

# Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucculata* and *Pinctada margarifera*

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**ABSTRACT:** Filter-feeding behaviours of the mussel *Perna viridis* and the oysters *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucculata* and *Pinctada margarifera* were compared during natural tidal variations in the concentration (6 to 40 dry mg total particulate mass l<sup>-1</sup>) and organic content (6 to 22%) of seston available in the Merbok mangrove system, Malaysia. In *P. viridis*, *C. belcheri* and *S. cucculata*, declining retention efficiencies for the largest available particle size classes of more than 6 to 12 µm diameter were associated with an overall organic enrichment of filtered relative to available matter. As seston availability increased, a minimum average of 71% of the additional filtered matter was rejected by each species as pseudofaeces prior to ingestion. And in all 5 species, preferential rejection as pseudofaeces of filtered particles with higher average inorganic content resulted in the net organic enrichment of ingested relative to filtered matter. In *P. viridis* and *C. belcheri*, the efficiency of that net organic selection declined for seston of lower organic content. Combining all data from each species, absorption efficiencies from ingested organics increased exponentially with the organic content of ingested matter. Collective findings suggest that key interrelations between component processes of nutrient acquisition were similar to those that have been established for the modeling of feeding, growth and environmental impact among filter-feeding bivalves from temperate latitudes. However, especially fast growth in *P. viridis* stemmed from higher average ( $\pm 2$  SE) clearance rates ( $13.2 \pm 7.0$  l h<sup>-1</sup> g<sup>-1</sup> when particulate organic matter < 1 mg l<sup>-1</sup>), greater average organic enrichment of filtered relative to available matter ( $0.99 \pm 0.67$ ) and greater average organic enrichment of ingested relative to filtered matter ( $0.63 \pm 0.03$ ) than have hitherto been recorded in any species of bivalve filter-feeder. In contrast, *P. margarifera* was least well adapted for the pre-ingestive selection of organic matter, with no differential retention on the gill and little selective rejection as pseudofaeces, representing at least part of the physiological basis for characteristically slow growth in pearl oysters.

**KEY WORDS:** Filter-feeding behaviour · Particle selection · Seston composition · *Perna viridis* · *Crassostrea belcheri* · *Crassostrea iradelei* · *Saccostrea cucculata* · *Pinctada margarifera*

## INTRODUCTION

Filter-feeding behaviour in bivalves is proving highly responsive to fluctuations in both the abundance and the composition of suspended seston (Hawkins & Bayne 1992, Bayne 1998). Further understanding of that behaviour is required to establish the role of bivalve shellfish in ecosystem processes (e.g.

Bayne & Hawkins 1992, Dame 1993, Herman 1993, Smaal & Prins 1993) and to predict the carrying capacity for shellfish culture within nearshore environments (e.g. Héral 1993). Findings illustrate a complex set of adaptations which not only help to maximise organic absorption, but also to maintain organic absorption relatively independent of short-term fluctuations in seston abundance and composition, including the 'dilution' of organic matter by silt that is typically resuspended within higher concentrations of natural

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seston (e.g. Hawkins et al. 1996, 1997, Urrutia et al. 1996, Navarro et al. 1997). Selective processes, and the consequences of those processes, are a particularly important feature of that behaviour. And because algal monocultures and other artificial suspensions do not afford utilisation of the full potential for particle selection, an emergent consensus now recognises that ecologically relevant responses are best observed when the bivalves are feeding upon natural seston (Foster-Smith 1975, Doering & Oviatt 1986, Cranford & Gordon 1992, Iglesias et al. 1992, 1996, Navarro et al. 1992, 1994, Bayne et al. 1993, MacDonald & Ward 1994, Hawkins et al. 1996, Soletchnik et al. 1996, Urrutia et al. 1996, Bacon et al. 1998, MacDonald et al. 1998).

Recent work in the cockle *Cerastoderma edule* (Urrutia et al. 1996), the oyster *Crassostrea gigas* (Soletchnik et al. 1996) and the mussel *Mytilus edulis* (Hawkins et al. 1996) feeding throughout the same natural tidal variations in seston availability has (1) identified a common set of equations that summarize functional interrelations between processes of particle filtration, pre-ingestive rejection and organic absorption, and (2) shown that those relations may be used to predict feeding behaviour and net organic absorption rate in all 3 species on the basis of seston abundance and seston organic content alone (Hawkins et al. 1998). These findings establish that similar functional interrelations control feeding responses in *C. edule*, *C. gigas* and *M. edulis*. We now need to test for the further generality of these key relations, for potential use in a common model that predicts filter-feeding and growth in separate species under different environmental conditions of food availability and composition.

To date, there have been no reports of the responses to variation in seston abundance or composition among filter-feeding bivalve shellfish from tropical latitudes. Yet shellfish dominate many nearshore communities in tropical environments. Work described here was undertaken to study the filter-feeding behaviour of the green mussel *Perna viridis* L., the mangrove oysters *Crassostrea belcheri* and *Crassostrea iradelei*, the rock oyster *Saccostrea cucullata*, and the pearl oyster *Pinctada margarifera*. All 5 species are cultured commercially throughout tropical waters (e.g. Rangarajan & Narasimham 1980, Sivalingam 1982, Yoo et al. 1986, Brohmanonda & Mutaransit 1988, Jarayabhand & Thavornnyutikarn 1995). To ensure natural behaviour and ecologically meaningful comparisons, responses to natural variations of seston were monitored within the Merbok mangrove system, Malaysia. Findings are used to examine whether functional interrelations that influence feeding responses in tropical species are similar to the common set of relations that have recently been established for use within models of feeding behaviour and growth in filter-feeding bivalves

from temperate latitudes (Hawkins et al. 1998). We also compare the feeding behaviour of our studied species with a view to understanding observed differences in growth rate and ecogeographical distribution.

## MATERIALS AND METHODS

Feeding behaviours of the mussel *Perna viridis* and the oysters *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucullata* and *Pinctada margarifera* were studied in response to natural variations of food availability during 3 complete tidal cycles at Kampong Bukit Kechik in the Merbok mangrove system, about 30 miles (48 km) north of Penang, Malaysia.

Whereas *Crassostrea iradelei* had been cultured at Kampong Bukit Kechik, the remaining species were collected from other sites as follows: *Perna viridis* from Pulau Aman, Penang; *Crassostrea belcheri* from Telaga Nenas, Perak; and both *Saccostrea cucullata* and *Pinctada margarifera* from Muka Head, Penang. Regardless of origin, all specimens were first acclimated to common conditions of  $27.0 \pm 1.0^\circ\text{C}$  and  $32.0 \pm 1.0\text{‰}$  while supplied with a copious through-flow of unfiltered natural seawater for 2 wk at the Muka Head Research Station, Universitat Sains Malaysia, Penang. Before experimentation, they were transported to Kampong Bukit Kechik, and placed within immersed plastic trays that were suspended below a raft owned by the Fisheries Research Institute of Penang. Starting 48 h later, and working from that same raft, we monitored feeding responses over the 6 to 8 h that spanned the rise from low to high tide on each of 9, 10 and 11 January 1996. Ranges of tidal rise and fall throughout those 3 d exceeded 1.8 m.

