

## Aspects of feeding, including estimates of gut residence time, in three mytilid species (*Bivalvia*, *Mollusca*) at two contrasting sites in the Cape Peninsula, South Africa

B. L. Bayne<sup>1</sup>, D.W. Klumpp<sup>2\*</sup>, and K.R. Clarke<sup>1</sup>

<sup>1</sup> NERC Institute for Marine Environmental Research, Prospect Place, Plymouth PL1 3DH, England

<sup>2</sup> Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa

**Abstract.** Individuals of three mytilid species (*Choromytilus meridionalis*; *Perna perna*; *Aulacomya ater*) from two sites characterised by different qualities of ration available to these suspension feeders showed different rates in some components of the physiological energy budget. These differences included higher feeding (=clearance) and respiration rates, but lower absorption efficiencies, in individuals from the site with the higher quality ration. A novel technique was employed to estimate the residence time of food particles in the digestive gland. Individuals showing higher feeding rates had shorter residence times than those feeding more slowly and a significant positive correlation was demonstrated between residence time and absorption efficiency. These relationships, together with an exponential increase in rates of respiratory heat loss with an increase in ingested ration, are suggested to provide these animals with a physiological flexibility to compensate for reduced food quality in a way consistent with some theoretical predictions. Such compensations are made more effective if the total gut capacity can also change in response to the quality of the ration.

The responses of suspension-feeding bivalves to variations in the quantity of suspended particulate matter (sston), which is available as food, have been studied extensively for many years (see review by Bayne and Newell 1983). Responses to variable food quality are much less well understood. Currently this topic is receiving some attention, largely in response to three considerations. Firstly, there has been an increased interest in relating the physiological energetics of various consumer species (and these commonly include populations of benthic suspension feeders) to seasonal variability in the supply of food and the qualitative differences (e.g. phytoplankton, detritus, bacteria) that this often represents. An example of this „budgetary” approach to production balances concerns work on the kelp ecosystem along the coasts of the Cape Peninsula, South Africa (Field 1983; Newell and Field 1983a, b).

A second consideration that directs attention to the effects of food quality on feeding behaviour concerns recent

findings that bivalves may select, at the gills or on the labial palps, between organically poor and rich particles, rejecting the former as pseudofaeces and disproportionately ingesting the latter (Kjørboe et al. 1980, 1981; Møhlenberg and Kjørboe 1981; Newell and Jordan 1983). Such an adaptation, the mechanistic basis for which is not yet understood, can represent an effective means of maintaining energy balance under conditions of high concentrations of sston of mixed quality.

Thirdly, and most fundamentally, recent theoretical treatments of feeding by suspension and deposit feeders, couched in terms of optimising energy yields when food varies both in quality and quantity, have led to certain predictions concerning the physiology of feeding that are testable by experiment (Calow 1975; Lehman 1976; Taghon et al. 1978; Cammen 1980; Taghon 1981). For example, Taghon (1981) concluded that the energetically optimal response to an increase in food quality is to increase the rate of feeding, even when this results in more rapid passage of food through the gut (i.e. reduced gut retention time) and a concomitant decline in the efficiency with which the ingested ration is absorbed. Taghon (loc. cit) pointed out that the evidence from previous studies on deposit and suspension feeders was conflicting, probably because of confounding factors which might disguise the true effects of variable food quality.

Previous experiments with microphagous molluscs have suggested that ingestion rate and absorption efficiency may indeed be inversely related (Calow 1975; Widdows 1978). Comparisons between bivalves feeding on pure cultures of algal cells and on natural food particles have indicated that absorption efficiency declines markedly at quite low concentrations of the former but is maintained at high values to much higher concentrations of natural sston (Bayne and Widdows 1978; Griffiths 1980b). However, the relationships between ingestion rate, absorption efficiency and coincident gut content remains uncertain (Hawkins and Bayne 1984). As Taghon et al. (1978) point out, there is a requirement in such studies to determine both gut passage time and absorption efficiency; to this we may add the need to relate these findings to other components of the energy budget in order to establish the implications to the net energy yield of changes in feeding behaviour.

The shores of Cape Peninsula, South Africa, afford an opportunity to explore some of these relationships, due to two factors. Firstly, at least three mytilid species, having

\* Present address: Biologische Anstalt Helgoland, Notkestrasse 31, D-2000 Hamburg 52, Federal Republic of Germany

Offprint requests to: B.L. Bayne

in common the same basic suspension-feeding mode of behaviour, frequently co-exist on these shores and are often to be found attached together on the same rock surface. Secondly, there are significant differences in the quality of the seston as food for these mussels, from shores which are close to the kelp beds and are therefore exposed to organically rich kelp debris in suspension (Stuart et al. 1982), to those which are relatively distant from the kelp and are characterised by a more organically poor seston (Griffiths 1980b). In this study we compared various aspects of feeding behaviour and of physiological energy balance in three species of mussel growing at two sites chosen to represent different qualities of diet. We were then able to assess whether physiological compensations of the kind predicted by theoretical analysis existed and, if so, whether these compensations differed between species.

