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The brown mussel *Perna perna* on the Natal coast, South Africa: utilization of available food and energy budget

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Abstract: The filtration rate of *Perna perna* (L.) at the approximate annual mean local water temperature (20 °C) is high, being 2.7×10^{-3} (shell length in mm)$^{1.86}$ l h^{-1} or 8.85 (dry flesh weight in g)$^{0.66}$ l h^{-1}. It was found to be able to filter latex particles down to at least 0.46 µm in diameter, these being roughly the mean size of free coccoid bacteria in the study area. Its mean assimilation efficiency, determined by the Conover method, was 61 % on a natural diet of particles < 100 µm in diameter which had a mean organic content of 3.16 mg l^{-1}. The faeces production rate was also established and an energy budget for *P. perna* is discussed in the light of available data.

INTRODUCTION

The brown mussel *Perna perna* is prolific on rocky reefs along the east coast of South Africa, and in a study of the ecology of a typical shallow reef community in Natal it proved to be by far the most important species in terms of biomass and production rate (Berry, 1982). Findings on reproduction, growth and production rate have been published by Berry (1978) and its rate of respiration has been established by Miller (in prep.). Considerable information is available on potential detrital and phytoplanktonic food material in suspension over the reef (Schleyer, 1979, 1980a, b, 1981). The purpose of the present paper is to examine the extent to which *P. perna* uses these potential food resources.

MATERIALS AND METHODS

Experimental material was obtained from the study area, a small isolated rocky reef 1646 m^2, situated in the littoral zone in front of the Oceanographic Research Institute (ORI) in Durban, South Africa. It is known as the ORI Reef and has been described by Berry (1978, 1982), Smale (1978) and Schleyer (1981).

Perna perna occurs in dense beds. Specimens were collected by carefully cutting their byssal attachments. In the laboratory they were 're-attached' in their natural position to apparatus with an elastic band or plasticine around the anterior byssal area. Experiments were then carried out at 20 °C, which was close to the annual mean surf temperature of 21.8 °C in the study area over a 16 yr period. Mean monthly temperature ranged from 19.8 to 25.3 °C.

Seawater analysis

Seawater samples were collected adjacent to and upcurrent of the ORI Reef. The samples were collected on the first 5 d of every month for 1 yr and on each occasion 500 ml of seawater were screened successively through a 200 µm and 100 µm sieve. The remaining particulate matter was filtered onto a pre-ashed 2 µm GFC filter of known weight, as were the fractions in each sieve after removal with 0.45 µm filtered seawater. The filters were then rinsed with an ammonium formate solution isotonic with seawater to remove sea salt and dried at 60 °C. After drying they were stored in a desiccator and flown to Cape Town where the samples were weighed on an electronic microbalance, ashed for 3 h in a muffle furnace at 450 °C and reweighed. The method employed was identical to that of Griffiths (1980a) and the facilities in her Cape Town laboratory were used for this purpose, ensuring maximum comparability with her results.

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Filtration rate

Filtration rates were determined using the technique described by Griffiths and King (1979) and Griffiths (1980a). Experiments were performed in Cape Town using Griffiths (1980a) apparatus and mussels were transported from Durban out of water for ca. 5 h in an insulated container. In the experiments mussels between 10 to 120 mm in shell length were cleared of epibiotic growth, attached to fine-meshed grids and suspended individually in 2 l beakers filled with 0.45 µm filtered seawater which was gently circulated by a magnetic stirrer bar. The mussels were fed on a suspension of unicellular alga *Dunaliella primolecta* and the decline in concentration of this was measured at 10 to 15 min intervals using a model TA II Coulter Counter with a 70 µm aperture. The concentration was raised to the original level by further addition of algal concentrate at each reading and this level was not allowed to drop by more than 20 %. Filtration rate was calculated according to the formula:

$$\text{Filtration rate } (\text{l h}^{-1}) = \frac{\log_e N_1 - \log_e N_2}{t_2 - t_1} \text{ X V} \quad (1)$$

where N_1 and N_2 = cell concentrations (l^{-1}) at times t_1 and t_2 respectively; V = experimental volume (l). For a derivation of this formula see Coughlan (1969). A filtration rate/shell length relationship determined in this manner at a temperature approximating to the annual mean was applied to monthly estimates of the mussel bed population on the ORI Reef determined by Berry (1978) over 2 yr. An annual estimate of the volume of water filtered by the mussel beds was thus obtained.

Particle retention

The smallest particle size which *Perna perna* is capable of filtering was determined using uniform latex particles dyed with fluorescent dyes (Dow Diagnostics, Dow Chemical Company, P.O. Box 68511, Indianapolis, Indiana 46268, USA) in a method developed by Schleyer (1980a). The manufacturer's specifications of these are listed in Table 1. Dilute suspensions of the particles, which ranged in diameter from 0.22 to 7.6 µm, were introduced separately into beakers containing mussels between 45 to 95 mm in shell length in gently agitated 0.2 µm filtered seawater. The fluorescent dyes enabled their decline in concentration in the seawater to be monitored by counting subsamples of the suspensions on 0.2 µm pore size polycarbonate filters (Nuclepore Corp., Pleasanton, California 94566, USA) using a Zeiss epifluorescence microscope fitted with a standard FITC filter pack and HBO 50 high pressure mercury light source. Sufficient fields were counted to provide a precision of >90 % at a confidence level of 95 % according to Cassell's (1965) graphical technique. The 0.22 µm diameter particles were collected on 0.1 µm pore size polycarbonate filters but could not be successfully counted since their size is at the limit of resolution of light microscopy. Faeces were checked for fluorescence as evidence of passage of latex particles through the digestive tracts of the mussels.

