Short-term changes in the energy balance of *Venerupis corrugatus* (Bivalvia) in relation to tidal availability of natural suspended particles

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ABSTRACT: This study further investigates the finding that a near doubling in clearance rates of *Venerupis corrugatus* correlated with a significant increase in natural particle concentration and silt load at high tide. At this time full extension of the siphons and open valves indicated increased pumping activity, whilst copious production of pseudofaeces showed that more filtered material was being rejected at high tide. After considering particle rejection, net organic ingestion (IR, mg h^{-1}) was related to clam size (W, g dry wt) by the allometric equations: $IR = 5.821\,W^{0.649}$ at low and $IR = 7.867\,W^{0.724}$ at high tide. This difference was significant, as was that between quantities of pseudofaeces produced (mg h^{-1}) at low ($2.498\,W^{0.447}$) and high tide ($4.686\,W^{0.582}$). Particle sorting efficiencies were size-dependent, ranging from 69 % for large clams to 63 % for juveniles at low tide and from 71 to 54 % at high tide. Thus with an increase in the particle load, sorting efficiency in adult clams changed little while that in juveniles was depressed. Absorption efficiency declined significantly from 49 % at low tide to 41 % on the flood tide. Respiration and excretion rates did not differ significantly between tides; common regressions were R (ml O$_2$ h^{-1}) $= 0.785\,W^{0.721}$ and U (μg NH$_4$-N h^{-1}) $= 2.733\,W^{1.343}$. Nonetheless potential for production (P) was significantly greater at high tide, being described by P (J h^{-1}) $= 15.751\,W^{0.696}$ compared with $P = 12.271\,W^{0.696}$ at low tide. Resultant net growth efficiencies were some 10 percentiles higher (49 to 53 %, depending on size) relative to low tide (37 to 42 %), a difference indicating successful and immediate exploitation of the tidally induced improvement in food supply. Elevated efficiencies were realised not by changes in absorption efficiency, respiration or excretion, but by an increase in clearance rates which, even after being balanced against a rise in pseudofaeces production, resulted in greater net organic ingestion at high tide. Short-term increases in production potential thus correlated with cyclic patterns of food supply. It is debated whether such production is a result of innate physiological regulation depending on nutritional needs or as a consequence of autonomous processes of water pumping and filtration efficiency.

KEY WORDS: Clam · Energy balance · Intertidal · Natural suspended particulates · Clearance · Ingestion

INTRODUCTION

In studies on bivalve energetics, there have consistently been 2 major ambiguities in extrapolating laboratory-based data on energy budgets to the natural environment. The first of these relates to diet and the second to natural temporal influences on food supply. While it is convenient to use an easily accessible food such as algae cultured in the laboratory or mixtures of algae and inert material to vary nutrient value, it is more meaningful in terms of extrapolating laboratory energy budgets to the field situation to use food derived from the natural habitat. Such food, for example powdered saltmarsh leaves (Lucas & Newell 1984, Newell & Langdon 1986) and detritus from kelp fronds (Stuart 1982), would reflect natural texture, palatability, composition and energy content (Wright et al. 1982, Newell & Jordan 1983, Lucas et al. 1987, Matthews et al. 1989, Stenton-Dozey 1989, Navarro et al. 1992, Urban & Kirchman 1992).

The second ambiguity, that of temporal influences on energy balance, has received little attention. Where it has been addressed, the focus has been on the effect of seasonal fluctuations in food concentration (Griffiths &

King 1979, Griffiths 1980) or episodic events such as upwelling (Stuart & Klumpp 1984, Seiderer & Newell 1985). However, these studies did not use natural diets or consider coinciding temporal changes in food quality. In this regard Kiørboe et al. (1981), Riisgård & Randløv (1981), Hawkins & Bayne (1985) and Hawkins et al. (1985) researched seasonal patterns of food processing and growth in *Mytilus edulis*.

As a contribution towards the understanding of bivalve energy budgets based on fluctuations in diets that are wholly natural, we undertook a study of *Venerupis corrugatus* (Gm.), a filter-feeding, burrowing clam found in sheltered intertidal areas of South Africa. Experimental design focused on the tidal availability and composition of natural suspended particulates in a rock pool with a sandy substrate inhabited by *V. corrugatus*. An earlier paper (Stenton-Dozey & Brown 1992) reported analyses of seawater samples, collected hourly during a 13 h spring tidal cycle, for particle size, particle quantity (counts, total and organic dry wt) and quality (organic content). Maximum particle size increased from 12 to 23 μm on the flood tide, while total particulate dry wt increased 4-fold to a maximum of 23 mg l^{-1}. Clearance rates, measured by following the decline in natural particulates in unfiltered seawater collected at low and high tide, were significantly related to tidal height and particle size plus an interaction of these 2 factors. When using high-tide water, larger particles were cleared at faster rates than in low-tide experiments, resulting in a substantial increase in the ingestion of organic material.