## Material and methods

### The animals and the sites

Specimens of *Choromytilus meridionalis* (Krauss), *Aulacomya ater* (Molina) and *Perna perna* (L.) were collected from the shore at Bloubergstrand in Table Bay, Cape Province (Fig. 1) and of *C. meridionalis* and *P. perna* from Bailey's Cottage in False Bay. Care was taken to select individuals of similar size which were growing at similar heights on the shore (approx. 0.3 m above low water spring tide mark, equivalent to the "midshore" site in Griffiths' (1981) study of *C. meridionalis* at Bailey's Cottage). Mean ( $\pm$  standard deviation, SD;  $n=20$ ) dry flesh weights for individuals used in experiments were as follows:

Species	Site	W:g
<i>C. meridionalis</i>	Bailey's Cottage	$1.11 \pm 0.29$
	Bloubergstrand	$1.02 \pm 0.41$
<i>P. perna</i>	Bailey's Cottage	$0.93 \pm 0.19$
	Bloubergstrand	$0.92 \pm 0.16$
<i>A. ater</i>	Bloubergstrand	$0.88 \pm 0.28$

Experiments were carried out in March and April. On each occasion when animals were sampled, 60 l of water were also collected directly adjacent to the animals on the shore. Immediately on return to the laboratory an aliquot of the water sample was taken for seston analysis (see below) and the remainder used to hold the animals overnight at 12° C in a constant temperature room. Experiments were carried out over the following day. Some individuals were used for determination of clearance and respiration rates; others were isolated for measurement of gut retention time and a third sample of animals, held with natural particulates overnight, was used for the collection of faeces and the determination of absorption efficiency.

### The measurements

1. *Food quality.* The seston from a measured volume of water was screened to exclude particles  $> 100 \mu\text{m}$  diameter

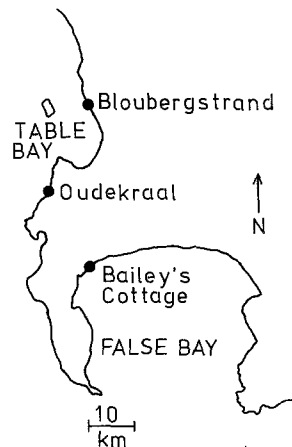


Fig. 1. A sketch map of the South Western Cape Province, South Africa, showing sites mentioned in the text

and then collected by filtration onto ashed, pre-weighed GF/C glass fibre filters with a retention efficiency of greater than 80% for particles larger than  $2 \mu\text{m}$  diameter (Sheldon 1972). The filters were washed with isotonic ammonium formate, dried and weighed to obtain the dry weight of seston per l of seawater. The filters were then combusted at 450° C for 5 h, cooled in a dessicator and weighed again, in order to determine, by difference, the weight of particulate organic matter. This procedure was repeated three times for samples from each of the two sites.

2. *Clearance rates and rates of oxygen consumption.* Ten specimens of each species from each site were placed in individual glass vessels in a temperature-controlled ( $12 \pm 0.5^\circ \text{C}$ ) apparatus of flowing seawater for the measurement of clearance rates by particle counts (Coulter Counter model TA II) on the water before and after passage through the experimental chamber; flow rates of water in the apparatus were controlled between 85 and  $100 \text{ ml min}^{-1}$ . The animals were allowed a period of 2 h to equilibrate to the equipment and to demonstrate steady rates of clearance. The experimental chambers were then isolated from the flowing seawater and rates of oxygen consumption measured using oxygen electrodes inserted through the top of the chambers, as the decline in oxygen concentration over a period of approximately 1 h. These procedures are similar to those described by Bayne et al. (1977) and employed by Griffiths (1980a) and Stuart (1982b) in their experiments with *C. meridionalis* and *A. ater*, respectively.

It did not prove possible with this system to measure clearance rates using natural particulates at ambient concentrations. We therefore measured clearance and respiration rates in mixed suspensions of the cells of *Dunaliella primolecta* and *Pheaeodactylum tricornutum*, taken from uni-algal laboratory cultures and added to the flowing seawater at a final concentration of between  $7$  and  $12 \times 10^3 \text{ cells ml}^{-1}$ , which was equivalent to approximately  $1 \text{ mg dry weight of algal cells l}^{-1}$ . At these cell concentrations, both *Choromytilus* and *Aulacomya* are expected to filter at rates that are relatively independent of slight changes in cell density (Griffiths and King 1979; Griffiths 1980a; Stuart 1982b), at least in the short term. We assume that these clearance rates are reliable measures of the animal's rates of feeding on naturally available food particles.

3. *Residence time of food particles in the digestive gland.* These measurements were based on a technique developed by M.N. Moore (Institute for Marine Environmental Research, Plymouth, UK; unpublished). The technique relies on two observations, a: suspension feeding bivalves will ingest bovine red blood cells when these are suspended in seawater, and the cells are then readily endocytosed into the digestive cells (Platt 1971) and b: the presence and the fate of these cells in the digestive system can be detected and followed quantitatively by cytochemical staining for the enzyme peroxidase which is associated with the blood cells.

Mussels were placed in GF/C filtered seawater (at 12°C) and bovine red blood cells added to the water at a concentration equivalent, in terms of spherical volume, to the concentrations of algal cells used in the measurements of clearance rate. One hour later the experimental trays were drained and re-filled with filtered seawater. Three individual animals (of each species and from each site) were removed immediately and then at 1, 3, 5, 7, 9 and 11 h; the 'control' sample, used to assess endogenous peroxidase activity in the digestive cells, consisted of three individuals not exposed to bovine blood cells.