In 2 experiments, a decline in number of a suspension of 0.460 µm latex particles in 1.5 l of 0.2 µm-filtered seawater containing 5 actively filtering *Perna perna* (45 to 95 mm shell length) was monitored over 4 to 6 h. Latex particles were added as they were filtered by the mussels and the particle concentration was kept roughly between the maximum and mean bacterial counts of 4.3×10^6 ml^{-1} and 2.0×10^6 ml^{-1} previously recorded on the ORI Reef (Schleyer, 1981). In one of the experiments air was displaced above the water with oxygen to maintain a higher level of dissolved oxygen and reduce any possibility of respiratory distress in the mussels. The water was not aerated since this might cause particle aggregation by jet drop enrichment (Blanchard, 1978). Gently agitated controls without mussels were monitored microscopically for latex particle aggregation, sedimentation or precipitation.

Choice of particle sizes was decided as a result of the finding that detritus particles had a mean diameter between 5 to 10 µm, that free-living coccoid bacteria had a mean diameter of 0.475 µm and that the smallest dimension (width) of microflagellates was ca. 2 µm (Schleyer, 1981).

Table 1. Manufacturer's specifications for dyed uniform latex particles used to establish the smallest size particle which *Perna perna* is capable of filtering

Mean diam. (µm)	± s. d.	Material	Dye	Density at 25 °C
0.220	± 0.0065	Polystyrene	Fluorescent green HW	1.05 g ml^{-1}
0.460	± 0.0048	Polystyrene	Fluorescent green HW	1.05 g ml^{-1}
0.806	± 0.0057	Polystyrene	Fluorescent green HW	1.05 g ml^{-1}
7.6	± 2.3	Styrene/Divinylbenzene	Fluorol 7 GA	1.05 g ml^{-1}

Assimilation efficiency

Assimilation efficiency was determined using the method of Conover (1966) in which the organic fraction in the food is related to the organic fraction in the faeces according to the formula:

$$\text{Assimilation efficiency (\%)} = \frac{F - E}{(1-E)F} \times 100 \qquad (2)$$

$$\text{where } F = \frac{\text{ash-free dry weight of food}}{\text{dry weight of food}};$$

$$E = \frac{\text{ash-free dry weight of faeces}}{\text{dry weight of faeces}}$$

In initial experiments using a suspension of *Dunaliella primolecta* as the food source, *Perna perna* assimilation was erratic and frequently zero. Thus an attempt was made to establish the assimilation of natural food instead. As the potential suspended food material consists largely of phytoplankton and detritus with associated microorganisms (Schleyer, 1981), not attempt was made to use a double labelling technique developed more recently to measure assimilation efficiency (Calow and Fletcher, 1972; Conover and Francis, 1973; Wightman, 1975; Cammen, 1977). Uniform labelling ot the food with an assimilable label (^{14}C) and unassimilable reference (^{51}Cr) is essential for its application to permit proportional measurement of assimilation of the former. Dual labelling of this nature was not considered possible with such a mixed food source.

Over a period of 1 yr, 19 experiments were performed by collecting 20 mussels between 50 to 60 mm in shell length at low tide and placing them within 10 min in beakers of sterile filtered seawater. Individuals that did not start pumping again within a few minutes were discarded and faeces from the others were collected continuously. These were placed in a watch glass with a minimum of water and at the end of the experiment the pooled faeces were filtered onto a preashed 2 µm GFC filter of known weight, rinsed with an ammonium formate solution isotonic with seawater to remove sea salt, and dried at 60 °C. After weighing with an electronic microbalance, the sample was ashed in a muffle furnace at 450 °C for 3 h and reweighed to determine the ratio of organic to inorganic material. In this way, an organic fraction of mussel faeces was obtained which could be directly related to that of the natural food upon which the mussels had been feeding before collection as no food was available in the sterile, filtered seawater.

A 500 ml seawater sample was collected upcurrent of the ORI Reef at the same time as the mussels and was screened (200 µm, then 100 µm) to eliminate sand grains and debris. The remaining particulate matter was then filtered onto a 2 µm pre-ashed, weighed GFC filter. These samples were also rinsed with ammonium formate and ashed and weighed to determine a ratio of organic to inorganic material likely to be representative of the food of the mussels. Some of the samples were accumulated in a desiccator and transported to Cape Town where they were ashed and weighed in order to obtain maximum comparability with Griffiths (1980b) results. Others were processed locally using the identical method.

These experiments were not done on a seasonal basis, but over a wide range of water conditions throughout the year.

Faeces production rate

Mussels between 35 and 97 mm in shell length were removed from the reef and placed in 2 l beakers as described above. Faeces from each mussel were removed as they were produced and accumulated in separate watch glasses over variable periods of time depending on the size of the mussel, but not exceeding 170 min. Only data from mussels which pumped continuously and in which there was no change in appearance of the faeces were used. Faeces were rinsed and dried as described above.

The caloric content of faeces was determined by combusting large samples (at least 200 mg), rinsed and dried as above, in an adiabatic bomb calorimeter. Benzoic acid of known caloric content was included to ensure complete combustion of samples.

