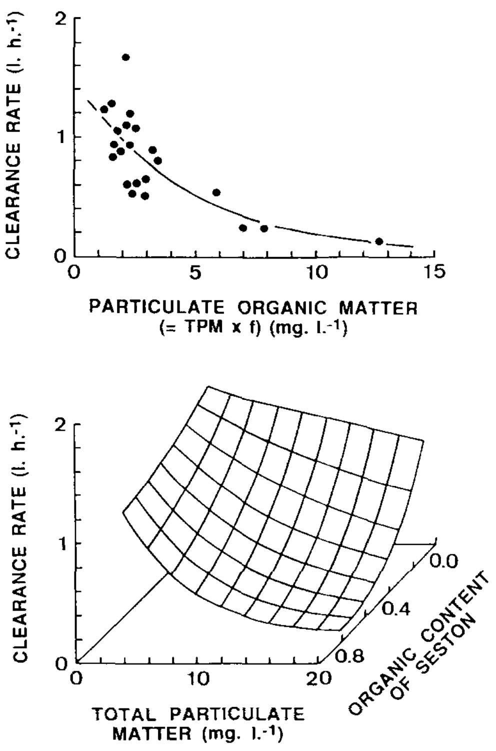

Fig. 1. A) Clearance rate (l h^{-1}) as a function of the interaction term between seston concentration and the organic content of the suspension. Points represent mean *CR* values obtained for different feeding conditions. The line corresponds to the function fitted to individual data (see Eq. (1)). B) Response surface representing the clearance rate for the range of total particulate matter concentration and organic content of seston recorded in the study.

seston concentrations inducing pseudofaeces production; thus, it would not be valid to describe the feeding behaviour of cockles at concentrations at or below the pseudofaeces threshold.

Filtration rates (*FR*: mg h^{-1}), computed as the product of *CR* and the corresponding *TPM* values, are plotted in Fig. 2 (upper panel). The response surface represented in this figure describes a complex dependence between *FR* and *TPM* and *f*. At low *f* (organic content) values, and in the range of *TPM* considered in this work, *FR* is always an increasing function of particulate matter concentration; however, this tendency lessens with increasing organic content and there is an inversion at high seston loads. In fact, for organic contents as high as 60%, filtration rate achieves a maximum at *TPM* concentrations around 5 mg l^{-1}.

4.3. Pseudofaeces production and ingestion rates.

Kiørboe et al. (1980) reported that pseudofaeces production rate was a simple, linear function of the rate of suspended matter filtration. More recently, Iglesias et al. (1992) have shown that the proportion of filtered matter being rejected as pseudofaeces depends

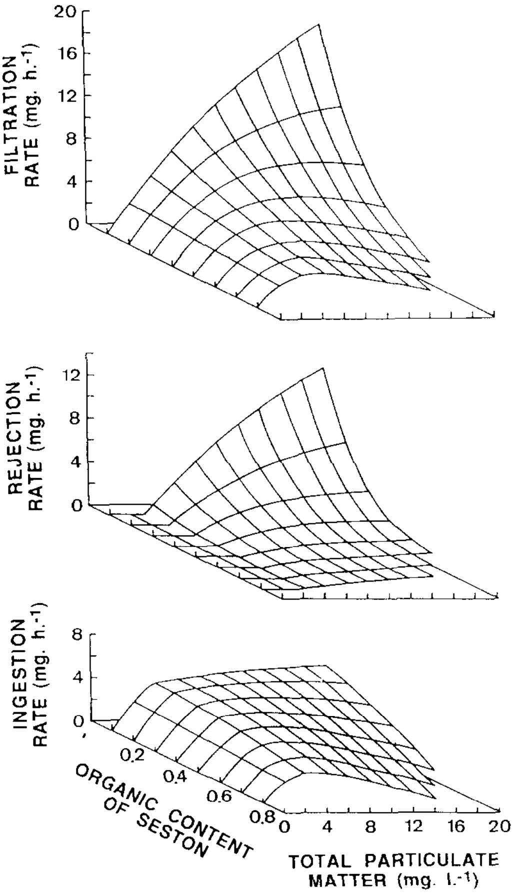

Fig. 2. Response surfaces representing variability in physiological parameters of seston processing as a simultaneous function of total particulate matter concentration and organic content of seston. Filtration, rejection and ingestion rates have been represented on the same scale to allow comparison.

