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Comparative allometries of gut-passage time, gut content and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*

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Abstract. Allometric relations were determined in bivalves collected from approximate mid-tide levels in Biscay, Spain, during March 1987. Species compared included the epifaunal suspension-feeder *Mytilus edulis* L. (9 to 1 108 mg dry soft-tissue weight) from a rocky-shore population at Meinakotz Beach, and the infaunal deposit-feeder *Cerastoderma edule* (L.) (1 to 192 mg dry soft-tissue weight) from the mudflats in Mundaka Ría. Relative to M. edulis, and compared per unit dry tissue weight, *C. edule* had similar palp areas but smaller gill areas. In addition, to help maximize absorption from organically-poor deposits, *C. edule* ingested three to four times as much food per hour, but had gut contents that were five to six times greater, so that gut-passage times available for the extraction of nutrients were 2.5 times longer. Metabolic faecal losses, which were comprised of endogenous materials lost from the bivalve into the gut, were two to three times greater in *C. edule,* but similar to those of *M. edulis* when expressed per unit mass ingested by each species. These losses were very substantial, being equivalent to as much as 15% of the ingested mass, and represent a significant indirect cost that is presumably incurred largely by the intracellular digestion characteristic of bivalves. Weight exponents indicated that such metabolic "investment" represented an unchanging proportion of the total costs of growth. They also showed that age-related constraints on total production did not stem from decreasing gut content. Rather, associated exponents identified limitations to the production in each species as being linked with marked reductions of gut-passage time and ingestion rate, and indicated that these limitations do not derive from corresponding decreases in gill or palp areas.

Introduction

Limits to increased net energy gain in bivalve molluscs are set primarily by functional constraints on ingestive and/or digestive capacity, rather than by the direct metabolic costs of feeding and growth (Bayne et al. 1989). Below these limits, bivalves display an impressive ability to regulate resource acquisition by adjusting parameters of feeding which include ingestion rate, gut content and/or activity of digestive enzymes (Bayne and Hawkins 1990). These adjustments, influencing gut-passage time and associated absorption (cf. Taghon et al. 1978), are known to effect seasonal regulation of energy acquisition (Hawkins and Bayne 1984), as well as compensations acting to maximize energy uptake in response to changes in dietary quantity and/or quality (Seiderer et al. 1982, Bayne et al. 1984, 1987, 1988, 1989).

Although it has been established that the above feeding components are involved in the active regulation of net energy gain, there is little insight into how they each change with body-size. Reduction of weight-specific energy intake is known to constrain total asymptotic production (both somatic and reproductive) with increasing age in bivalves (Jørgensen 1976, Bayne and Newell 1983). These relations do not, however, identify those feeding components which limit energy uptake. To date, there have only been studies on the effects of animal size on absorption efficiency and/or gill area (Dral 1967, Hughes 1969, Vahl 1973 b, Thompson and Bayne 1974, Foster-Smith 1975, Theisen 1982). We are not aware of any previous work relating gut-passage time to body size, and limited data on gut content have been presented in relation to shell length alone (Hughes 1969, Wikander 1980). Similarly, there is no information concerning effects of body size upon metabolic faecal losses, which comprise endogeneous materials lost from the animal following secretion, exocytosis and/or abrasion in the gut. Such losses are known to be unusually large in bivalves (Hawkins and Bayne 1984, 1985), representing an indirect cost of digestion and absorption, and setting minimal limits to the organic content of food capable of supporting growth (Bayne and Hawkins 1990).

The present paper documents allometric relations for gill and palp areas, gut-passage time, gut content, ingestion rate and metabolic faecal loss determined simultaneously for both the suspension-feeder *Mytilus edulis* L.

and the fine deposit-feeder *Cerastoderma edule* (L.). Findings are discussed in relation to constraints upon total production, and these constraints are considered in relation to the contrasting strategies of feeding and digestion revealed for each species.

Materials and methods

Bivalves were collected from approximate mid-tide levels in Biscay, Spain, during March 1987; *Mytilus edulis* L. (12 to 65 mm shell length) from a rocky-shore population at Meinakotz Beach, and *Cerastoderma edule* (L.) (10 to 25 mm shell height) from the mudflats in Mundaka Ría.

The bivalves were immediately transported to the Laboratory of Animal Physiology at the University of País Vasco, cleared of epibionts, and air-dried before glueing (fast-setting Araldite) each individual by its exterior shell surface to the internal wall of an open-topped plastic tray. Individuals were positioned with exhalent siphons pointed downwards, about 1 cm from base-level, and were immersed in tanks of seawater within 4 h of collection. Positioning as above aided settlement of egesta for subsequent collection from discrete areas beneath each individual. All seawater was replaced daily, and maintained at the natural salinity (32.0 ± 1.0‰ S) and temperature ($12.5\,°C \pm 2.0\,C°$) during continuous aeration.