An estimate of the total annual faeces production at a temperature approximating to the annual mean was obtained by determining the faeces production/shell length relationship and applying it to monthly estimates of the population in mussel beds on the ORI Reef made by Berry (1978) over 2 yr.

RESULTS

Seawater analysis

Seasonal abundance of organic matter in different size particle fractions in seawater is summarised in Table 2. Organic matter was generally most abundant in the smallest particles (2 to 100 µm) and the annual mean organic fraction was greatest in these particles (24.8 %). The increase in the organic fraction in the larger particles in summer and autumn was due to a reduction of inorganic matter rather than an increase in organic content, and the conspicuous quantity of

Table 2. Mean seasonal abundance of organic and inorganic material (mg l^{-1}) in different size particle fractions in seawater collected upcurrent of ORI Reef

	Particle size (μm)			
	2–100	100–200	>200	Total
WINTER: (Jul–Sep)				
Organic material	2.363	1.606	3.082	7.051
Inorganic material	11.779	34.476	112.970	159.225
% Organic material	*16.71*	*4.54*	*2.66*	*4.24*
SPRING: (Oct–Dec)				
Organic material	2.499	0.890	1.619	5.008
Inorganic material	10.573	8.497	20.116	39.186
% Organic material	*19.12*	*9.48*	*7.45*	*11.33*
SUMMER: (Jan–Mar)				
Organic material	4.291	1.520	0.822	6.633
Inorganic material	9.030	1.903	0.525	11.458
% Organic material	*32.21*	*44.41*	*61.02*	*36.67*
AUTUMN: (Apr–Jun)				
Organic material	3.208	1.509	0.645	5.362
Inorganic material	8.233	3.311	7.090	18.634
% Organic material	*28.04*	*31.31*	*8.34*	*22.35*
ANNUAL				
Organic material (n=60)	3.161	1.373	1.339	5.873
Range	0.244–25.364	0.214–24.646	0.056–10.504	
Inorganic material	9.608	9.450	26.352	45.410
Range	0.398–112.310	0.070–76.276	0.014–830.948	
% Organic material	*24.76*	*12.69*	*4.84*	*11.45*

inorganic matter in larger particles in winter consisted largely of sand grains, probably the result of periodic non-seasonal sanding up of the reef (Berry, 1978). The presence of larger particles was also strongly influenced by wave action resulting in a greater size range of particulate matter in suspension.

Griffiths (1980b) in a similar study on the utilisation of available food by *Choromytilus meridionalis* in the surf zone at False Bay in the Cape Province, found that sand particles in faeces of *C. meridionalis* seldom exceed 100 μm in diameter and particles larger than this in the water consist mainly of sand grains with little adhering organic matter. She concluded that the bulk of food available to the mussels occurs in particles <100 μm in diameter and in her study these had a mean organic content of 2.65 mg l^{-1} and 5.69 mg l^{-1} of inorganic material. This size range of particle in the ORI Reef water also contains the most organic material and probably constitutes the major food resource of *Perna perna*. An annual mean value of 3.16 mg l^{-1} was obtained for the organic content of these particles and the inorganic content was 9.6 mg l^{-1}. The mean organic fraction of 24.76 % derived from these figures is lower than the value of 31.8 % found by Griffiths (1980b) in her Cape study.

Filtration rate

The following regression equation was derived from results of the filtration rate experiments (Fig. 1):

$$\text{Filtration rate } (l\ h^{-1}) = 2.7 \times 10^{-3} \text{ (shell length in mm)}^{1.86};\ r^2 = 0.97 \quad (3)$$

By substitution of a conversion from shell length to dry flesh weight (Berry, 1978), the equation becomes.

$$\text{Filtration rate } (l\ h^{-1}) = 8.85 \text{ (dry flesh weight in g)}^{0.66} \quad (4)$$

Standard deviation around the mean filtration rate of many of the size classes was high because the mussels did not filter at the same rate continuously but had cycles of activity.

The estimated potential volume of water filtered annually by the mussel population on the ORI Reef was 143 876 000 l m^{-2} in 1975/76 and 157 346 000 l m^{-2} in 1976/77.

Assuming no localised depletion and 100 % retention by *Perna perna* of 2 to 100 μm particles containing 3.16 mg l^{-1} organic material (Table 2), the mussel beds on the ORI Reef could potentially have filtered an estimated annual total of 454 792 g m^{-2} of organic

