Feeding physiology of infaunal (*Mulinia edulis*) and epifaunal (*Mytilus chilensis*) bivalves under a wide range of concentrations and qualities of seston

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ABSTRACT: A comparative study was carried out on the functional feeding behavior of the infaunal clam *Mulinia edulis* and the epifaunal mussel *Mytilus chilensis* from Yaldad Bay, southern Chile, in response to broad fluctuations in quantity and quality of seston. A number of physiological variables were quantified and compared, including clearance, filtration and ingestion rates; pseudofeces production and pre-ingestive selection efficiency. Relative sizes of the ctenidia and labial palps were measured for both species to determine if the size of the organs was related to their capacity for filtration and pre-ingestive particle selection. Both species showed high rates of clearance at lower seston concentrations (<3 to 5 mg l^{-1}). Above these concentrations, both species regulated both the quantity and quality of material ingested. When the seston concentration was relatively low and/or its quality high, regulation of food ingested was accomplished primarily by reduction in clearance rate, while at high seston concentrations and/or low quality, this parameter was regulated primarily by the expulsion of pseudofeces with a lower content of organic matter. Ingestion regulation was higher in *M. chilensis*. In general, both species showed a capacity for pre-ingestive particle selection, which increased with seston concentration and the proportion of organic matter present. In diets containing more than 60 % organic matter, selection efficiency in *M. chilensis* became slightly reduced, while in *M. edulis* it remained stable; this observation is explained by the larger relative size of the labial palps in *Mulinia edulis*. Generally, feeding rates of *M. chilensis* were higher than those of *M. edulis*; this may be attributable to the former's larger-sized ctenidia, which are able to filter more food.

KEY WORDS: *Mulinia edulis* · *Mytilus chilensis* · Infaunal and epifaunal bivalves · Feeding behavior · Particle selection · Diet quality · Chile tidal flats

INTRODUCTION

Numerous species of bivalve filter-feeders inhabit the estuaries and tidal flats in southern Chile, often at high population densities. The seston in these regions, upon which the bivalves feed, commonly undergoes major fluctuations in concentration and quality, as it participates in sedimentation and resuspension cycles produced by the extreme tidal ranges in this ecosystem (Rojas 1984, Navarro et al. 1993). One of the bivalves present is the infaunal clam *Mulinia edulis* King, 1831, which inhabits the low intertidal zone (Jaramillo et al. 1985, Asencio et al. 1993). Also present in this region is the epibenthic mussel *Mytilus chilensis* Hupe, 1854, which lives attached to hard substrates in the medium-high intertidal zone (Winter et al. 1982). *M. edulis* is exposed to greater fluctuations in seston than *M. chilensis*, as the former occupies very fine sediments that are more easily resuspended than those of the coarser sands around mussel habitats (Winter et al. 1982, Clasing et al. 1998).

Numerous studies have examined the feeding physiology of filter-feeding bivalves as it relates to the concentration and quality of the seston (Winter 1970,

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Foster-Smith 1975, Kiørboe & Møhlenberg 1981, Newell & Jordan 1983, Iglesias et al. 1992, 1996, Navarro et al. 1992, 1994, Ward & MacDonald 1996, Navarro & Widdows 1997). These studies suggest that both infaunal and epifaunal bivalves are able to affect pre-ingestive particle selection, which improves the quality of the matter ingested. In this manner, these organisms are able to adjust their feeding rates in order to maximise their acquisition of energy and avoid functional problems associated with particle saturation. A majority of studies on this topic were carried out using a narrow range of seston concentrations (2 to 30 mg l^{-1}) in seawater that did not necessarily reflect natural seston concentrations, which may range to over 100 mg l^{-1} with extreme values of 500 mg l^{-1} (Falconer & Owens 1990). The few studies which have included high ranges of seston concentration (>100 mg l^{-1}) used natural seston or diets made up of varying quantities of sediment to which known amounts of phytoplankton had been added (Widdows et al. 1979, Hawkins et al. 1996, Urrutia et al. 1996, Navarro & Widdows 1997). In these studies, the concentration of seston was inversely correlated with the proportion of organic matter, and thus the physiological responses recorded were difficult to interpret due to simultaneous changes in the quality and quantity of the seston.

The present laboratory study was carried out using cultured algae mixed with natural fine sediment to elucidate the functional responses of infaunal (*Mulinia edulis*) and epibenthic (*Mytilus chilensis*) bivalves exposed to broad fluctuations in the availability and quality of food material in the seston. Measurements were made on several physiological variables related to feeding, including clearance, filtration and ingestion rates, production of pseudofeces and pre-ingestive selection efficiency. Other measurements included areas of the ctenidia and labial palps of these bivalves to determine any relationship between the size of these organs and their relative capacity for filtration and pre-ingestive selection of particles from the seston.

MATERIALS AND METHODS

Collection and acclimation of bivalves. Adult *Mulinia edulis* and *Mytilus chilensis* were collected from the tidal flat at Yaldad Bay, Chile (43° 08′ S; 73° 44′ W) and maintained in continuously flowing natural seawater enriched with laboratory-cultured microalgae (*Isochrysis galbana*) at 14°C and a salinity of 30‰, which represented typical annual averages for this bay (Navarro et al. 1993). Thirty specimens of each species were collected, with *M. edulis* individuals measuring 50.2 ± 1.1 mm in length and 1.36 ± 0.36 g in dry tissue weight, and the *M. chilensis* individuals measuring 50.7 ± 0.7 mm and 1.04 ± 0.36 g dry tissue weight.

Feeding experiments. Experimental diets were prepared by mixing cultured microalgae (*Isochrysis galbana*) with natural sediment collected from the top (0.5 cm) of the tidal flat at Yaldad, with the aim of simulating ranges of concentration and organic matter content typically measured at this location. The sediment was diluted in seawater and screened through a 40 μm mesh screen. The microalgae were cultured in f/2 medium (Guillard 1974) and had a particle size ranging between 3 and 7 μm spherical diameter; they contained 70 to 90% organic material. The sediment particles were in the 3 to 15 μm size range and contained 13 to 15% organic material; 100% of the microalgae particles were smaller than 7 μm, whereas only 80% of the sediment particles were smaller than 7 μm. Quantification of the contents of each diet was as follows: the number of particles equivalent to 1 mg dry weight was determined on 3 replicates of each basic solution of algae and sediment, with each replicate divided into 2 subsamples. Of these 2 subsamples, 1 was analyzed with an ELZONE 180 XY particle counter using an aperture opening of 120 μm (detecting particles between 2.9 and 75.6 μm diameter) which estimated the total particulate matter (TPM) as particles per liter. The second subsample was analyzed for total dry weight and particulate organic matter using the methods of Strickland & Parsons (1972). Each subsample was filtered on glass-fiber filters (diameter = 0.45 μm; Millipore) which had been previously washed with distilled water, ashed at 450°C for 4 h, and weighed. The filtrate was washed with 3% ammonium formate, dried at 70°C for 48 h, and weighed; the net dry weight represented the total seston (TPM, mg l^{-1}) in the diet. The particulate organic material (POM) content of the samples was determined from the ash-free dry weight, obtained by ashing the filters at 450°C for 4 h and re-weighing.