The present paper aims to identify any short-term increase in production potential (P = somatic growth, reproduction and/or deposition of energy reserves) of *Venerupis corrugatus* following a tidally induced rise in food supply. Rates of ingestion derived from indirect measurements of clearance rates of natural particulates are balanced against rates of ammonia excretion, defaecation and respiration. These data are discussed with reference to the recent debate on whether production potential in a bivalve is determined by innate physiological processes (Hawkins et al. 1985, Bayne et al. 1989, Bayne & Hawkins 1990) or simply by the rate at which the filtration mechanism processes particulate material (Jørgensen 1990).

MATERIALS AND METHODS

Rock-pool environment. The study site was located at Bloubergstrand, just north of Cape Town, on the west coast of South Africa, and comprised a large rock pool with a sandy bottom. At low tide the pool is isolated from the sea by a rocky outcrop, beyond which lies an extensive kelp bed. Temperature and oxygen content of the rock pool were monitored every hour between low and high tides. Water warmed up from 13 to 18 °C while the pool was isolated (4 to 5 h), falling to 14 °C after inundation. Oxygen levels ranged from 8 to 10 mg l^{-1}, supersaturation being reached at high tide.

Experimental clams were collected in summer when a light southeasterly wind prevailed. At the same time, 50 l of rock-pool water was sampled at low and high tides, when low and high particle densities could respectively be expected (Stenton-Dozey & Brown 1992). Clams were maintained in rock-pool water overnight so they could feed on natural particulates before experiments were conducted the following day.

Clearance rates. Detailed methodology can be found in Stenton-Dozey & Brown (1992). Briefly, clearance rates were determined indirectly by measuring the decline in natural particle densities within 1 μm diameter size categories. Two sets of experiments were conducted, one using unfiltered seawater collected at low tide, and the other water collected at high tide. The total number of particles, including bacteria, cleared from suspension was calculated by summation of numbers of particles in each size category before and after each experimental period. These data were then used in the equations of Coughlan (1969) to calculate overall clearance rates for clams ranging in size from 26 to 867 mg soft tissue dry wt (17 to 53 mm shell length). Results are presented as allometric equations relating body weight to clearance rate.

Ingestion rates. Ingestion rates as mg inorganic and/or organic dry wt ingested h^{-1} individual^{-1} were calculated from mean particle concentration × clearance rate. A distinction was made between gross ingestion (i.e. the particulate quantity cleared from suspension) and net ingestion (the quantity entering the mouth after rejected material has been released as pseudofaeces). This was achieved by subtracting the mean total and organic dry wt of pseudofaeces produced h^{-1} from the overall quantity of material ingested h^{-1}. Once again ingestion rates were related to body weight in allometric equations.

Absorption efficiencies. The ash-ratio method (Conover 1966) was used to estimate absorption efficiencies as given by the following formula:

$$AE = \frac{f - e}{(1 - e)f} \times 100$$

where AE = absorption efficiency; f = organic fraction of food; and e = organic fraction of faeces.

Faeces were collected immediately after they emerged from the exhalant siphon, suctioned onto ashed (460 °C for 6 h), pre-weighed 25 mm Whatman GF/F filters and rinsed with ammonium formate to remove salts. These filters were dried at 60 °C for 2 d to obtain total dry wt, then ashed at 460 °C for 20 h,

reweighed, and the organic content of faeces determined by difference. The Conover ratio implicitly assumes non-selective feeding. However, during experiments *Venerupis corrugatus* produced copious amounts of pseudofaeces, which constitute the rejection of some organic material after particles have been filtered but not yet ingested. This necessitated estimating an organic fraction for *f* in the Conover ratio which was the balance between the organic fraction filtered and that lost in pseudofaeces. This was possible by collecting all pseudofaeces produced during experiments and determining their total weight and organic content.

Metabolic expenditure. Rates of excretion were estimated by measuring ammonium N. During and after feeding experiments, replicate 5 ml samples were taken at 1 h intervals for 5 h for an indophenol-blue spectrophotometric determination of ammonia as modified from Koroleff (1976). Excretion rates were calculated over 4 h from regression slopes of μg NH_4-N clam^{-1} against time (h) for different body sizes.

