

# Feeding physiology of *Cerastoderma edule* in response to a wide range of seston concentrations

J. M. Navarro\*, J. Widdows

Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, United Kingdom

**ABSTRACT:** The suspension-feeding activity of *Cerastoderma edule* (L.) was investigated in response to a wide range of experimental seston concentrations which approximated the changes in seston quality and quantity found in the natural environment over tidal cycles of sediment resuspension. The different seston concentrations were produced by adding increasing quantities of resuspended fine sediment to a relatively low and constant algal concentration ( $0.59 \text{ mg dry wt l}^{-1}$ ). The total seston concentrations (total particulate matter) varied over a wide range from 1.6 to  $570 \text{ mg l}^{-1}$ , and the organic fraction (particulate organic matter) between  $0.62$  and  $79.8 \text{ mg l}^{-1}$ . The organic content of the diets decreased with the increasing seston concentration, from 38.8% at the lowest concentration to 14% at the highest concentration. A significant negative relationship was found between clearance rate of *C. edule* and seston concentration, with very low values at  $570 \text{ mg l}^{-1}$  of total seston. Filtration rate increased with seston concentration from a minimum value of  $2.67 \text{ mg h}^{-1}$  at the lowest concentration to a maximum of  $84.0 \text{ mg h}^{-1}$  at a concentration of  $300 \text{ mg l}^{-1}$ . Above  $300 \text{ mg l}^{-1}$  there was an abrupt decline in filtration rate. Pseudofaeces production started at a concentration of  $4.8 \text{ mg l}^{-1}$ , showing its highest values at around  $300 \text{ mg l}^{-1}$ . The organic content of pseudofaeces was significantly lower than the organic content of the seston, suggesting that *C. edule* is able to preferentially select organic particles for ingestion instead of inorganic particles. Selection efficiency was maintained at a high and constant level at seston concentrations between  $4.8$  and  $97 \text{ mg l}^{-1}$ , declining at the highest seston concentrations with the lowest organic content. Thus the physiological sorting and selection mechanism appears to be very effective at seston concentrations below  $100 \text{ mg l}^{-1}$ , this ability declining abruptly at higher concentrations. Ingestion rate was constant in the lower range of seston concentration ( $1.6$  to  $34 \text{ mg l}^{-1}$ ), increased at concentrations around  $250 \text{ mg l}^{-1}$ , and declined abruptly at the higher food rations. Absorption efficiency appeared relatively independent of seston concentrations over a large range, but it was reduced at concentrations above  $250 \text{ mg l}^{-1}$ . We found a very effective digestive mechanism to regulate absorption rate at seston concentrations between  $1.6$  and  $250 \text{ mg l}^{-1}$ . The results suggest that *C. edule* can compensate efficiently for a decrease in seston quality over a wide range of seston concentration ( $1.6$  to  $300 \text{ mg l}^{-1}$ ) by maintaining an effective preingestive mechanism of selection for organic particulate matter, as well as increasing filtration and rejection rates. As a consequence, this species is well adapted to living in turbid environments, such as intertidal mudflats, which are characterised by marked fluctuations in seston quality and quantity, caused by resuspension of fine sediments during periods of high current velocities on the flood or ebb tides.

**KEY WORDS:** Feeding behaviour · Preingestive selection · Seston load · Diet quality · *Cerastoderma edule*

## INTRODUCTION

Shallow soft-bottom estuaries or bays are characterised by large fluctuations in the quantity and composition of the suspended particulate matter (SPM).

The main cause of changes in SPM is the resuspension of fine sediments during periods of high current velocity on flood and ebb tides, wind-wave activity and intermittent storm events. The physical resuspension of the bottom sediments has a significant effect on the quantity and quality of the SPM available to filter-feeders (Anderson & Meyer 1986, Berg & Newell 1986, Hawkins et al. 1996, Urrutia et al. 1996). While this process produces an increase in total particulate mat-

\*Present address: Instituto de Biología Marina, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.  
E-mail: jnavarro@valdivia.uca.uach.cl

ter (TPM) and particulate organic matter (POM), the relative organic content of the seston can be markedly reduced due to the dilution effect of the higher proportion of inorganic matter contained in the resuspended sediment. Therefore both the quantity and quality of the seston can be altered under these environmental conditions.

The functional response of filter-feeders to the variation in the quantity and quality of SPM has been discussed by many authors (Winter 1976, 1978, Bayne & Newell 1983, Shumway et al. 1985, Bayne et al. 1987, 1989, Iglesias et al. 1992, Navarro et al. 1992, Hawkins et al. 1996, Urrutia et al. 1996). The results of these studies have shown that filter-feeders are able to compensate for reductions in food quality or quantity by means of physiological mechanisms which enhance the energy gain from environments characterised by large fluctuations in the quantity and quality of seston. It has been reported that filter-feeding bivalves are able to compensate for the 'dilution' of the organic fraction by the inorganic fraction of the seston by preferential ingestion of organic particles from the filtered matter and selective rejection of the inorganic matter within the pseudofaeces (Kiørboe & Møhlenberg 1981, Newell & Jordan 1983, Iglesias et al. 1992, 1996, Bayne et al. 1993, Navarro & Iglesias 1993, Hawkins et al. 1996). However, most of these studies have not been carried out over a wide environmental range of seston concentrations, typically  $<30 \text{ mg l}^{-1}$  of total seston (Bayne et al. 1987, 1993, Iglesias et al. 1992, Navarro et al. 1992, 1993). Only recently have studies addressed concentrations up to  $100 \text{ mg l}^{-1}$  (Hawkins et al. 1996, Urrutia et al. 1996). However, it has been observed that filter-feeders inhabiting mudflats and estuaries can experience seston concentrations up to  $500 \text{ mg l}^{-1}$  (e.g. Humber Estuary, England) during resuspension events (Falconer & Owens 1990). Significant differences in the physiological responses of epifaunal and infaunal bivalves, such as *Cerastoderma edule* and *Mytilus edulis*, have been reported by Hawkins et al. (1990). *C. edule* shows higher ingestion rates than the epibenthic *M. edulis*, probably to maximise the amount of food absorbed from the organically poor seston available to this infaunal species. It was also suggested that *M. edulis* requires many days to compensate and adjust its digestive system to changes in food quality, while the infaunal *C. edule* appears to be able to adapt more quickly to higher seston concentrations of low quality (Hawkins et al. 1985).

*Cerastoderma edule* is an infaunal bivalve which shows high physiological plasticity when exposed to changes in seston quality over a relatively narrow concentration range of between 1 and  $30 \text{ mg l}^{-1}$  (Iglesias et al. 1992, Navarro et al. 1992). Preferential ingestion of organic particles has been described in this species

when exposed to seston concentrations above the threshold of pseudofaeces production (Navarro et al. 1992, Urrutia et al. 1996). Such a mechanism can play a significant role in the maximisation of net rates of energy intake, which is considered as a basic characteristic of fitness (Taghon 1981, Willows 1992).

The main objective of the present study was to investigate the effects of a wide range of environmentally realistic seston concentrations on the feeding activity of *Cerastoderma edule*. The range of seston concentrations ( $1.6$  to  $570 \text{ mg l}^{-1}$ ) was more extensive than those examined in previous studies, and with different proportions of organic matter (0.14 to 0.39).

## MATERIAL AND METHODS

**Site of collection and experimental animals.** Specimens of the bivalve *Cerastoderma edule* (cockles) of a similar shell height ( $2.66 \pm 0.02 \text{ cm}$ , mean  $\pm$  SE) and having a mean dry tissue weight of  $214 \pm 13.2 \text{ mg}$  ( $\pm$  SE), were collected on 3 occasions (between May and August 1995) during low tide from an intertidal population near the mouth of the River Exe, southwest England. They were transported immediately to the Plymouth Marine Laboratory and were acclimated to laboratory conditions for 1 wk prior to any measurement. Cockles were allowed to bury into sediment trays and were held in an aquarium ( $3 \text{ m}^3$ ) of recirculating seawater collected offshore (Eddystone) and maintained at  $15^\circ\text{C}$  and at a salinity of 32 to 34 psu. Cockles were fed with a unialgal diet of *Isochrysis galbana*.