A total of 48 feeding experiments were carried out, each consisting of a different diet, with variations between 1.91 and 203.13 mg l^{-1} and organic material percentages between 18 and 91%. Each experiment lasted 5 h; the first 2 h were used to acclimate the bivalves to the diet, and physiological measurements were made during the subsequent 3 h. The acclimation time represented the time required for ingested particles to appear in the feces of the organisms, determined using particles containing fluorescent markers. This assured that the digestive tract contained particles of the experimental diet being tested. Diets were administered using an open system comprising 18 bivalve chambers, a constant flow of seawater, a vessel containing the basic diet (sediment + microalgae), and a peristaltic pump that delivered measured dosages to a mixing chamber from which the diet flowed continuously to each chamber containing the test bivalves. Each experiment was comprised of 8 replicates per species and a control chamber, which contained a pair of empty valves of the

corresponding species in order to correct for the retention and/or sedimentation of particles in the chambers arising from physical factors.

Physiological measurements. Clearance, filtration, rejection and ingestion rates were carried out as follows.

Clearance rate: This rate was determined by measuring the difference between particles in the control chambers (C_1) and experimental chambers, each containing a bivalve (C_2) every 30 min during each experiment. At the same time, flow rate (F) was determined for each chamber, and a difference of 20 to 40% in particle numbers was maintained between the chambers containing bivalves and the control chambers as described by Navarro & Thompson (1996). Clearance rate (CR) was calculated from:

$$CR\ (l\ h^{-1})\ =\ F \times [(C_1 - C_2)/C_1]$$

Filtration rate: The quantities of total (FR) and organic particulate matter (OFR) removed from the water per unit time were estimated from the following equations (Widdows 1985):

$$FR\ (mg\ h^{-1})\ =\ CR \times TPM$$
$$OFR\ (mg\ h^{-1})\ =\ CR \times POM$$

Rejection rate and pre-ingestive selection efficiency: At the end of each experiment, pseudofeces were collected quantitatively with Pasteur pipettes, and their dry weight and organic matter content were measured following the same methods as described for the seston. The rate of total production of pseudofeces and organic matter (RR and ORR, mg h^{-1}) were calculated by dividing the total pseudofeces produced by the time of duration of each experiment.

The efficiency of pre-ingestive selection (SE) represented the efficiency with which particles of higher organic content were retained for ingestion. This was calculated after Bayne et al. (1993) as:

$$SE\ =\ 1 - (p/f) \times 100$$

where p = % organic matter in pseudofeces and f = % organic matter in the diet.

Ingestion rate: When no pseudofeces were produced, the total filtration and organic filtration rates represented the total ingestion rate (IR) and organic ingestion rate (OIR), respectively. With concurrent pseudofeces production, the ingestion rate was calculated by subtracting the total pseudofeces production rate (RR) or the organic pseudofeces production rate (ORR) (Bayne et al. 1993):

$$IR\ (mg\ h^{-1})\ =\ FR - RR$$
$$OIR\ (mg\ h^{-1})\ =\ OFR - O$$

Area of pallial organs. Thirteen specimens of *Mulina edulis* (length = 51.89 ± 0.59 mm) and 15 *Mytilus*

chilensis (length = 50.69 ± 0.86 mm) obtained from the Yaldad tidal flats were dissected to obtain the ctenidia and labial palps. The organs from individual specimens were spread on a flat surface and photographed and their surface areas were then determined using a Scion image program Version 3.0b.

Standardization and transformation of variables. The physiological rates and areas of pallial organs were converted to a 'standard' individual of 1 g tissue weight; for this, the soft tissues were dried at 70°C for 48 h and then individually weighed. Standardization employed the equation of Bayne et al. (1987):

$$Y_s\ =\ (W_s/W_e)^b \times Y_e$$

where Y_s = the clearance rate or area of pallial organs for an individual of standard weight, W_s = its standard weight, W_e = its observed weight, Y_e = the uncorrected measured clearance rate or area of its pallial organs, and b = the weight exponent. The weight exponents for clearance rates were 0.5 and 0.61 for *Mulinia edulis* and *Mytilus chilensis*, respectively. For the pallial organ area in both species, the weight exponents used were 0.1 and 0.61 for ctenidia and palps, respectively.

Statistical analysis. Tests for normality and homocedasticity were carried out on the physiological variables according to Sokal & Rohlf (1979). Clearance, filtration, and ingestion were $\log_{10}$-transformed, production of pseudofeces was transformed to square roots, and an arcsine transformation was applied to the selection efficiency data. Multiple linear and nonlinear regression analyses were carried out to determine the dependency of the physiological variables on the concentration and/or the quality of the seston. Analyses of covariance were applied to detect differences between the physiological variables between the 2 species. Finally, a 1-way ANOVA was carried out to reveal any differences between the organic fraction of the food and that of the pseudofeces produced by *Mulinia edulis* and *Mytilus chilensis*, as well as any differences between their pallial organ area. ANCOVA calculations were performed with the general linear model procedure (GLM) of the SAS 6.1 program (SAS Institute). The non-linear models and graphics were prepared using the least-squares estimation procedures and the quasi-Newton estimation method of the STATISTICA program. Significance levels were determined at $\alpha = 0.05$.

RESULTS

Clearance and filtration rates

Over the range of seston concentration tested (1 to 200 mg l^{-1}), the clearance rate for *Mulinia edulis* varied

Table 1. *Mulinia edulis* and *Mytilus chilensis*. Regressions (mean ± SE) between concentration of seston (total particulate matter, TPM), its organic content (particulate organic matter, POM) and feeding rates. CR: clearance rate; FR: total filtration rate; OFR: organic filtration rate; RR: rate of pseudofeces production; SE: efficiency of pre-ingestive selection; IR: total ingestion rate; OIR: organic ingestion rate