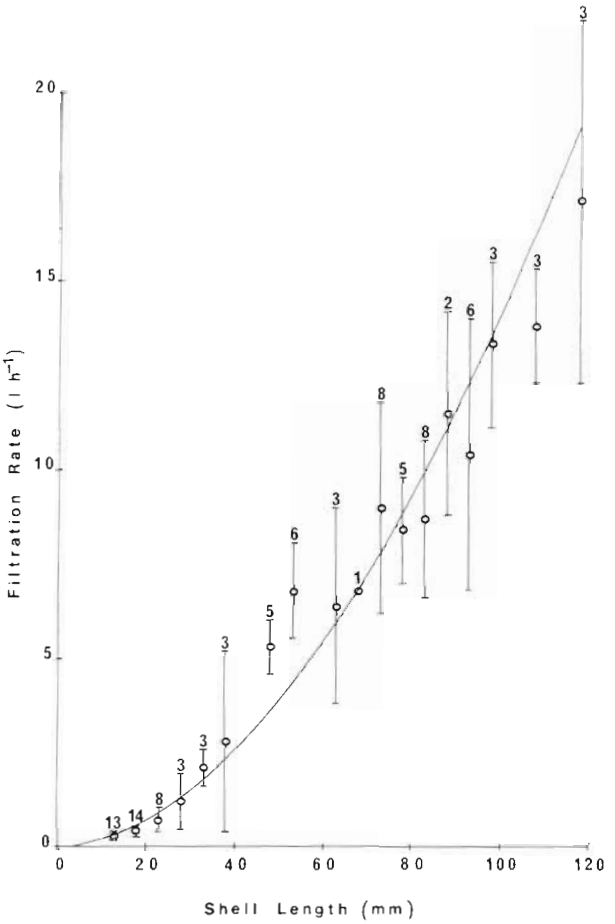

Fig. 1. *Perna perna*. Mean filtration rates of 5 mm size classes fed on a suspension of *Dunaliella primolecta*. Vertical bars: standard deviation around mean; figure above each mean: number (n) of mussels in each size class. Six readings were taken for every mussel. Filtration rate (l h^{-1}) = 2.7 × 10^{-3} (shell length in mm)$^{1.86}$; r^2 = 0.97

material in 1975/76 and 497 370 g m^{-2} in 1976/77. These estimates, based on a filtration rate determined at 20 °C, are likely to be slightly conservative as the annual mean was 21.8 °C, but as the range was only 19.8 to 25.3 °C they should adequately reflect annual totals. These values would be equivalent to 8.64 × 10^6 kJ m^{-2} and 9.45 × 10^6 kJ m^{-2} respectively if the organic material has a calorific value typical of macrophyte detritus, i.e. 19 kJ g^{-1}. Calorific values of this magnitude are listed by Schleyer (1981) for terrestrial plant debris and seaweed on the ORI Reef and by Cummins (1967) for macrophytic detritus in a stream.

Particle retention

Perna perna proved capable of reducing the concentration of a suspension of 7.6 µm latex particles fairly rapidly and produced both fluorescent faeces and pseudofaeces within 1 h. Successively smaller latex particles were filtered more slowly and they were not rejected as pseudofaeces but appeared in the faeces after a longer period of time (Table 3). In faeces the particles were heavily concentrated, but in patches where this was not the case most particles were observed microscopically to be single and non-aggregated. The 0.22 µm particles took the longest time to appear as fluorescence in faeces and no other details are presented for them in Table 3 since microscopic counts were not possible.

Results of uptake of 0.46 µm particles by 5 mussels over 4 to 6 h are presented in Fig. 2. In the first instance (Fig. 2A) filtration of the particles was very rapid but the high filtration rate may have been caused by respiratory distress as the water was not oxygenated. In the second experiment with oxygenation (Fig. 2B) filtration was at first not evident, but on addition of further particles, counts of both the single particles (broken line) and total particles (solid line) declined. Control counts in both cases are of single particles revealing gradual aggregation. In all experiments, particle aggregation occurred far slower over the experimental period in controls than the rate of filtration by mussels (for examples see Fig. 2).

It is concluded that *Perna perna* is capable of filtering particles down to 0.46 µm, but the low retention of 0.22 µm particles was possibly achieved by filtration of small particle aggregates. Its ability to filter particles as small as free-living coccoid bacteria with a mean diameter of 0.476 µm has also been substantiated in the field by measurement of a drop in number in water moving across the reef (Schleyer, 1981).

Table 3. *Perna perna*. Latex particle retention by 45 to 95 mm shell-length individuals in 0.5 l of 0.2 µm-filtered seawater

Latex particle Ø (µm)	7.6	0.806	0.460	0.220
n	4	4	4	4
Particle count at start (ml^{-1})	0.1 × 10^6	12 × 10^6	19 × 10^6	?
Particles filtered after 2 h	55 % – 98 %	25 % – 84 %	11 % – 64 %	?
Fluorescent pseudofaeces produced	yes	no	no	no
Fluorescent faeces produced after	~1 h	~2 h	~3.5 h	~5 h

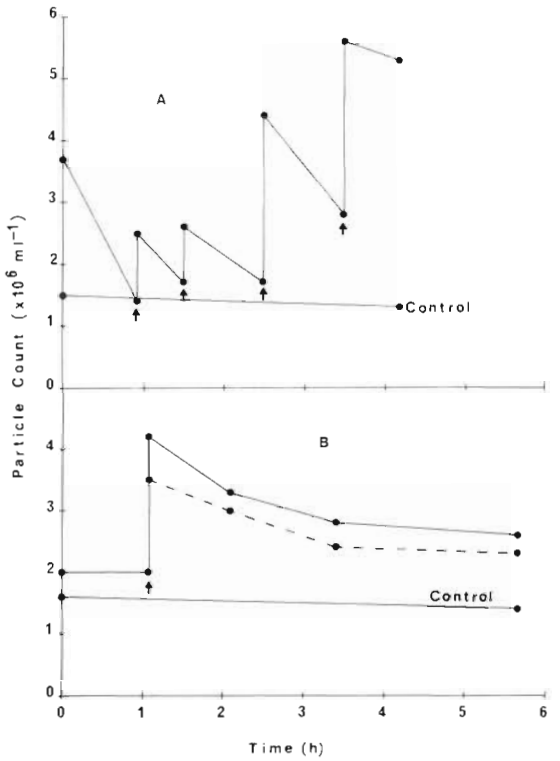

Fig. 2. *Perna perna.* Decline in number of a suspension of 0.460 μm latex particles in 1.5 l of 0.2 μm filtered seawater containing 5 actively feeding mussels between 45 and 95 mm in shell length. Addition of latex particles indicated by arrows. Results of 2 experiments (A, B) are presented (details explained in text)