**Experimental seston concentrations.** The filter-feeding activity of *Cerastoderma edule* was determined in response to a wide range of experimental seston concentrations which approximated the changes in seston quality and quantity found in the natural environment over tidal cycles of sediment resuspension (e.g. Humber Estuary; Falconer & Owens 1990). The different experimental seston concentrations varied between 1.6 and  $570 \text{ mg l}^{-1}$ , with an organic content ranging between 38.8 and 14% (Table 1). The range of seston concentrations was produced by adding increasing quantities of resuspended fine surficial sediment to a constant, but relatively small, amount of the unicellular algae *Isochrysis galbana* ( $20 \times 10^6 \text{ cells l}^{-1}$  or  $0.59 \text{ mg dry wt l}^{-1}$ ). A stock of surficial sediment (1 cm depth) was collected from mudflats in the Lynher Estuary, southwest England, and stored at  $5^\circ\text{C}$  in the dark. Subsamples were then homogenised by strong aeration and stirring before sieving through a  $30 \mu\text{m}$  Nitex screen. Particle size distribution of the seston was measured with a Coulter Multisizer fitted with a  $100 \mu\text{m}$  orifice tube. The differential and cumulative curves describing the particle size distribution (Fig. 1) show that the median parti-

Table 1. Composition of the experimental diets supplied to *Cerastoderma edule*. TPM: total particulate matter; POM: particulate organic matter

Diet	TPM (mg l <sup>-1</sup> )	POM (mg l <sup>-1</sup> )	Organic content (%)
1	1.6	0.62	38.8
2	4.8	1.09	22.7
3	11.0	2.74	24.9
4	34.0	7.11	20.9
5	97.0	19.40	20.0
6	142.0	25.70	18.1
7	219.0	45.11	20.6
8	302.0	53.61	17.8
9	368.0	65.32	17.8
10	448.0	62.72	14.0
11	570.0	79.80	14.0

cle size was approximately 5 µm diameter (spherical equivalent). The concentrations of TPM and POM in the experimental diets were established by sampling known volumes of the suspensions (3 replicates). Each sample was filtered through washed, precombusted, preweighed Whatman GF/C filters of 4.7 cm and rinsed with 20 ml of isotonic ammonium formate to remove salt and prevent cell lysing. These filters were then dried at 90°C for 24 h, weighed, combusted at 450°C for 3 h and reweighed after cooling in a desiccator. Or-

ganic content of each diet was obtained from the difference between dry and ash weights.

**Physiological measurements. Clearance and filtration rate:** Clearance rate was estimated by measuring the removal of suspended particles from the water flowing through a system of raceways with 10 channels (50 × 5 × 7 cm; length × width × depth) containing individual cockles. The system to measure clearance rate was composed of a 20 l container of stock solution, a peristaltic pump discharging the stock solution at a required rate into a mixing chamber with a magnetic stirrer, and thence via 2.5 mm bore tubing through 8 experimental raceways containing the individual cockles and 2 other control channels without animals which accounted for any sedimentation. The cockles were held overnight in the system with similar experimental diets and allowed to bury into the sediment (coarse sediment 0.5 to 1 mm diameter) contained in small trays of 12 × 5 × 4 cm (length × width × depth) held inside each raceway. The cockles were oriented with the inhalant siphon facing the inflow of the water and were left undisturbed for 1 h before the start of measurements. Clearance rates were determined by using appropriate flow rates through each raceway (ca 100 to 140 ml min<sup>-1</sup>). These were low enough to record a significant difference between the particle concentration in the outflows from the controls and experimental chambers with cockles (max. 40%), but sufficient to eliminate the

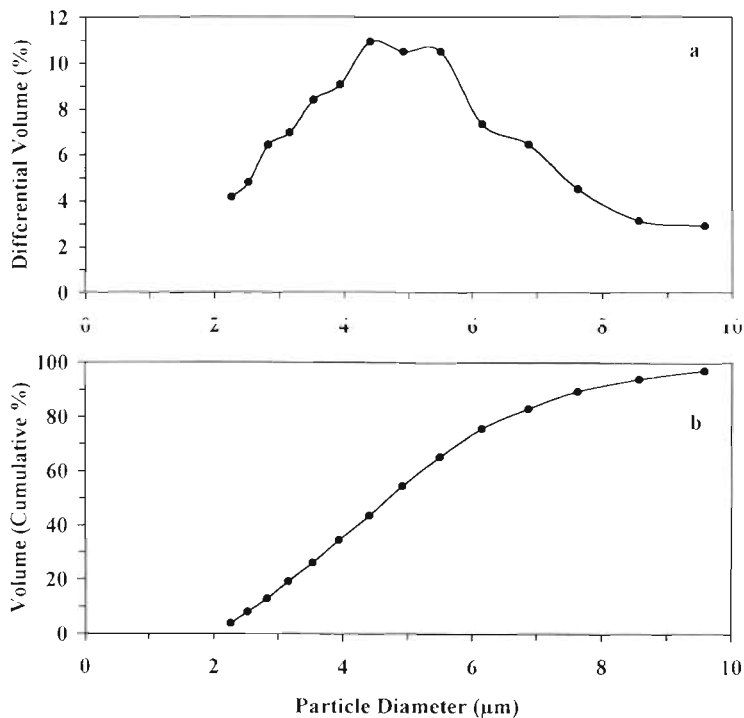


Fig. 1. (a) Differential and (b) cumulative volume in relation to particle diameter (in spherical equivalent) of the experimental seston concentrations

possibility of recirculation of water through the mantle cavity. Flow rates through each channel were determined by simultaneously collecting and measuring the volume of water from each outflow in a given period of time. A Coulter Multisizer fitted with a 100 µm orifice tube was used to determine the difference between the particle concentration in the outflow from the control channel ( $C_1$ ) and the outflow from each experimental raceway ( $C_2$ ). Clearance rate was calculated as flow rate multiplied by  $(C_1 - C_2)/C_1$ . Experiments were run for 4 to 6 h on each occasion and the mean clearance rates were calculated based on several measurements (5 to 10). The mean rate includes some periods of inactivity or transition between feeding and inactivity. To avoid the inclusion of periods of inactivity, maximum clearance rates were also calculated, based on the maximum values recorded for each individual in each experiment.

Filtration rate represents the amount of seston (mg h<sup>-1</sup>) which is filtered from a suspension, and it was calculated as the product of clearance rate and the particle concentration. Below the threshold of pseu-

dofaeces production, filtration rate is equal to ingestion rate and above this threshold, filtration rate represents the sum of ingested matter plus rejected matter as pseudofaeces (Widdows et al. 1979).

**Biodeposition and ingestion rate:** Faecal pellets produced by *Cerastoderma edule* during the experiments were either collected quantitatively using a micropipette (e.g. at low seston concentration), or the faeces which had settled on the sediment were siphoned off together with the coarse surficial sediment and the faeces were then separated under a stereomicroscope. Pseudofaeces are ejected from the inhalant siphon and are deposited as a separate pile from the faeces. A proportion of the pseudofaeces is also resuspended by the ejection force out of the inhalant siphon created by sudden valve adduction. These clouds of resuspended pseudofaeces are lost from the experimental system, and therefore only a representative fraction was collected separately from the faeces, which was enough to measure their organic and inorganic composition. Total egestion rate was estimated directly by quantitative collection of faecal pellets, while total rejection rate (or pseudofaecal production) was estimated from the difference between the filtration rate and ingestion rate. Faeces and pseudofaeces were filtered through GF/C filters and treated as described above for determination of the seston concentration of the experimental diets.

Ingestion rate was calculated from the composition of the experimental diet and the egestion rate, using the inorganic fraction of the diets and faecal pellets as indicators, assuming that there is minimal absorption of inorganic material during its passage through the digestive tract. Cockles also have the ability to preferentially select organic matter relative to the inorganic matter at seston concentrations where pseudofaeces are produced. Therefore ingestion rate was corrected according to the percentage of selection efficiency.