Gut-passage time

The bivalves were laboratory-acclimated for 3 d, during which time they were fed the alga *Phaeodactylum tricornutum* Bohlin diluted to an organic content of 50 ± 5% total dry weight with sediment freshly scraped from the surface 5 mm of the natural mudflat. The suspended concentrations of this diet available to bivalves in the laboratory were monitored with a Coulter Counter (Model ZB), and maintained between 10 and 20×10^3 particles cm^{-3}. To measure gut-passage time, *P. tricornutum* was labelled with ^{14}C as described by Hawkins and Bayne (1984). Following transfer of the bivalves to individual trays, labelled algae were mixed with the sediment and administered, for 1 h, during which time the particle concentrations were maintained similar to those during acclimation. The bivalves were then returned to their unlabelled diet, and faeces were collected at intervals that varied between 0.25 and 2 h for a total of up to 24 h from up to 12 groups each of between three and ten individuals, spanning the size-range available for each species. Samples were pipetted directly onto 75 mm Millipore membrane-filters before dissolution of each filter with 2.5 ml 2-methoxyethanol (Chemische Fabrik), digestion with 1 ml Tissue Solve (Ferosa) at 60 °C for 24 h, neutralization with 0.5 ml sulphuric acid, and addition of 10 ml (Ferosa) scintillation cocktail. Following instrument equilibration, β-emissions were determined with a liquid scintillation spectrophotometer, and ^{14}C-hexadecane internal standards (Amersham) were used to determine absolute counting efficiencies for each vial before expressing results as disintegrations per minute (dis/min) per faecal sample per mussel.

For the estimation of gut-passage time, data indicating a transient peak of the ^{14}C label in the faeces were modelled using an iterative least-squares algorithm to fit a one-compartment model as follows:

$$\text{when } 0 < t < t_1, \quad \text{then } y = 0; \tag{1}$$

$$\text{when } t_1 < t < t_2, \quad \text{then } y = a_1 (1 - e^{-a_2 (t - t_1)}); \text{ and} \tag{2}$$

$$\text{when } t_2 < t, \quad \text{then } y = a_1 (1 - e^{-a_2 \cdot t_2})\, e^{-a_2 (t - t_2)}; \tag{3}$$

where y = absolute dis/min at time t, t_1 = "transit time" to the first appearance of faecal ^{14}C, $t^2 = t^1 + 1$, and a_1 and a_2 are parameters describing the maximum value for y and the rate of decrease for y with t, respectively. Final egestion occurs at an exponentially reducing rate (cf. Ruggerone 1989), so that there is no theoretical time at which all ^{14}C has been completely removed from the gut. Gut-passage time was therefore estimated as the time at which cumulative dis/min integrated under the model curve reached 90% of the total egested dis/min.

Gut content

Egesta derived from particles ingested in the natural environment were sampled at intervals that varied between 4 and 15 h up to a total of 47 h after immersion of freshly-collected individuals in filtered (2 μm) seawater. Faeces were siphoned with a glass pipette from between 6 and 8 replicate groups each of between 2 and 15 individuals spanning the available size-range in each species. The pooled faeces from each group were filtered onto pre-ashed (450 °C for 4 h) and weighed Millipore GFC filters, rinsed with 0.9% (w:v) ammonium formate, and dried to constant weight at 80 °C. Egestion was then quantified in terms of total dry matter and inorganic matter from increments in weight measured both before and after re-ashing each filter.

To estimate gut content, cumulative results indicating decreasing rates of egestion with time following the immersion of bivalves in filtered seawater were modelled using least-squares regression to fit exponential curves described by the following equation:

$$y = a_1 (1 - e^{-a_2 \cdot t}), \tag{4}$$

where y = cumulative weight of either inorganic or total egesta, t = time since re-immersion, and a_1 and a_2 are parameters describing the maximum value for y and the rate of increase for y with t, respectively.

To account for a sustained loss of organics egested within faeces (see "Results – Metabolic faecal loss") and because the exponential function in Eq. (4) precludes prediction of the time at which all material had been egested, fitted curves were used to quantify gut content (mg total dry weight) as total egestion prior to the time at which cumulative egestion reached 95% of the maximum value predicted for inorganic matter alone.

Ingestion rate

Ingestion rate (IR; mg total dry wt h^{-1}) may be calculated according to Hawkins and Bayne (1984) as follows:

$$\text{IR} = \frac{\text{gut content (mg)}}{\text{gut passage time (h)}}. \tag{5}$$

However, in the present paper, gut-passage time and gut content were not determined in the same individuals. Accordingly, the relation between ingestion rate and dry soft-tissue weight was derived by dividing the regression equation relating gut content with dry soft-tissue weight by the regression equation relating gut-passage time with dry soft-tissue weight.