Samples were collected over separate experimental periods of 1 to 3 h during each tidal cycle. Species were on occasion exchanged between periods of measurement, allowing >1 h to adapt following handling. For each period of measurement, up to 11 individual shellfish were each maintained separately in 1 l plastic trays that were supplied with seawater ( $27.0 \pm 1.0^\circ\text{C}$ ) pumped from beneath the raft. Rates of seawater supply were first adjusted to ensure that concentrations of suspended particles were not reduced by more than 25% between the inflow and outflow from each shellfish tray, and then maintained at constant rates which differed between 170 and  $450 \text{ ml min}^{-1}$  throughout each experimental period. There were no significant differences between particle sedimentation rates at different flow rates, and maximal flow rates in each shellfish tray of  $<0.5 \text{ cm s}^{-1}$  were well below rates of  $>15 \text{ cm s}^{-1}$  that have been shown to inhibit filter-feeding in other species of bivalve shellfish (e.g. Wildish & Saulnier 1993). At each collection time, rate of current

flow at the experimental site was measured by timing the passage of an immersed piece of coconut husk over 2 m alongside the raft. Water temperature was also recorded, and salinity measured with a refractometer. In addition, 1 l of seawater was sampled from the outflows of each tray containing an experimental individual, including 1 empty 'control' tray. Then, the flow rate through each tray was recorded, and all true faeces and all pseudofaeces collected separately. To obtain sufficient precision in our measures of faecal production and faecal composition, the true faeces or pseudofaeces were each combined from replicate groups of 2 to 3 individual shellfish, before being homogenised by rapid repeat-pipetting. Aliquots of seawater and faecal samples were filtered onto separate pre-weighed and ashed Whatman GF/C filters. All filters were dried at 60°C before re-weighing and calculation of the total dry sample weight per filter. Each filter was then ashed at 450°C for 4 h prior to final weighing, allowing further calculation both of the ash (inorganic) and ash-free (organic) masses of each filtered sample.

Seston abundance was measured as the total dry particulate mass (TPM; mg l<sup>-1</sup>) of all available seston, and seston quality as the organic content of total dry seston (OCS; fraction). Measures of TPM and OCS were undertaken assuming that concentrations measured in the outflow from the empty 'control' tray were representative of the available particulates.

Each water sample from both experimental and control outflows were analysed for both particle count and size distribution. These and other measures were made using a Coulter Channelyser and associated tube with orifice diameter of 100 µm, recording the particle numbers per 2 ml of sample within each of 32 size channels over the range 3 to 17 µm equivalent spherical diameter. Efficiencies with which filtered particles within specific size classes were retained on the gill (REP, fraction) were calculated as:

$$\text{REP} = (\text{inflow particle counts ml}^{-1} \text{ within size class} - \text{outflow particle counts ml}^{-1} \text{ within size class}) / (\text{inflow particle counts ml}^{-1} \text{ within size class})$$

where the inflow particle counts were measured within outflow water from the control chamber without an experimental individual.

Clearance rate (CR; l h<sup>-1</sup>) with which each shellfish species removed particles from seawater was calculated as:

$$\text{CR} = (\text{number of particles ml}^{-1} \text{ within the inflow} - \text{number of particles ml}^{-1} \text{ within the outflow}) / (\text{number of particles ml}^{-1} \text{ within the outflow}) \times \text{litres of water flow h}^{-1} \text{ through tray}$$

Particle retention efficiencies declined for particles larger than about 12 µm equivalent spherical diameter

(refer to 'Results'). Therefore, to approximate pumping rate as closely as possible, CR was only calculated for particles of 3 to 8 µm.

Retention efficiencies (REO, fraction) with which the organic content of filtered particles (OCF; fraction) was enriched compared with the organic content of the all available seston (OCS; fraction) were calculated as:

$$\text{REO} = (\text{OCF} - \text{OCS}) / \text{OCS}$$

Other processes of feeding and absorption were calculated according to the basic procedures of Hawkins et al. (1996, 1998), Soletchnik et al. (1996) and Urrutia et al. (1996). All calculations are summarized with acronyms in Table 1. Note that these calculations assume no significant delay in the deposition of filtered particles, estimating particle availability as the integrated average over corresponding periods of faecal collection. Note also that REO, NOSE (net organic selection efficiency), NOIR (net organic ingestion rate), NOAR (net organic absorption rate), NAEFO (net absorption efficiency from filtered organics) and NAEIO (net absorption efficiency from ingested organics) are net measures; REO, NOSE and NOIR being influenced by particle losses or mucous losses from the shellfish, whereas NOAR, NAEFO and NAEIO are influenced both by mucous losses and by metabolic faecal losses.

Following all experimentation, the soft tissues were excised from each shellfish and dried at 60°C before measuring the total soft tissue dry weight. Feeding responses were standardised to those for an equivalent individual of 1 g soft tissue dry weight as follows:  $Y_s = (W_s/W_e)^b Y_e$ , where  $Y_s$  is the standardised parameter,  $W_s$  is the standard weight (1 g),  $W_e$  is the weight or length of the experimental individual,  $Y_e$  is the uncorrected parameter, and  $b$  is the average size exponent of 0.62 for feeding processes in a variety of suspension-feeding shellfish (Bayne & Newell 1983). This standard weight of 1 g soft tissue dry weight compared with averages ( $\pm 2$  SE) for all experimental individuals of each species as follows: 0.40  $\pm$  0.03 g for *Perna viridis*, 1.02  $\pm$  0.07 g for *Crassostrea belcheri*, 0.91  $\pm$  0.11 g for *Crassostrea iradelei*, 0.48  $\pm$  0.08 g for *Saccostrea cucullata* and 0.86  $\pm$  0.24 g for *Pinctada margarifera*.

It was not possible to study the feeding behaviour of all 5 species simultaneously. This meant that measures were made over different average periods of food availability (TPM; mg l<sup>-1</sup>). However, measures in *Perna viridis* and *Crassostrea belcheri* were undertaken together over a common range of TPM from 7 to 15 mg l<sup>-1</sup>, and measures in *Saccostrea cucullata* and *Pinctada margarifera* were undertaken together over a similar common range of TPM from 10 to 23 mg l<sup>-1</sup>. Measures in *Crassostrea iradelei* were made over a limited range of TPM from 8 to 9 mg l<sup>-1</sup>. Measures of feeding behaviour were each made upon a different replicate group

Table 1. Definitions and descriptions of the calculation of separate components of feeding behaviour