also on the organic content of the food suspension. Both findings led Navarro and Iglesias (1993) to express the rate of pseudofaeces rejection as a simultaneous function of both the filtration rate and the organic content of filtered matter. Taking a similar approach, the rate of pseudofaeces production (*RR*: mg h^{-1}) has been also treated here as a linear, multiple function of filtration rate (*FR*), organic content of the suspended matter (f) and the interaction term ($FR \times f$). However, a multiple regression model based only on these potential predictors of *RR* did not accurately predict pseudofaeces production rates at the extreme *TPM* and f values studied in this work. After a detailed analysis of individual data, we concluded that, for a given *FR* value, pseudofaeces production was also dependent on seston concentration. Introduction of *TPM* as a new independent variable together with the corresponding interaction terms with other variables in the model (*FR* and f) greatly increased its predictive value. The fitted equation was:

$$RR = -4.201 + 0.885\,(\pm 0.037)\,FR + 4.490\,(\pm 0.709)f + 0.099\,(\pm 0.019)\,TPM$$
$$-\,0.968\,(\pm 0.192)\,FR \times f \qquad (2)$$

$$\text{d.f.} = 111,\ r^2 = 0.969,\ F = 825.15,\ p = 0.0001$$

All variables retained in this equation are highly significant ($p = 0.001$) but FR is mainly responsible for variability recorded in RR, as indicated by the maximum partial F (585.04). The interaction term $FR \times f$ is the second variable in order of significance level, and this term reflects the fact that slopes of the lines relating RR to FR are dependent (negatively) on the organic content of filtered matter. This means that for a given rate of filtration, the amount of material rejected as pseudofaeces increases as the seston organic content decreases. f is the third term in order of significance ($F = 40.64$), but the meaning of this term is complicated by the above interaction. A positive coefficient accounts for the fact that intercepts of lines RR vs. FR are an increasing function of food organic content; however, since the slopes of these lines rapidly decrease with f (see above), the resultant effect is the intersection of lines at very low FR values and so, pseudofaeces rejection is always higher with poorer quality of suspensions. Although explaining a relatively minor proportion of variability recorded in the dependent variable ($F = 26.89$), TPM specifically affects the rate of pseudofaeces production, in addition to the main effect predicted via filtration rate.

The relationship between rate of pseudofaeces production (i.e., rejection rate) and dietary descriptors considered, TPM and f, has been represented in the second panel in Fig. 2. The profile of surfaces for rejection and filtration rates are very similar, which reflects the strong effect of FR on RR. The main difference refers to the behaviour at high concentration of particles, where FR may present a decline for high qualities while RR is always a positive function of TPM. Another important feature shown in Fig. 2 is that the proportion of filtered matter being rejected as pseudofaeces always increases in response to rising TPM concentrations, and decreases as the organic content of filtered seston rises.

By subtracting rates of pseudofaeces rejection from filtration rates, we estimated rates of seston ingestion (IR: mg h^{-1}) which are represented in Fig. 2 (lower panel). As shown, under feeding conditions excluding pseudofaeces production, where ingestion rates equal filtration rates, these appear as a rising function of seston concentration. Above the pseudofaeces threshold, however, ingestion rate remains nearly constant, which is the consequence of two mechanisms acting together: a) Reducing CR in response to increasing seston levels and b) increasing amounts of pseudofaeces as filtration rates and particle concentration rise. The relative importance of each of these regulatory mechanisms varies with the organic content of filtered matter. At low f values, adjusting CR in response to changes in seston concentration is of minor relevance, and the rejection of variable amounts of pseudofaeces is the main mechanism for adjusting ingestion rates. Conversely, at high f values, pseudofaeces production does not constitute a significant component of feeding processes and ingestion is controlled by adjusting CR.

4.4. Selection efficiencies and rate of food ingestion.

In this study, efficiency of food selection at the preingestive level has been estimated for different descriptors of the diet: total organics, chlorophyll *a*, organic carbon and organic nitrogen. The SE_0 index represents the efficiency with which cockles select organics from the matter retained by the gill. It has been previously established (Iglesias et al., 1992) that SE is independent of the concentration of particulate matter in suspension but varies with its organic content. According to observed trends, we have expressed SE as a polynomial function of f. The following equation was fitted to all individual data points:

$$SE_0 = -0.354 + 5.364\,(\pm 1.074)f - 11.794\,(\pm 2.830)f^2 + 7.108\,(\pm 2.225)f^3 \quad (3)$$

$$\text{d.f.} = 111;\ r^2 = 0.646;\ F = 65.1;\ p = 10^{-4}$$

This function has been plotted in Fig. 3, where points represent mean values for the different feeding conditions. Maximum SE_0 values correspond to intermediate (around 0.35) f values, decreasing at lower and higher organic contents. For comparison, selection efficiencies for chlorophyll *a*, carbon and nitrogen have been plotted in panels from Fig. 3, together with the curve obtained for SE_0 . Points representing preingestive