Aerobic respiration rates were measured in a flow-through respirometer, fitted with YSI (Yellow Springs Instrument Co.) dissolved-oxygen probes and housed in a constant temperature room set at 15 °C. Unfiltered seawater collected from the pool was used in the respirometer so that respiration rates would reflect filtration activity. Seawater flowed from an upper reservoir through 4 respiration chambers into a bottom reservoir, from where it was returned to the top reservoir via a pump. The chambers, fitted with YSI probes, could be shut off from flowing seawater by tourniquet valves on the inlet and outlet hoses. At all times these chambers were submerged to prevent air leakage, while magnetic stirrers ensured circulation within. The probes were linked to an oxygen meter interfaced to a computer programmed to regress the decline in oxygen content against time.

Production potential. Rates of respiration (R) and excretion (U) were balanced against the absorbed ration (Ab = ingestion rate × absorption efficiency) to arrive at the potential for production (growth, reproduction and deposition of energy reserves = P, in J h^{-1}) for standardised weights of clams. P is substituted for the more commonly used term 'scope for growth' (SFG) in light of recent interpretive criticisms (Jørgensen 1990). For metabolic expenditure the following energy conversions were used: 1 ml O_2 = 20.08 J (Gnaiger 1983) and 1 mg NH_4-N = 24.87 J (Elliot & Davison 1975).

The energy of suspended particulate material was based on a ratio of 1 mg organic dry wt = 9.72 J (± 0.85, n = 6). This food value was determined by concentrating the filtrate of rock-pool seawater on membrane filters, scraping the filtrate onto glass slides, drying at 60 °C for 24 h followed by combustion in a microbomb calorimeter. Three replicates were processed for each tidal height but since negligible differences were found, data on the energy content of particulates at low and high tide were pooled.

RESULTS

Resource availability

A detailed account of suspended material present in seawater collected at Bloubergstrand and used in feeding experiments is given in Stenton-Dozey & Brown (1992). Briefly, summation of particle numbers, dry and organic weight from 1 μm particle size classes covering a diameter spectrum of 0.6 to 12 μm at low tide gave 3.4×10^9 particles l^{-1} totaling 6.7 mg dry wt l^{-1} of which 61 % was organic. At high tide the spectrum expanded to include 23 μm diameter particles with an increase in suspension densities to 5.6×10^9 l^{-1} representing 9.6 mg dry wt l^{-1} with a reduced organic content of 51 %.

Clearance and ingestion rates

Coincident with more particulates at high tide, clearance rates were nearly double that at low tide (Fig. 1). Indeed ANOVA indicated that clearance rates were significantly affected not only by tidal height, but also by particle size as well as by an interaction between these 2 factors (Table 2 in Stenton-Dozey & Brown 1992).

Ingestion rates (Fig. 1) are quantified as inorganic and/or organic intake (mg dry wt h^{-1}) and also expressed in gross and net terms. Differences between these categories were used to quantify the amount of inert material filtered by *Venerupis corrugatus* but then rejected as pseudofaeces. A doubling of clearance rates on the flood tide resulted in a 1.5-fold increase in gross ingestion, that is from 14.0 mg filtered h^{-1} at low tide to 21.2 mg h^{-1} at high tide. The gross organic yield from this material amounted to 8.5 mg h^{-1} at low tide which means that 39 % of total intake was inert material; the equivalent at high tide was 11.3 mg h^{-1} and 47 %.

At high tide net ingestion, i.e. the amount of material entering the digestive system once refractory material had been discarded as pseudofaeces, was between 1.15 and 1.35 times that at low tide. Student *t*-testing of equality between regression coefficients (Table 1) showed that the increase in ingestion rates at high tide was significant. Increased clearance and ingestion rates were associated with the observation that the siphons of individual clams held in high-tide water were often extended and fully open for long periods whereas among clams supplied with low-tide water,