DISCUSSION

The mean value for total particulate carbon (POC) larger than 0.2 μm diameter measured upcurrent of the ORI Reef was 3.53 mg l^{-1} (Schleyer, 1981). This conforms with values for particulate organic matter (POM) in Table 2 if an approximate ratio of 1 : 2 for carbon to organic material is assumed (Lenz, 1977). The slightly higher than usual values for POM measured in both the present study and that by Griffiths (1980b) are to be expected as both were conducted in the surf zone where particulate matter is held in suspension.

Griffiths (1980b) obtained an energy value of 6.1 kJ g^{-1} ash free dry weight by direct measurement for particles <100 μm. This is markedly lower than values obtained by Widdows et al. (1979) who calculated energy values for particulate matter on the basis of determinations of the proportional content of protein, lipid and carbohydrate. The mean of their listed values is 23.6 kJ g^{-1} and is similar to that of 18.8 kJ g^{-1} provided by Cummins (1967) for freshwater stream detritus of macrophytic origin. The value used in the present study (19 kJ g^{-1}) results in a calorific value for seawater of 60 J l^{-1} when only particles <100 μm are considered.

Potential suspended food material on the ORI Reef has been extensively studied (Schleyer, 1980b, 1981). The total particulate organic matter <100 μm available is 3.16 mg l^{-1} of which the most important component in terms of biomass is detritus with attached bacteria (2.97 mg l^{-1}). A small biomass (170.1 μg l^{-1} dry weight) of phytoplankton, predominantly microflagellates, is also available to suspension-feeders, while the biomass of free-living bacteria appears to be insignificant (16.5 μg l^{-1} dry weight). However, it was estimated that heterotrophic activity of unattached bacteria, which comprise 79 % of the total bacteria exceeds phytoplanktonic production by at least 4 times.

Utilization of detritus by detritivores can take place in one of 2 ways:

(a) Only the microorganisms attached to ingested detritus are digested and the undigestible detritus is voided as faeces, which are then recolonised by microorganisms and may be re-ingested by detritivores (Newell, 1965; Darnell, 1967; Odum, 1970). (b) A proportion of the detritus itself, as well as the attached microorganisms, is digested (Adams and Angelovic, 1970; Bowen, 1976, 1979). The dry organic content of suspended food available to *Perna perna* is ~ 25 %. Of this, in calorific terms, detritus comprises about 94.1 %, phytoplankton 5.4 % and free bacteria 0.5 %. As its assimilation efficiency is at least 40 % this indicates that *P. perna* belongs to the latter category of detritivore.

Digestive enzymes in mussels suggest a complete range of digestive ability. They include carbohydrases and cellulases commensurate with a detrital diet as well as peptidases and lipases (Bayne et al., 1976). McHenery et al. (1978) also found lysozyme and suggested that its role is in the digestion of bacteria. This has recently been confirmed in *Mytilus edulis* (Birkbeck and McHenery, 1982), the enzyme being found to be effective on Gram-negative bacteria which are predominant in the marine environment.

Although it is generally accepted that mussels do not discriminate between particles on the basis of size (Bayne et al., 1976), it has recently been demonstrated that qualitative selection does occur in a number of bivalve species before and after injestion (Kiørboe and Møhlenberg, 1981; Birkbeck and McHenery, 1982). Our results establish that *Perna perna* is capable of filtering particles of the size of the free-living bacteria available to it and these may have a nutritionally more important role than their relatively low calorific value might suggest if a selective mechanism is operative.

The weight exponents of *Perna perna* found in relating filtration rate to size would rank among the highest

of those of different bivalves summarised by Bayne et al. (1976). The filtration rate of *P. perna* is also higher than that measured for *Choromytilus meridionalis* by Griffiths (1980a), filtration rates of individuals 50 mm in shell length being 4.0 l h^{-1} (*P. perna* at 20 °C) and 3.1 l h^{-1} (*C. meridionalis* pooled data, 12 and 18 °C). The dry flesh weights of the 2 species at this shell length are 0.29 g *(P. perna)* and 0.39 g *(C. meridionalis)*.

Mean assimilation efficiency of *Perna perna* was 61 % which is higher than the value of 40 % for *Choromytilus meridionalis* (Griffiths, 1980b). However, this parameter was probably overestimated for reasons outlined below. Of necessity specimens were collected only at low tide when accessible and the diminished water flow (10 to 60 cm deep) moving across the reef was likely to have resulted in food depletion. In *Mytilus edulis* ingestion increases with increasing food concentration until a threshold is reached after which the excess is rejected as pseudofaeces (Foster-Smith, 1975; Widdows et al., 1979). Ingested material is initially assimilated by the digestive gland at high efficiency, but as ingestion increases, food bypasses the digestive gland to the intestine and assimilation efficiency declines (see Widdows et al., 1979). Digestion in *P. perna* is probably similar and the conditions of depleted food under which specimens were collected could have resulted in measurements of above average assimilation efficiency. This error could have been exacerbated by collecting the faeces for the Conover method under foodless conditions. Finally, in the Conover method it is assumed that assimilation of inorganic material in the food does not occur. Animals such as bivalves would utilise a proportion of the inorganic material ingested for shell production and this has been shown to be the case in other organisms, particularly crustacea (e.g. Prus, 1971). Once again this would result in an overestimation of the assimilation efficiency.