Selection efficiency (SE) was calculated according to Bayne & Hawkins (1990) and Iglesias et al. (1992), where the organic content was used to evaluate the preferential ingestion of organic matter instead of inorganic matter from the food. For this purpose it is necessary to know the organic content of the food ( $f$ ) and pseudofaeces ( $p$ ) to use the formula:

$$SE = 1 - (p/f)$$

When  $SE = 0$ , there is no selection ( $f = p$ ) and when  $SE = 1$ , there is complete selection and ingestion of organic particles.

**Net absorption efficiency:** Due to the cockle's ability to select organic particles in preference to inorganic particles at experi-

mental suspensions above the threshold of pseudofaeces production, net absorption efficiency was estimated by using the organic and inorganic (ash) content of the food ingested and the faeces, following the ratio method of Conover (1966). Absorption rate was calculated as the product of the organic ingestion rate and absorption efficiency.

**Statistical analysis.** Regression analysis and curve fitting using different models were performed with Excel 5.0 to represent the dependence of the feeding and digestive processes on the different seston concentrations. Analysis of covariance (ANCOVA) was applied to compare the regression lines (slopes and elevations) of the mean and maximum clearance rates. Analysis of variance (ANOVA) followed by a test of significance (Tukey's) was applied to compare the organic content of the seston, faeces and pseudofaeces. All these analyses were carried out with the statistical package Systat (v. 5.3; Systat Inc.) for Windows™.

## RESULTS

### Experimental seston concentrations

Experimental seston concentrations (TPM) varied over a wide range from 1.6 to 570  $\text{mg l}^{-1}$ , and POM varied between 0.62 and 79.80  $\text{mg l}^{-1}$  (Table 1). The organic content of the diets (Fig. 2) decreased with the increasing seston concentration, from 38.8% at the lowest seston concentration to 14% at the highest concentration. This relationship was best described by the following power function:

$$OC = 34.528 x^{-0.1272} \quad (R^2 = 0.81)$$

where OC is the % organic content and  $x$  is the seston concentration ( $\text{mg l}^{-1}$ ).

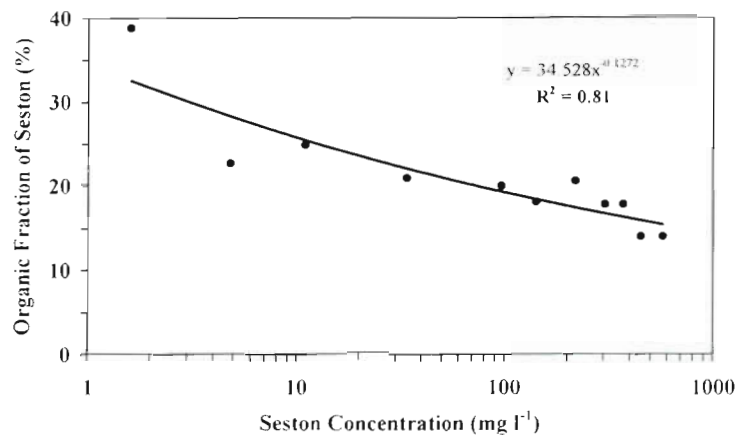


Fig. 2. Relationship between the organic fraction and total seston concentration. Curve was best fitted by a power function

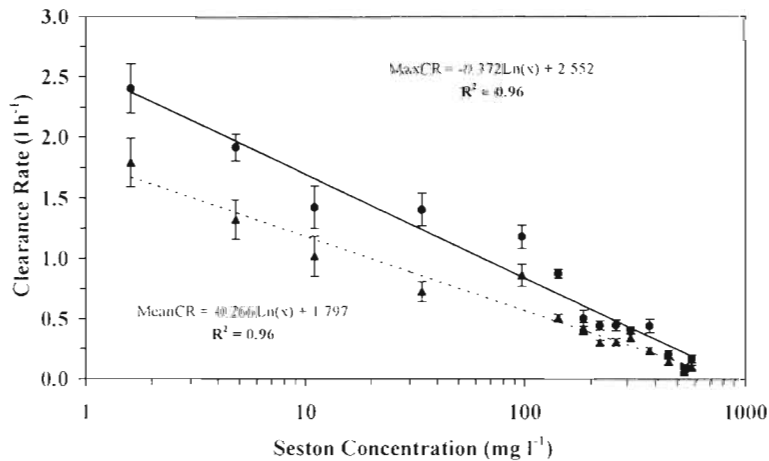


Fig. 3. *Cerastoderma edule*. Maximum (●) and mean (▲) clearance rates (CR) in relation to seston concentration ( $x$ ). Curves were fitted by linear functions

### Physiological measurements

#### Clearance rate

There is a significant negative relationship between the clearance rate of *Cerastoderma edule* and seston concentration (Fig. 3) which can be described by the following equations:

$$\text{Mean CR} = -0.266 \ln(x) + 1.797 \quad (R^2 = 0.96)$$

$$\text{Max. CR} = -0.372 \ln(x) + 2.552 \quad (R^2 = 0.96)$$

where CR is the clearance rate ( $l h^{-1}$ ) and  $x$  is the seston or TPM concentration ( $mg l^{-1}$ ).

The ANCOVA showed that there were no significant differences between the slopes ( $p = 0.17$ ) of the mean and maximum clearance rates of *Cerastoderma edule*. However, significant differences were found when the elevations were compared ( $p = 0.02$ ). The highest CR values [max.:  $2.4 \pm 0.20 l h^{-1}$  ( $\pm SE$ ); mean:  $1.79 \pm 0.20 l h^{-1}$  ( $\pm SE$ )] were obtained at the lowest seston concentration (i.e.  $1.6 mg l^{-1}$ ), with a gradual decline in CR with increasing seston concentration. At the highest concentration of  $526 mg l^{-1}$  the maximum and mean clearance rates had declined to  $0.09 \pm 0.033 l h^{-1}$  ( $\pm SE$ ) and  $0.06 \pm 0.026 l h^{-1}$  ( $\pm SE$ ), respectively.

#### Filtration rate

The total filtration rate (TFR) in  $mg h^{-1}$  (organic + inorganic matter  $h^{-1}$ ) increased with seston concentration from a minimum value of  $2.67 mg h^{-1}$  at the lowest concentration ( $1.6 mg l^{-1}$ ) to a maximum of  $84.0 mg$

$h^{-1}$  at  $300 mg l^{-1}$ . Above ca  $300 mg l^{-1}$  there was a decline in TFR (Fig. 4). Less variation was recorded in the organic filtration rate (OFR), which ranged from  $1.07 mg h^{-1}$  at the lowest seston concentration to  $17.02 mg h^{-1}$  at  $259 mg l^{-1}$  (Fig. 4). With increasing seston concentration there was a decline in OFR (i.e.  $>260 mg l^{-1}$ ) but the values did not fall below  $8 mg h^{-1}$ . The relationships between TFR/OFR and seston concentration are described by polynomial models according the following equations:

$$\text{TFR} = -0.0007x^2 + 0.463x + 9.05 \quad (R^2 = 0.97)$$

$$\text{OFR} = -0.0001x^2 + 0.092x + 2.196 \quad (R^2 = 0.93)$$

where TFR is the total filtration rate (inorganic and organic matter) in  $mg h^{-1}$ , OFR is the organic filtration rate in  $mg h^{-1}$  and  $x$  is the seston concentration in  $mg l^{-1}$ . The resulting models were highly significant ( $p < 0.001$ ), with a good fit to the data.