Metabolic faecal loss

Metabolic faecal loss (MFL; $\mu g\ h^{-1}$) was calculated using fitted parameters predicted by Eq. (4) as follows:

$$\text{MFL} = \frac{E_{T_{95}} - E_{I_{95}}}{T_T - T_I}, \tag{6}$$

where $E_{T_{95}}$ and $E_{I_{95}}$ are 95% of the maximum predicted values for cumulative egestion of the total dry matter and inorganics, respectively; and T_T and T_I are the associated times taken for cumulative egestion of the total dry matter and inorganics, respectively, to reach 95% of maximum predicted values. This calculation assumes the inorganic content of metabolic faecal loss to be insignificant.

Gill area and palp area

Following the above measurements, the left valve and mantle were removed from each individual, which was then placed in seawater in a petri dish. An outline of the outer left gill was traced onto paper placed over the dish cover, and the dimensions of each palp were measured using a stereoscopic microscope with eyepiece micrometer. Gill area was calculated from the weight of paper enclosed by each trace, and palp area from recorded dimensions assuming palp outline to be an isosceles triangle. Areas were doubled to account for each side of the demibranch or palp, and multiplied by the number of demibranches (4) or palps (2) to compute the total area for each individual.

The remaining soft tissues were excised from these same individuals, pooled with associated gills and palps, and dried at 80 °C for 24 h before measuring total soft-tissue weights.

Allometric relationships could then be defined using Type I least-squares regression, and treatments compared by covariance analysis (Sokal and Rohlf 1981).

Results

Shell and dry-tissue allometry

Relations between dry soft-tissue weight (y, mg) and either the shell length (x, mm) of *Mytilus edulis* or the shell height (x, mm) of *Cerastoderma edule* were described by the following regressions (ranges in parentheses represent 95% confidence intervals):

$$M.\ edulis,\ y = 0.008\,x^{2.82\,(\pm 0.18)} \quad (n=28,\ r=0.995,\ P<0.001); \tag{7}$$

$$C.\ edule,\ y = 0.005\,x^{3.23\,(\pm 0.14)} \quad (n=22,\ r=0.997,\ P<0.001). \tag{8}$$

Gill area and palp area

Relations between dry soft-tissue weight (x, mg) and either gill or palp area (y, mm^2) for *Mytilus edulis* and *Cerastoderma edule* are illustrated in Fig. 1 and described by the following regressions:

$$M.\ edulis;\ \text{gill area}\quad y = 29.90\,x^{0.72\,(\pm 0.08)} \quad (r=0.997,\ n=6,\ P<0.001); \tag{9}$$

$$M.\ edulis;\ \text{palp area}\quad y = 0.35\,x^{0.68\,(\pm 0.19)} \quad (r=0.982,\ n=6,\ P<0.001); \tag{10}$$

$$C.\ edule;\ \text{gill area}\quad y = 6.74\,x^{0.72\,(\pm 0.15)} \quad (r=0.994,\ n=5,\ P<0.001); \tag{11}$$

$$C.\ edule;\ \text{palp area}\quad y = 0.17\,x^{0.80\,(\pm 0.22)} \quad (r=0.989,\ n=5,\ P<0.001). \tag{12}$$

Gill areas documented here for *M. edulis* were virtually identical to those expressed per unit tissue weight by Vahl (1973 b) (see present Fig. 1). Comparisons using Eqs. (7) and (8) show that the present data are also comparable with previous gill and/or palp areas expressed per unit shell length or height (Dral 1967, Foster-Smith 1975, Theisen 1982). Slopes of regressions relating log gill area and log shell length of *M. edulis* (2.02 ± 0.06) and *C. edule* (2.30 ± 0.76) are not significantly different from 2, in accordance with proportionality to the square of shell length (Hughes 1969, Foster-Smith 1975, Theisen 1982, Worrall et al. 1983).