LOW TIDE
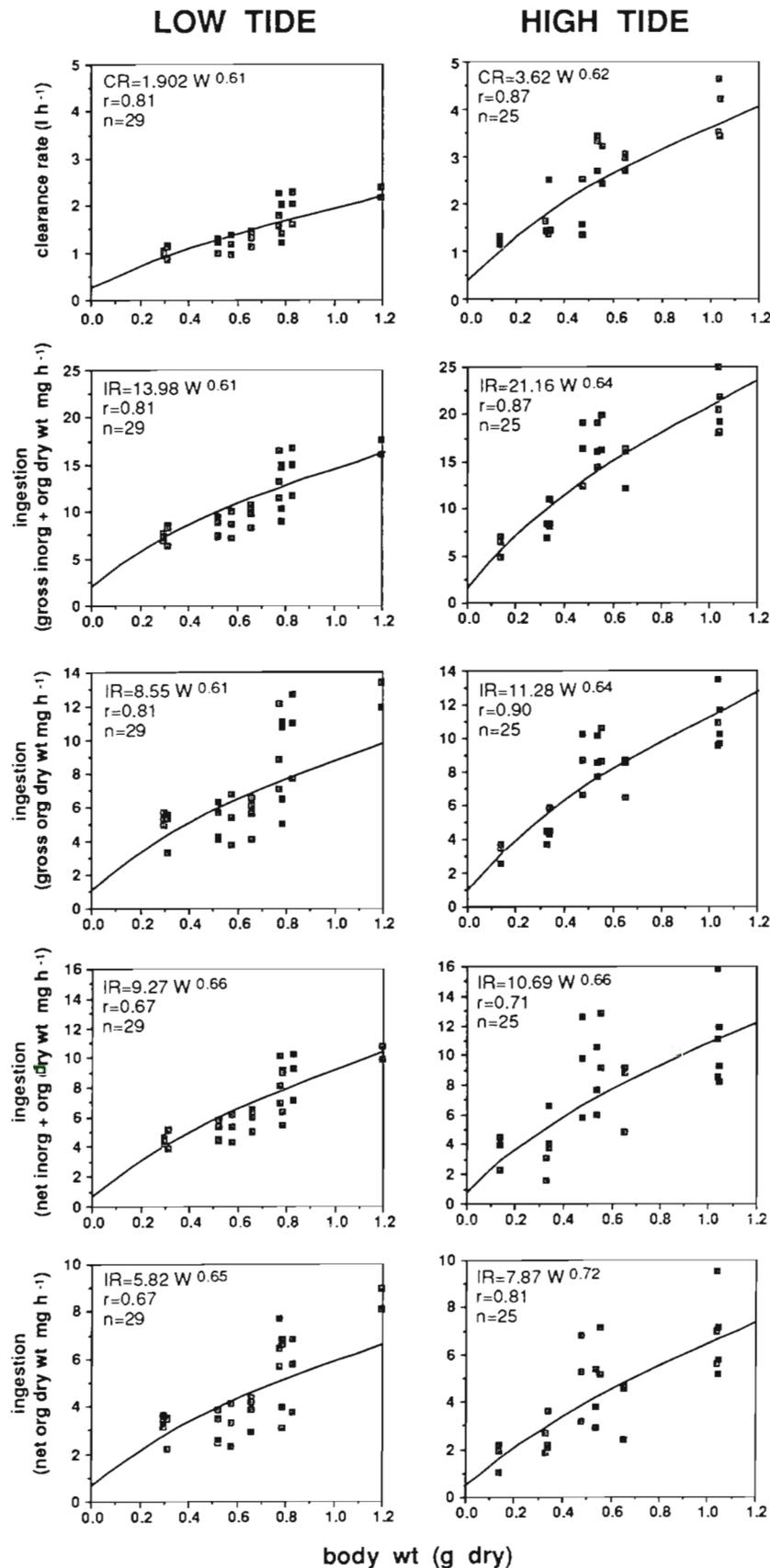
HIGH TIDE

the siphons were not fully extended and closed intermittently. Valve gape was also noted to increase when high-tide water was supplied.

In association with increased particle concentration and gross ingestion rates at high tide, *Venerupis corrugatus* produced large quantities of pseudofaeces (Fig. 2) at rates significantly greater (Table 2) than in experiments using low-tide water. Even though more pseudofaeces was released at high tide, the proportion of organics filtered from suspension but then rejected as pseudofaeces differed little between low and high tides. Percentages were size-dependent, ranging from 31 % for large clams to 37 % for small ones at low tide, the equivalent at high tide being 29 to 46 %. These data can also be viewed in terms of the efficiency with which particles are sorted; % efficiency = $100[1 - (P/F)]$, where P and F represent the organic content, by weight, of material rejected in pseudofaeces and found in filtered material (Navarro et al. 1992). At low tide these efficiencies range from 69 % for large *V. corrugatus* to 63 % for small ones and at high tide, from 71 to 54 %. This indicates that with the increased particle load at high tide, sorting efficiency in adult clams changed little while that of juveniles was depressed.