Parameter	Acronym	Unit	Calculation
Clearance rate <sup>a</sup>	CR	l h <sup>-1</sup>	(number of particles ml <sup>-1</sup> within the inflow – number of particles ml <sup>-1</sup> within the outflow)/(number of particles ml <sup>-1</sup> within the outflow) × litres water flow h <sup>-1</sup> through tray
Filtration rate	FR	Total mg h <sup>-1</sup>	(mg inorganic matter egested both as true faeces and pseudofaeces h <sup>-1</sup> )/(1 – OCF)
Retention efficiency for filtered particles	REP	Fraction	(inflow particle counts ml <sup>-1</sup> within size class – outflow particle counts ml <sup>-1</sup> within size class)/(inflow particle counts ml <sup>-1</sup> within size class)
Retention efficiency for filtered organic matter	REO	Fraction	(OCF – organic fraction within total particulates available in tray inflow)/organic fraction within total particulates available in tray inflow
Organic content of filtered matter	OCF	Fraction	(mg particulate organic matter l <sup>-1</sup> within tray inflow – mg particulate organic matter l <sup>-1</sup> within tray outflow)/(mg total particulate matter l <sup>-1</sup> within tray inflow – mg total particulate matter l <sup>-1</sup> within tray outflow)
Rejection rate	RR	Total mg h <sup>-1</sup>	mg total pseudofaeces egested h <sup>-1</sup>
Net organic selection efficiency	NOSE	Fraction	1 – (organic fraction within pseudofaeces)/(organic fraction within total particulates available in tray inflow)
Net organic ingestion rate	NOIR	mg h <sup>-1</sup>	(FR × OCF) – (RR × organic fraction within pseudofaeces)
Net organic absorption rate	NOAR	mg h <sup>-1</sup>	NOIR – [(mg total true faeces egested h <sup>-1</sup> ) × (organic fraction within true faeces)]
Net absorption efficiency from filtered organics	NAEFO	Fraction	NOAR/(FR × OCF)
Net absorption efficiency from ingested organics	NAEIO	Fraction	NOAR/NOIR
Organic content of ingested matter	OCI	Fraction	NOIR/(FR – RR)

<sup>a</sup>Calculated for particles from 3 to 8 µm diameter (refer to 'Material and methods')

of 2 to 3 individuals (refer above), and differed in number (n) between species, with n = 12 in *P. viridis* and *C. belcheri*, n = 6 in *S. cucullata* and *Pinctada margaritifera*, and n = 7 in *C. iradelei*. For all 5 species, average performance is compared, and the natural variation between measures is used to compare functional inter-relationships between separate component processes of feeding physiology. In *P. viridis* and *C. belcheri*, the range of food availability and number of measures were sufficient to identify influences of TPM on feeding behaviour (refer to 'Results'). Where present data did not allow resolution of the exact form of relations, equations were fitted on the basis of a common set of relations that have previously been shown to satisfactorily predict responses observed in other suspension-feeding bivalve molluscs (Hawkins et al. 1997). All statistical tests and procedures used in these analyses and in the presentation of data were undertaken using SYSTAT for Windows, Version 7 (SYSTAT Inc., Evanston, IL, USA). Variables were only included as additional predictors in multiple regression if the probability of their correlation with residuals was less than 2.5%. To further avoid constructing multicollinear

models with unstable regression coefficient estimates, we also excluded any variable with a tolerance of <0.1 (calculated as 1 minus the squared multiple correlation between a predictor and the other predictors in a model).

## RESULTS

### Seston availability

Throughout all 3 tidal cycles, natural seston availability measured as TPM (mg l<sup>-1</sup>) varied from 6 to 40 mg l<sup>-1</sup>. The temporal pattern of variation in TPM was different on each day, and did not correlate ( $p > 0.05$ ) with current speed, which ranged from 0.01 to 0.5 m s<sup>-1</sup>. Surface water temperature and salinity throughout all measurements averaged ( $\pm$  maximum range) 27.3  $\pm$  0.8°C and 27.9  $\pm$  1.5‰, respectively. Combining the data from all measures of seston availability and quality, Fig. 1 illustrates how the OCS (fraction) decreased from a maximum of 0.22 to a minimum of 0.09 with increasing TPM up to 40 mg l<sup>-1</sup>, according

to a negative relation that was best described by the equation:

$$\text{OCS} = 0.25(0.18, 0.34) \times \text{TPM}^{-0.26(\pm 0.14)}$$

where  $r^2 = 0.24$ , residual  $df = 43$ ,  $p = 0.001$ , and bracketed values indicate 95 % confidence limits.

### Average feeding behaviour

Average ( $\pm 2$  SE) REP (fraction) within separate 2 mm size classes that averaged 4, 6, 8, 10, 12, 14 and 16  $\mu\text{m}$  equivalent spherical diameter are illustrated for each species in Fig. 2. REPs of 0.25 to 0.35 for the smaller particles of less than about 8 mm equivalent spherical diameter were essentially similar in all 5 species (Fig. 2). However, REPs for the largest particle size class with an average diameter of 16  $\mu\text{m}$  were significantly lower than for the smallest particles with an average diameter of 4  $\mu\text{m}$  in *Perna viridis* ( $t = 2.51$ , residual  $df = 13$ ,  $p = 0.03$ ), *Crassostrea belcheri* ( $t = 2.73$ , residual  $df = 25$ ,  $p = 0.01$ ) and *Crassostrea iradelei* ( $t = 7.08$ , residual  $df = 18$ ,  $p = 0.000001$ ). These reductions appeared to begin for particles larger than about 12  $\mu\text{m}$  diameter in *P. viridis* and *C. belcheri*, and for particles larger than only about 6  $\mu\text{m}$  diameter in *C. iradelei* (Fig. 2). No such reductions were apparent in either *S. cucullata* or *P. margarifera* ( $p > 0.05$ ).

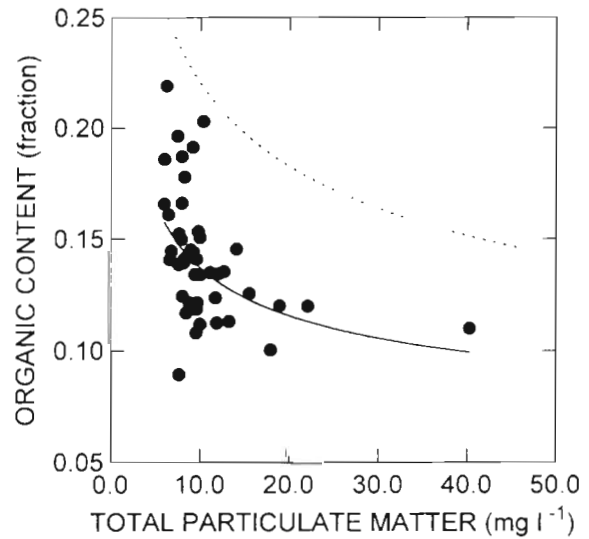


Fig. 1. Relationship between the organic content (OCS; fraction) and total particulate mass (TPM;  $\text{mg l}^{-1}$ ) of seston collected over 3 separate tides in the Merbok mangrove estuary, Malaysia. Both lines were fitted by least squares; the solid line to illustrated data from the Merbok mangrove estuary (refer to 'Results' for the equation), and the dashed line to data from the bay of Marennes-Oléron, France [where  $\text{OCS} = 0.41(0.29, 0.56) \times \text{TPM}^{-0.27(\pm 0.09)}$ ; from Hawkins et al. (1996)]

Table 2 summarises average ( $\pm 2$  SE) measures of feeding physiology computed over the full range of seston