Papers reviewed by Bayne et al. (1976) reported an inverse relationship between assimilation efficiency and the proportion of organic to inorganic material in the suspended food of bivalves. The converse appeared to be true with *Perna perna* in which assimilation increased with the organic fraction in the food (Fig. 3). Although a similar result for absorption efficiency has been reported for *Mytilus edulis* (Bayne and Worrel, 1980), the possibility that the sampling bias discussed above might account for this in *P. perna* cannot be discounted, as it seems likely that there is a direct relationship between wave action (turbulence) and the quantitity of inorganic material suspended in the water over-lying the mussels. As conditions become progressively calmer, the relative proportion of organic to inorganic material would increase

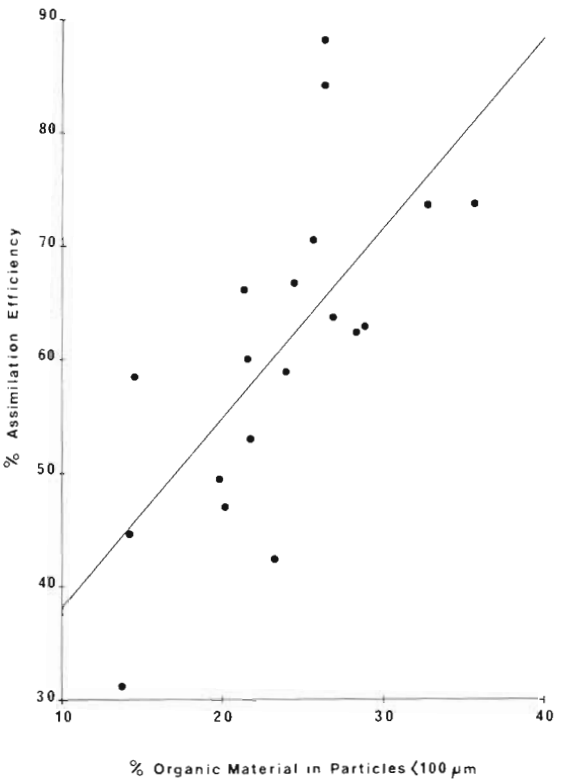

Fig. 3. *Perna perna*. Assimilation efficiency of 50 to 60 mm shell-length individuals plotted as function of the organic fraction in 2 to 100 µm particles in seawater collected at the same time as the mussels. % assimilation efficiency = 1.67 (% organic material in 2 to 100 µm particles) + 21.39; r^2 = 0.47

because the heavier inorganic sand would settle. At the same time the absolute quantity of particulate matter would decrease due to localised depletion over the reef, resulting in increased assimilation efficiency by the mussels.

The respiration rate of *Perna perna* has been determined by Miller (in prep.) using the method described by Caulton (1978). The experiments were conducted in a flow-through system at temperatures between 15 and 25 °C. The results are expressed by the equation:

$$\text{oxygen consumption } (\mu l\ h^{-1}) = 10.176\ (\text{dry flesh weight in g})^{0.731} x\ (\text{temperature in °C})^{1.24} \quad (5)$$

This was applied to Berry's (1978) monthly records of the ORI Reef mussel bed population in 5 mm size classes at the appropriate temperatures to obtain an annual estimate of respiration for the 2 yr sampled. The oxycaloric equivalent of 20.79 J ml^{-1} oxygen consumed (Hughes, 1970) was used to convert the value for respiration into energy terms. Together with the present results, this enables the formulation of an energy budget for the *Perna perna* beds on the ORI Reef on the basis of a mean annual value for *P. perna* production obtained from Berry (1978).

Following IBP terminology (Crisp, 1971) the components of the energy budget, consumption (C), somatic production (P), gonad output (G), respiration (R), egesta (F) and excreta (U) are related in the equation:

$$C = P + G + R + F + U \quad (6)$$

The substituted values (kJ m^{-2} yr^{-1}) for *P. perna* are:

P	G	R	F	C
141 653	+ 25 160	+ 139 668	+ 424 677	= (732 158)

In the equation U has been ignored as it is generally low in energy terms and difficult to measure in an aquatic animal. C has been derived by addition and would be the energy consumed from a total of 9.05×10^6 kJ m^{-2} yr^{-1} filtered by the mussel bed population, assuming 100 % retention of particles <100 µm. This leaves a balance in excess of requirements of 8.31×10^6 kJ m^{-2} yr^{-1} or 92 %. Although *Perna perna* does produce quantities of pseudofaeces in the field, it seems unlikely that it rejects so large a proportion of filtered food material. Therefore, either retention of particles less than 100 µm is much less than 100 % which, even allowing for possible low filtration efficiency of free bacteria, would not account for a discrepancy of this magnitude or, more plausibly, the actual quantity of food available may be less than the estimated potential quantity. Localized food depletion over the reef, shown to occur under calm conditions (Schleyer, 1981), may also occur under normal conditions of turbulence considering the high density of filter feeders present. The mean density of mussels in mussel beds alone is 10 600 m^{-2} (Berry, 1978) while other filter feeders for which the filtration rates are unknown also occur on the reef at high densities – the oyster *Saccostrea cucullata* has a mean density of ~ 500 m^{-2} over the whole reef, Cirripedia occur at ~ 2550 m^{-2}, and *Porcellana dehaanii* at ~ 50 m^{-2} (Berry, 1982). At such high densities competition for food seems likely to occur, in which case measurement of POM over the reef itself rather than adjacent to it would have been more appropriate.