On removal from the experimental trays each individual mussel was opened, the digestive gland dissected free of other tissue and placed in Bakers formalin fixative for 2–3 h at 4°C. The glands were then rinsed free of fixative and stored in gum sucrose (also at 4°C). Just prior to sectioning the glands were cooled to –70°C in hexane/liquid nitrogen and then cut (10 µm section thickness) in a cryostat with the knife cooled in dry ice. Peroxidase activity was induced by reaction with 30% (v:v) hydrogen peroxide in an acetate buffer (pH 5.0) and visualised with amino-ethylcarbazole dissolved in dimethyl formamide, following incubation for 20 min at 22°C. The enzyme activity was quantified by microdensitometry.

The microdensitometer readings were corrected for control (=baseline) values and the results (see Fig. 4) fitted by an exponential model using an iterative least squares procedure (Nash 1979):

$$y = \alpha K t e^{-Kt} \quad (1)$$

where  $\alpha$  is a normalisation (scaling) factor for the y-axis,  $K$  is the fitted rate parameter and  $t$  is time in hours from the end of the bovine blood cell feeding period. This model has empirical and some theoretical justification as the solution of a set of first-order differential equations, defining rates of uptake and absorption as a constant proportion

of the measured peroxidase activity. It follows that  $t = 1/K$  corresponds to the time at which  $y = y_{\max}$ . For  $y = 0.5 y_{\max}$ ,  $Kt$  is the solution of:

$$(Kt)e^{-(Kt)} = 1/2e. \quad (2)$$

This equation was solved numerically to provide an estimate of the time for which the blood cells were retained within the digestive gland (i.e. the apparent gut retention time); it signifies the time taken for approx. 95% of the ingested ration to be either absorbed or otherwise lost from the digestive cells. The fitting technique employed to estimate  $K$  provided a measure of variance which was then used to determine the standard deviation on the calculated value for the mean gut retention time.

4. *Absorption efficiency.* Faeces were collected from mussels held in the laboratory over 12 h whilst feeding on natural particulates. The pooled faeces samples from ten individuals were rinsed in ammonium formate, dried, weighed, then ashed and weighed again for the determination of absorption efficiency according to Conover (1966). The absorption efficiency is taken to be the efficiency with which ingested food is absorbed across the gut wall and differs from assimilation efficiency in that it takes no account of excretory losses.

## Results

*Food value.* Seston concentrations were higher, but the particles were of lower organic content, at Bailey's Cottage than at Blouberg (Table 1). This is in agreement with independent studies by Griffiths (1980b) and Stuart (1982b). Stuart (1982a) derived a simple regression equation to relate seston energy content (as Joules per mg dry weight) to percentage organic matter (legend Table 1) and this equation was used to calculate energy equivalents for the two sites. The available ration, estimated as Joules per litre, was slightly higher at Blouberg than at Bailey's Cottage and the quality of the ration ( $\text{J mg}^{-1}$ ) was very much better at the former site.

*Clearance rates.* The results are shown as means ( $\pm$  one standard deviation) in Fig. 2, together with regression lines, taken from the literature, which describe the relationship between clearance rates and body size. These regressions are plotted from the following sources: (1) *Choromytilus meridionalis* from Griffiths (1980a) who sampled from the same population at Bailey's Cottage used in this study. (2)

**Table 1.** Energy available, as particles less than 100 µm diameter, to mussels at two sites

Site	Seston conc; mg dry wt l <sup>-1</sup>		% organic matter		Energy equivalent		Ration level
	Observed	Literature	Observed	Literature	J mg dry wt <sup>-1</sup>	J mg POM <sup>-1</sup> J l <sup>-1</sup>	
Bailey's Cottage	7.11 ± 0.6	8.34 ± 3.75 <sup>a</sup>	29	32	2.44 <sup>c</sup>	9.4 <sup>d</sup>	17.3
Bloubergstrand	3.27 ± 1.2	3.28 ± 2.40 <sup>b</sup>	49	48	6.24 <sup>c</sup>	12.7 <sup>d</sup>	20.4

Measured seston concentration (mean  $\pm$  SD for  $n=3$ ) and percent organic matter are compared with literature values (<sup>a</sup> Griffiths, 1980b; <sup>b</sup> Stuart 1982b). <sup>c</sup> Energy equivalents, as Joules per mg dry seston, are calculated from a regression equation derived by Stuart (1982a) viz:  $\text{J mg}^{-1} = 0.19 \times \% \text{ organic matter} - 3.07$ . The resulting values are similar to mean energy equivalents for seston at Bailey's Cottage and Oudekraal (near Blouberg) calculated by Griffiths (2.8  $\text{J mg}^{-1}$ ) and Stuart (6.0  $\text{J mg}^{-1}$ ), respectively. <sup>d</sup> This calculation assumes all available energy is due to particulate organic matter (POM)

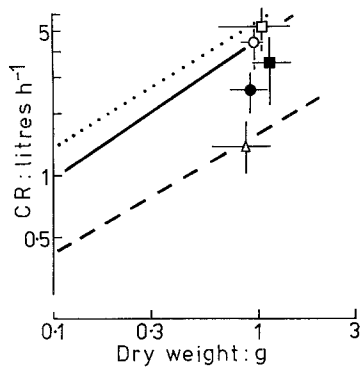


Fig. 2. The rates of clearance of mussels at two sites. Clearance rates, CR, are plotted as litres water cleared of particles  $>2\ \mu\text{m}$  per h (mean  $\pm$  SD,  $n=10$ ).  $\square$ , *Choromytilus* from Blouberg;  $\blacksquare$ , *Choromytilus* from Bailey's Cottage;  $\circ$ , *Perna* from Blouberg;  $\bullet$ , *Perna* from Bailey's Cottage;  $\triangle$ , *Aulacomya* from Blouberg. The plotted regression lines are from the literature; dotted line for *Choromytilus* (Griffiths 1980a); full line for *Perna* (Berry and Schleyer 1983); dashed line for *Aulacomya* (Stuart 1982b)