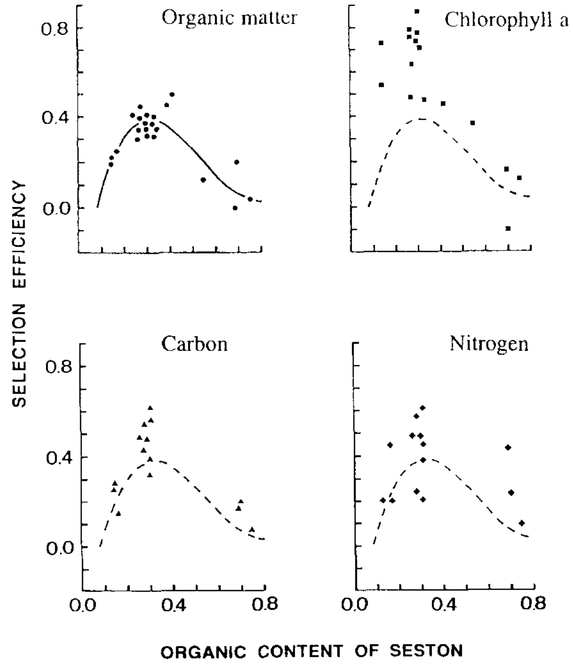

Fig. 3. Selection efficiency of organic matter (circles), chlorophyll *a* (squares), carbon (triangles) and nitrogen (rhombuses), as a function of seston organic content. The curve shown is a third degree polynomial, fitted by least squares to selection efficiency values for total organic matter (see Eq. (3)). For comparison, this same curve (dotted lines) is presented together with other estimations of selection efficiency.

selection of algal particles (chlorophyll *a*) are well above the curve for organic matter, which indicates a more effective selection of algae compared with average organic particles. However, neither carbon nor nitrogen appear to be selected differentially, and both elements follow the same trend as has been recorded for SE_0.

Selection efficiencies provided by Eq. (3) combined with rates of ingestion were used to obtain rates of organic matter ingestion (*OIR*: mg h^{-1}) in the range of feeding conditions illustrated in Fig. 2. Fig. 4 shows the evolution of organic filtration (calculated as $FR \times f$) (solid lines), organic ingestion (broken lines) and absorption rates (dotted lines) with increasing seston concentration in the range of 0–20 mg l^{-1}, and variable organic contents of the seston; namely, A, B and C correspond, respectively, to f values of 0.15, 0.45 and 0.75. For ease of discussion, rates of food processing have been plotted against particulate organic availability. From comparing A, B and C, it can be seen that whereas organic filtration rate is almost independent of the organic content of the seston, organic ingestion is positively affected by this quality term. This effect is mainly due to the higher proportion of pseudofaeces produced when filtered matter is of low organic content, coupled to moderate selection efficiencies found with this poor quality food (4A). With seston of better quality (4B and 4C), the proportion of filtered matter that is rejected decreases and therefore, organic ingestion rate is closer to organic

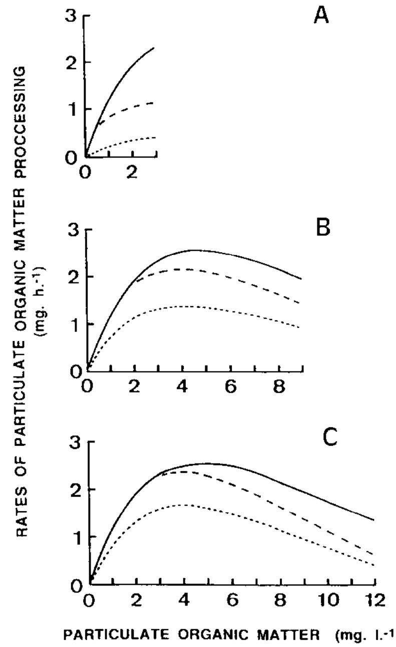

Fig. 4. Rates of organic matter processing as a function of organic matter availability (*POM*: mg l^{-1}) corresponding to three different organic contents of the food (f): A) f=0.15; B) f=0.45 and C) f=0.75. Chosen range of total seston concentration was 0–20 mg l^{-1}, which generates variable ranges of *POM* depending on the organic content of seston. Solid, broken and dotted lines correspond to rates of organic matter filtration, organic matter ingestion and absorption, respectively.

filtration rate reaching higher values. However, with diets of high organic content (4B and 4C) the increase in organic matter availability above 4–6 mg l^{-1} leads to a reduction in the rate of organic matter ingestion, as a consequence of reducing clearance rate. This decrease is more pronounced for diets of higher organic content (4C) because, added to a sharper decline in clearance rate (see Eq. (1)) selection efficiencies fall to minimum values (see Fig. 3) under these specific feeding conditions.