It further seems likely that R in the energy budget is underestimated. Although Griffiths (1980a) found that oxygen consumption by *Choromytilus meridionalis* was not influenced by food concentration, workers such as Thompson and Bayne (1974) who worked on *Mytilus edulis* have shown that it increases with an increase in the concentration of suspended particles. Also, as discussed by Nixon et al. (1971), water currents may affect the respiration rate of bivalves. R in the present case was measured in a flow-through system in which there was no suspended food material and in which the rate of flow was in no way comparable to that experienced by *Perna perna* under natural conditions. More refined measurements of R might therefore improve the present energy budget which

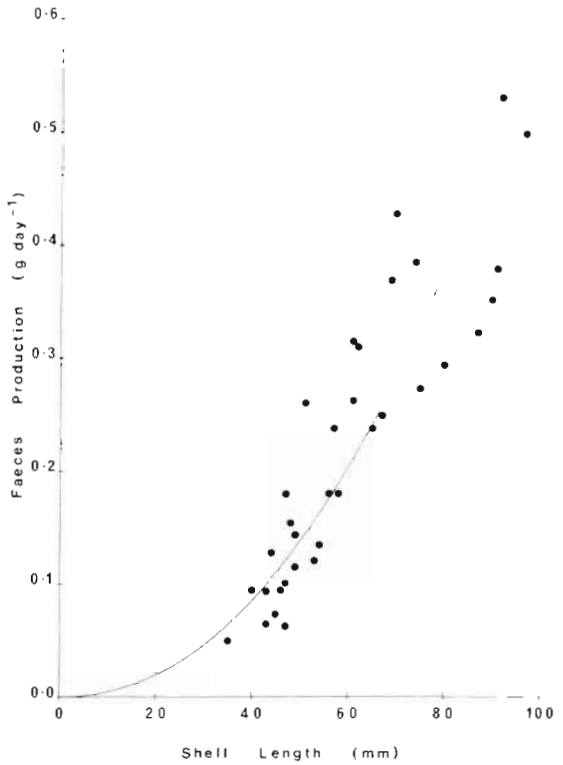

Fig. 4. *Perna perna*. Faeces production of 35 to 97 mm shell-length individuals. Faeces production (g d^{-1}) = 3.2×10^{-5} (shell length in mm)$^{2.14}$; $r^2 = 0.8$

yields assimilation and production efficiencies that are relatively high: Assimilation efficiency

$$\left(\frac{P+G+R}{C} \times 100\right)$$

is 42 %, which is lower than the experimentally determined value of 61 % but this is in accord with the suggestion that this parameter was overestimated. The production efficiency

$$\left(\frac{P+G}{P+G+R} \times 100\right)$$

derived from the budget is 54.6 %; yet the mean production efficiency of 36 % obtained from published results for 23 non-insect invertebrate detritivores is considerably lower (Humphreys, 1979; May, 1979). However, even if the true value of R was double the present estimate, the resultant assimilation efficiency (51 %) and production efficiency (38 %) would both still be high, making it apparent that *P. perna* operates very efficiently, i.e. at a relatively low metabolic cost. This is attributed to the physical energy subsidy and multiplier effect of the surf it inhabits which maintains particulate food in suspension and transports it continuously across the reef. The surf also generates and maintains a high O_2 tension and removes faeces and

pseudofaeces that are produced at a rate that would otherwise smother the mussels.

In conclusion, at subtropical temperatures (19.8 to 25.5 °C) in the surf zone, *Perna perna* is an unusually productive organism. Not only does it have a faster growth rate than most temperate mussel species but it is very shortlived – only 0.1 % of the population on the ORI Reef survive into their third year. It attains high density and biomass; the mean dry biomass for ORI Reef mussel beds is 1720 g m^{-2} with a mean annual $P/\bar{B}$ of 4.8 (Berry, 1978). Consequently, a feature of this study is the high value obained for each component of the energy budget.

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LITERATURE CITED

Adams, S. M., Angelovic, J. W. (1970). Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Sci. 11: 249–254

Bayne, B. L., Thompson, R. J., Widdows, J. (1976). Physiology: I. In: Bayne, B. L. (ed.) Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge, p. 121–206

Bayne, B. L., Worrel, C. M. (1980). Growth and production of mussels *Mytilus edulis* from two populations. Mar. Ecol. Prog. Ser. 3: 317–328

Berry, P. F. (1978). Reproduction, growth and production in the mussel, *Perna perna* (Linnaeus), on the east coast of South Africa. Invest. Rep. oceanogr. Res. Inst. (48): 1–28

Berry, P. F. (1982): Biomass and production rate in the ascidian *Pyura stolonifera* on a littoral rock reef on the Natal Coast, South Africa with estimates of biomass of other detritivores. Invest. Rep. oceanogr. Res. Inst. (53): 1–12

Birkbeck, T. H., McHenery, J. G. (1982). Degradation of bacteria by *Mytilus edulis*. Mar. Biol. 72: 7–15