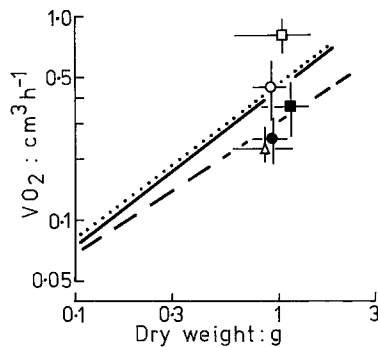


Fig. 3. Rates of oxygen consumption ( $\text{VO}_2$ ;  $\text{cm}^3\ \text{h}^{-1}$ ; mean  $\pm$  SD,  $n=10$ ) for mussels from two sites. For symbols and regression lines, see legend to Fig. 2

*Aulacomya ater* from Stuart (1982b) who sampled at Oudekraal (see Fig. 1). (3) *Perna perna* from Berry and Schleyer (1983) who sampled this species at a site near Durban (Natal, South Africa); the regression as plotted has been corrected for the temperature difference between the two studies ( $20^\circ\text{C}$  at Durban,  $12^\circ\text{C}$  in the present experiments) by using a  $Q_{10}$  of 2.36 calculated by Miller (quoted by Berry and Schleyer, l.c.) from measurements of the rate of oxygen consumption by *Perna* (i.e. we assume the same temperature coefficient to apply to clearance rate).

*C. meridionalis* from Blouberg showed the highest clearance rates and *A. ater*, also from Blouberg, the lowest. For both *C. meridionalis* and *P. perna* mean clearance rates were higher at Blouberg than at Bailey's Cottage ( $t_{(18\text{d.f.})}=3.35$ ,  $P<0.01$  and  $t_{(18\text{d.f.})}=3.04$ ,  $P<0.01$ , for the two species, respectively). Agreement with previously published values was good for *A. ater* and for *P. perna* at Blouberg, but measurements for *C. meridionalis* and *P. perna* at Bailey's Cottage were somewhat lower than would have been predicted from the regression equations.

**Rates of oxygen consumption.** The results are shown as means ( $\pm$  one standard deviation) in Fig. 3, together with regression lines from the same literature sources used in

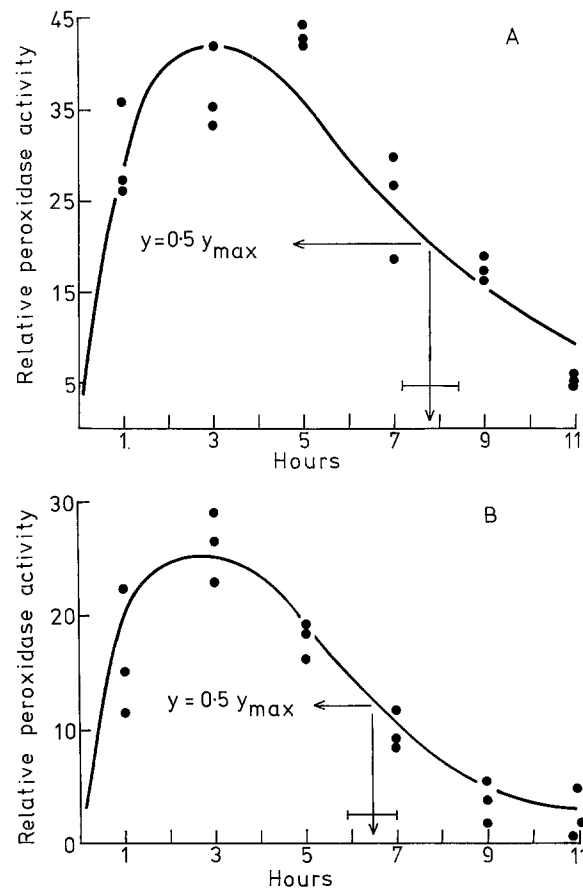


Fig. 4. A, B. Activity of the enzyme peroxidase, measured in arbitrary units by microdensitometry, as a marker of the residence of food particles in the digestive gland of mussels (see text). The time at which enzyme activity was half maximum value was taken as the "retention time" and is shown together with one standard deviation. A *Choromytilus* at Bailey's Cottage. B *Aulacomya* at Blouberg. The plotted values are the means of ten determinations, made on duplicate slides, for each of three individuals at each sampling

Fig. 2. Rates of oxygen consumption by *Choromytilus* and *Perna* were higher in individuals from Blouberg ( $t_{(18\text{d.f.})}=4.61$ ,  $P<0.001$ , and  $t_{(18\text{d.f.})}=5.13$ ,  $P<0.001$ , respectively). *Aulacomya* had the lowest rates of oxygen consumption. Agreement between measured values and predictions from the published regression equations were fair.

**The relationship between clearance rates and oxygen consumption.** This relationship, assessed in terms of litres of water cleared of particulate material per  $\text{cm}^3$  oxygen consumed, fell between  $11.3\ \text{l cm}^{-3}$  (*Perna* at Bailey's Cottage) and  $6.6\ \text{l cm}^{-3}$  (*Aulacomya* at Blouberg). By converting to energy equivalents ( $1\ \text{cm}^3$  oxygen consumed  $\equiv 20.08$  Joules), these values suggest a mean routine ration requirement of approx.  $2.5\ \text{J l}^{-1}$  which is equivalent to 14% and 12%, respectively, of the available ration at Bailey's Cottage and Blouberg (see Table 1).