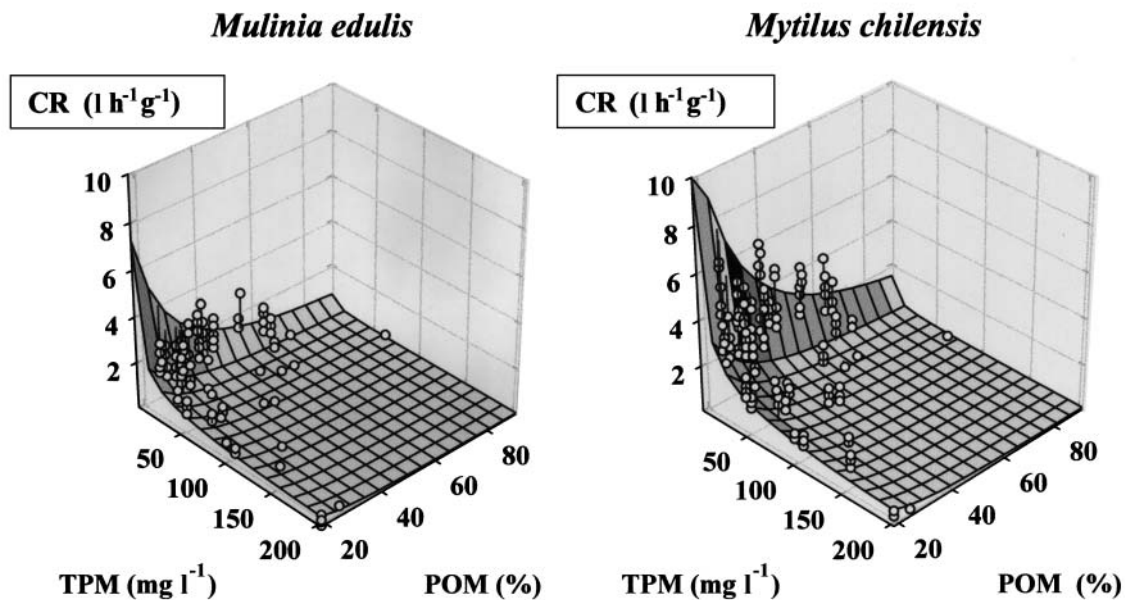| Equation	r^2	p <	n
Mulinia edulis			
$CR = 10^{(2.95\,[\pm 0.11] - 0.59\,[\pm\,0.02]\,\log_{10}TPM - 1.53\,[\pm 0.07]\,\log_{10}POM)}$	0.815	0.0001	341
$FR = 10^{(2.95\,[\pm 0.11] + 0.41\,[\pm 0.02]\,\times\,\log_{10}TPM - 1.53\,[\pm 0.07]\,\times\,\log_{10}POM)}$	0.815	0.0001	341
$OFR = 10^{(1.15\,[\pm 0.13] + 0.38\,[\pm 0.02]\,\times\,\log_{10}TPM - 0.61\,[\pm 0.08]\,\times\,\log_{10}POM)}$	0.671	0.0001	341
$RR = (-9.75\,[\pm 1.36] + 17.77\,[\pm 0.97]\,\log_{10}TPM + 5.19\,[\pm 0.85]\,\log_{10}POM$ $- 9.18\,[\pm 0.63]\,\log_{10}TPM \times \log_{10}POM)^2$	0.908	0.0001	273
$SE = 100 \times \sin\,(-5.41\,[\pm 1.60] + 1.66\,[\pm 0.54]\,\times\,\log_{10}TPM + 5.19\,[\pm 1.75]$ $\times\,\log_{10}POM - 0.62\,[\pm 0.27]\,\times\,\log_{10}TPM \times \log_{10}POM - 0.20\,[\pm 0.07]$ $\times\,[\log_{10}TPM]^2 - 1.16\,[\pm 0.50]\,\times\,[\log_{10}POM]^2)$	0.255	0.0229	180
$IR = 10^{(1.09\,[\pm 0.11] + 0.57\,[\pm 0.13]\,\times\,\log_{10}TPM - 0.16\,[\pm 0.06]\,\times\,\log_{10}TPM^2 - 0.26\,[\pm 0.03]\,\times\,[\log_{10}POM])}$	0.528	0.0044	211
$OIR = 0.69\,(\pm 0.19) + 2.69\,(\pm 0.17)\,\times\,\log_{10}TPM$	0.532	0.0001	211
Mytilus chilensis			
$CR = 10^{(2.94\,[\pm 0.14] - 0.61\,[\pm 0.02]\,\times\,\log_{10}TPM - 1.33\,[\pm 0.08]\,\times\,\log_{10}POM)}$	0.826	0.0001	274
$FR = 10^{(2.95\,[\pm 0.14] - 0.39\,[\pm 0.02]\,\times\,\log_{10}TPM - 1.33\,[\pm 0.08]\,\times\,\log_{10}POM)}$	0.753	0.0001	274
$OFR = 10^{(0.96\,[\pm 0.14] + 0.39\,[\pm 0.012]\,\times\,\log_{10}TPM - 0.39\,[\pm 0.08]\,\times\,\log_{10}POM)}$	0.597	0.0001	274
$RR = (14.71\,[\pm 0.58] - 7.08\,[\pm 0.39]\,\log_{10}TPM \times \log_{10}POM)^2$	0.875	0.0001	239
$SE = 100 \times \sin\,(-6.95\,[\pm 1.18] + 1.43\,[\pm 0.29]\,\times\,\log_{10}TPM + 7.68\,[\pm 1.38]$ $\times\,\log_{10}POM - 0.45\,[\pm 0.15]\,\times\,\log_{10}TPM \times \log_{10}POM - 0.25\,[\pm 0.04]$ $\times\,[\log_{10}TPM]^2 - 2.08\,[\pm 0.41]\,\times\,[\log_{10}POM]^2)$	0.328	0.0026	289
$IR = 0.18\,(\pm 0.02)\,\times\,\log_{10}TPM + 0.35\,(\pm 0.02)\,\times\,\log_{10}POM - 0.0007\,(\pm 0.0001)$ $\times\,(\log_{10}TPM)^2 - 0.004\,(\pm 0.0004)\,\times\,(\log_{10}POM)^2$	0.363	0.0001	167
$OIR = -5.41\,(\pm 1.33) + 0.17\,(\pm 0.01)\,\times\,TPM + 0.35\,(\pm 0.06)$ $\times\,POM - 0.0007\,(\pm 0.0001)\,\times\,TPM^2 - 0.003\,(\pm 0.0034)\,\times\,POM^2$	0.594	0.0001	167

Fig. 1. *Mulinia edulis* and *Mytilus chilensis.* Relation between concentration of seston (TPM), its organic content (POM) and clearance rate (CR)

between 0.05 and 2.22 l h^{-1} g^{-1} while that of *Mytilus chilensis* was between 0.05 and 4.40 l h^{-1} g^{-1}. These values declined with increasing concentration of the seston and increasing percentage of the organic content of the seston (Fig. 1). The regression models that were best fitted to the effect of concentration and quality of the diet on the clearance rates are described by the equations in Table 1. Although the tendency appeared the same for both species, the ANCOVA demonstrated that the clearance rate of *M. chilensis* was significantly higher than that of *M. edulis* (Table 2) at any given seston concentration.

Over the spectrum of seston concentrations tested, the total filtration rate of *Mulinia edulis* varied between 2.65 and 144.19 mg h^{-1} g^{-1} and that of *Mytilus chilensis* between 3.28 and 189.81 mg h^{-1} g^{-1} (Fig. 2).

The organic filtration rate of *M. edulis* fluctuated between 1.33 and 17.09 mg h^{-1} g^{-1} while that of *M. chilensis* ranged between 2.93 and 35.07 mg h^{-1} g^{-1} (Fig. 2). In general terms, the total particulate matter and organic matter filtered by both species increased with increasing seston concentration. This increase was also noted when there was a decrease in the organic content of the seston (Fig. 2). The regression models that were best fitted to the effect of concentration and quality of the diet on the total and organic matter filtration rates are described by the equations in Table 1.