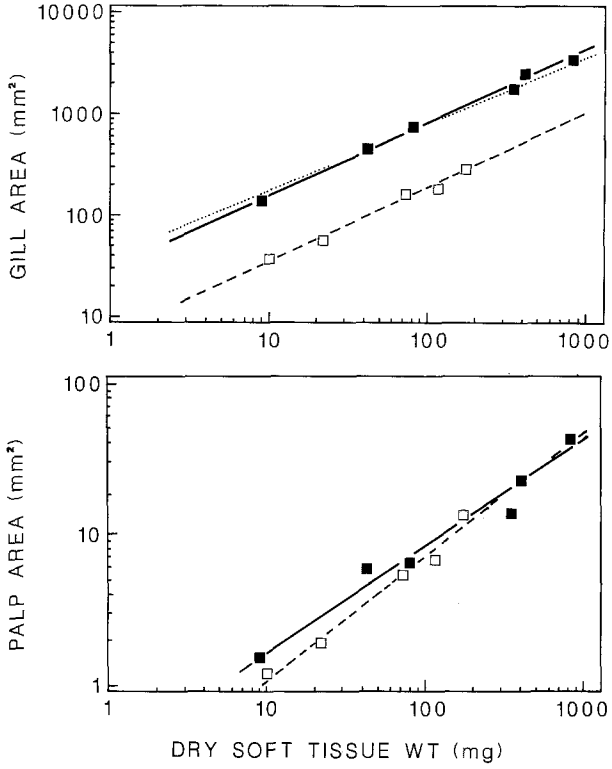

Fig. 1. *Mytilus edulis* (■) and *Cerastoderma edule* (□). Relations between dry soft-tissue weight and either gill area or palp area. Lines fitted by least-squares ["Results – Shell and dry-tissue allometry": Eqs. (9) to (12)]. A previous regression describing gill area in *M. edulis* (Vahl 1973 b) is shown for comparison (dotted line)

Covariance analyses identified significant differences between species in gill area per unit body weight, and confirmed that there were no statistical differences between species in palp area per unit body weight (Fig. 1). For gill area, Eqs. (9) and (11) possess similar weight exponents ($t=0.044$, 9 DF, $P>0.05$) but different intercept values ($t=6.229$, 9 DF, $P<0.001$), confirming that relative to *Cerastoderma edule* and irrespective of body size, the gill area of *Mytilus edulis* was four to five times greater per unit dry soft tissue (Fig. 1).

Gut-passage time

An example of the curves fitted statistically to peaks of ^{14}C in the faeces is illustrated with the associated estimation of gut-passage time in Fig. 2. Following logarithmic transformation of each variable, fitted relations between dry tissue weight (x, mg) and gut-passage time (y, hours) were statistically significant, as follows:

$$Mytilus\ edulis\quad y = 1.30\,x^{0.34\,(\pm 0.12)} \quad (r=0.890,\ n=12,\ P<0.001); \tag{13}$$

$$Cerastoderma\ edule\quad y = 1.71\,x^{0.41\,(\pm 0.32)} \quad (r=0.787,\ n=8,\ P<0.050). \tag{14}$$

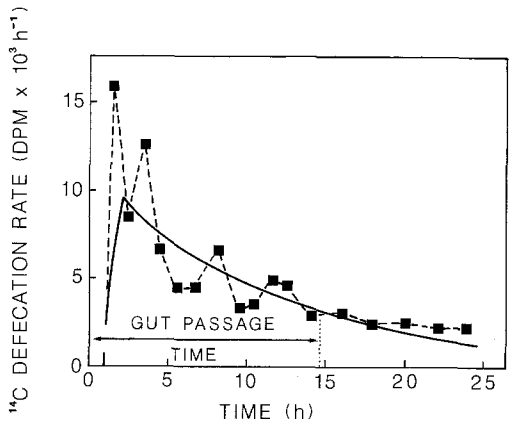

Fig. 2. *Mytilus edulis*. Example of disintegrations per minute for faecal ^{14}C over time following ingestion of ^{14}C-labelled alga, together with associated estimation of gut-passage time. Data represent total egestion from largest size-class ($n=3$ individuals with mean dry soft-tissue wt of 604 mg). Model curves were fitted by least-squares as described in "Materials and methods – Gut-passage time"

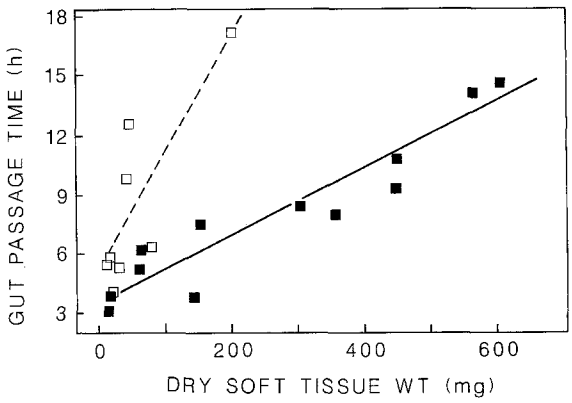

Fig. 3. *Mytilus edulis* (■) and *Cerastoderma edule* (□). Relations between dry soft-tissue weight and gut-passage time. Lines fitted by least-squares ["Results – Gut-passage time": Eqs (15) and (16)]

However, these dependencies are better defined by linear relations, as illustrated in Fig. 3 and described by the following regressions:

$$M.\ edulis,\ y=3.50+0.017(\pm0.004)x \quad (r=0.943, n=12, P<0.001); \quad (15)$$

$$C.\ edule,\ y=5.02+0.060(\pm0.041)x \quad (r=0.827, n=8, P<0.020). \quad (16)$$

Comparison of the intercept values for these linear regressions indicated similar gut-passage times in the smallest individuals of each species ($t=1.034$, 18 DF, $P>0.050$). Slopes, however, were significantly different ($t=2.592$, 18 DF, $P<0.020$), reflecting gut-passage times in the largest *C. edule* that were 2.5 times longer than in *M. edulis* of equivalent dry tissue weight (Fig. 3).