4.5. Absorption efficiencies and absorption rates.

Although variability in absorption efficiency (*AE*) across feeding conditions is relatively small, lower *AE* values were recorded with diets of low organic content. According to Bayne et al. (1987), absorption efficiency is a positive function of food quality which, for quality given as mg *POM* per mm^3 of ingested particles, could be described by an asymptotic exponential. Since volumetric recordings of pseudofaeces were not performed in the present work, we lacked estimates of ingested volumes and our estimations of quality are in mass terms ($i = OIR/IR$). Following in the other respects Bayne et al. (1987), points representing individual absorption efficiencies against the corresponding i values were fitted with the following exponential equation:

$$AE = 0.729\,(\pm 0.028)(1 - e^{(-4.976(\pm 0.975)(i - 0.059(\pm 0.031)))}) \qquad (4)$$

$$r^2 = 0.598, n = 112$$

where 0.729 is the maximum asymptotic absorption efficiency, 4.976 represents the rate at which that absorption efficiency is reached with increasing i, and 0.059 is the value of i at which AE equals 0. The curve described by Eq. (4) has been represented in Fig. 5, where points represent mean AE values recorded for the different dietary conditions.

In order to evaluate a possible differential absorption of carbon and/or nitrogen, individual absorption efficiency values for these elements were plotted as a function of

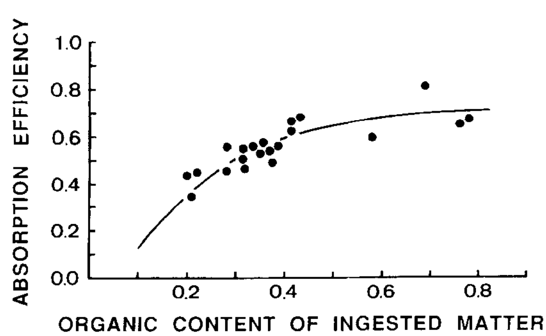

Fig. 5. Absorption efficiency as a function of the organic content of ingested matter. For clarity, individual data points have not been included, each point representing the mean value obtained for individuals exposed to the same dietary conditions. The curve has been fitted to individual data and equation is given in the text (See Eq. (4)).

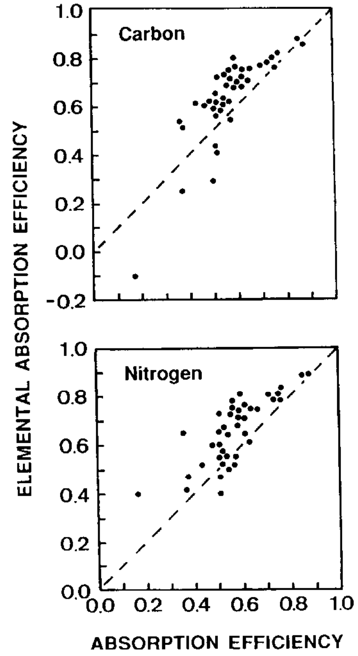

Fig. 6. Elemental absorption efficiency for carbon and nitrogen as a function of the absorption efficiency estimated for overall organic matter. The broken line in both panels is the 45° diagonal and has been drawn as the reference for complete absence of differential absorption efficiency.

the net absorption efficiency for the whole organic ration (Fig. 6). The broken line represents coincidence between elemental and overall absorption efficiency for organics. So, departure from this line would indicate differential absorption. On average, carbon is absorbed with less efficiency than nitrogen, but the difference is only evident at *AE* values lower than 0.5 (points below the broken line). Progressive loss of differences between C and N as overall *AE* approaches 1 is, however, an expectable result, given that for complete food absorption both elements have also to be totally absorbed. Absorption efficiency of carbon at low overall absorption efficiencies is clearly diminished compared to the absorption efficiency for nitrogen, but more data would be needed in the lower range of net absorption efficiencies to attain definitive conclusions about differences in elemental absorption.