The ANCOVA showed that the rates of total and organic matter filtration by *Mytilus chilensis* were significantly greater than those of *Mulinia edulis* (Table 2).
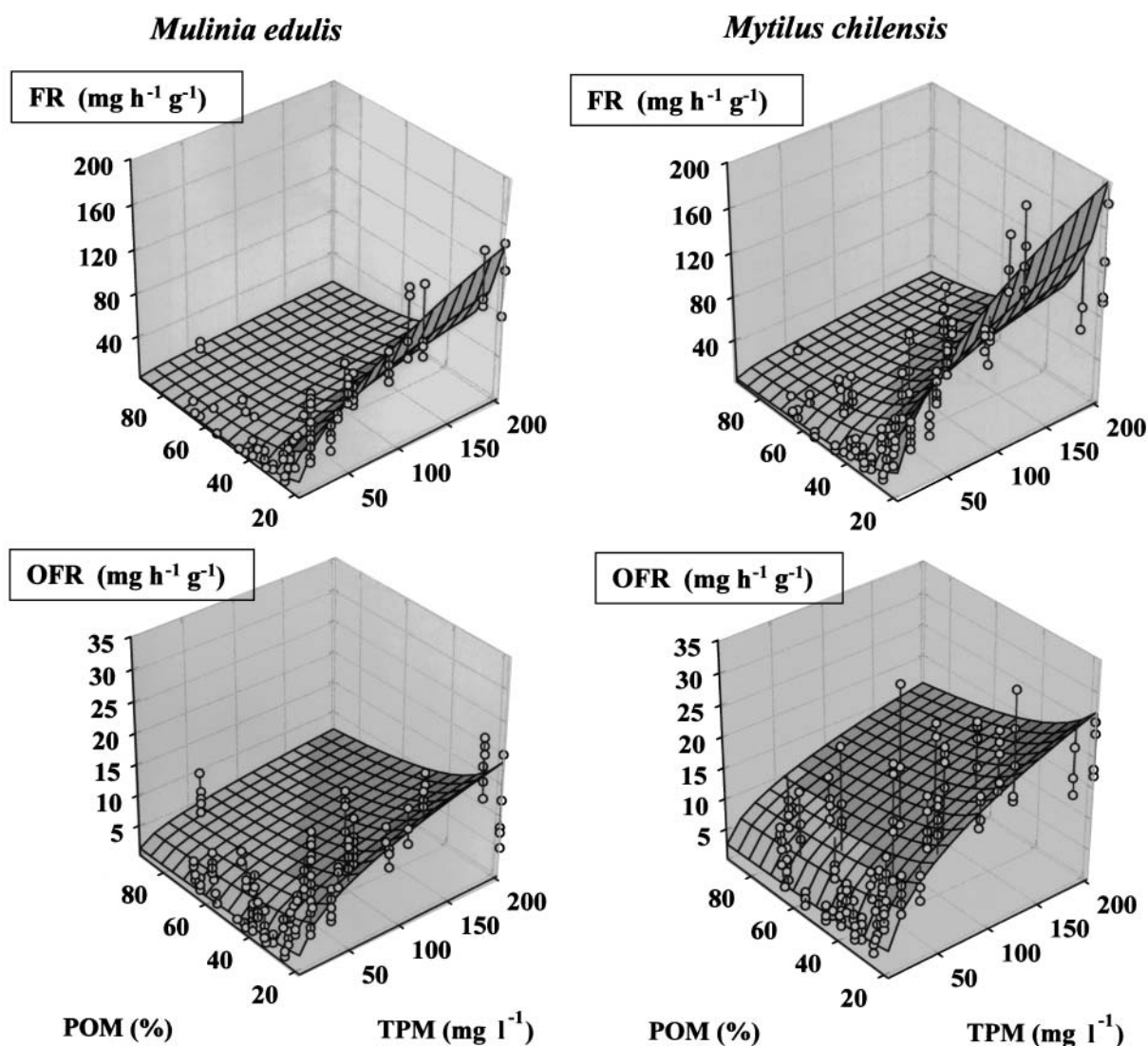

Fig. 2. *Mulinia edulis* and *Mytilus chilensis.* Relation between concentration of seston (TPM), its organic content (POM), total filtration rate (FR) and organic filtration rate (OFR)

Table 2. *Mulinia edulis* and *Mytilus chilensis.* ANCOVA for physiological variables (GLM procedure; model: physiological variable = species TPM or POM). p > |T| H_0: probability of getting a larger |T| value under the hypothesis. (1) *M. edulis* and (2) *M. chilensis.* (A very small value for this probability leads to the conclusion that the independent variable contributes significantly to the model.) CR: clearance rate; FR: total filtration rate; OFR: organic filtration rate, RR: rate of pseudofeces production; SE: efficiency of pre-ingestive selection; IR: total ingestion rate; OIR: organic ingestion rate

Physio-logical variable	Species	Least square (LS) mean	SE	p > |T| H_0: LS mean = 0	p > |T| H_0: LS mean (1) = LS mean (2)
CR	(1) *Mulinia edulis*	1.08	0.05	0.0001	0.0001
	(2) *Mytilus chilensis*	2.08	0.05	0.0001	
FR	(1) *M. edulis*	18.28	1.16	0.0001	0.0001
	(2) *M. chilensis*	33.08	1.33	0.0001	
OFR	(1) *M. edulis*	5.17	0.29	0.0001	0.0001
	(2) *M. chilensis*	9.90	0.32	0.0001	
RR	(1) *M. edulis*	7.69	0.82	0.0001	0.0001
	(2) *M. chilensis*	14.60	0.91	0.0001	
SE	(1) *M. edulis*	27.55	1.70	0.0001	0.7056
	(2) *M. chilensis*	28.49	1.37	0.0001	
IR	(1) *M. edulis*	8.13	0.29	0.0001	0.1275
	(2) *M. chilensis*	8.79	0.33	0.0001	
OIR	(1) *M. edulis*	3.28	0.16	0.0001	0.0001
	(2) *M. chilensis*	4.62	0.18	0.0001	

Rejection rate

Production of pseudofeces by *Mulinia edulis* began at seston concentrations just above 4.5 mg l^{-1} when the percentage of organic matter in the diet was 30%, and at 6 mg l^{-1} when the organic content was 60%. The production of pseudofeces in *Mytilus chilensis* occurred at seston concentrations just above 2.7 mg l^{-1}, with no apparent relation to organic matter content. At lower seston concentrations pseudofeces were produced sporadically in minor amounts; pseudofeces production increased as the amount of seston increased, and with a decrease in organic content (Fig. 3). The greatest production of pseudofeces occurred at 108.5 mg l^{-1} of seston for both species, reaching 134.5 mg h^{-1} g^{-1} in *M. edulis* and 177.4 mg h^{-1} g^{-1} in *M. chilensis.* The joint effect of concentration and quality of the diet on the production of pseudofeces is described in Table 1.

The ANCOVA showed significantly higher production of pseudofeces by *Mytilus chilensis* (Table 2).