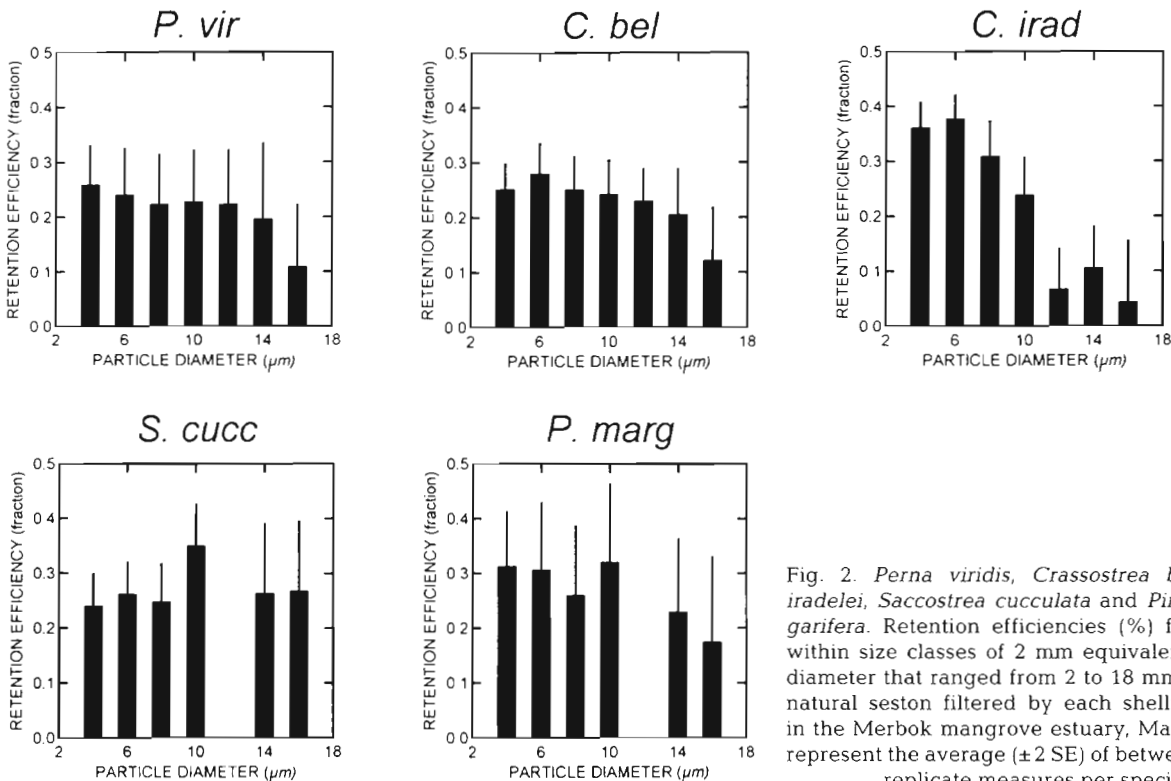


Fig. 2. *Perna viridis*, *Crassostrea belcheri*, *C. iradelei*, *Saccostrea cucullata* and *Pinctada margarifera*. Retention efficiencies (%) for particles within size classes of 2 mm equivalent spherical diameter that ranged from 2 to 18 mm within the natural seston filtered by each shellfish species in the Merbok mangrove estuary, Malaysia. Data represent the average ( $\pm 2$  SE) of between 8 and 31 replicate measures per species



Table 2. Average ( $\pm$  SE) clearance rates for particles of between 3 and 8  $\mu\text{m}$  diameter (CR;  $\text{l h}^{-1}$ ), net organic retention efficiencies (REO, fraction), net organic selection efficiencies (NOSE, fraction), net organic ingestion rates (NOIR;  $\text{mg organics g}^{-1} \text{h}^{-1}$ ) and net organic absorption rates (NOAR;  $\text{mg organics g}^{-1} \text{h}^{-1}$ ) recorded for each species. All data are standardised for shellfish of 1 g dry soft tissue weight

Species	CR	REO	NOSE	NOIR	NOAR
<i>Perna viridis</i>	$7.2 \pm 3.1$	$+0.99 \pm 0.67$	$0.63 \pm 0.03$	$24.8 \pm 3.6$	$21.5 \pm 3.4$
<i>Crassostrea belcheri</i>	$4.6 \pm 1.0$	$+0.35 \pm 0.21$	$0.39 \pm 0.04$	$9.5 \pm 1.4$	$6.0 \pm 0.9$
<i>Crassostrea iradelei</i>	$4.1 \pm 1.5$	$+0.36 \pm 0.23$	$0.39 \pm 0.03$	$7.2 \pm 1.6$	$4.7 \pm 1.2$
<i>Saccostrea cucullata</i>	$4.9 \pm 1.2$	$+0.04 \pm 0.24$	$0.38 \pm 0.09$	$6.9 \pm 1.7$	$4.0 \pm 1.5$
<i>Pinctada margarifera</i>	$5.5 \pm 1.3$	$-0.11 \pm 0.17$	$0.22 \pm 0.09$	$2.0 \pm 1.6$	$1.3 \pm 0.9$

availability for each studied species. Compared with the 4 oyster species, *Perna viridis* showed the highest average values for CR ( $\text{l h}^{-1}$ ), REO (fraction), NOSE (fraction), NOIR ( $\text{mg organics h}^{-1}$ ) and NOAR ( $\text{mg organics h}^{-1}$ ) (Table 2). In particular, comparisons of REO indicate that the organic content of matter filtered by *P. viridis* was virtually double that in the total available seston. In contrast, there was no such enrichment in either *Saccostrea cucullata* or *Pinctada margarifera*, and although significant in *Crassostrea belcheri* and *Crassostrea iradelei*, average percentage increases were only about one-third that in *P. viridis* (Table 2). Similarly, although all 4 species of oysters selectively enriched the organic content of ingested matter relative to filtered matter, their average NOSEs were less than  $(0.39/0.63) \times 100 = 62\%$  of that in *P. viridis* (Table 2). The result was that average NOAR in *P. viridis* was 3 to 5 times greater than in the *Crassostrea* spp., and 16 times greater than in *P. margarifera* (Table 2).

#### Responses associated with changing seston availability

CR for particles of between 3 and 8  $\mu\text{m}$  diameter ( $\text{l h}^{-1}$ ) in *Perna viridis* decreased from maxima of more than  $15 \text{ l h}^{-1}$  to minimal values of less than  $5 \text{ l h}^{-1}$  with the increasing availability of POM ( $\text{mg l}^{-1}$ ) up to  $2.5 \text{ mg l}^{-1}$ , as is illustrated in Fig. 3 according to a relation that was best described by the following allometric equation:

$$\text{CR} = 12.2(9.6, 15.4) \times \text{POM}^{-0.90(\pm 0.54)}$$

where  $r^2 = 0.33$ , residual df = 22 and  $p = 0.003$ . Multiple stepwise regression indicated that neither TPM nor OCS explained any ( $p > 0.05$ ) of the remaining variance in CR. No relation was evident between CR and either TPM, OCS or POM in *Crassostrea belcheri* ( $p > 0.05$ ), despite being measured over the same ranges of seston availability as in *P. viridis*. Nor was any such relation evident in any of the 3 remaining oyster species ( $p > 0.05$ ).