Rates of food absorption were estimated, in the range of feeding conditions presented before, by multiplying rates of organic ingestion (Fig. 4, broken lines) by their corresponding absorption efficiencies derived from Eq. (4). These rates are represented in Fig. 4 by dotted lines. Rates of absorption follow the trend found for rates of organic ingestion, although differences between both lines tend to decrease with increasing organic matter availability; decreasing trends recorded for rates of ingestion at rising *POM* are less pronounced in terms of organic (Fig. 4) than total matter (Fig. 2), due to the effects of preingestive selection for organics. Absorption efficiency improves, thus, as a result from the increase in quality of ingested food at high ration.

Differences in absorption rate related to the quality of suspended matter (compare A, B and C) become more pronounced than differences in organic ingestion rate, due to the positive dependence of absorption efficiency on the organic content of ingested food.

5. Discussion

5.1. Rates of clearance, filtration and pseudofaeces production

Previous works performed with *Cerastoderma edule* (Iglesias et al., 1992; Navarro et al., 1994) have evidenced the plasticity of feeding behaviour in this species when exposed to variable food conditions including changes in both seston concentration and its nutritional value. Other bivalves, like mussels *Mytilus edulis* (Bayne et al., 1989; Bayne et al., 1993), adjust their feeding parameters in a similar way, suggesting this kind of behaviour would be a general feature of bivalve feeding physiology (Bayne, 1993). One of the aims of this work was to test whether previously observed variability in feeding processes of cockles could be extrapolated to a much wider range of variation in the dietary regime.

The equation describing variability in clearance rate as a function of seston concentration and organic content of the seston (Eq. (1)) predicts results quite similar to those obtained for cockles fed various mixtures of silt and phytoplankton (Navarro et al., 1994) for seston concentrations above the pseudofaeces production threshold. The main difference refers to the value for the intercept. After correction for size differences, this discrepancy indicates that clearance rates of present cockles appeared consistently reduced by ca. 25% compared with previous estimations. However, the general meaning of the equation remains, and the minor disagreement between models is probably a consequence of the thermal regime under which different experiments were performed. Present determinations were done at temperatures that are the environmental extremes in the Bay of Marennes-Oleron and, probably, close to the maximum for the range of distribution of *Cerastoderma edule*; it is well known for a variety of bivalve species that above a certain temperature, clearance rates reduce with further temperature increase (Ali, 1970; Walne, 1972).

In the range of particle concentrations used in this work, *CR* variability is mainly explained by the interaction between food quality and concentration, reflecting the fact that reduction in clearance rate with particle concentration occurs at higher rates for higher qualities of available food. Thus, *CR* reduction constitutes the basis for a strict regulation of the rate of particle filtration, and hence ingestion, in the case of particles presenting high organic contents; under these circumstances pseudofaecal rejection constitutes a minor fraction of total filtered matter, and does not significantly contribute to regulation of ingestion rate. Declining filtration and ingestion rates at very high *TPM* concentrations (Fig. 2) cannot be considered to have functional value on energetic grounds; rather, it should be regarded as a response of the filtration apparatus to avoid malfunctioning by saturation of the gill at such extreme seston loads. A comparable response does not occur with suspensions of low quality, but particulate volumes for a given *TPM* are much higher in the case of diets based on phytoplankton with a low specific gravity (up to ten times higher: Table 1).

For low dietary qualities, rates of reduction of clearance rate with seston concentration are lower than for high food qualities. Therefore, resulting rates of filtration present a positive, although attenuating, dependence on *TPM* concentration. Under these dietary conditions, production of pseudofaeces constitutes a higher proportion of filtered matter, which also results in a strict regulation of ingestion rate.

Energetic advantages of regulating ingestion rates across food concentrations have been extensively discussed by Navarro and Iglesias (1993) and Navarro et al. (1994) who indicated that lack of strict regulation would lead to: a) very short passage times of the food through the digestive system and consequently, reduced absorption efficiency and b) disproportionate losses of endogenous material which is not reabsorbed (the so called 'metabolic faecal losses'; Hawkins and Bayne, 1985; Bayne and Hawkins, 1990), that would constitute a negative component as regards net absorption. The two regulation alternatives have been previously described in cockles (Iglesias et al., 1992) and mussels (Bayne et al., 1993), although for ranges of seston concentration much narrower than tested in the present work.