#### Biodeposition rate

Egestion rate (i.e. faeces production) and rejection rate (i.e. pseudofaeces production) combined represent the biodeposition rate. There were significant differences between these 2 processes, egestion rate increased slightly with seston concentration, from  $1.25 mg h^{-1}$  to  $3.41 mg h^{-1}$  at  $1.6$  and  $311 mg l^{-1}$ , respectively. Pseudofaeces production was not observed at the lowest experimental diet ( $1.6 mg l^{-1}$ ), but it

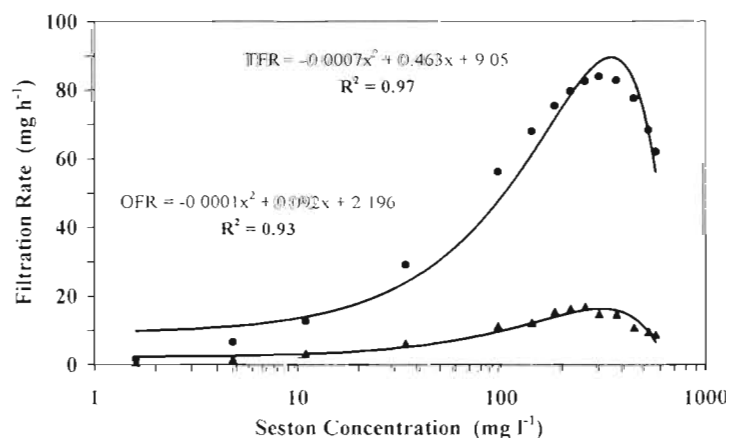


Fig. 4. *Cerastoderma edule*. Total (●, TFR) and organic (▲, OFR) filtration rates in relation to seston concentration. Curves were described by polynomial functions



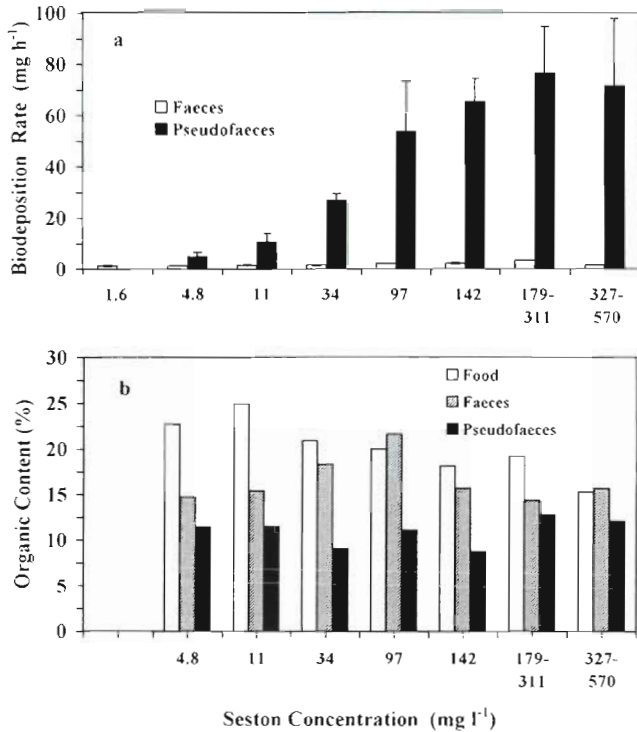


Fig. 5. *Cerastoderma edule*. (a) Biodeposition rate in relation to seston concentration. (b) Organic content of food, faeces and pseudofaeces in relation to seston concentration

increased significantly from 4.86 mg h<sup>-1</sup> at a seston concentration of 4.8 mg l<sup>-1</sup> to 76.20 mg h<sup>-1</sup> at 311 mg l<sup>-1</sup> (Fig. 5a). Faeces production declined by 60% while pseudofaeces production was only reduced slightly at the higher concentrations (>327 mg l<sup>-1</sup>). The organic content of pseudofaeces was significantly lower than the organic content of the seston (p < 0.01), suggesting

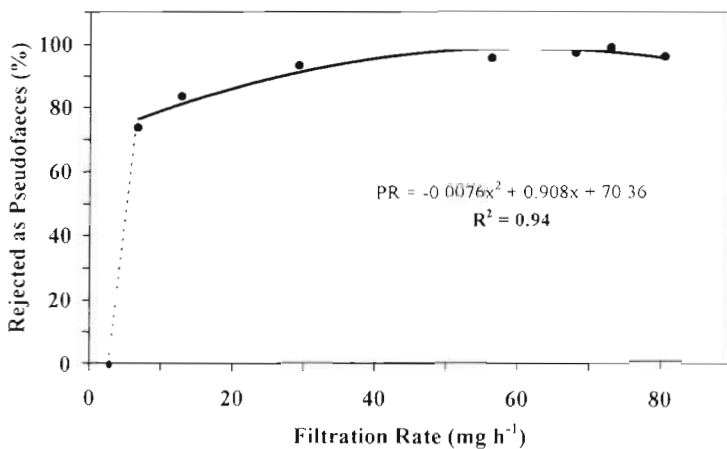


Fig. 6. *Cerastoderma edule*. Material rejected as pseudofaeces in relation to different levels of filtration rate. Curve (continuous line) was fitted by a polynomial function. PR: pseudofaeces rejection; x: filtration rate

that *Cerastoderma edule* is able to preferentially select organic particles for ingestion instead of inorganic particles, and thus increase the % inorganic content of the pseudofaeces. Significant differences were also found between faeces and pseudofaeces (p < 0.01) when the organic content of these biodeposits was compared (Fig. 5b). Rejection rate followed a similar pattern to filtration rate and the proportion of filtered material which was rejected as pseudofaeces increased from zero to 97.6% at 2.67 and 84 mg h<sup>-1</sup> of FR, respectively (Fig. 6).

#### Selection efficiency and ingestion rate

*Cerastoderma edule* showed preferential ingestion of organic particles instead of inorganic particles contained in the seston. Selection efficiency was maintained high and constant (ca 0.50) at seston concentrations between 4.8 and 97 mg l<sup>-1</sup>, and then declined to lower values (ca 0.15) at the highest seston concentrations (between 450 and 570 mg l<sup>-1</sup>). This relationship is presented in Fig. 7a and described by the following exponential equation:

$$SE = 0.617e^{-0.0026x} \quad (R^2 = 0.89)$$

where SE is selection efficiency and x is the seston concentration (mg l<sup>-1</sup>).

The preferential ingestion of organic matter from the seston produces an organic enrichment of the food ingested. Consequently the organic content of the filtered material ranged between 24.9 (at 11 mg l<sup>-1</sup>) and 14% (at 570 mg l<sup>-1</sup>), while the organic content of the material ingested varied between 43 and 16%, at the same respective seston concentrations (Fig. 7b). The difference between the 2 curves presented in Fig.

7b (filtration and ingestion) represents the effect of selection efficiency in *Cerastoderma edule*. At seston concentrations below ca 100 mg l<sup>-1</sup> (20% organic content) the physiological sorting and selection mechanism appears to be very effective, but the ability to select then declined abruptly at higher concentrations.

Total ingestion rate (TIR) showed constant values, ca 2 mg h<sup>-1</sup>, at the lower seston concentrations (1.6 and 34 mg l<sup>-1</sup>), increasing slowly up to 4.2 mg h<sup>-1</sup> at concentrations around 250 mg l<sup>-1</sup>, but then declined abruptly at the higher food rations (Fig. 8). Organic ingestion rate (OIR) followed a more constant trend, ranging from 0.64 mg h<sup>-1</sup> at the lower seston concentrations (i.e. <100 mg l<sup>-1</sup>) to 1.25 mg h<sup>-1</sup> at ca 200 mg l<sup>-1</sup>. The relationships between these physiological rates and the