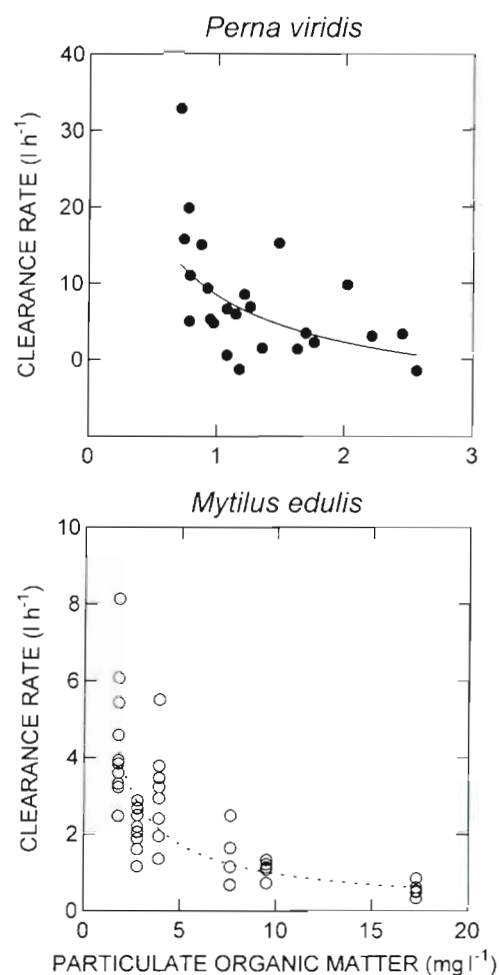


Fig. 3. *Perna viridis* and *Mytilus edulis*. Short-term responses in clearance rate for particles of between 3 and 8  $\mu\text{m}$  diameter (CR;  $\text{l h}^{-1}$ ) to the particulate organic matter within natural seston (POM;  $\text{mg l}^{-1}$ ) available to *P. viridis* in the Merbok mangrove estuary, Malaysia. The solid line was fitted by least squares (refer to 'Results' for equation). Data are also presented for *M. edulis* [where  $\text{CR} = 4.2(3.2, 5.5) \times \text{POM}^{-0.64(\pm 0.08)}$ , from Hawkins et al. (1996)]. All data are standardised to 1 g dry soft tissue weight, and represent separate replicate measures upon individual mussels

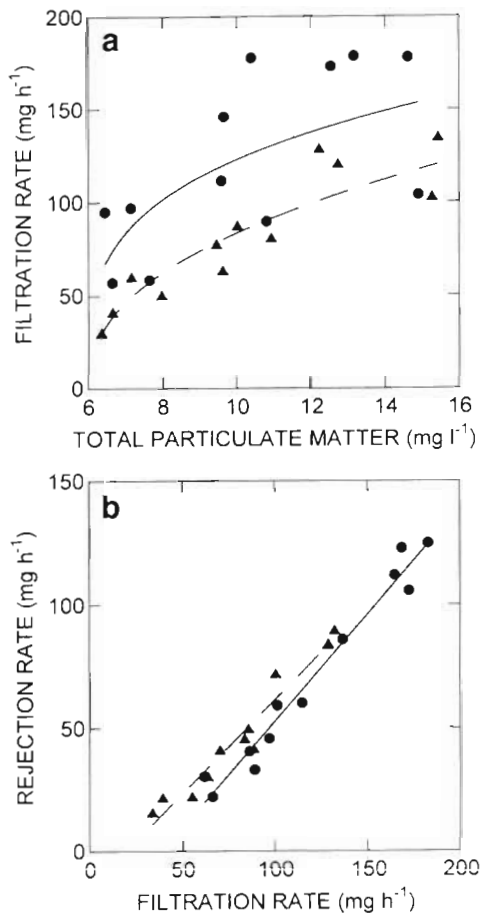


Fig. 4. *Perna viridis* and *Crassostrea belcheri*. Short-term responses in (a) filtration rate (FR;  $\text{mg h}^{-1}$ ) to the total particulate matter within available seston (TPM;  $\text{mg l}^{-1}$ ), and (b) the relation between rejection rate (RR;  $\text{mg h}^{-1}$ ) and FR in both *P. viridis* (●, —) and *C. belcheri* (▲, —) feeding upon natural seston in the Merbok mangrove estuary, Malaysia. Lines were fitted by least squares (refer to 'Results' for equations). All data are standardised to 1 g dry soft tissue weight, and represent the average for single measures upon separate replicate groups, each of 2 to 3 shellfish

Filtration rates (FR; total  $\text{mg h}^{-1}$ ) in both *Perna viridis* and *Crassostrea belcheri* increased with TPM as is illustrated in Fig. 4 according to relations that were described by the following allometric equations (cf. Hawkins et al. 1997):

*Perna viridis*

$$\text{FR} = 13.8(\pm 3.9) \times \text{TPM}^{0.91(\pm 0.59)}$$

where  $r^2 = 0.49$ , residual df = 10 and  $p = 0.01$ ; and

*Crassostrea belcheri*

$$\text{FR} = 2.8(\pm 2.4) \times \text{TPM}^{1.43(\pm 0.38)}$$

where  $r^2 = 0.85$ , residual df = 10 and  $p = 0.00002$ .

There was no indication that either REP or REO varied with TPM, OCS or FR ( $p > 0.05$ ). But in all 5 species,

FR was the main determinant of pseudofaecal rejection rate (RR; total  $\text{mg h}^{-1}$ ) as illustrated for *Perna viridis* and *Crassostrea belcheri* in Fig. 4 according to relations that were best described by the following linear relations:

*Perna viridis*

$$\text{RR} = -33.5(\pm 12.6) + 0.87(\pm 0.10)\text{FR}$$

where  $r^2 = 0.97$ , residual df = 10 and  $p = 0.00000001$ ;

*Crassostrea belcheri*

$$\text{RR} = -14.6(\pm 9.6) + 0.76(\pm 0.11)\text{FR}$$

where  $r^2 = 0.95$ , residual df = 10 and  $p = 0.00000006$ ;

*Crassostrea iradelei*

$$\text{RR} = -11.0(\pm 6.8) + 0.75(\pm 0.11)\text{FR}$$

where  $r^2 = 0.97$ , residual df = 6 and  $p = 0.000008$ ;

*Saccostrea cucullata*

$$\text{RR} = -9.7(\pm 15.8) + 0.71(\pm 0.24)\text{FR}$$

where  $r^2 = 0.89$ , residual df = 4 and  $p = 0.004$ ; and

*Pinctada margarifera*

$$\text{RR} = -1.1(\pm 4.3) + 0.81(\pm 0.14)\text{FR}$$

where  $r^2 = 0.97$ , residual df = 4 and  $p = 0.0003$ .

These equations indicate that for every measured increment in FR, a minimum average of 71% of the additional filtered matter was rejected as pseudofaeces, and which averaged as much as 87% of that additional filtered matter in *P. viridis*.

NOSE (fraction) in *Perna viridis*, *Crassostrea belcheri* and *Saccostrea cucullata* increased with OCS as is illustrated in Fig. 5 according to relations that were

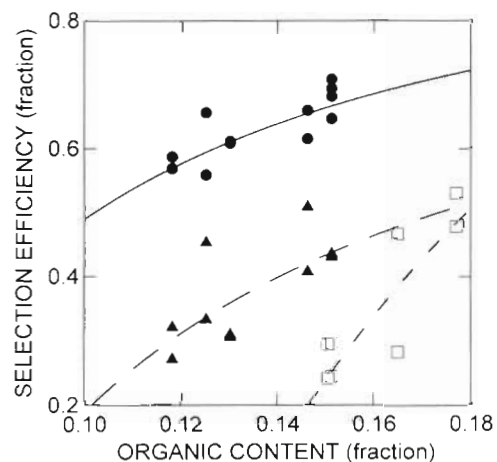


Fig. 5. *Perna viridis*, *Crassostrea belcheri* and *Saccostrea cucullata*. Short-term responses in net organic selection efficiency (NOSE; fraction) to the organic content of natural seston (OFS, fraction) available to *P. viridis* (●, —), *C. belcheri* (▲, —) and *S. cucullata* (□, ---) in the Merbok mangrove estuary, Malaysia. Lines were fitted by least squares (refer to 'Results' for equations). All data are standardised to 1 g dry soft tissue weight, and represent the average for single measures upon separate replicate groups, each of 2 to 3 shellfish

described by the following hyperbolic equations (cf. Hawkins et al. 1997):