An evaluation of the observed variability in clearance rates and implications of this variability in terms of regulation of the ingestion rate requires considering the advantages derived from each regulatory mechanism. Since pseudofaeces production implies an organic enrichment of ingested food compared with filtered seston (to be discussed later), there are obvious advantages associated with high rates of pseudofaeces production, which, in turn, requires high filtration rates. This is the behaviour observed when seston organic contents are low. However, when suspended food is organically rich, lower proportions of filtered matter are rejected prior to ingestion and regulation is mainly achieved by adjusting clearance rate. The explanation we give to this differential behaviour is that, under conditions of high dietary quality, possibilities of preingestive organic enrichment are necessarily less, as most suspended particles are of high food value, which establishes a limit to the proportion of filtered matter that can be rejected. In fact, the proportion of rejected to filtered matter should never exceed the inorganic content of suspended particles or preingestive selection would become suboptimal, in the sense that a certain amount of organic material would be voided in the pseudofaeces, together with particles of low food value. Regarding this point, it is important to note that slope of lines relating rejection to filtration derived from Eq. (2), which represent the maximum asymptotic proportion of filtered matter being rejected, take values close to the inorganic content of filtered matter.

Although reported so far only for cockles (Iglesias et al., 1992) and mussels (Bayne et al., 1993), this behaviour is probably common to most bivalves, as variability in feeding conditions occurs in most habitats and capacity for preingestive selection has been reported for different species (Kiørboe and Møhlenberg, 1981).

5.2. Preingestive food selection

Selection efficiency for total organics is a curvilinear function of the organic content of suspended matter. This finding agrees with previous results of experiments with *Cerastoderma edule* fed mixtures of natural resuspended silt and particles of the alga

Tetraselmis suecica (Iglesias et al., 1992), particularly for low organic contents of food. For organic contents greater than 0.4, however, selection efficiencies reported here are well below previous data. This discrepancy can be attributed to differences in the phytoplanktonic component in both experiments. Selection efficiencies reported by Iglesias et al. (1992) at high f values reflect the ability of cockles to discriminate between silt particles and *Tetraselmis* cells. In the present experiments the organic fraction at high f values is a mixture of three algal species, and differences in selection efficiency among them are possible, as demonstrated by Shumway et al. (1985) with suspensions of heterogeneous specific composition. Under this assumption, were one of the algal species to be selectively rejected, the selection efficiency based on organic contents of pseudofaeces and food would tend to decrease, even if efficient selection between algae occurs.

Determinations of chlorophyll *a* content in the seston and in the pseudofaeces has allowed us to evaluate the efficiency with which algal particles are specifically selected. As shown in Fig. 3, efficiency for chlorophyll *a* presents higher values than efficiency estimated for total organic matter (dotted line in the figure). Newell and Jordan (1983) reported a similar difference in studies on preingestive selection performed with *Crassostrea virginica*, and proposed that this difference could be attributed to a preferential ingestion of algae compared with other forms of particulate organic matter. In support of this hypothesis, Urban and Kirchman (1992) have also observed that *C. virginica* preferentially rejects rice starch particles when offered in combination with *Isochrysis galbana* cells. On the other hand, Iglesias et al. (1992) have also suggested that, as pseudofaeces include mucus from the gill, selection efficiency for total organics would necessarily take lower values than efficiency for chlorophyll *a*; also, if that mucus constituted an approximately constant proportion of total rejected matter, the difference would rise with decreasing organic content of the seston.

Data reported here on selection efficiency of carbon and nitrogen indicate that these elements are not selected for differential ingestion (Fig. 3). This observation contrasts with results obtained by Newell and Jordan (1983), who measured higher carbon and lower nitrogen contents in the pseudofaeces of *C. virginica* compared with filtered matter. According to these authors, a higher C/N ratio in pseudofaeces than in food would be the consequence of preferential rejection of organic matter of non-algal origin, giving support to the idea of algae being selected with higher efficiency. Our present results do not invalidate these conclusions by Newell and Jordan (1983), as C/N ratios measured for the food suspensions used in this work are low and virtually indistinguishable from values considered normal for phytoplankton; consequently, the scope for a further nitrogen enrichment of ingested matter would be minimum.