Gut content

Examples of the curves fitted statistically to data indicating decreasing rates of egestion with time following the immersion of bivalves in filtered seawater are illustrated with associated estimations of gut content in Fig. 4. In turn, fitted relations between each measure of gut content (y, mg total dry wt) and corresponding body size (x, mg dry soft-tissue) are illustrated in Fig. 5 and described by the following regressions:

$$Mytilus\ edulis \quad y=0.080\,x^{0.68(\pm0.06)} \quad (r=0.991, n=16, P<0.001); \quad (17)$$

$$Cerastoderma\ edule \quad y=0.507\,x^{0.64(\pm0.12)} \quad (r=0.968, n=12, P<0.001). \quad (18)$$

These regressions possess similar weight exponents ($t=0.699$, 25 DF, $P>0.050$) but different intercept values ($t=7.747$, 25 DF, $P<0.001$), confirming that relative to *M. edulis* and irrespective of body weight, gut contents in *C. edule* were five to six times greater per unit dry body-tissue (Fig. 5).

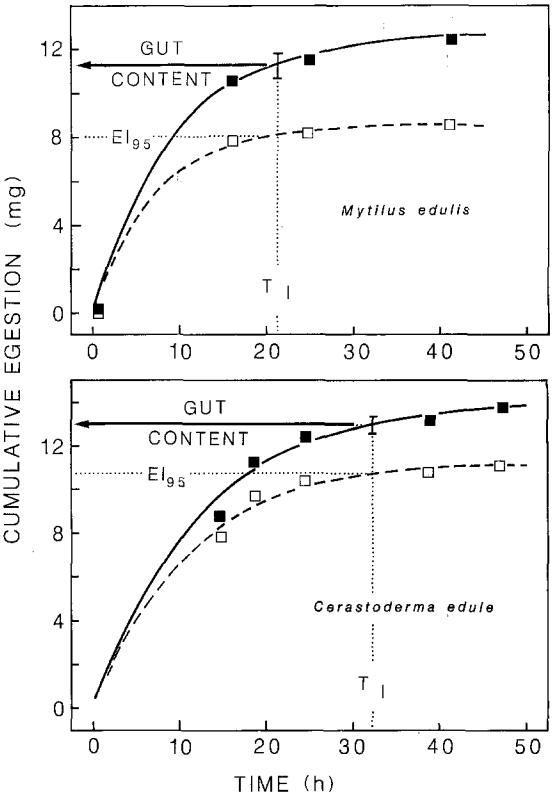

Fig. 4. *Mytilus edulis* and *Cerastoderma edule*. Examples of cumulative egestion with time following immersion in filtered seawater. Data (±95% confidence intervals) are presented both for total dry matter (■) and for inorganic matter (□). Curves fitted by least-squares; gut content (mg total dry matter) is total cumulative egestion prior to time (T_I) at which cumulative egestion reached 95% of maximum value predicted for inorganics alone ($E_{I_{95}}$) (see "Materials and methods – Gut content")

Ingestion rate

Relations between dry soft-tissue weight (x, mg) and rate of ingestion (y, mg h^{-1}) were derived from Eqs. (13), (14), (17) and (18) [see "Materials and methods (Eq. 5) for

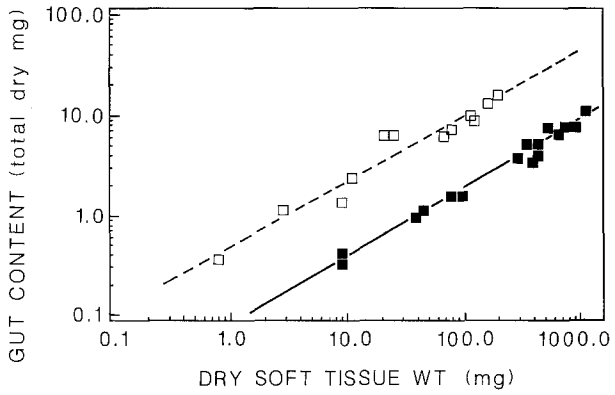

Fig. 5. *Mytilus edulis* (■) and *Cerastoderma edule* (□). Relations between dry soft-tissue weight and voided gut content. Lines fitted by least-squares ["Results – Gut content": Eqs. (17) and (18)]