*Perna viridis*

$$\text{NOSE} = 1.01(\pm 0.18) - [0.052(\pm 0.024) \times (1/\text{OFS})]$$

where  $r^2 = 0.63$ , residual df = 10 and  $p = 0.002$ ;

*Crassostrea belcheri*

$$\text{NOSE} = 0.92(\pm 0.31) - [0.073(\pm 0.042) \times (1/\text{OFS})]$$

where  $r^2 = 0.54$ , residual df = 10 and  $p = 0.006$ ; and

*Saccostrea cucullata*

$$\text{NOSE} = 1.84(\pm 0.90) - [0.24(\pm 0.15) \times (1/\text{OFS})]$$

where  $r^2 = 0.72$ , residual df = 10 and  $p = 0.03$ .

Multiple stepwise regression confirmed that FR did not explain a significant proportion of the remaining variance for NOSE in any of these 3 species ( $p > 0.05$ ).

Combining all data from each species, NAEIO (fraction) increased with the organic content of ingested matter (OCI; fraction) in a strong common relation that was best described by the exponential equation:

$$\text{NAEIO} = 0.89(\pm 0.06) \times (1 - e^{-8.58(\pm 3.36)[\text{OCI} - 0.13(\pm 0.03)]})$$

where  $r^2 = 0.87$ , residual df = 40 and  $p = 0.00000003$ .

This relation is illustrated in Fig. 6, showing how NAEIO increased from as low as 0.3 to maximal values of more than 0.8 at the highest OCI.

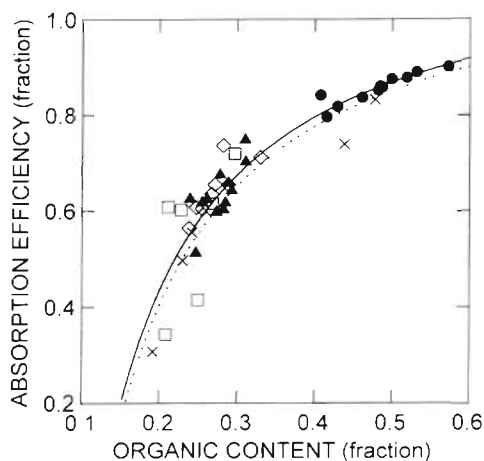


Fig. 6. *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucullata*, *Pinctada margarifera* and *Mytilus edulis*. Short-term responses in net absorption efficiency from ingested organics (NAEIO; fraction) to the organic content of matter ingested (OCI; fraction) by *P. viridis* (●), *C. belcheri* (▲), *C. iradelei* (◇), *S. cucullata* (□) and *P. margarifera* (×) feeding upon natural seston in the Merbok mangrove estuary, Malaysia. The solid line was fitted by least squares to all data combined (refer to 'Results' for equation). The dotted line illustrates the same relation for *M. edulis* [NAEIO =  $1.15(\pm 0.03) - 0.149(\pm 0.004) \times (1/\text{OCI})$ ] feeding upon natural seston from the bay of Marennes-Oléron, France (from Hawkins et al. 1997). All data are standardised to 1 g dry soft tissue weight, and represent the average for single measures upon separate replicate groups, each of 2 to 3 shellfish.

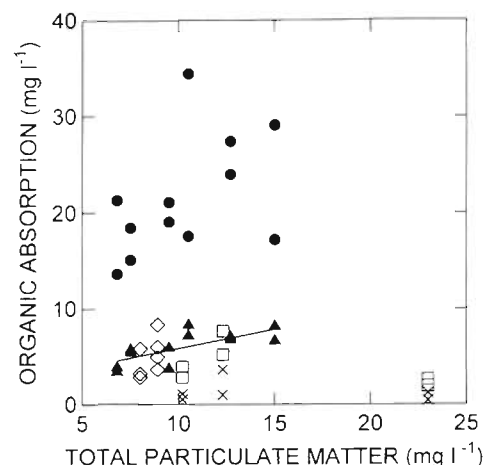


Fig. 7. *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucullata* and *Pinctada margarifera*. Short-term responses in net organic absorption rate (NOAR;  $\text{mg h}^{-1}$ ) to the total particulate mass (TPM;  $\text{mg l}^{-1}$ ) of natural seston available to *P. viridis* (●), *C. belcheri* (▲), *C. iradelei* (◇), *S. cucullata* (□) and *P. margarifera* (×) feeding upon natural seston in the Merbok mangrove estuary, Malaysia. The line was fitted by least squares to data for *C. belcheri* alone (refer to 'Results' for equation). All data are standardised to 1 g dry soft tissue weight, and represent the average for single measures upon separate replicate groups, each of 2 to 3 shellfish.

Despite significant ranges of food availability, short-term responses in NOAR ( $\text{mg h}^{-1}$ ) did not vary with TPM in either *Perna viridis*, *Saccostrea cucullata* or *Pinctada margarifera* ( $p > 0.05$ ). Alternatively, as is illustrated in Fig. 7, a significant positive relation between NOAR and TPM suggests that absorption would have increased at higher food availabilities in *Crassostrea belcheri*.

## DISCUSSION

The form and slope of the relation between OCS and TPM of seston available at our experimental site in the Merbok mangrove estuary were similar to those observed in the bay of Marennes-Oléron, France (refer to 'Results' and Fig. 1). This suggests 'dilution' of organic matter by the silt that is typically resuspended within higher concentrations of natural seston (e.g. Widdows et al. 1979). However, OCS at any given TPM in the Merbok estuary was almost half that observed in the bay of Marennes-Oléron (Fig. 1). We are not aware of other comparable data from tropical waters.

Filter-feeding behaviour in bivalve molluscs is highly flexible in response to changes in both the amount and composition of available seston (Hawkins & Bayne 1992, Bayne 1998). In particular, feeding rate decreases in exponential relation with increasing con-