5.3. Absorption efficiency

The efficiency with which ingested food is absorbed by a suspension feeding bivalve is a parameter that has been shown to change over different time scales according to variability in seston characteristics (see review by Bayne and Newell, 1983). Particularly, when feeding on natural seston or on suspensions resembling natural conditions, organic food quality appears as the main factor controlling absorption efficiency (Bricelj and Malouf, 1984; Bayne et al., 1987; Goulletquer et al., 1989; Navarro et al., 1991). Navarro et al. (1994) have analysed the way in which absorption efficiency of cockles is affected by dietary characteristics, to find that there is a complex dependence of *AE* on both the organic content of ingested food (with positive effect) and the rate of ingestion (with negative effect). In the present study lack of a negative effect of food concentration on absorption efficiency is probably due to the ingestion rate being maintained almost constant (see Fig. 2) in the full range of *TPM* concentrations used. According to previous statements, without such a strict regulation of ingestion rate, absorption efficiency would had been probably depressed to levels resulting in rates of absorption lower than actually achieved.

As regards the effect of the organic content of ingested food on absorption efficiency, the relationship fitted to data from this work indicates a maximum asymptotic efficiency (AE_{max}) of 0.73 and negative *AE* at i values lower than $0.059(i_o)$. Assuming that, on average, 1 mg of ingested particles occupies 0.75 mm^3, present values compare well with estimations derived from the general expression obtained by Navarro et al. (1994) for this same species: $AE_{max}=0.77$ and $i_o=0.07$.

Previous studies reporting differential absorption efficiencies for carbon and nitrogen are scarce in marine bivalves. Hawkins and Bayne (1985), for instance, measured similar absorption efficiencies of both elements in mussels fed the diatom *Phaeodactylum tricornutum*. Grant and Cranford (1991), however, found that *Placopecten magellanicus* absorbed nitrogen with higher efficiency than carbon and, as reported here for cockles (Fig. 6), the difference between both absorption efficiencies becomes wider for decreasing net absorption efficiency. Prins and Smaal (1989) have also reported higher absorption efficiencies for nitrogen than for carbon in *Mytilus edulis* and *Cerastoderma edule* feeding on natural seston but, in this case, measured efficiencies were based on total biodeposition and, therefore, are not strictly comparable to our determinations.

Greater absorption efficiency for N than for C may be attributed to two different causes: a) greater lipid and/or carbohydrate contents of metabolic faecal losses; b) easier digestion and absorption of proteins compared with carbohydrates and/or lipids. This would particularly be the case if low quality food comprises particles with a significant proportion of refractory (indigestible) carbohydrates. None of these explanations can currently be supported by experimental evidence and thus, more information is needed to elucidate these fundamental aspects of the digestive physiology of filter feeding bivalves.

On the other hand, differential absorption of C and N reported here should be taken with some reserve. Differences are only evident at low absorption efficiencies, where scarcity of data makes plain the need of further research with diets of low quality. If present results were confirmed however, their implications in terms of elemental balance would be of great relevance. As documented by Hawkins and Bayne (1991), growth efficiencies for protein exceed those for energy in mussels, which is the consequence of a faster turnover for carbon than for nitrogen in these organisms. The implication of this finding is that growth might be more limited by energy than by nitrogen, and in that case, reduced absorption efficiency for C would tend to magnify energy limitations to growth. In food environments dominated by phytoplankton, low C/N of living algal cells would be compensated for, in terms of energy, by high absorption efficiencies, for which no differential elemental absorption is expected. Conversely, with low quality food, where phytoplankton represents a minor proportion of the organic fraction of available seston and hence, C/N ratio may be high (i.e., detritus, vascular plant debris, etc.), higher absorption and growth efficiencies for nitrogen than for energy would constitute valuable physiological traits as they act to compensate for reduced environmental nitrogen availability.

5.4. Food absorption in cockles under natural conditions of food availability

When analysing the consequences of feeding responses, which have previously been discussed in terms of food acquisition, account should be taken of the fact that some of the feeding conditions used in this work are not environmentally realistic. In nature, high organic contents usually occur at low seston loads, while as particle concentration rises there is a concomitant decrease in the organic content of the seston. Such a negative correspondence is evident either from comparisons between locations of typically low (e.g., the Ría de Arosa, N. Spain: Navarro et al., 1991) and high seston loads (e.g., the Bay of Marennes-Olerón: Goulletquer et al., 1989; Razet et al., 1990) or from consideration of seasonal variations in seston concentration and composition at a single site (Berg and Newell, 1986). Due to their position in the substrate, cockles collect particles from the near-bottom water mass, where sediment resuspension may lead to pulses of particle concentration of a considerable magnitude. As the organic content of sedimentary matter is usually lower than that of other suspended materials, a rather dramatic decrease in the organic richness of seston is likely to occur when particle concentration rises in the close vicinity of cockles' feeding siphons.