Pre-ingestive selection efficiency

In both species, material rejected as pseudofeces had a significantly lower organic content than the diet offered (p = 0.001; Fig. 4). Selection efficiency of the particles varied between −4 and 65% in *Mulinia edulis* and between 1 and 66% in *Mytilus chilensis*. In both species the selection efficiency increased with increasing concentration and organic fraction of the seston; however, at levels greater than 60% organic matter, *M. chilensis* showed a mild reduction in its selective capacity, while
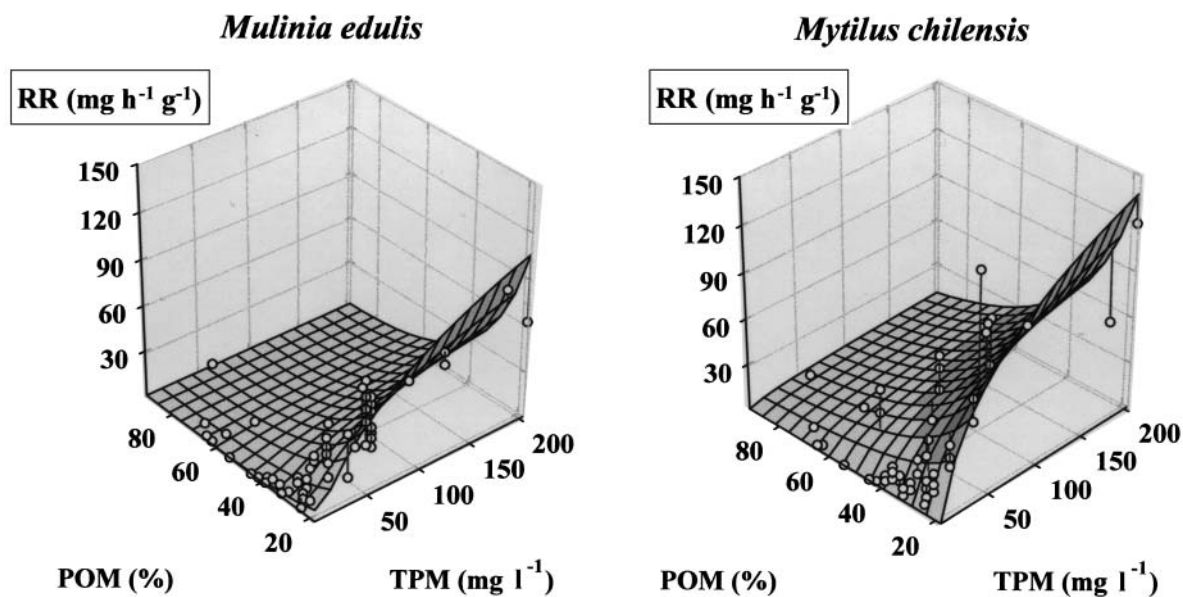

Fig. 3. *Mulinia edulis* and *Mytilus chilensis.* Relation between concentration of seston (TPM), its organic content (POM) and the rate of production of pseudofeces (RR)

this parameter became stable in *M. edulis* (Fig. 5). Table 1 presents the equations which best describe the seston effects on selection efficiency.

ANCOVA revealed no significant differences between the selective efficiencies of the 2 species (Table 2).

Ingestion rate

Over the range of seston concentrations tested (1 to 200 mg l^{-1}), the total ingestion rate fluctuated between 2.65 and 19.58 mg h^{-1} g^{-1} in *Mulinia edulis* and between 2.06 and 22.12 mg h^{-1} g^{-1} in *Mytilus chilensis*, whereas organic ingestion varied between 1.31 and 7.8 mg h^{-1} g^{-1} in *M. edulis* and between 2.02 and 15.65 mg h^{-1} g^{-1} in *M. chilensis*. The ingestion rate of *M. edulis* increased up to 10–20 mg l^{-1}, and then remained stable at the higher concentrations. *M. chilensis* showed a sustained increase up to 100 mg l^{-1} g^{-1}, decreasing thereafter (Fig. 6). An increase in total and organic ingestion with decreasing organic fraction of the diet was observed in both species except for the organic ingestion rate of *M. edulis*. In *M. chilensis* there was also a decline, with the seston containing less than 40 % organic matter. The regression models which best describe these relations in the 2 species are detailed in Table 1.

The ANCOVA showed that there were no significant differences between total ingestion rates of the 2 species, whereas the organic ingestion rates of *Mytilus chilensis* was significantly higher than that of *Mulinia edulis* (Table 2).
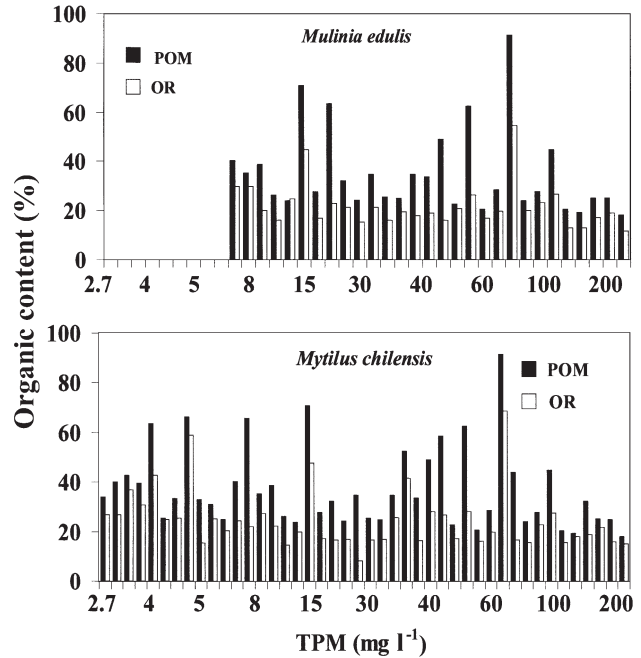

Fig. 4. *Mulinia edulis* and *Mytilus chilensis.* Relation between organic content of food (POM) and that of pseudofeces (OR) produced at different seston concentrations (TPM) in the laboratory

Area of pallial organs

In *Mulinia edulis*, the ctenidial area measured about 0.71 mm^2 g^{-1}, whereas this value was 1.29 mm^2 g^{-1} for *Mytilus chilensis*. The labial palps of *M. edulis* mea-
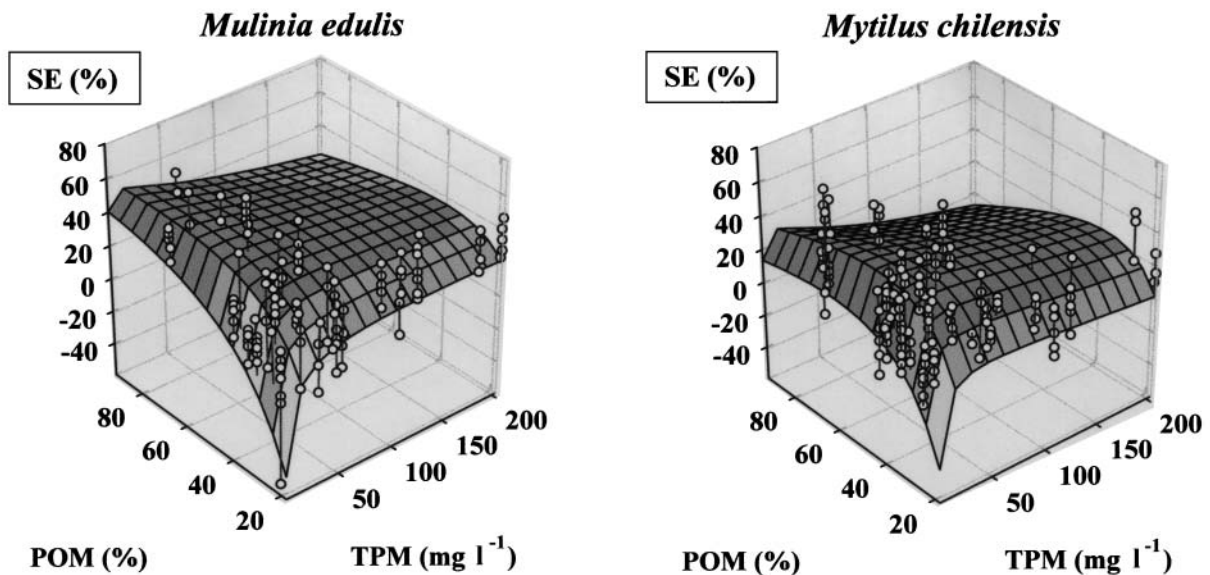