Absorption efficiencies, which were calculated from the net organic fraction ingested by *Venerupis corrugatus* and which therefore accounted for pseudofaeces production, averaged 49 ± 7 % at low tide (n = 9) and 41 ± 5 % (n = 9) at high tide. A 2-sample *t*-test (Zar 1984) identified a significant difference between these means ($t = 2.813$, n = 18, $0.01 < p < 0.05$). The

body wt (g dry)

Fig. 1 *Venerupis corrugatus*. Scatter plots of original data on clearance rates ($l\ h^{-1}$) and ingestion rates (mg inorganic and/or organic dry wt h^{-1}) in relation to body wt (mg dry wt) of clams at low and high tide. Superimposed on these data are graphs depicting allometric equations in Table 1

Table 1 *Venerupis corrugatus*. Student t-testing of equality between regression coefficients of allometric equations for ingestion rates at low and high tide as given in Fig. 1b. b_c: common slope; p = 0.05 (after Zar 1984)

Ingestion rates (mg h^{-1})	Between slopes					Between elevations			
	MS	SE	df	t	b_c	SS	MS	df	t
Gross inorg. + org.	0.011	0.133	50	± 0.289	0.644	0.358	0.007	51	± 4.248
Gross org.	0.011	0.133	50	± 0.289	0.644	0.364	0.007	51	± 4.628
Net inorg. + org.	0.024	0.203	50	± 0.266	0.661	1.197	0.024	51	± 2.181
Net org.	0.012	0.410	50	± 0.409	0.698	0.658	0.013	51	± 3.673

increase in particle concentration, and most probably associated changes in particle sizes and composition that take place on the flood tide, appeared to depress absorption efficiency in *V. corrugatus*.

LOW TIDE

PF$_{inorg + org}$ = 4.42 W$^{0.49}$, r = 0.85, n = 9
PF$_{org}$ = 2.50 W$^{0.45}$, r = 0.64, n = 9

HIGH TIDE

PF$_{inorg + org}$ = 10.22 W$^{0.67}$, r = 0.97, n = 9
PF$_{org}$ = 4.69 W$^{0.58}$, r = 0.88, n = 9

body wt (g dry)
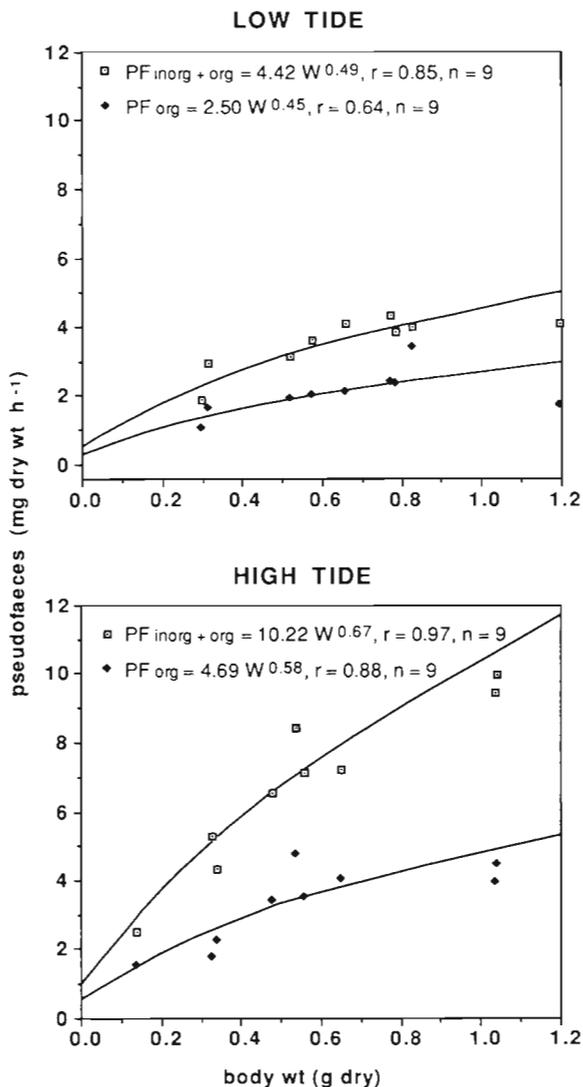
pseudofaeces (mg dry wt h^{-1})

Fig. 2. *Venerupis corrugatus*. Scatter plots of original data on pseudofaeces production (mg dry wt) of clams at low and high tide. Superimposed on these data are graphs depicting allometric equations in Table 2