**The retention time of food in the digestive gland.** Figure 4 shows the intensity of peroxidase staining over time in the digestive cells of *Choromytilus* at Bailey's Cottage (Fig. 4A) and *Aulacomya* at Blouberg (Fig. 4B), together with curves fitted by equation 1 (Material and methods). The y-axis

**Table 2.** The estimated retention time for food particles in the digestive gland of three species of mussel at two sites

Species	Site	Retention time (h) <sup>a</sup>	Gut content <sup>b</sup> mg
<i>C. meridionalis</i>	Bailey's Cottage	7.81 ± 0.66	173
	Bloubergstrand	1.40 <sup>c</sup>	24
<i>P. perna</i>	Bailey's Cottage	8.34 ± 0.90	168
	Bloubergstrand	2.40 ± 0.21	34
<i>A. ater</i>	Bloubergstrand	6.44 ± 0.45	35

<sup>a</sup> The retention time (±SD) is estimated from equations 1 and 2

<sup>b</sup> The gut content is calculated as ingestion rate (mg dry seston h<sup>-1</sup>) × retention time for the digestive gland

<sup>c</sup> The statistical fit of the model (Eq. 1) did not fully converge with these data; for the estimate of retention time quoted here, the sum-of-squares function is probably within 0.01% of its minimum value

**Table 3.** Absorption efficiencies for three species of mussel from two sites, measured for natural particulates; values are means ± range for *n* = 3

Species	Site	Absorption efficiency (mean ± range)	Literature value
<i>C. meridionalis</i>	Bailey's Cottage	0.66 ± 0.09	0.47 ± 0.15 <sup>a</sup>
	Bloubergstrand	0.43 ± 0.04	—
<i>P. perna</i>	Bailey's Cottage	0.65 ± 0.10	(0.58 ± 0.11) <sup>b</sup>
	Bloubergstrand	0.40 ± 0.05	—
<i>A. ater</i>	Bloubergstrand	0.52 ± 0.12	0.49 ± 0.10 <sup>c</sup>

The literature values are: <sup>a</sup> from Griffiths (1980b); <sup>b</sup> from Berry and Schleyer (1983; calculated from their data, derived for *Perna* from Natal); <sup>c</sup> from Stuart et al. (1982)

(stain intensity) is scaled in arbitrary units, set to zero in terms of baseline values of peroxidase activity as determined for individuals prior to their feeding on the bovine blood cells. From the fitted equations, the "retention time" of food in the digestive gland is calculated, in h, equivalent to the time at which stain intensity has declined from its maximum value ( $y_{\max}$ ) to 0.5  $y_{\max}$  (Fig. 4). These estimates of retention time are listed in Table 2 as means ± standard deviation.

**Table 4.** A calculation of net energy balance in three species of mussel at two sites. The calculation ignores energy losses due to excretion. CR, clearance rates (±SD; Fig. 2). *C*, ingested ration, calculated for natural seston at the relevant sites (Table 1). *e*, absorption efficiency (Table 3). *A*, absorbed ration. *R*, heat loss, calculated as cm<sup>3</sup> O<sub>2</sub> h<sup>-1</sup> (Fig. 3) × 20.08 J cm<sup>-3</sup>. *A* - *R*, the net balance. Values for mean scope for growth, taken from the literature, are also listed: *C. meridionalis* at Bailey's Cottage from Griffiths (1980a); *P. perna* from Berry and Schleyer (1983), temperature corrected by  $Q_{10} = 2.36$ ; *A. ater* interpolated from Stuart (1982b), determined at Oudekraal

Species	Site	CR (lh <sup>-1</sup> )	<i>C</i> (Jh <sup>-1</sup> )	<i>e</i>	<i>A</i> (Jh <sup>-1</sup> )	<i>R</i> (Jh <sup>-1</sup> )	<i>A</i> - <i>R</i> (Jh <sup>-1</sup> )	Scope for growth (Jh <sup>-1</sup> ) from literature
<i>C. meridionalis</i>	Bailey's Cottage	3.13 ± 0.75	54.1	0.66	35.7	7.3	28.4	21.0
	Bloubergstrand	5.30 ± 1.21	108.1	0.43	46.5	16.2	30.3	
<i>P. perna</i>	Bailey's Cottage	2.84 ± 0.84	49.1	0.65	31.9	5.1	26.8	19.1
	Bloubergstrand	4.39 ± 0.51	89.5	0.40	35.8	9.1	26.7	
<i>A. ater</i>	Bloubergstrand	1.66 ± 0.46	33.9	0.52	17.6	5.0	12.6	10.2

Striking differences are apparent in the retention time between sites, with mussels (*Choromytilus* and *Perna*) retaining material in the digestive gland for approximately 8 h at Bailey's Cottage compared with approx. 2 h at Blouberg; *Aulacomya* at Blouberg had a longer retention time than the other two species. There is a high positive correlation in these data between estimated gut retention time and absorption efficiency (cp. Tables 2 and 3:  $r^2 = 0.95$ ;  $n = 5$ ;  $P < 0.01$ ) and a negative exponential relationship between clearance rate and estimates of the retention time for food in the digestive gland which is just statistically significant ( $r^2 = -0.88$ ;  $n = 5$ ;  $P = 0.05$ ).