Fig. 5. *Mulinia edulis* and *Mytilus chilensis.* Relation between concentration of seston (TPM), its organic content (POM) and efficiency of pre-ingestive selection (SE)
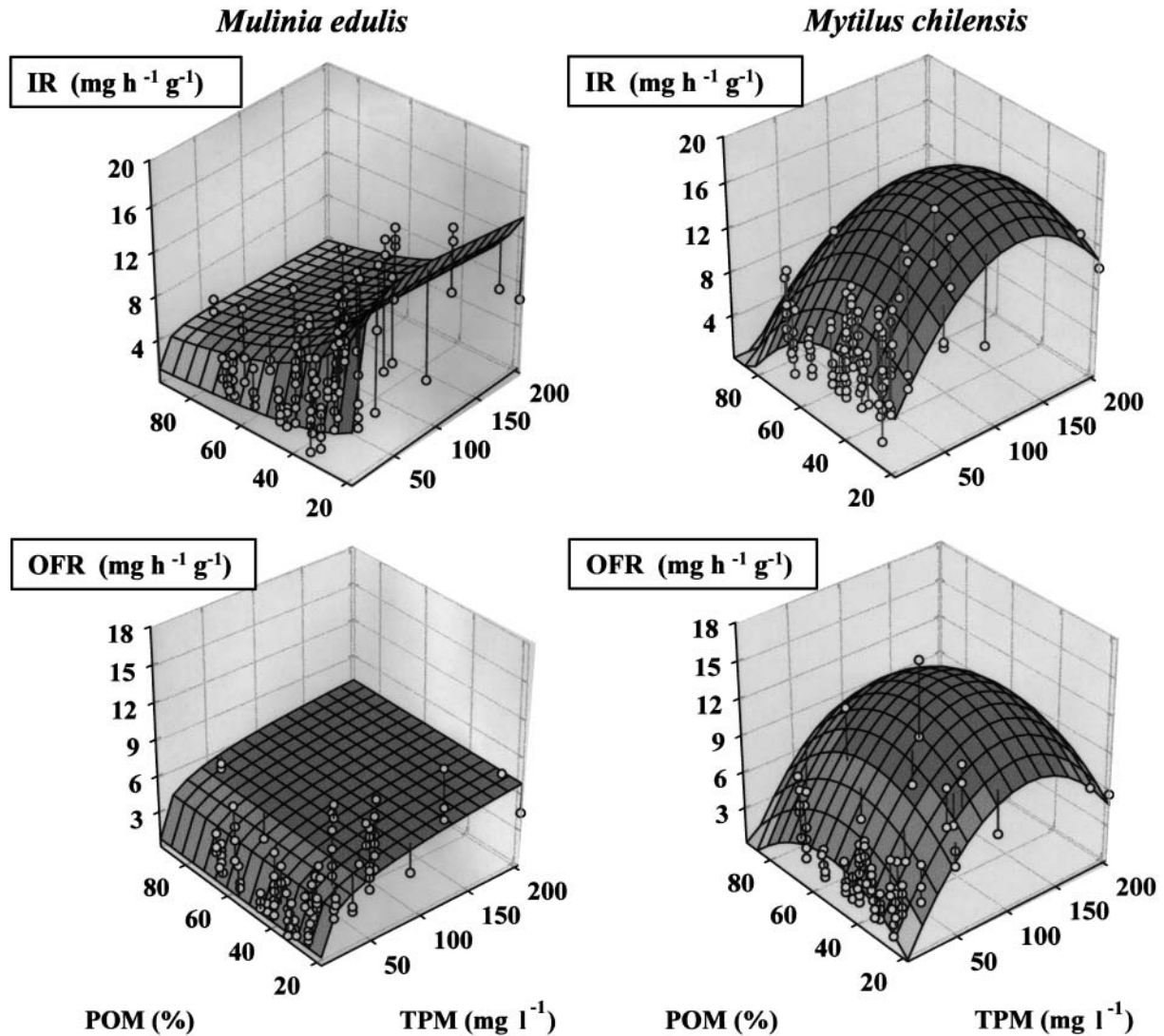
Fig. 6. *Mulinia edulis* and *Mytilus chilensis*. Relation between concentration of seston (TPM), its organic content (POM), rates of total ingestion (IR) and organic ingestion (OIR)

sured about 0.23 mm^2 g^{-1} of the organism, while this parameter was 0.1 mm^2 g^{-1} for *M. chilensis*. The ANCOVA showed that the ctenidial area of *Mulinia* was significantly higher than that of *M. chilensis* (df = 26, *F* = 141.1, p = 0.0001), while the labial palps area of *M. edulis* was significantly lower than that of *M. chilensis* (df = 26, *F* = 57.4, p = 0.0001).

DISCUSSION

Clearance and filtration rates

The higher rates of clearance in *Mulinia edulis* and *Mytilus chilensis* with lower concentrations and qual-

ity of seston has been observed in other bivalves, and has been explained as a mechanism for maximising food uptake during periods of limited food availability (Bayne et al. 1987, Willows 1992). The decrease in feeding rate with increased seston concentration may be a response mechanism for the regulation of ingestion rate to avoid saturation of the ctenidia and labial palps (Iglesias et al. 1992). The reduction in clearance rate with increasing seston quality has been described as a mechanism to conserve energy when pre-ingestive selection efficiency is irrelevant, as with monoalgal diets (Navarro et al. 1992). Thus, both species studied control the amount of particles retained by means of reducing water flow through the ctenidia and/or perhaps closing the ventral feeding tracts, as

has been observed in various bivalve species (Ward et al. 1994, Beninger et al. 1997). The decline in clearance rate may also be due to other factors, such as reduction in retention efficiency of small particles (<7 µm) by the ctenidia when there is an increase in seston, as observed in other bivalves (Wilson 1983, Barillé et al. 1993, 1997). The same inverse relationship of clearance rate to seston concentration has been described for other bivalves, such as *Arctica islandica* (Winter 1970), *Cerastoderma edule* (Navarro et al. 1992, 1994, Iglesias et al. 1996, Urrutia et al. 1996, Navarro & Widdows 1997), *M. chilensis* (Navarro & Winter 1982), and *M. edulis* (Winter 1976, Widdows et al. 1979, Kiørboe et al. 1980, 1981, Clausen & Riisgård 1996). Other authors found that the clearance rate was independent of the concentration of seston (Møhlenberg & Kiørboe 1981, Cranford et al. 1998), and yet others have observed increases in clearance rate with an increase in seston concentration (Newell & Shumway 1993, Hawkins et al. 1996, Urrutia et al. 1996). These variations are related to the different types of particles in the seston and the range of seston concentration used in the studies cited (Hawkins et al. 2001).