centrations of POM, presumably because the gut becomes saturated with organics (e.g. Iglesias et al. 1992, Hawkins et al. 1997) (Fig. 3). This means that high feeding rates are observed at low availabilities of organically rich food as in artificial diets comprised mainly of cultured unicellular alga or algae (e.g. Møhlenberg & Riisgård 1979, Riisgård 1988, Jørgensen 1996, Hawkins et al. 1997). But the reverse may occur for natural seston of lower (<25%) OCS, for which feeding rate has been observed to increase to maximal rates at higher concentrations (e.g. Iglesias et al. 1992, Newell & Shumway 1993, Hawkins et al. 1996), only decreasing upon clogging of the gills at the very greatest loads (Widdows et al. 1979, Barillé et al. 1997). This is because OCS typically decreases with the increasing TPM of natural seston, due to 'diluting' effects of suspended silt. Further, unlike monocultures of alga, natural seston affords the opportunity for particle selection, which is most efficient at those maximal rates of feeding (Hawkins et al. 1998). Given these selective processes, there is no guarantee that the same maximal feeding rates occur when shellfish filter natural particle mixtures as when they filter cultured alga or algae. It is therefore important that behaviour be compared under similar feeding conditions. In the present study of responses to natural seston, average ( $\pm 2$  SE) CR ( $l\ g^{-1}\ h^{-1}$ ) for particles of between 3 and 8  $\mu m$  diameter in all 5 species ranged from  $4.1 \pm 1.5$  to  $7.2 \pm 3.1\ l\ g^{-1}\ h^{-1}$  (Table 2). Comparable averages across full ranges of experimental food availabilities have not exceeded  $3.0\ l\ g^{-1}\ h^{-1}$  in all previous studies for a variety of temperate species feeding upon natural seston, including *Cerastoderma edule* (Navarro et al. 1994), *Crassostrea gigas* (Soletchnik et al. 1996), *Mya arenaria* (Bacon et al. 1998), *Mytilus edulis* (Bayne et al. 1993, Newell & Shumway 1993, Hawkins et al. 1996), *Mytilus galloprovincialis* (Navarro et al. 1996) and *Placopecten magellanicus* (Cranford & Gordon 1992, MacDonald & Ward 1994, Bacon et al. 1998). On this basis, it is tempting to speculate that average CR may be faster in the tropical species studied here. But confirmation of any such trend must await further comparison over a wider range of feeding conditions. Present measures did not include all feeding conditions experienced by each species in their natural environments.

Although present experimental ranges of food availability differed between some species (refer to 'Materials and methods'), there are certain clear findings of interest. A key finding from the present study has been that average REP (fraction) of approximately 3 to 8  $\mu m$  equivalent spherical diameter were essentially similar in all 5 species, but that average retention efficiencies for the largest filtered particle size class with an average diameter of 16  $\mu m$  were significantly lower than for the smallest particles with an average diameter of

approximately 3  $\mu m$  in *Perna viridis*, *Crassostrea belcheri* and *Crassostrea iradelei* (Fig. 2). Many previous investigations of particle retention efficiency in a variety of filter-feeding bivalve shellfish have reported that REP generally increased to constant maxima at the largest particle diameters (e.g. Hawkins & Bayne 1992, Barillé et al. 1993). However, it has also been observed that REP decreased with increasing particle diameter above about 8  $\mu m$  in the scallop *Placopecten magellanicus* from temperate latitudes (Cranford & Grant 1990, MacDonald & Ward 1994). MacDonald & Ward (1994) suggested that this may have been an artefact caused by the lower number of particles in larger size classes. We do not agree that such an artefact occurred in our work here. Differences were statistically significant (refer to 'Results'). In addition, independent measures of the average ( $\pm 2$  SE) REO (fraction) show that the organic contents of matter filtered by *P. viridis* ( $0.99 \pm 0.67$ ), *C. belcheri* ( $0.35 \pm 0.21$ ) and *C. iradelei* ( $0.36 \pm 0.23$ ) were all significantly higher than the organic content of available seston. These are the same 3 species that showed reduced retention of the largest filtered particle size class. Yet in both *Saccostrea cucullata* and *Pinctada margarifera*, we observed neither any reduced retention of larger particles nor any net organic enrichment of filtered matter. Most importantly, these collective findings are consistent with past studies establishing that the smallest suspended particles have highest organic contents within natural seston from both temperate and tropical environments (Defossey & Hawkins 1997), explaining how reduced retention of larger particles may result in the greater proportional retention of organic matter. In a related phenomenon, Defossey & Hawkins (1997) reported differential size-dependent rejection of larger particles within pseudofaeces from the temperate filter-feeding bivalves *Mytilus edulis*, *Ruditapes philippinarum* and *Tapes decussatus*, pointing out how rejection observed on the basis of particle size alone may effect the organic enrichment of natural filtered seston. It seems then, that larger particles may be relatively 'undesirable', for which both a declining retention efficiency on the gill and an increasing efficiency of rejection as pseudofaeces may additively effect the pre-ingestive selection of organically rich matter.

We suspect that methodological differences may explain the contrast between past reports that REP increased to constant maxima with increasing particle diameter, and our present findings in *Perna viridis*, *Crassostrea belcheri* and *Crassostrea iradelei*, including past findings in *Placopecten magellanicus* (Cranford & Grant 1990, MacDonald & Ward 1994). Both our present work and that in *P. magellanicus* compared particle-size distributions within the inflow and outflow from separate trays that each contained 1 shell-

fish, when high throughflows ensured that test individuals did not remove more than 30% of the particles suspended within previously unused seawater. In contrast, other measures of particle retention efficiency in filter-feeding bivalves have all monitored the relative decline of different size-fractions whilst experimental individuals were maintained within static containers of seawater, or with very slow throughflows (refer Barillé et al. 1993 for summary of past literature). Under such circumstances of limited throughflow, repeated re-filtering of water may result in the ultimate removal of all larger particles, and possible overestimation of the associated retention efficiencies.

Negative influences of TPM have been recorded upon retention efficiencies for small particles in temperate species that include *Crassostrea virginica* (Loosanoff & Engle 1947), *Mytilus edulis* (Davids 1964), *Agopecten irradians* (Palmer & Williams 1980), *Ostrea edulis* (Wilson 1983) and *Crassostrea gigas* (Barillé et al. 1993). It is possible that the same may have occurred in the present species over larger ranges of seston availability than were studied here. However, whether particle retention efficiency varies within and/or between species, our findings suggest that variation is of both physiological and ecological importances. Compared with the available seston, the organic content of filtered particles was increased by averages of about 35% in *Crassostrea belcheri* and *Crassostrea iradelei*, and by an average of as much as 99% in *Perna viridis* (Table 2). Differential retention of filtered particles has been well established using flow cytometry in many shellfish species (e.g. Bougrier et al. 1997, and references therein). For these reasons, it may not be acceptable to calculate FR ( $\text{mg h}^{-1}$ ) indirectly as the product of CR ( $\text{l h}^{-1}$ ) and food availability measured either as TPM ( $\text{mg l}^{-1}$ ) or POM ( $\text{mg l}^{-1}$ ).

In addition to establishing differential retention of filtered particles on the gill, we have shown that all 5 species studied here were able selectively to enrich the organic content of ingested matter relative to filtered matter, preferentially rejecting particles of higher inorganic content as pseudofaeces prior to ingestion. Previous work in temperate species feeding upon the same natural seston in the bay of Marennes-Oléron, France, has shown that efficiencies of that selection (NOSE) in the cockle *Cerastoderma edule*, the oyster *Crassostrea gigas* and the mussel *Mytilus edulis* each varied positively with both the organic content of available seston (OCS) and the mass of seston filtered  $\text{h}^{-1}$  (FR) (Hawkins et al. 1998). Stepwise multiple regressions confirmed that NOSE increased in strong positive relations with OCS alone in *Perna viridis*, *Crassostrea belcheri* and *Saccostrea cucullata* studied here. It is uncertain whether NOSE declines with OCS due to a relatively constant enrichment of pseudofaeces by

mucus (Hawkins et al. 1996), or because algae are more easily transported on ciliary currents to the mouth, and may be proportionally more abundant than silt in seston of higher OCS (Jørgensen 1996). In either case, we suspect that the lack of any significant additional influence of FR on NOSE may be ecologically relevant in these tropical species. In temperate species, increased NOSE at faster FR is an important response which helps to maintain nutrient acquisition independent of fluctuations in seston availability and composition, because the general negative relation between OCS and TPM (Fig. 1) means that filtered material is increasingly 'diluted' by silt as the concentrations of available seston increase to levels that often exceed  $200 \text{ mg TPM l}^{-1}$  (Hawkins et al. 1996). This response may not be as important in tropical waters, where TPM is on average lower, and where seasonal fluctuations in seston availability are on average less extreme.