**Estimates of digestive gland (gut) content.** This has been estimated (Table 2) as the product of mean clearance rate (lh<sup>-1</sup>), seston concentration (mg dry matter. l<sup>-1</sup>) and the retention time for food in the digestive gland (h). The estimated gut contents are higher for individuals from Bailey's Cottage than for Bloubergstrand and differences between sites are greater than those between species.

**Absorption efficiency.** For both *C. meridionalis* and *P. perna*, absorption efficiencies were lower at Blouberg than at Bailey's Cottage, and values for *Aulacomya* were intermediate (Table 3).

**Net energy balance.** An estimate of net energy balance, which ignores losses due to excretion, is shown in Table 4. Since no pseudofaeces were produced during feeding on natural particulates (see also Griffiths 1980b), the ingested ration (*C*: Jh<sup>-1</sup>) is given as the product of clearance (= feeding) rate and the energy available as suspended particulates (Jl<sup>-1</sup>) at the site and times of sampling. This value, weighted by the absorption efficiency, gives the absorbed ration (*A* = *C* × *e*; Jh<sup>-1</sup>) which, on subtraction of the estimated respiratory heat loss (*R*) yields the net balance (*A* - *R*; Jh<sup>-1</sup>). These results suggest (a) a close similarity between *Choromytilus* and *Perna*, (b) a similarity, within each of these species, at the two sites, and (c) that the net energy balance for *A. ater* is reduced, relative to the other two species.

## Discussion

The rations available, as suspended particulate matter, to mussels at the two sites studied were markedly different. At Bailey's Cottage the seston was at high concentration but of low organic and energy content; at Bloubergstrand, on the other hand, the seston was at lower concentration

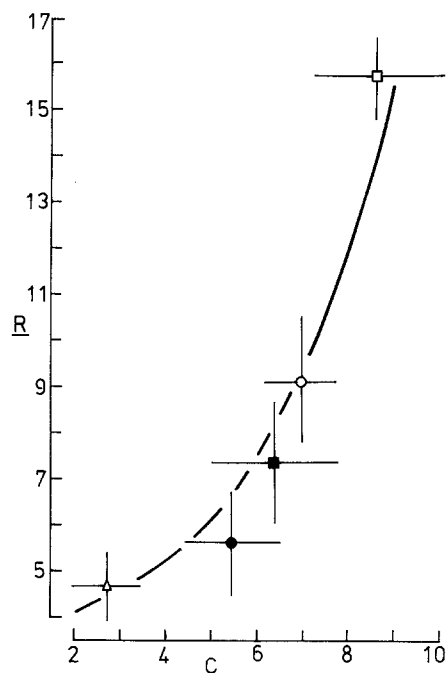


Fig. 5. Mean values for rates of respiratory heat loss ( $R$ ;  $\text{Jh}^{-1}$ ) plotted against ingested ration ( $C$ ;  $\text{mg POM h}^{-1}$ ) for three mussel species at two sites.  $\square$ , *Choromytilus* at Blouberg;  $\blacksquare$ , *Choromytilus* at Bailey's Cottage;  $\circ$ , *Perna* at Blouberg;  $\bullet$ , *Perna* at Bailey's Cottage;  $\Delta$ , *Aulacomya* at Blouberg. The curve is fitted according to the expression:  $R = 2.45 e^{(0.2C)}$ , for which  $r^2 = 0.89$ ,  $n = 5$

and of a higher organic and energy content. At Blouberg the suspended organic material is rich in kelp detritus whereas at Bailey's Cottage there is often a high concentration of inorganic material in suspension. Brown (1981) reviewed data for primary production in False Bay, concluding that production was much lower than in Table Bay. In spite of these differences in available ration, *Choromytilus* and *Perna* at the two sites expressed a similar net energy balance, when calculated according to certain simplifying assumptions. The reasonable measure of agreement (Table 4) between values calculated in this study and previously published estimates lends some confidence to the following interpretations.

Three fundamental relationships appear to comprise the physiological responses to differences in food quality that are apparent in these results. Firstly, there is a negative relationship between clearance rate and the retention time of food particles in the digestive gland (the "gut retention time"); a more rapid rate of feeding tends to result in an increased rate of passage of material through the digestive system (but see Fig. 7 and later discussion). Secondly, gut retention time and absorption efficiency are strongly positively related; an increase in retention time was consistent in these data with an increased absorption efficiency. Thirdly, an exponential relationship appears to hold between ingested ration and respiratory heat losses (Fig. 5), in agreement with previous studies on other bivalve species (reviewed by Bayne and Newell 1983).

The extent to which a suspension-feeding bivalve may invoke these relationships in order to compensate for a decline in food quality by optimising clearance rate is illustrated in Fig. 6. This Fig. is based on a simple simulation using relationships indicated in this study:

- Ingestion rate ( $C$ ) is calculated in terms of  $\text{mg particu-$

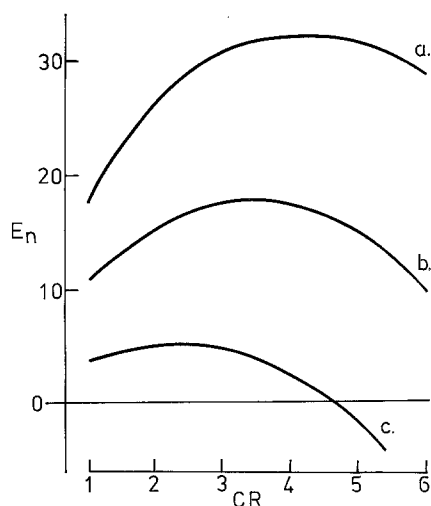


Fig. 6. Net energy balance ( $E_n$ ;  $\text{Jh}^{-1}$ ) related to clearance rate ( $CR$ ;  $1 \text{ h}^{-1}$ ) at three values for the energy equivalence of particulate organic matter;  $a$   $12 \text{ Jmg}^{-1}$ ,  $b$   $8 \text{ Jmg}^{-1}$ ,  $c$   $4 \text{ Jmg}^{-1}$ . These are the results of a simple simulation as described in the text