Although the feeding activity of *Mulinia edulis* and *Mytilus chilensis* decreased with increasing seston concentration, the amount of seston and amount of organic matter filtered increased. It was also found that the increases in total and organic matter filtration by both species that occurred when the organic content of the diet decreased was due to a slight increase in clearance rate. This relationship has also been observed in other bivalves such as *Cerastoderma edule* (Navarro et al. 1994, Iglesias et al. 1996, Hawkins et al. 1998), *Crassostrea gigas* (Hawkins et al. 1998), and *Mytilus edulis* (Bayne et al. 1993).

The higher rates of clearance and filtration observed in *Mytilus chilensis* support the results from earlier studies that compared epifaunal non-siphonate species with infaunal siphonate species (Tenore & Dunstan 1973, Foster-Smith 1975, Bacon et al. 1998). This difference may be related to the higher water-pumping rate in the pallial cavity of *M. chilensis*, a greater efficiency in the retention of small particles, and/or a larger ctenidial surface compared with the infaunal species. However, as Jørgensen & Riisgård (1988) and Jørgensen (1990) demonstrated that frictional resistance to flow is very low even in long siphons, and Grizzle et al. (1992) demonstrated that siphonate taxa typically have greater inhalant pumping speeds than non-siphonate taxa, it is improbable that the water-pumping rate is lower in siphonate species. Although the retention efficiency of small particles was not examined, this was unlikely to have been a factor in the differences observed in clearance rates between the 2 species, since in the diet 80% of the particles were greater than 4 µm in diameter, i.e. in the size range that is retained with 100% efficiency (Vahl 1973, Bayne & Newell 1983). Accordingly, the most probable reason for the higher feeding rates in *M. chilensis* is its large ctenidia, which can retain larger quantities of particulate material than the small ctenidia of *Mulinia edulis*. The relationship between ctenidial area per unit weight and clearance rate has previously been described at interspecific (Foster-Smith 1975, Hawkins et al. 1990) and intraspecific (Jones et al. 1992, Bayne 1993) levels. Also, the greater feeding activity of *M. chilensis* could be related to its type of ctenidia and its superior capacity for processing the material that these retain: whereas *Mulinia edulis* is a homorhabdic eulamellibranch, *M. chilensis* is a homorhabdic filibranch. According to Ward et al. (1993) and Beninger et al. (1997), homorhabdic eulamellibranchs can transport retained particles toward the labial palps only by means of the ventral tracts, whereas homorhabdic filibranchs are able to transport them by both ventral and dorsal tracts.

Rejection rate and pre-ingestive selection efficiency

The capacity for processing particulate food is subject to certain limitations, above which excess retained food is rejected in the form of pseudofeces. It is not clear if this limitation is morphological or functional, or whether it is imposed by the digestive tract, the ctenidia and/or labial palps. According to Bayne et al. (1989), maximum ingestion coincides with the seston concentration at which pseudofeces production begins. In the present study, however, the highest ingestion rates for both species were obtained at seston concentrations above the threshold levels for pseudofeces production. It is thus probable that pseudofeces production did not arise from saturation of the digestive tract.

The threshold for production of pseudofeces in *Mulinia edulis* was higher than that in *Mytilus chilensis*. This was related to the lower quantity of material retained on the smaller ctenidia of *M. edulis*: the larger labial palps become saturated at seston concentrations higher than the saturation concentrations for *M. chilensis*, which has large ctenidia and small labial palps. Navarro et al. (1992) associated the higher threshold of pseudofeces production in *Cerastoderma edule* with this species' higher capacity to reduce clearance rates compared to *M. edulis*. This situation appears hardly probable for *M. chilensis* and *M. edulis*, since they have similar capacities for reducing their clearance rates (the slopes relating these rates to seston concentration were –0.61 for *M. chilensis* and –0.60 for *M. edulis*). On a better-quality diet, the threshold for pseudofeces production was higher in *M. edulis*,

but not in *M. chilensis.* (*C. edule* showed similar behavior to that of *M. edulis*: Iglesias et al. 1996.) This, together with the low and sporadic production of pseudofeces by *M. chilensis* at low seston concentrations, may be an indication that the low rate is not due to morphological limitations or to digestive functions, but is rather a response that can be suppressed when no nutritional advantage is to be gained.

Above the threshold of pseudofeces production, *Mulinia edulis* rejected 11 to 80% and *Mytilus chilensis* 15 to 90% of filtered materials. The highest rejection percentages occurred for diets with high seston concentrations and low organic matter content, indicating that the production of pseudofeces in both bivalves is a mechanism that permits regulation of the rate of ingestion, especially when the diet is excessively concentrated and/or of low quality. The increase in the production of pseudofeces with increasing concentration and decreasing quality of the seston agrees with previous data for other bivalves (Kiørboe et al. 1980, Bayne et al. 1993, Iglesias et al. 1996, Hawkins et al. 1998). However, in some bivalves such as *Mya arenaria*, the production of pseudofeces was reported not to increase with increasing seston concentration (Bacon et al. 1998): this may have been due to the limited range of seston concentrations used in the measurements.

Release of pseudofeces by *Mytilus chilensis* was continuous compared with that by *Mulinia edulis*, in which accumulations of these biodeposits were observed to be periodically ejected by contraction of the siphons and rapid abduction of the valves. This behavior in *M. edulis* may be related to its long incurrent siphon, which impedes the removal of pseudofeces. Observations by Beninger et al. (1997) on the eulamellibranchs *Mya arenaria* and *Spisula solidissima* showed that the labia below the mouth may temporarily shut, thus accumulating excess material until this is trapped by the cilia of the labial palps and diverted toward the exit stream of the pseudofeces. The present study found that *M. chilensis* produced greater quantities of pseudofeces than *M. edulis* due to the greater amounts of material filtered by the former. Similar results were described in comparisons of other epibenthic and infaunal species: *Placopecten magellanicus* produced greater quantities of pseudofeces than *Mya arenaria* (Bacon et al. 1998) and *M. edulis* greater quantities than *Mercenaria mercenaria* (Tenore & Dunstan 1973) and *Cerstoderma edule* (Hawkins et al. 1998).