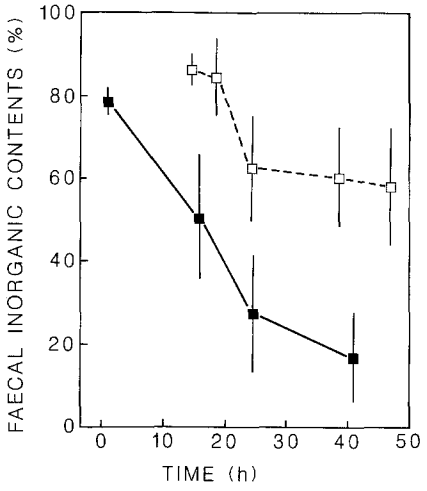

Fig. 6. *Mytilus edulis* (■) and *Cerastoderma edule* (□). Inorganic contents of faeces egested with time following immersion of bivalves in filtered seawater. Data are means (±95% confidence intervals) for all size classes combined

calculation], and are described as follows:

$$\textit{Mytilus edulis} \qquad y = 0.061\,x^{0.35(\pm 0.12)}; \tag{19}$$

$$\textit{Cerastoderma edule} \quad y = 0.296\,x^{0.23(\pm 0.28)}. \tag{20}$$

These regressions possess similar weight exponents ($t = 0.747$, 12 DF, $P > 0.05$) but different intercept values ($t = 13.639$, 12 DF, $P < 0.001$), indicating that relative to *M. edulis* and irrespective of body size, rates of ingestion by *C. edule* were three to four times greater when expressed as dry mg per unit body tissue.

Metabolic faecal loss

Considering all size classes combined, fitted regressions describing cumulative egestion following the immersion of bivalves in filtered seawater (e.g. Fig. 4) indicate that 95% of inorganic material had been egested within 15.8 ± 3.2 h (mean ± 95% confidence interval) and 28.3 ± 2.4 h for *Mytilus edulis* and *Cerastoderma edule*, respectively. Alternatively, and without exception, significant accumulation of total dry faeces continued throughout the period of experimental collection (47 h; Fig. 4), which period was three times longer than the slowest gut-passage time recorded following the ingestion of ^{14}C-labelled alga (Fig. 3). This indicates a sustained loss of organics that was reflected, as illustrated in Fig. 6, by a decreasing proportion of the inorganics egested within faeces. Assuming gut-passage times for ingested organics to be broadly equivalent to those for ingested inorganics, we consider this continuing organic egestion to represent metabolic faecal loss (described in "Introduction" and "Discussion"), quantified as described in "Materials and methods (Eq. 6)."

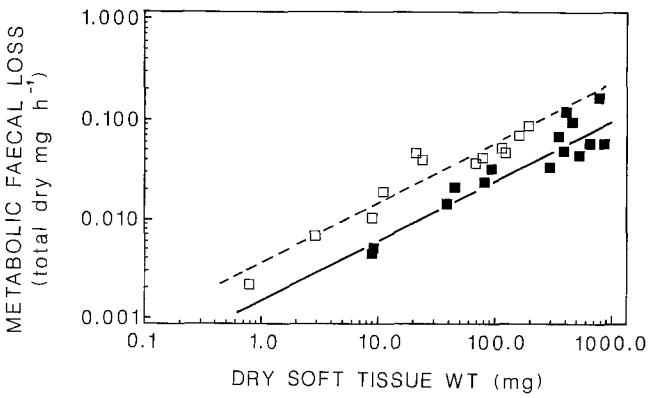

Fig. 7. *Mytilus edulis* (■) and *Cerastoderma edule* (□). Relations between dry soft-tissue weight and metabolic faecal loss. Lines fitted by least-squares ["Results – Metabolic faecal loss": Eqs. (21) and (22)]

Relations between dry soft-tissue weight (x, mg) and metabolic faecal loss (y, μg h^{-1}) are illustrated in Fig. 7 and described by the following regressions:

$$\textit{Mytilus edulis} \qquad y = 1.33\,x^{0.64(\pm 0.15)} \quad (r = 0.933,\ n = 15,\ P < 0.001); \tag{21}$$

$$\textit{Cerastoderma edule} \quad y = 3.55\,x^{0.60(\pm 0.14)} \quad (r = 0.952,\ n = 12,\ P < 0.001); \tag{22}$$

These regressions possess similar weight exponents ($t = 0.452$, 25 DF, $P > 0.050$) but different intercept values ($t = 2.289$, 25 DF, $P < 0.050$), confirming that relative to *M. edulis* and irrespective of body size, metabolic faecal losses from *C. edule* were two to three times greater per unit dry body-tissue (Fig. 7).

Eqs. (19) to (22) above were used to derive further regressions defining the relations between dry soft-tissue weight (x, mg) and metabolic faecal loss per unit ingestion (y, μg metabolic faecal loss mg^{-1} ingestion), described as follows:

$$\textit{Mytilus edulis} \qquad y = 21.6\,x^{0.30(\pm 0.18)}; \tag{23}$$

$$\textit{Cerastoderma edule} \quad y = 12.0\,x^{0.37(\pm 0.31)}. \tag{24}$$

These regressions possess similar weight exponents ($t = 0.410$, 12 DF, $P > 0.050$) that each differ significantly from zero ($P < 0.05$), as well as similar intercept values ($t = 0.793$, 12 DF, $P > 0.050$). Thus, per unit ingestion, metabolic faecal losses were greater in larger individuals of each species. However, irrespective of body size, there were no statistical interspecific differences in metabolic faecal losses per unit ingestion.