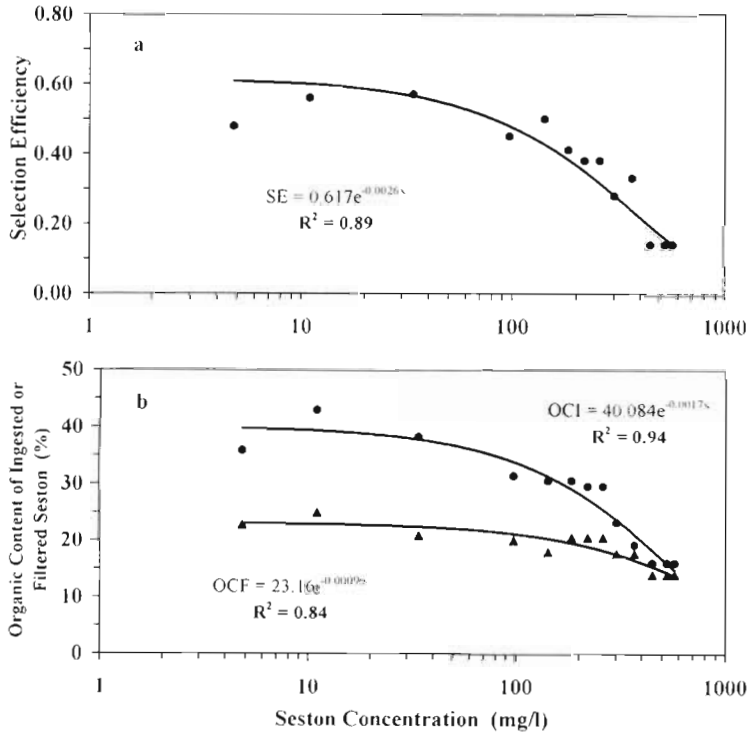


Fig. 7 *Cerastoderma edule*. (a) Selection efficiency (SE) in relation to seston concentration (x). (b) Organic content of ingested (OCI; ●) or filtered (OCF; ▲) seston in relation to seston concentration (x). Curves for (a) and (b) were fitted by exponential functions

experimental seston concentrations are described by the following polynomial models:

$$\begin{aligned} \text{TIR} &= -3 \times 10^{-5} x^2 + 0.01x + 1.859 \quad (R^2 = 0.62) \\ \text{OIR} &= -7 \times 10^{-6} x^2 + 0.003x + 0.752 \quad (R^2 = 0.63) \end{aligned}$$

where TIR is the total ingestion rate in  $\text{mg h}^{-1}$ , OIR is the organic ingestion rate and x is the seston concentration ( $\text{mg l}^{-1}$ ).

Net absorption efficiency

Absorption efficiency (AE) was estimated from the food ingested (after preingestive selection) and the faeces according to the ash ratio technique (Conover 1966), which has been found to give reproducible data for filter-feeders (Navarro & Thompson 1994). High values between 50 and 70% were registered at the lower seston concentrations (1.6 to 34  $\text{mg l}^{-1}$ ), but this was followed by a progressive decline to 8.7% at the highest food ration (548  $\text{mg l}^{-1}$ ) (Fig. 9a). Thus AE appears to be relatively independent of seston concentrations over a large range (1.6 to 250  $\text{mg l}^{-1}$ ), and it is only reduced at concentrations above

250  $\text{mg l}^{-1}$ . This relationship can be represented by an exponential model according to the following equation:

$$\text{AE} = 70.817e^{-0.0036x} \quad (R^2 = 0.78)$$

where AE is the absorption efficiency (%) and x is the seston concentration ( $\text{mg l}^{-1}$ ).

When absorption efficiency was related to the organic content of the material ingested there was a clear increase from 8.7% for low organic content (0.15) to values as high as 65% at a middle organic content (0.25), which continued at a relatively constant level to the highest values of organic content (0.4) tested in this study (Fig. 9b). This relationship is described by the following logarithmic equation:

$$\text{AE} = 122.8 \ln(x) + 249.42 \quad (R^2 = 0.71)$$

where AE is the absorption efficiency (%) and x is the organic fraction of ingested seston.

The rate of food absorption (AR) was very constant (ca 0.5  $\text{mg h}^{-1}$ ) at seston concentrations from 1.6 to 250  $\text{mg l}^{-1}$ . At higher seston concentrations this was followed by a rapid decline in AR, with minimum values around 0.04  $\text{mg h}^{-1}$  at rations above 300  $\text{mg l}^{-1}$  (Fig. 10). This suggests that there is a very effective digestive mechanism to regulate AR at experimen-

tal seston concentrations between 1.6 and 250  $\text{mg l}^{-1}$ , and the rapid decrease at higher concentrations appears to reflect a failure of the feeding system, which is not able to maintain selection mechanisms and high ingestion rates. The relationship between AR and seston concentration is described by a polynomial

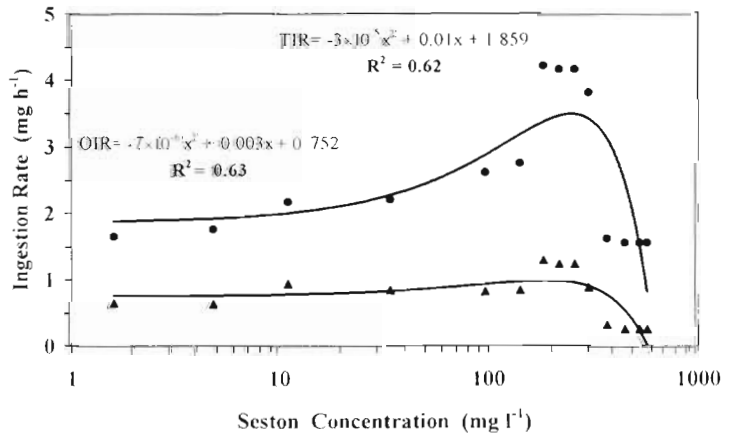


Fig. 8 *Cerastoderma edule*. Total (TIR; ●) and organic (OIR; ▲) ingestion rates in relation to seston concentration (x). Curves were fitted by polynomial functions

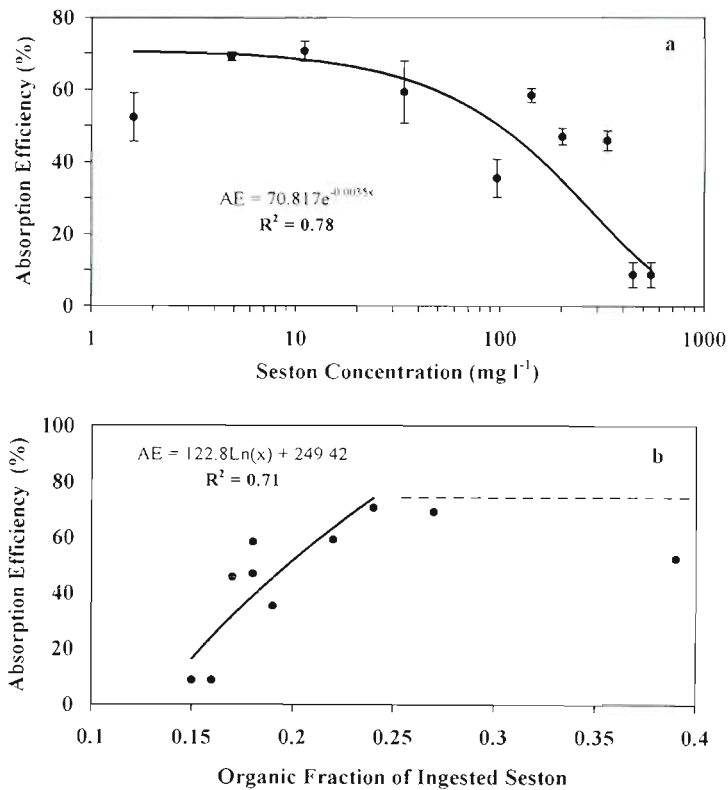


Fig. 9. *Cerastoderma edule*. (a) Absorption efficiency (AE) in relation to seston concentration ( $x$ ); curve was fitted by an exponential function. (b) Absorption efficiency (AE) in relation to the organic fraction of ingested seston; curve was fitted by a logarithmic function

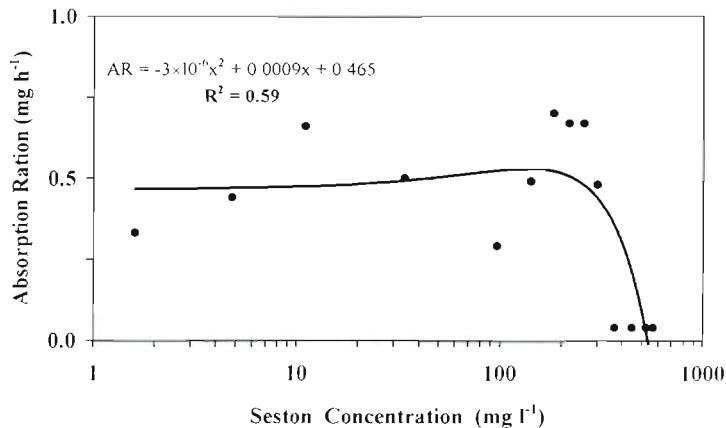


Fig. 10. *Cerastoderma edule*. Absorption ratio (AR) in relation to seston concentration ( $x$ ). Curve was fitted by a polynomial function

model according to the formula:

$$AR = -3 \times 10^{-6}x^2 + 0.0009x + 0.465 \quad (R^2 = 0.59)$$

where AR is the absorption rate ( $\text{mg h}^{-1}$ ) and  $x$  is the seston concentration ( $\text{mg l}^{-1}$ ).