Pseudofeces produced by both *Mulinia edulis* and *Mytilus chilensis* contained lower amounts of organic matter than were introduced with the seston diets, which suggests the presence of pre-ingestive mechanisms that allow rejection of particles of low organic content and ingestion of organically rich particles. This

capacity has been recognised previously by numerous authors working with other bivalve species (Kiørboe & Møhlenberg 1981, Newell & Jordan 1983, Iglesias et al. 1992, Navarro et al. 1992). Some species however do not have this capacity (e.g. *Venerupis pullastra:* Foster-Smith 1975, *Mya arenaria:* Bacon et al. 1998, and *Pinctada imbricata*, Ward & MacDonald 1996).

Pre-ingestive particle selection in bivalves occurs both at the ctenidia and at the labial palps (Ward et al. 1994, Beninger et al. 1997). It is not clear if selection of material is made on the basis of its chemical composition or physical characteristics of the particles related to their organic or inorganic nature. Some authors have suggested that hardness and flexibility may play an important role in the selection process (Bougrier et al. 1997). Other authors have suggested that the type of microalgae and its chemical composition are determining factors (Newell & Jordan 1983, Shumway et al. 1985). Finally, some authors have demonstrated selection on the basis of particle size, whereby particles or microalgae of relatively large sizes are preferentially rejected (Defossez & Hawkins 1997, Navarro & Thompson 1997). In the present study, the pre-ingestive selection of particles with high organic content may be related to the capacity of the bivalves to recognise the chemical nature of the particles, or to some morphological characteristic linked to their organic content (e.g. size, density, form, flexibility, or hardness).

The capacity of *Mulinia edulis* and *Mytilus chilensis* for particle selection decreased with decreasing quality of the seston. In *M. edulis* this also decreased slightly when the quality of the seston was very high (>60% organic matter) as observed in other bivalves (Hawkins et al. 1996, 1998, Iglesias et al. 1996, Wong & Cheung 1999). The decline in selection efficiency with decreasing quantities of seston may be explained by the higher dilution of organic material with inorganic material, and the difficulty in perception of this by the receptors in the bivalves (Newell et al. 1989). The decrease in selection efficiency by *M. chilensis* fed seston of very high quality probably arose from the small nutritive advantage to be gained from increased selection on this type of diet, and to organic enrichment of the mucus accompying pseudofeces production (pseudofecal metabolic loss), which represents a high energetic cost (Bayne et al. 1993). The fact that *M. edulis* does not experience a reduction in selection efficiency with high-quality diets may be explained by the higher capacity of selection associated with its relatively large labial palps.

The selection efficiency of both bivalves increased markedly with increasing food supply, remaining relatively constant and high with the highest seston concentrations. This is in agreement with data of Hawkins

et al. (1998) for *Crassostrea gigas* and *Mytilus edulis*, but in contrast to data for *Cerastoderma edule*, in which a decrease in efficiency selection was observed with increasing concentration of seston (Navarro & Widdows 1997, Hawkins et al. 1998). Pseudofecal metabolic losses were most obvious at low seston concentrations, being responsible for negative selection efficiencies. Similar negative selections were observed when the quality of the food was low. Conversely, the high selection efficiency observed at high seston concentrations may have been due to the capacity of the labial palps to differentiate and separate particles with different levels of organic content.

Although the labial palps of *Mulinia edulis* are larger than those of *Mytilus chilensis*, their selection efficiency was similar. Other interspecific comparisons found correlations between palp size and selection efficiency (Kiørboe & Møhlenberg 1981). Bacon et al. (1998) demonstrated that the epifaunal species *Placopecten magellanicus* was more efficient in rejecting inorganic particles than the infaunal *Mya arenaria* when seston concentrations were between 3 and 14 mg l^{-1}, however these authors did not evaluate these results in reference to the relative sizes of the labial palps. As shown by Hawkins et al. (1990) for *Cerastoderma edule* and *M. edulis*, there may be a general tendency for the labial palps of infaunal species to be larger than those of epifaunal species. Other factors, such as the degree of specialisation of the labial palps and/or the ctenidia, may play an important role in the process of particle selection. Since the gills of *M. chilensis* are able to transport retained particles toward the mouth both by dorsal and ventral feeding tracts (Ward et al. 1993, Beninger & St-Jean 1997), it is possible that qualitative particle separation may occur in the gills. This would compensate for the poor particle selection efficiency of its small labial palps. Conversely, the small size of the ctenidia in *M. edulis* results in particle selection by its relatively larger labial palps.

Ingestion rate

The ingestion rate of *Mulinia edulis* and *Mytilus chilensis* increased with increasing seston concentration and decreasing seston quality. The degree of regulation of material ingested was greater in *M. chilensis*, with a reduction in ingestion rate at high concentrations and low quality, while in *M. edulis* it remained constant. Morphological or functional saturation of the ctenidia, palps, or digestive tract may explain the decrease in ingestion rate at high seston concentrations, but for low concentrations and quality of seston this explanation does not apply. It is probable that with seston at high concentrations and/or of low quality, the efficiency of particle selection at the level of the labial palps declines and the reduction in ingestion rate represents a compensatory mechanism that permits maintenance of high absorption efficiency. Both the increase in and the regulation of the ingestion rate with increasing seston concentration have been observed in other bivalve species such as *Cerastoderma edule* (Navarro et al. 1994, Iglesias et al. 1996, Navarro & Widdows 1997), *Crassostrea gigas* (Hawkins et al. 1998), *M. edulis* (Bayne et al. 1989), and *M. mercenaria* (Bricelj & Malouf 1984).

There were no differences between total ingestion rate of the 2 species, although *Mytilus chilensis* filtered more food than *Mulinia edulis*: this is explainable by the higher proportion of material rejected by *M. chilensis.* In contrast, *M. chilensis* ingested more organic food than *M. edulis*, probably due to the larger amount of organic material it filtered. These results coincide with those of Hawkins et al. (1998), who reported the rate of ingestion of organic material of an epifaunal species (*M. edulis*) to be greater than that of an infaunal species (*Cerastoderma edule*).

It has been reported that species better adapted to high-turbidity environments (infauna and species with siphons) regulate ingestion primarily by production of pseudofeces. Those not similarly adapted (epifaunal and non-siphonate species) regulate their ingestion rates by reduction in clearance rate (Foster-Smith 1975, Bricelj & Malouf 1984, Bacon et al. 1998). Both species studied here had both mechanisms for regulating their ingestion rate. However, at low concentrations of seston and/or with high seston quality, reduction of clearance rate with increasing TPM was more marked than any increase in pseudofeces production. At median or high seston concentrations and/or with low seston quality, the situation was reversed. Regulation of the ingestion rate by means of coordination of the clearance rate and production of pseudofeces is a mechanism that contributes to maximisation of energy gain under varying conditions of food availability. Thus, a reduction in clearance rate is more beneficial than production of pseudofeces when the diet is of high quality, since it is practically impossible to optimise such a diet; in addition, the organic enrichment of the mucus that accompanies the production of pseudofeces would be an unnecessary energy expenditure. When, however, the diet is of low quality, it may be advantageous for bivalves not to reduce the clearance rate in order to filter large quantities of particles and thus be able to preferentially select and ingest particles of higher nutrient value.

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