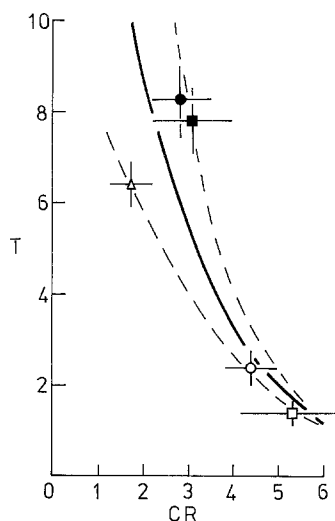


Fig. 7. Gut retention time ( $T$ ;  $\text{h}$ , as measured by the peroxidase technique) related to clearance rate ( $CR$ ;  $1 \text{ h}^{-1}$ ). The symbols are the same as in Fig. 5. The full line plots the relationship according to the equation: Retention time  $= 23.6 e^{(-0.49 CR)}$ ; this provides a fit that is only just statistically acceptable ( $r^2 = -0.88$ ;  $n = 5$ ;  $P = 0.05$ ). The dashed lines represent an alternative (and hypothetical) relationship in which the mussels are assumed able to adjust gut capacity in a manner allowing constant gut retention time whilst increasing clearance rate; these lines are drawn by eye to link points from each of the two sites separately

late organic matter (POM) per h. Respiratory heat loss is a function of ingestion rate (see Fig. 5):  $R = 2.45 e^{(0.2C)}$ . Gut retention time ( $T$ ) is calculated as an exponential function of clearance rate (see Fig. 7):  $T = 23.6 e^{(-0.49 CR)}$ . Absorption efficiency ( $e$ ) is linearly related to gut retention time (see Tables 2 and 3):  $e = 0.34 + 0.036 T$ . The absorbed ration ( $A$ ) is the product of ingestion rate, absorption efficiency and a term ( $S$ ) which defines the energy value of the POM, as Joules per mg. The net energy balance ( $E_n$ ) is then  $A - R$ . In Fig. 6 this simulation has been run for three values of  $S$ ; 12, 8 and  $4 \text{ J mg POM}^{-1}$ . The optimum clearance rate, at which  $E_n$  is maximised, declines from 4.5 to 3.5 to  $2.3 \text{ l h}^{-1}$  with reduced food quality.

A fourth component to this overall physiological compensation is possible and is hinted at in the present data (Table 2) viz. an increase in the capacity of the digestive gland or, as estimated here, in gut content. One interpretation of the data is offered in Fig. 7, where gut retention time is related to clearance rate. We postulate that, both on a seasonal time scale (Hawkins and Bayne 1984) and in response to site-specific differences in ration, the mussels might increase the volume capacity of the digestive system, whilst holding the clearance rate constant, and so increase gut retention time and absorption efficiency. Slight increases in the gut content significantly add to the degree of physiological compensation possible in responding to reduced food quality, although they will require longer periods of time than changes in clearance rate and gut retention.

The analysis offered here is a simple one and it disregards other features of digestion in these animals, some of which have only recently been recognised, such as the potential rôle of extra-cellular digestion (Seiderer et al. 1982) and of metabolic faecal losses (Hawkins and Bayne 1984). Nevertheless, even in its present form, this analysis suggests that suspension feeding bivalves may possess adaptive features in their feeding behaviour additional to those currently recognised (Bayne and Newell 1983). At the least, by varying the rate at which material is processed through the digestive system, the animals may modify the energetic consequences of a decline in the quality of the available ration and help to maintain a high net rate of energy gain over a wide range of feeding conditions. A higher ingestion rate by animals feeding on a more energy-rich diet is consistent with the theoretical predictions of Taghon (1981), derived from an optimality model in which absorption efficiency was assumed to decline with increased rates of ingestion. The general findings of this study are also consistent with our unpublished observations that *Mytilus edulis* living in conditions of high inorganic seston concentrations have consistently lower clearance rates than individuals growing at lower seston loadings of higher organic content.

Finally, our estimates of net energy balance suggest that *Aulacomya ater* would grow at a slower rate, at Bloubergstrand, than *Choromytilus meridionalis* of a similar size. This is consistent with the studies of Griffiths and King (1979; on *Aulacomya*) and Griffiths and Buffenstein (1981; on *Choromytilus*) at a site approximately 10 km north of Blouberg, where *C. meridionalis* does indeed grow more rapidly than *A. ater*. In trying to identify processes relevant to competition between these species, these quantitative differences in their physiological energetics may be relevant insofar as they affect rates of growth in newly colonised space. The results reported here also suggest, however, that similar compensatory trends exist in these three bivalves, as regards their feeding behaviour and physiology when faced with changes in food quality.