Above the threshold of pseudofaeces production (i.e.  $4.8 \text{ mg l}^{-1}$ ) ingestion rate represented a very small frac-

tion of the filtered material, ranging from  $26.6\%$  ( $1.76 \text{ mg h}^{-1}$ ) at a concentration of  $4.8 \text{ mg l}^{-1}$  to  $2\%$  ( $1.55 \text{ mg h}^{-1}$ ) at concentrations above  $368 \text{ mg l}^{-1}$ . The highest ingestion rates were obtained at concentrations between  $180$  and  $250 \text{ mg l}^{-1}$  with values above  $4.2 \text{ mg h}^{-1}$  ( $5\%$  of the filtered material). Ingestion rate did not increase to the same degree as filtration rate, and the progressive difference between these 2 rates as seston concentration rises (up to ca  $250 \text{ mg l}^{-1}$ ) reflects the increase in the rate of pseudofaeces production, with a slight reduction at the higher seston concentrations. According to these results, ingestion rate is regulated by 2 different feeding processes as the seston concentration increases. Firstly, the reduction in clearance rate and secondly, the increase in pseudofaeces production. Absorption rate was very constant within a wide range of seston concentrations ( $1.6$  to  $250 \text{ mg l}^{-1}$ ) representing a very low amount of the ingested material and declining to zero at concentrations  $>350 \text{ mg l}^{-1}$ .

## DISCUSSION

The present study exposed the bivalve *Cerastoderma edule* to a very wide range of seston concentrations, with different proportions of organic matter, with the aim of simulating environmental conditions found in turbid estuaries inhabited by this infaunal bivalve (e.g. Humber Estuary; Falconer & Owens 1990). Resuspension of fine sediments will result in a progressive decrease of the % organic content (quality) as seston concentration increases. These negative relationships have been described in many marine environments (Widdows et al. 1979, Newell & Bayne 1980, Navarro et al. 1991, 1993).

ANCOVA showed that there were no significant differences between the slopes of regressions relating mean and maximum clearance rate (CR) with total seston concentrations. However, significant differences were found between the elevations, suggesting that *Cerastoderma edule* combines peri-

ods of high feeding activity with other less active periods. The mean CR were consistently about  $60$  to  $70\%$  of the maximum CR over the wide range of seston concentrations. The functional feeding response of *C. edule* was characterised by a significant reduction of CR with increasing seston concentration, which is in agreement with Winter (1978), who postulated the



ability of filter-feeders to regulate pumping rate in response to increasing seston concentrations. Similar effects of seston load on CR have been described by Foster-Smith (1975) for *C. edule* and also for the clam *Venerupis pullastra*. More comprehensive studies carried out recently by Navarro et al. (1992, 1994) and Iglesias et al. (1996) on *C. edule* showed similar effects of increasing seston concentrations within a range of 1 to 30 mg l<sup>-1</sup>. The results of the present study have demonstrated that this negative relationship between CR and seston concentration extends over a very wide range of seston concentrations (1.6 to 570 mg l<sup>-1</sup>). This shows that a reduction in CR is one important compensatory mechanism to regulate ingestion rate when *C. edule* is exposed to conditions of increased turbidity and seston concentration, similar to those associated with intertidal mudflats in estuaries with high tidal ranges (e.g. 5 to 7 m).

Many studies have been carried out relating food availability and filtration rate in marine bivalves, but most of them have used seston concentrations below the threshold of pseudofaeces production (Riisgard & Randlov 1981, Navarro & Winter 1982, Winter et al. 1984, Bayne et al. 1989). Other authors have conducted similar studies above the threshold of pseudofaeces production (Foster-Smith 1975, Widdows et al. 1979, Iglesias et al. 1992, Navarro et al. 1992, Bayne et al. 1993, Hawkins et al. 1996). Very different feeding behaviours have been described in both cases, showing the importance of evaluating physiological responses to seston concentrations of similar quantity and quality to those measured in the natural environment. The present study showed that filtration rate (FR) increased with seston concentration up to a maximum of 300 mg l<sup>-1</sup>, and then declined at higher concentrations. Iglesias et al. (1992) and Navarro et al. (1992, 1994) also found an increase in FR in *Cerastoderma edule*, within a smaller range of seston concentrations (1.53 to 29.8 mg l<sup>-1</sup>) than those used in the present experiment (1.6 to 570 mg l<sup>-1</sup>). Similar behaviour was observed in *Mytilus edulis* by Bayne et al. (1993). Iglesias et al. (1992) concluded that there was an interactive effect between seston quantity and quality and the feeding behaviour of *C. edule*, describing 2 main responses: (1) filtration rates are constant when *C. edule* is exposed to increasing particle concentration of high quality, and (2) filtration rates increase progressively with seston concentrations of low food quality. Our results are very similar to this within a wider range of seston concentrations, where FR was almost constant between 1.6 and 11 mg l<sup>-1</sup> when the quality of the seston was high (organic content = 39 to 25%). However, FR increased rapidly with increasing concentration from 11 to 300 mg l<sup>-1</sup> and decreasing quality of the rations (organic content = 25 to 18%). The presence of

high FR appears as an efficient mechanism to enhance the energy gain from a turbid environment, because these species can process large amounts of particulate matter. They have the capacity to sort and preferentially ingest organic particles instead of inorganic particles, and reject a high proportion of inorganic matter in the form of pseudofaeces. This feeding behaviour results in an enrichment of the ingested matter. The decrease of FR at concentrations above 300 mg l<sup>-1</sup> suggests a gradual failure of the filtration, particle selection and ingestion systems, and an inability to function effectively at these higher seston loads.

Rejection of pseudofaeces has been described as a second regulatory mechanism of ingestion rate (Foster-Smith 1975, Widdows et al. 1979, Iglesias et al. 1992, Navarro et al. 1992). Hawkins et al. (1996) found that the production of pseudofaeces in *Mytilus edulis* depends on the FR, which increased with seston concentration up to the highest level tested by these authors (112 mg l<sup>-1</sup>). Similar results were obtained in the present study, where *Cerastoderma edule* increased the rejection rate with the increase in FR, from zero at 1.6 mg l<sup>-1</sup> to nearly 80 mg h<sup>-1</sup> at 300 mg l<sup>-1</sup>, while egestion rate was maintained very constant between the same food concentrations. Rejection rate (RR) was low at the lower seston concentrations (Fig. 5a), but increased steadily from 34 to 300 mg l<sup>-1</sup>, following a similar pattern to FR. The relationship between FR and RR was fitted by a polynomial model (Fig. 6) and is in agreement with that reported by Hawkins et al. (1996) for *M. edulis*. *C. edule* appears to show both mechanisms for regulating ingestion, one is by reducing CR and the other by increasing the production of pseudofaeces. However, the relative importance of these 2 mechanisms appears to be modified by the quantity and quality of the suspended particulate matter, and different results can be obtained when only the effects of the quality of the diet are tested. Iglesias et al. (1992) and Navarro et al. (1992) concluded that the mechanism of regulation in *C. edule* is determined by food composition, with CR providing the main mechanism under high quality (energy rich) rations, and the production of pseudofaeces as the main mechanism under low quality rations.