Discussion

It is important to note that our present measures of gut content in *Mytilus edulis* and *Cerastoderma edule* were of voided material (cf. Hughes 1969, Wikander 1980), all of which had been subject to absorption both within the digestive tubules and intestine (Hawkins et al. 1986). Our "voided" gut contents are thus smaller than the "true" gut contents being digested within individuals feeding normally. Given $<20\%$ organics in fresh faeces (Fig. 6), and assuming a net absorption efficiency of 60% of the organic weight, then gut contents measured in terms of voided material may have been up to 23% less than the mass of that same material upon ingestion. However, true gut content lies between ingested and voided masses, and may be calculated as the mass of material remaining in the gut midway through one gut-passage time (cf. Bayne et al. 1987). It may be assumed that gut content reduces at an exponential rate with passage of material through the gut, and that this rate [e.g. Parameter a_2 in Eq. (4)] is described by the fitted value of 0.2 determined in *M. edulis* by Bayne et al. (1987) from a relationship between gut-passage time and absorption efficiency. On this basis, gut content measured in terms of voided material did not underestimate the true gut content by more than 10%. Such errors are too small to have significantly affected the large interspecific differences seen here for gut content and ingestion rate. Furthermore, absorption efficiency is independent of size (Vahl 1973b, Thompson and Bayne 1974), so that the weight exponents documented here for voided gut content are representative of individuals feeding in their natural environment.

Relative to *Mytilus edulis,* then, and compared per unit dry soft-tissue weight, *Cerastoderma edule* had faster rates of ingestion, but was digesting so much more food that gut-passage times were substantially slower. Despite faster ingestion, we have also shown that *C. edule* had smaller gill areas which, compared with *M. edulis,* are known to be less porous as indicated both by lower ostial area and by lower rates of pumping per unit gill area (Foster-Smith 1975).

Seasonal cycles in dry soft-tissue weight are similar in *Mytilus edulis* and *Cerastoderma edule* from comparable latitudes (e.g. Hawkins et al. 1985, Navarro et al. 1989). The present results for nearby populations in northern Spain therefore reflect different strategies of feeding and digestion. *M. edulis* is epifaunal and non-siphonate, feeding primarily on suspended particulate matter. In contrast, *C. edule* is an infaunal siphonate, feeding mainly upon fine surficial deposits available at high concentrations – when too high a filtration per unit gill area may choke the gill with sediment. Similarly, given constant filtration per unit gill area, too large a gill may incur saturation of other feeding processes, as suggested by Hughes (1969) in explanation of small gill area in the deposit-feeder *Scrobicularia plana.*

Sibly and Calow (1986) explained why larger guts help to maximise the net rate of obtaining energy from poorer foods. In addition, proportionally more nutrient is derived from digesta retained longer within the gut (Calow 1977), as has been verified in molluscs by positive relationships between gut-passage time and absorption efficiency (Bayne et al. 1984, 1987, 1988). Presumably, then, both larger gut content and longer retention time helped *Cerastoderma edule* to maximise absorption from organically-poor deposits. This is exemplified by net absorption efficiencies of more than 20% in *C. edule* ingesting natural deposits with organic contents that are typically $\sim 10\%$ total dry weight (Navarro et al. 1990). In contrast, maximal net absorption efficiencies are seen in *Mytilus edulis* feeding upon organically-rich natural suspensions, but these decline exponentially to negative values for diets with organic contents of $\lesssim 20\%$ (Bayne et al. 1987).

Sustained egestion of organics (Figs. 4 and 6) represented metabolically derived material excreted to the alimentary canal and therefore assayed with faeces (cf. Forster and Gabbott 1971, Calow and Fletcher 1972). To some extent, this material must represent an indirect cost of the intracellular digestion characteristic of bivalve digestive cells, for this entails rejection of cellular contents within residual bodies exocytosed during cycles of digestion and reconstitution (Platt 1971). Other sources of metabolic faecal loss may include digestive enzymes, mucus bound to faecal ribbons (Arakawa 1970), bacteria incubated within the digestive system (Prieur 1981), and/or metabolic end products (Hawkins et al. 1983).

Metabolic faecal losses were first recognised in *Mytilus edulis* from analyses of faecal nitrogen content (Hawkins et al. 1983) and isotope depuration (Famme and Kofoed 1982, Hawkins and Bayne 1984). Hawkins and Bayne (1985) then compared measures of gross and net absorption efficiencies, showing that as much as 67% of the organic nitrogen within faeces from *M. edulis* may be of metabolic origin. Present results confirm similar losses, determined using an independent technique. Calculating the mean for individuals of all sizes combined, then metabolic faecal losses over one gut-passage time [predicted from Eqs. (15)–(16)] comprised 61.6 ± 3.6 ($n=15$) and 107.4 ± 14.3 ($n=12$) percent of organic matter in the gut contents voided from *M. edulis* and *Cerastoderma edule,* respectively. Such losses will have a profound effect on apparent absorption determined gravimetrically, and lead to consistent underestimation of the gross uptake as measured using isotopes (e.g. Hawkins and Bayne 1985).