In order to asses the effect of simultaneous changes in seston concentration and composition that occur environmentally, on the rate of energy acquisition by cockles, we have considered *TPM* values ranging from 1 to 40 mg l^{-1}, estimated the corresponding values of organic content (f) according to the expression: $f=0.5\ TPM^{b}$, and substituted them in the equations for feeding rates and efficiencies presented here. In order to simulate the organic dilution of seston with sediments of different food value, we have considered different b values that, according to the above expression, resulted in different rates of reduction in the organic content with rising concentration of suspensions. Specifically we have set b values at -0.19, -0.31 and -0.57 (conditions **a**, **b** and **c**), which results in minimum f values of 0.25, 0.15 and 0.05 respectively, for the maximum *TPM* concentration (40 mg l^{-1}), while $f=0.5$ at $TPM=1$ mg l^{-1} for all conditions. Results obtained from this simulation have been plotted in Fig. 7, where curves **a**, **b** and **c** represent absorption rate for each of the three conditions referred to above; dotted lines 1, 2 and 3 have been drawn to connect estimates of absorption corresponding to 1, 2 and 3 mg *POM* l^{-1}, respectively. As shown, only for condition **a** (minimum organic content of resuspended materials = 25%) is there a significant interval where a positive dependence exists between absorption and *TPM*, which comes from increasing food availability combined with selection efficiencies that are still maintained at relatively high levels. Above 12 mg l^{-1} for condition **a** and in all the range of *TPM* for conditions **b** and **c**, there is a reduction in the absorption rate with increasing particle concentration. When the organic fraction of resuspended sediment is particularly low (**c**

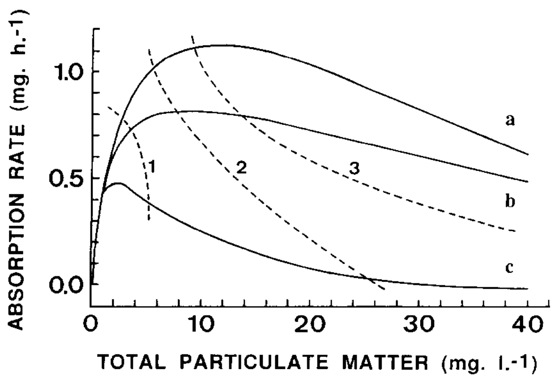

Fig. 7. Absorption rate as a function of total particulate matter concentration, for three conditions (**a**, **b** and **c**) simulating different degrees of organic 'dilution' of suspended matter caused by resuspension events (see Section 5.4). Dotted lines 1, 2 and 3 join absorption rate values estimated for 1, 2 and 3 mg *POM* l^{-1}, respectively.

condition), the reduction in the organic content of suspended matter leads to very low selection and absorption efficiencies that, in addition, tend to decrease as *TPM* concentration rises; these negative effects overcome the benefits of a slight elevation in *POM* concentration. For intermediate conditions (**b**), absorption rate is much less dependent on seston concentration. The merit of this analysis is to show the significant effects that variability in the organic content of resuspended sediments exerts in terms of energy acquisition. In that sense, this approach provides a physiological explanation to previous observations by Bodoy and Plante-Cuny (1984), who found that growth of *Ruditapes decussatus* (L.) correlates better with Chl *a* in the bottom sediments than with Chl *a* in the water column, as well as results by Grant et al. (1990) reporting that daily growth of *Ostrea edulis* (L.) appeared correlated with both the increment in sedimentary Chl *a* and gross resuspension of sediment.

As has been illustrated, resuspension of bottom sediments may elicit important and opposing effects on the energy balance of cockles, depending on the organic content of that sediment. However, it is important to point out that, had not the cockle this capacity to adjust feeding behaviour in response to simultaneous changes in seston concentration and composition, the effect of resuspended sedimentary matter would always be negative in terms of absorption, due to the organic 'dilution' of suspended particles. In summary, cockles increase clearance and, thus, filtration rates in response to elevations in seston concentration that are accompanied by a reduction in its organic content. Under these conditions, increasing amounts of pseudofaeces are rejected whereas ingestion rates are being maintained almost constant. In this process, the organic enrichment of ingested matter derived from preingestive selection helps to compensate for the reduced food value of filtered matter in terms of both organics ingestion and absorption efficiency. The alternative way for regulating ingestion rate in order to avoid oversaturation of the digestive capacity would have been to adjust the clearance rate. In this case, however, no preingestive food enrichment would occur and, consequently, any elevation in the proportion of inorganic matter in suspension would lead to decreasing ingestions of organic matter and absorption efficiencies.

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