ANOVA followed by Tukey's test of significance showed that the organic content of the pseudofaeces was significantly lower than the organic content of the seston filtered (Fig 5b), indicating selection with organic enrichment and preferential ingestion of organic particles at concentrations when pseudofaeces are produced by *Cerastoderma edule*. This feeding response of *C. edule* was first identified by Kjørboe & Møhlenberg (1981) using the chlorophyll *a* ratio in the food and pseudofaeces. They found this species was able to select phytoplankton cells with selection effi-

ciencies as high as 77%. Bayne et al. (1989) modified this index using the organic fraction in food and pseudofaeces and reported values around 50% for *Mytilus edulis*. The present study also demonstrated that selection efficiency (SE) was a very effective physiological mechanism in *C. edule* up to a seston concentration of 100 mg l<sup>-1</sup> (20% organic content), but declined abruptly at higher concentrations (Fig. 7a) and lower organic contents. This decrease may also be related to the decreasing quality of the experimental rations with the increasing seston concentrations, as reported by Navarro et al. (1992) for the same species. Our results of SE do not agree with those of Hawkins et al. (1996), who recorded a positive relationship between SE and filtration rate in *M. edulis*. However, there is agreement when results are expressed in terms of the positive relationship between organic content (between 0.14 and 0.40) of the food and SE. The decreasing difference between the organic fractions of filtered and ingested matter represents the effects of SE, and showed that SE was negatively related to seston concentration, but positively related to the organic content of the seston. These relationships were represented by exponential equations (Fig. 7b), showing that by means of this mechanism organic ingestion rate was increased by ca 70% (i.e. 25% organic in seston to 43% organic in ingested matter; Fig. 7b) at the lower concentrations (i.e. 11 mg l<sup>-1</sup>, high quality) and ca 2.0% at the highest concentrations (low quality). It is not clear if this significant decrease of SE at higher seston loads is related to the less efficient mechanism of filtration when it is necessary to process large amount of filtered material or to the effects of the increasing fraction of mucus in the organic content of the pseudofaeces as the quantity of the seston increases and its quality decreases. Iglesias et al. (1992) assumed that the rejected material by *C. edule* at food qualities below 40% of organic matter contains approximately constant fractions of mucus and that pseudofaecal mucus loss could be the explanation of the lower values of SE. These same authors suggested that the secreted mucus in the pseudofaeces would be a similar loss to the metabolic faecal losses associated with digestive processes, and thus the SE represents net selection efficiency. Urrutia et al. (1996) reported a very similar dependence of SE on the organic content of the seston, however their values were higher than those found in the present study within a range of 10 to 20% of organic content. The significantly higher seston concentration used in the present study could be producing the lower values of SE, showing the interactive effects of TPM and organic content of the seston on the feeding response of *C. edule*.

In contrast to filtration rate, ingestion rate was maintained independent of seston concentration of *Cerasto-*

*derma edule* with very constant values (around 2 mg h<sup>-1</sup>) between 1.6 and 100 mg l<sup>-1</sup>. However, there was an increase in the total ingestion rate of ~80% between 100 and 300 mg l<sup>-1</sup>, and thus it was related with a very high filtration rate at those rations. The abrupt decrease in ingestion rate at higher concentrations was associated with a marked decline in clearance rate and by a reduction in filtration rate. Organic ingestion rate was more efficiently regulated than total ingestion rate, being very constant over a wide range of seston concentrations (1.6 to 300 mg l<sup>-1</sup>). This was primarily due to the efficient particle selection mechanism, which increased the amount of organic matter ingested relative to the organic content of the seston filtered. The total amount of ingested matter at concentrations ranging from 1.6 to 100 mg l<sup>-1</sup> was approximately twice that reported by Hawkins et al. (1990) for the same species, possibly because they used a very low food concentration (20 × 10<sup>3</sup> particles ml<sup>-1</sup>) with a higher organic content, which could result in similar organic ingestion rate to that obtained in the present study (around 0.8 mg h<sup>-1</sup>). Our results therefore indicate that *C. edule* has a very efficient mechanism of regulating the amount of food ingested over a very wide range of seston concentrations, by simultaneously reducing clearance rate and increasing production of pseudofaeces.

Net absorption efficiency, unlike gross absorption efficiency, takes into consideration the organic matter which is secreted or abraded inside the gut lumen during the process of digestion and absorption, and which is not then absorbed but eliminated together with the faeces (Hawkins & Bayne 1985, 1992). Absorption efficiency in filter-feeding bivalves has been reported as a physiological process highly affected by the quantity and quality of the diet (Bayne & Newell 1983). At algal cell concentrations below the threshold of pseudofaeces production the absorption efficiency for species of *Mytilus* has been found to decline with increasing ingestion rate (Thompson & Bayne 1972, 1974, Widdows 1978, Navarro & Winter 1982). Although when bivalves are feeding on diets similar to those found in the natural environment, many species appear to have preingestive mechanisms to select and preferentially ingest organic particles from the seston. The organic content of the food ingested is therefore the main factor determining absorption efficiency (Bricelj & Malouf 1984, Iglesias et al. 1992, Navarro et al. 1993). Net absorption efficiency (AE) measured in the present study was high (50 to 70%) and very constant at the lower seston concentrations (1.6 to 34 mg l<sup>-1</sup>), declining only slightly up to seston concentrations of 300 mg l<sup>-1</sup>. This lack of a negative relationship between TPM and AE is primarily due to the occurrence of a constant ingestion

rate over this range (Fig. 8). The slight reduction of AE between 34 and 300 mg l<sup>-1</sup> can be explained by the slight increase in ingestion rate. The decline in AE at the higher seston concentrations tested is probably due to the rapid decrease in the quantity and quality of food ingested combined with the negative effect of metabolic faecal losses. According to Hawkins & Bayne (1992) and Navarro et al. (1994), this organic component forms a constant fraction of the food ingested and will therefore represent an increasing proportion of the faecal organic content and will lower absorption efficiency in response to ingested seston with low organic content. Our results are in good agreement with the findings of these authors, because absorption efficiency was markedly reduced when *Cerastoderma edule* ingested seston with an organic content lower than 0.2 (Fig. 9b). From our results, negative values of absorption efficiency are predicted at high seston concentrations with organic contents lower than 0.14. Similar results were obtained by Cranford (1995), with zero absorption efficiencies for *Placopecten magellanicus* at rations with organic contents of 0.14. Navarro et al. (1992) also reported similar results of AE for *C. edule*, with zero values at rations with organic content around 0.09. According to Navarro et al. (1992), the organic content at which absorption efficiency reaches zero can be used as an index of the capacity of the animal to survive in environments with low quality diets. However, this single parameter is not enough, and it is also necessary to consider other physiological parameters (e.g. metabolic costs) to establish whether an animal has the energy available to survive (to grow and reproduce) in a given environment.

Absorption rate was very constant throughout a wide range of seston concentrations (1.6 to 300 mg l<sup>-1</sup>), mainly as the result of the almost constant absorption efficiency between 1.6 and 200 mg l<sup>-1</sup> (Fig. 9a) and the highly regulated organic ingestion rate between this range (Fig. 8). Our results suggest that at concentrations above 300 mg l<sup>-1</sup> the energy intake of *Cerastoderma edule* is significantly reduced as a result of the reductions in clearance rate, filtration rate, ingestion rate and absorption efficiency. *C. edule* is therefore a species which can compensate efficiently for a decrease in seston quality (0.4 to 0.2) over a wide range of seston concentrations (1.6 to 300 mg l<sup>-1</sup>) by maintaining an effective preingestive mechanism of selection for organic particulate matter, as well as increasing filtration and rejection rates. As a consequence, this species is well adapted to living in environments with marked fluctuations in seston quality and quantity caused by resuspension of fine sediments during periods of high current velocities on the flood or ebb tides.