**Acknowledgements.** This work was carried out in the Department of Zoology at the University of Cape Town. We wish to acknowledge the financial support of the University and the hospitality and enthusiasm of the staff of the Department and, most particularly, Professor John Field. We gratefully acknowledge the co-operation of Dr. M.N. Moore (IMER, Plymouth) in our application of his peroxidase technique and Ms. Mandy Day (also of IMER) for skilled assistance. This work forms part of the Adaptive Processes programme of the Institute for Marine Environmental Research, a component laboratory of the Natural Environment Research Council, U.K.

## References

- Bayne BL, Widdows J (1978) The physiological ecology of two populations of *Mytilus edulis* L. *Oecologia* (Berlin) 37:137–162
- Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: Saleuddin ASM, Wilbur KM (eds) *The Mollusca*, Vol 4, Physiology, Part 1. Academic Press, New York, pp 407–514
- Bayne BL, Widdows J, Newell RIE (1977) Physiological measurements on estuarine bivalve molluscs in the field. In: Keegan BF, O'Ceidigh P, Boaden PJS (eds) *Biology of benthic organisms*. Pergamon Press, Oxford, pp 57–68
- Berry PF, Schleyer MH (1983) The brown mussel *Perna perna* on the Natal coast, South Africa: utilisation of available food and energy budget. *Mar Ecol Prog Ser* 13:201–210
- Brown PC (1981) Pelagic phytoplankton, primary production and nutrient supply in the southern Benguela region. *Trans R Soc S Africa* 44:347–355
- Calow P (1975) The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* Müll. and *Planorbis contortus* Linn. (Pulmonata), in terms of ingestion rates and absorption efficiencies. *Oecologia* (Berlin) 20:33–49
- Cammen KN (1980) Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia* (Berlin) 44:303–310
- Conover RJ (1966) Assimilation of organic matter by zooplankton. *Limnol Oceanogr* 11:338–345
- Field JG (1983) Coastal ecosystems: flow patterns of energy and matter. In: Kinne O (ed) *Marine Ecology Vol 5*, Springer, Berlin (in press)
- Griffiths RJ (1980a) Filtration, respiration and assimilation in the black mussel, *Choromytilus meridionalis*. *MarEcolProgr Ser* 3:63–70
- Griffiths RJ (1980b) Natural food availability and assimilation in the bivalve *Choromytilus meridionalis*. *MarEcolProgr Ser* 3:151–156
- Griffiths RJ (1981) Population dynamics and growth of the bivalve *Choromytilus meridionalis* (Kr) at different tidal levels. *Est Coast Shelf Sci* 12:101–118
- Griffiths RJ, Buffenstein R (1981) Aerial exposure and energy input in the bivalve *Choromytilus meridionalis* (Kr). *J exp mar Biol Ecol* 52:219–229
- Griffiths CL, King JA (1979) Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Mar Biol* 51:141–149
- Hawkins AJS, Bayne BL (1984) Seasonal variation in the balance between physiological mechanisms of feeding and digestion in *Mytilus edulis* (Bivalvia: Mollusca) *Mar Biol* (in press)
- Kjørboe T, Møhlenberg F, Nøhr O (1980) Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia* 19:193–205
- Kjørboe T, Møhlenberg F, Nøhr O (1981) Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Mar Biol* 61:283–288
- Lehman JT (1976) The filter feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol Oceanogr* 21:501–516
- Møhlenberg F, Kjørboe T (1981) Growth and energetics in *Spisula subtruncata* (da Costa) and the effect of suspended bottom material. *Ophelia* 20:79–90
- Nash JT (1979) Compact numerical methods for computers: Linear algebra and functional minimisation. Adam Hilger, Bristol
- Newell RC, Field JG (1983a) The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community. *Mar Biol Lett* 4:23–36
- Newell RC, Field JG (1983b) Relative flux of carbon and nitrogen in a kelp-dominated system. *Mar Biol Lett* 4:249–257
- Newell RIE, Jordan SJ (1983) Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. *Mar Ecol Progr Ser* 13:47–53
- Platt AM (1971) Studies on the digestive diverticula of *Mytilus*

- edulis* L. PhD Thesis, Queens University, Belfast, Northern Ireland
- Seiderer LJ, Newell RC, Cook PA (1982) Quantitative significance of style enzymes from two marine mussels (*Choromytilus meridionalis* Kr. and *Perna perna* L.) in relation to diet. *Mar Biol Lett* 3:257–271
- Sheldon RW (1972) Size separation of marine seston by membrane and glass-fibre filters. *Limnol Oceanogr* 17:494–498
- Stuart V (1982a) Studies on the utilisation of kelp detritus by the ribbed mussel *Aulacomya ater* (Molina). PhD Thesis, University of Cape Town, South Africa
- Stuart V (1982b) Absorbed ration, respiratory costs and resultant scope for growth in the mussel *Aulacomya ater* (Molina) fed on a diet of kelp detritus of different ages. *Mar Biol Lett* 3:289–306
- Stuart V, Field JG, Newell RC (1982) Evidence for absorption of kelp detritus by the ribbed mussel *Aulacomya ater* using a new  $^{51}\text{Cr}$  labelled microsphere technique. *Mar Ecol Progr Ser* 9:263–271
- Taghon GL (1981) Beyond selection: Optimal ingestion rate as a function of food value. *Am Natur* 118:202–214
- Taghon GL, Self FRL, Jumars PA (1978) Predicting particle selection by deposit feeders: A model and its implications. *Limnol Oceanogr* 23:752–759
- Widdows J (1978) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J Mar Biol Ass UK* 58:109–124

Received April 25, 1984