The physiological consequences of NOSE were amplified by a common positive exponential relation between NAEIO (fraction) and OCI (fraction) (Fig. 6). Similar relations have previously been observed within *Cerastoderma edule*, *Crassostrea gigas* and *Mytilus edulis* feeding upon natural seston in temperate waters; the relation observed in *M. edulis* was similar to the common relation observed here (Fig. 6) (Hawkins et al. 1998). The reason for these relations is presently unclear. Hawkins et al. (1996) suggested that dependence of NAEIO on OCI may stem from the metabolic faecal losses that are incurred through normal digestive processes, and which appear reasonably constant per unit of total mass ingested (Hawkins et al. 1990), thereby exerting proportionally greater influence upon net efficiencies of absorption from ingested matter of increasingly lower organic contents. Alternatively, it has been proposed that lower efficiencies of organic selection may result in lower digestibility of the organic matter ingested from available seston of low OCS (Jørgensen 1996).

Resulting absorption and growth in *Perna viridis* may have been close to their maxima across the full range of experimental seston availability, as indicated by (1) the reduction in CR to values that approximated zero when exposed to more than about  $2.5 \text{ mg POM l}^{-1}$  (Fig. 3), and (2) the lack of any clear change in NOAR over the full range of experimental TPM (Fig. 7). This suggests that *P. viridis* was well-adapted to the ranges of seston abundance and quality experienced in the Merbok mangrove estuary, and may perform equally well in less turbid water with lower POM. However, in *Crassostrea belcheri* exposed to identical ranges of TPM and OC (refer to 'Materials and methods'), there was no decline in CR ( $p > 0.05$ ) and a linear increase in NOAR with TPM (Fig. 7). Apparently, *C. belcheri* would have ingested more and grown faster at higher

food availabilities than were experienced here, as is consistent with the natural distribution of this fast-growing oyster in turbid waters (e.g. Yoo & Ryu 1984).

NOAR ( $\text{mg organics g}^{-1} \text{ h}^{-1}$ ) represents the energy available for metabolism and production. The average NOAR of  $21.5 \text{ mg organics h}^{-1} \text{ g}^{-1}$  that we report here in *Perna viridis* represents an organic ingestion rate of nearly 52% of total dry soft tissue per day. Shafee (1979) reported that the energy deposited within tissue (= net growth or production) represented a maximum of 56% of the energy absorbed in *P. viridis*. Assuming that the energy content of absorbed organic matter was  $7.25 \text{ J mg}^{-1}$  (Hawkins et al. 1996), the resulting energy available for production in *P. viridis* of  $1 \text{ g}$  dry soft tissue may be calculated as  $[0.56 \times (21.5 \times 7.25)] = 87 \text{ J h}^{-1}$ . Mussel tissue has an energy content of about  $23.5 \text{ J mg}^{-1}$  (Slobodkin & Richman 1961), so that the present estimate of average NOAR indicates potential net growth of about 9% soft tissue  $\text{d}^{-1}$  in *P. viridis* of  $1 \text{ g}$  dry soft tissue. Equivalent calculations based upon measures of NOAR in the temperate mussel *Mytilus edulis* indicated that maximal growth associated with apparent saturation of digestive processes represented only  $4.0\% \text{ g}^{-1} \text{ dry soft tissue d}^{-1}$ , which matched seasonal maxima in the natural environment (Hawkins et al. 1997). This contrast is consistent with observations that shell length in *P. viridis* may increase by an average of as much as  $13 \text{ mm mo}^{-1}$  during growth from seed ( $<30 \text{ mm}$ ) to marketable size ( $>75 \text{ mm}$ ) (Kuriakose 1980, Rangarajan & Narasimham 1980), compared with a maximum of only  $7 \text{ mm mo}^{-1}$  in *M. edulis* and various other mussel species of comparable size from temperate waters (Hickman 1979).

Fast growth in *Perna viridis* stems from a combination of interrelated differences in feeding behaviour. Maximal CR recorded in *P. viridis* at our lowest seston availabilities of  $\text{POM} < 1 \text{ mg l}^{-1}$  averaged  $13.2 \pm 7.0 \text{ l h}^{-1} \text{ g}^{-1}$  ( $n = 9$ ,  $\pm 2 \text{ SE}$ ), which was more than double average maxima of less than  $5 \text{ l h}^{-1} \text{ g}^{-1}$  recorded over the same range of natural POM in the temperate mussel *Mytilus edulis* (e.g. Hawkins et al. 1996, 1998) (Fig. 3). Further, the average ( $\pm 2 \text{ SE}$ ) REO of  $0.99 \pm 0.67$  in *P. viridis* was significantly greater than in all 4 oyster species (Table 2), and the average NOSE of  $0.63 \pm 0.03$  in *P. viridis* was significantly higher than has previously been reported in any species to date (e.g. Hawkins et al. 1996, 1998, Iglesias et al. 1996, Soletchnik et al. 1996, Bacon et al. 1998).

As in *Perna viridis*, present findings suggest that organic absorption and growth in both *Saccostrea cucullata* and *Pinctada margarifera* were already maximal at our lowest experimental seston concentrations of about  $10 \text{ mg TPM l}^{-1}$  (Fig. 7). *S. cucullata* is generally found on rocky or firm substrata in relatively open waters, whereas *Pinctada* species are often character-

istic of other clearer water, including coral reefs. Certainly, compared with other filter-feeding bivalve shellfish from tropical waters, *Pinctada* species grow very slowly, with an annual increase in shell length of less than  $3 \text{ cm}$  (Yoo et al. 1986, Numaguchi 1996). This was reflected by the average NOAR of  $1.3 \pm 0.9 \text{ mg h}^{-1}$  recorded in *Pinctada margarifera* of  $1 \text{ g}$  dry soft tissue here, and which was only 6% of the average NOAR recorded in *P. viridis* (Table 2). CR in *P. margarifera* was comparable with the other studied species, but with little pre-ingestive selection, as REO was insignificant, and NOSE only averaged  $0.22 \pm 0.09$  (Table 2). Significantly, Ward & MacDonald (1996) did not observe selective rejection of inorganic matter in the sub-tropical pearl oyster *Pinctada imbricata*, which appeared to produce pseudofaeces solely as a means of regulating ingestion rate. Our collective findings therefore suggest that *Pinctada* spp. may not be well-adapted for the differential retention or rejection of POM, which constitutes at least part of the physiological basis for comparatively slow growth.

In conclusion, we have shown that key interrelations between component processes of nutrient acquisition in tropical bivalves were similar to those among temperate species. Our findings also establish significant differences in the feeding behaviour of functionally similar species from tropical latitudes. Although subtle, these differences are likely to be of ecological consequence, reflecting the importance of species diversity. Further studies over complete natural ranges of seston availability and composition are required before the development of models that predict relative impacts of different bivalve filter-feeders upon particle fluxes, nutrient dynamics and community structure.

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