Expressed per unit total dry weight of ingested particulates, metabolic faecal losses were similar in each species. Eqs. (23) and (24) indicate that these losses represented between 7 and 9% of the total dry mass ingested by individual *Mytilus edulis* and *Cerastoderma edule* of 100 mg dry soft-tissue weight. Given that proportional losses increased with size, comprising as much as 15% of ingested mass in *M. edulis* of 600 mg dry soft-tissue weight, then the present findings are consistent with a seasonal range of 7 to 24% estimated previously for nitrogen alone in *M. edulis* of 295 to 990 mg dry soft-tissue weight, these percentages being derived assuming that nitrogen contributes 10% of organic dry weight (Hawkins and Bayne, 1984). These losses were considerably greater than in other species with predominantly extracellular digestion (Hawkins and Bayne 1984), and indicate com-

parable metabolic "investment" per unit mass of the total particulate matter ingested by each species. For a given body size, such consistency accounts for observations that digestive efficiencies (efficiencies with which chlorophyll were degraded) may be independent of organic content of the diet (Hawkins et al. 1986), whereas net absorption efficiencies become progressively reduced for diets with an increasing ash content (Hawkins et al., 1986, Bayne et al. 1987, 1988).

Gut-passage times recorded here are consistent with previous data for *Mytilus edulis* (Hawkins and Bayne 1984, Bayne et al. 1987). However, different methods of measurement preclude comparison of our own data with those previously documented for other species. In particular, Hughes (1969), Hylleberg and Gallucci (1975) and Wikander (1980) measured the rates of passage of dyed or of ashed food-particles from the mouth or stomach to anus of deposit-feeders from the genera *Scrobicularia* ($\approx$8 h), *Macoma* (1 to 9 h) and *Abra* (12 to 19 h). These times represent the "transit time", which is generally faster than the time measured in the present study for complete evacuation of one meal (Utley et al. 1970). Gut-evacuation times in the above deposit-feeders may therefore be substantially slower than in *Mytilus edulis*, which is consistent with the longer retention of particles ingested by *Cerastoderma edule*.

Exponents of the regressions describing relations between dry soft-tissue weight and either gill area, palp area, gut content or metabolic faecal loss in both *Mytilus edulis* (0.72 ± 0.08, 0.68 ± 0.19, 0.68 ± 0.06 and 0.64 ± 0.15, respectively) and *Cerastoderma edule* (0.72 ± 0.15, 0.80 ± 0.22, 0.64 ± 0.12 and 0.60 ± 0.14, respectively) were similar to theoretical expectations ($b = 0.75$) that have been experimentally confirmed for energy expenditure measured either as oxygen uptake (Vahl 1973 a, b, Bayne and Newell 1983) or as total heat dissipation (Widdows 1987). Such consistency suggests a general mechanistic integration between rate of metabolism, the surface area of the primary site for extraction of oxygen from water, surface areas enabling the retention and sorting of food, as well as the amount of food being processed at any one time. It also suggests an associated integration with the energy investment in food-processing, this investment being represented by metabolic faecal losses so that, irrespective of size, significant indirect costs of feeding comprise a relatively constant proportion of the total metabolic expenditure.

Compared with the exponents for gill area, palp area, gut content and metabolic faecal loss, those for gut-passage time and ingestion rate were significantly reduced in both *Mytilus edulis* (0.34 ± 0.12 and 0.35 ± 0.12, respectively) and *Cerastoderma edule* (0.41 ± 0.32 and 0.23 ± 0.28, respectively). These values complement those previously recorded for ingestion in bivalves feeding upon natural particulates ($b = 0.44 \pm 0.12$, $n = 10$; Bayne and Newell 1983), as well as earlier findings that weight exponents for pumping rate were lower than for oxygen consumption in these same species (Vahl 1973 a, b). As for direct costs measured as oxygen consumption, metabolic faecal losses were greater per unit mass ingested by larger individuals of each species. Moreover, relative to total heat dissipation and metabolic faecal losses, similar weight exponents for gut content indicate that declining production efficiencies with age did not stem from weight-specific decreases in the amount of food being digested at any one time. Rather, low exponents for both gut-passage time and ingestion rate identify limitations to the production of each species as being linked with marked reductions in the rates with which these filter-feeders collect particles and pass them through their digestive system. Whilst not identifying the basis of these reductions, associated exponents indicate that these limitations were not imposed by corresponding decreases in the surface areas of gills or palps.

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