Blanchard, D. C. (1978). Jet drop enrichment of bacteria, virus and dissolved organic material. Pure Appl. Geophys. 116: 302–308

Bowen, S. H. (1976). Feeding ecology of the cichlid fish *Sarotherodon mossambicus* in Lake Sibaya, Kwazulu. Unpubl. Ph. D. thesis, Rhodes University, Grahamstown

Bowen, S. H. (1979). A nutritional constraint in detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Ecol. Monogr. 9: 17–31

Calow, P. P., Fletcher, C. R. (1972). A new radio-tracer technique involving ^{14}C and ^{51}Cr for estimating the assimilation efficiencies of aquatic, primary producers. Oecologia 9: 155–170

Cammen, L. M. (1977). On the use of liquid scintillation counting of ^{51}Cr and ^{14}C in the twin tracer method of measuring assimilation efficiency. Oecologia (Berl.) 30: 249–251

Cassell, E. A. (1965). Rapid graphical method for estimating the precision of direct microscopic counting data. Appl. Microbiol. 13: 293–296

Caulton, M. S. (1978). The effect of temperature and mass on routine metabolism in *Sarotherodon* (= *Tilapia*) *mossambicus* (Peters). J. Fish Biol. 13: 195–201

Conover, R. J. (1966). Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 338–345

Conover, R. J., Francis, V. (1973). The use of radioactive isotopes to measure the transfer of materials in aquatic food chains. Mar. Biol. 18: 272–283

Coughlan, J. (1969). The estimation of filtering rate from the clearance of suspensions. Mar. Biol. 2: 356–358

Crisp, D. J. (1971). Energy flow measurements. In: Holme, N. A., McIntyre, A. D. (ed.) Methods for the study of marine benthos. Blackwell, Oxford and Edinburgh, p. 197–279

Cummins, K. W. (1967). Calorific equivalents for studies in ecological energetics. University of Pittsburgh, Pittsburgh

Darnell, R. N. (1967). Organic detritus in relation to the estuarine ecosystem. In: Lauff, G. H. (ed.) Estuaries. Publs Am. Ass. Advmt Sci. 83: 276–382

Foster-Smith, R. L. (1975). The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullustra* (Montagu). J. exp. mar. Biol. Ecol. 17: 1–22

Griffiths, C. L., King, J. A. (1979). Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. Mar. Biol. 51: 141–149

Griffiths, R. J. (1980a). Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis* (Kr.). Mar. Ecol. Prog. Ser. 3: 63–70

Griffiths, R. J. (1980b). Natural food availability and assimilation in the bivalve *Choromytilus meridionalis*. Mar. Ecol. Prog. Ser. 3: 151–156

Hughes, R. N. (1970). An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa). J. Anim. Ecol. 39: 357–381

Humphreys, W. F. (1979). Production and respiration in animal populations. J. Anim. Ecol. 48: 427–453

Kiørboe, T., Møhlenberg, F. (1981). Particle selection in suspension-feeding bivalves. Mar. Ecol. Prog. Ser. 5: 291–296

Lenz, J. (1977). Seston and its main components. In: Rheinheimer, G. (ed.) Microbial ecology of a brackish water environment. Springer Verlag, Berlin, p. 37–60

May, R. M. (1979). Production and respiration in animal communities. Nature, Lond. 282: 443–444

McHenery, J. G., Birkbeck, T. H., Allen, J. A. (1978). The occurrence of lysozyme in marine bivalves. Comp. Biochem. Physiol. 63B: 25–28

Newell, R. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. J. Zool. 144: 25–45

Nixon, S. W., Ovlatt, C. A., Rogers, C., Taylor, K. (1971). Mass and metabolism of a mussel bed. Oecologia 8: 21–30

Odum, W. E. (1970). Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. In: Steele, J. H. (ed.) Marine food chains. University of California Press, Berkeley, California, p. 222–240

Prus, T. (1971). The assimilation efficiency of *Assellus aquaticus* L. (Crustacea, Isopoda). Freshwat. Biol. 1: 287–305

Schleyer, M. H. (1979). Preliminary results of a comparative study of the role of bacteria and phytoplankton in the littoral waters of Natal. S. Afr. J. Sci. 75: 566

Schleyer, M. H. (1980a). The role of microorganisms and detritus in the water column of a subtidal reef of Natal,

South Africa. Unpublished Ph. D. thesis, University of Natal, Durban

Schleyer, M. H. (1980b). A preliminary evaluation of heterotrophic utilisation of a labelled algal extract in a subtidal reef environment. Mar. Ecol. Prog. Ser. 3: 223–229

Schleyer, M. H. (1981). Microorganisms and detritus in the water column of a subtidal reef of Natal. Mar. Ecol. Prog. Ser. 4: 307–320

Smale, M. J. (1978). Migration, growth and feeding in the Natal rock lobster *Panulirus homarus* (Linnaeus). Invest. Rep. oceanogr. Res. Inst. (47): 1–56

Thompson, R. J., Bayne, B. L. (1974). Some relationships between growth, metabolism and food in the mussel, *Mytilus edulis*. Mar. Biol. 27: 317–326

Widdows, J., Fieth, P., Worrall, C. M. (1979). Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. Mar. Biol. 50: 195–207

Wightman, J. A. (1975). An improved technique for measuring assimilation efficiency by the $^{51}Cr - ^{14}C$ twin tracer method. Oecologia 19: 273–284

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