**Acknowledgements.** The authors gratefully acknowledge M. Brinsley, P. Salkeld and F. Staff for their help during this study and to the British Council and Fundación Andes of Chile for post doctoral support to J.M.N. This is LOIS publication number 91 of the LOIS Community Research Programme, carried out under a Special Topic Award from the Natural Environment Research Council.

#### LITERATURE CITED

- Anderson FE, Meyer LM (1986) The interaction of tidal currents on a disturbed intertidal bottom with a resulting change in particulate matter quantity, texture and food quality. *Estuar Coast Shelf Sci* 22:19–29
- Bayne BL, Hawkins AJS (1990) Filter feeding in bivalve molluscs: controls on energy balance. In: Mellinger J, Truchot JP, Lahlou B (eds) *Animal nutrition and transport processes*, No. 1. Nutrition in wild and domestic animals. *Comparative physiology*, Vol 5. Karger, Basel, p 70–83
- Bayne BL, Hawkins AJS, Navarro E (1987) Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *J Exp Mar Biol Ecol* 111:1–22
- Bayne BL, Hawkins AJS, Navarro E, Iglesias JIP (1989) Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. *Mar Ecol Prog Ser* 55: 47–54
- Bayne BL, Iglesias JIP, Hawkins AJS, Navarro E, Heral M, Deslous-Paoli JM (1993) Feeding behaviour of the mussel, *Mytilus edulis* L.; responses to variations in both quantity and organic content of seston. *J Mar Biol Assoc UK* 73: 813–829
- Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: de Saleuddin ASMM, Wilbur KM (eds) *The Mollusca*, Vol 4. *Physiology*, part 1. Academic Press, New York, p 407–515
- Berg JA, Newell RIE (1986) Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar Coast Shelf Sci* 23: 375–386
- Bricelj VM, Malouf RE (1984) Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. *Mar Biol* 84: 155–165
- Conover RJ (1966) Assimilation of organic matter by zooplankton. *Limnol Oceanogr* 11:338–345
- Cranford PJ (1995) Relationships between food quantity and quality and absorption efficiency in the sea scallops *Placopecten magellanicus* (Gmelin). *J Exp Mar Biol Ecol* 189: 123–142
- Falconer RA, Owens PH (1990) Numerical modelling of suspended sediment fluxes in estuarine waters. *Estuar Coast Shelf Sci* 31:745–762
- Foster-Smith RL (1975) The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). *J Exp Mar Biol Ecol* 17:1–22
- Hawkins AJS, Bayne BL (1985) Seasonal variation in the relative utilisation of carbon and nitrogen by the mussel *Mytilus edulis*: budgets, conversion efficiencies and maintenance requirements. *Mar Ecol Prog Ser* 25:181–188
- Hawkins AJS, Bayne BL (1992) Physiological interrelations, and the regulation of production. In: Gosling E (ed) *The mussel Mytilus: ecology, physiology, genetics and culture*. Elsevier Science Publishers, Amsterdam, p 171–222
- Hawkins AJS, Navarro E, Iglesias JIP (1990) Comparative

- allometries of gut content, gut passage time and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. Mar Biol 105:197–204
- Hawkins AJS, Smith RFM, Bayne BL, Héral M (1996) Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis* L. Mar Ecol Prog Ser 131:179–190
- Iglesias JIP, Navarro E, Alvarez-Jorna P, Armentia Y (1992) Feeding, particle selection and absorption in cockles *Cerastoderma edulis* exposed to variable conditions of food concentration and quality. J Exp Mar Biol Ecol 162:177–198
- Iglesias JIP, Urrutia MB, Navarro E, Alvarez-Jorna P, Larretxea X, Bougrier S, Héral M (1996) Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. J Exp Mar Biol Ecol 162:177–198
- Kjørboe T, Møhlenberg F (1981) Particle selection in suspension-feeding bivalves. Mar Ecol Prog Ser 5:291–296
- Navarro E, Iglesias JIP (1993) Infaunal-filter-feeding bivalves and the physiological response to short term fluctuations in food availability and composition. In: Dame RF (ed) Bivalve filter feeders in estuarine and coastal ecosystems processes. NATO ASI Series, Vol G 33. Springer-Verlag, Heidelberg, p 25–56
- Navarro E, Iglesias JIP, Ortega M (1992) Natural sediment as a food source for the cockle *Cerastoderma edule* (L.): effect of variable particle concentration on feeding, digestion and the scope for growth. J Exp Mar Biol Ecol 156:69–87
- Navarro E, Iglesias JIP, Ortega M, Larretxea X (1994) The basis for a functional response to variable food quantity and quality in cockles *Cerastoderma edule* (Bivalvia, Cardiidae). Physiol Zool 67:468–496
- Navarro E, Iglesias JIP, Perez Camacho A, Labarta U, Beiras R (1991) The physiological energetics of mussels (*Mytilus galloprovincialis* Lmk.) from different cultivation rafts in the Ria de Arosa (Galicia, N.W. Spain). Aquaculture 94:197–212
- Navarro JM, Clasing E, Urrutia G, Asencio G, Stead R, Herrera C (1993) Biochemical composition and nutritive value of suspended particulate matter over a tidal flat of southern Chile. Estuar Coast Shelf Sci 37:59–73
- Navarro JM, Thompson RJ (1994) Comparison and evaluation of different techniques for measuring absorption efficiency in suspension feeders. Limnol Oceanogr 39:159–164
- Navarro JM, Winter JE (1982) Ingestion rate, assimilation efficiency and energy balance in *Mytilus chilensis* in relation to body size and different algal concentrations. Mar Biol 67:255–266
- Newell RIE, Bayne BL (1980) Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium (Cerastoderma) edule* (Bivalvia: Cardiidae). Mar Biol 56:11–19
- Newell RIE, Jordan SE (1983) Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. Mar Ecol Prog Ser 13:47–53
- Riisgard HU, Randlov A (1981) Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar Biol 61:227–234
- Shumway SE, Cucci TL, Newell RC, Yentsch CM (1985) Particle selection, ingestion and absorption in filter-feeding bivalves. J Exp Mar Biol Ecol 91:77–92
- Taghon GL (1981) Beyond selection: optimal ingestion rate as a function of food value. Am Nat 118:202–214
- Thompson RJ, Bayne BL (1972) Active metabolism associated with feeding in the mussel *Mytilus edulis* L. J Exp Mar Biol Ecol 8:191–212
- Thompson RJ, Bayne BL (1974) Some relationships between growth, metabolism and food in the mussel, *Mytilus edulis*. Mar Biol 27:317–326
- Urrutia MB, Iglesias JIP, Navarro E, Prou J (1996) Feeding and absorption in *Cerastoderma edule* under environmental conditions in the bay of Marennes-Oleron (W. France). J Mar Biol Assoc UK 76:431–450
- Widdows J (1978) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J Mar Biol Assoc UK 58:109–124
- Widdows J, Fieth P, Worrall CM (1979) Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar Biol 50:195–207
- Willows RI (1992) Optimal digestive investment: a model for filter feeders experiencing variable diets. Limnol Oceanogr 37:829–847
- Winter JE (1976) Feeding experiments with *Mytilus edulis* L. at small laboratory scale. II. The influence of suspended silt in addition to algal suspensions on growth. In: Persoone G, Jaspers E (eds) Proc 10th Eur Mar Biol Symp, Vol 1. Universa Press, Wetteren, p 583–600
- Winter JE (1978) A critical review on some aspects of filter-feeding in lamellibranchiate bivalves. Haliotis 7:71–87
- Winter JE, Acevedo MA, Navarro JM (1984) Quempillén estuary, an experimental oyster cultivation station in Southern Chile. Energy balance in *Ostrea chilensis*. Mar Ecol Prog Ser 20:151–164

This article was submitted to the editor

Manuscript first received: September 24, 1996

Revised version accepted: April 7, 1997