Respiration and excretion

The relationship between body wt and respiration rates $(R$, ml O$_2$ h$^{-1})$ at 15 °C was calculated as $R = 0.773 W^{0.701}$ (r = 0.81, n = 22) at low tide and $R = 0.791 W^{0.731}$ (r = 0.90, n = 23) at high tide. However, no significant differences could be found between regression coefficients (Student t-test), indicating that neither the state of the tide nor, indirectly, the increase in clearance and ingestion rates associated with tidal inundation influenced respiration rates. Thus a common equation was computed (after Zar 1984): $R = 0.785 W^{0.721}$ (r = 0.89, n = 45; between slopes $t = 1.38$, $0.2 < p < 0.1$; between elevations $t = 1.96$, df = 41, $0.1 < p < 0.05$).

Excretion rates (U) as µg NH$_4$-N h^{-1} were related to body weight by $U = 2.594 W^{1.316}$ (r = 0.86, n = 8) at low tide and $2.759 W^{1.269}$ (r = 0.96, n = 9) at high tide. Once again Student t-tests revealed no significant differences between elevations or weight exponents. Excretion rates could thus be expressed by 1 equation, $U = 2.733 W^{1.343}$ (r = 0.90, n = 17; between slopes $t = 0.117$, df = 13, p > 0.5; between elevations $t = 1.913$, df = 14, $0.1 < p < 0.05$).

Production potential

The above equations relating body weight of *Venerupis corrugatus* to rates of ingestion, respiration and excretion, were used to calculate an energy budget for standardised weights of clams in terms of J h^{-1}. At both low and high tide the production potential (P) for all sizes of *V. corrugatus* remained positive when $R + U$ were balanced against the absorbed ration (Ab) (Table 3). At high tide this balance was such that more energy was available for growth and reproduction than at low tide.

Allometric equations were calculated from data in Table 3: low tide, $P = 12.271 W^{0.663}$ (n = 7, r = 0.98); and high tide, $P = 15.751 W^{0.729}$ (n = 7, r = 0.98). Given that data used to derive P (IR and ration) showed significant differences, the increase in energy gain at high tide must clearly hold some significance too. Indeed, net

Table 2. *Venerupis corrugatus*. Student *t*-testing of equality between regression coefficients of allometric equations for pseudofaeces production at low and high tide as shown in Fig. 2. b_c: common slope; p = 0.05 (after Zar 1984)

Pseudofaeces production (mg h^{-1})	Between slopes					Between elevations			
	MS	SE	df	t	b_c	SS	MS	df	t
Inorg. + org.	0.003	0.135	14	± 1.394	0.609	0.054	0.004	15	± 10.961
Org.	0.011	0.227	14	± 0.595	0.535	0.152	0.011	15	± 4.939

Table 3. *Venerupis corrugatus*. Energy budget (J h^{-1}) for a selected size range of clams at low (LT) and high (HT) tide. Energy uptake calculated from net organic ingestion (*IR*) (Fig. 1) where 1 mg organic dry wt = 9.72 J. Absorbed rations (*Ab*) were based on absorption efficiencies of 49% at LT and 41% at HT. Respiration (*R*, ml O_2 h^{-1}) = 0.785 $W^{0.721}$ where 1 ml O_2 = 20.08 J (Gnaiger 1983). Excretion (*U*, µg NH_4-N h^{-1}) = 2.733 $W^{1.343}$ where 1 mg NH_4-N = 24.87 J (Elliot & Davison 1975). *P*: production

Low tide						High tide					
Body wt (g dry wt)	IR (J h^{-1})	Ab (J h^{-1})	R (J h^{-1})	U (J h^{-1})	P (J h^{-1})	Body wt (g dry wt)	IR (J h^{-1})	Ab (J h^{-1})	R (J h^{-1})	U (J h^{-1})	P (J h^{-1})
0.1	12.773	6.239	2.991	0.003	2.335	0.1	14.437	5.919	2.991	0.003	2.925
0.2	19.926	9.764	4.941	0.008	4.816	0.2	23.846	9.777	4.941	0.008	4.829
0.4	31.201	15.288	8.142	0.020	7.076	0.4	39.388	16.149	8.142	0.020	7.987
0.6	40.629	19.908	10.907	0.034	8.967	0.6	52.827	21.659	10.907	0.034	11.618
0.8	48.989	24.005	13.420	0.050	10.535	0.8	65.059	26.674	13.420	0.050	13.204
1.0	56.570	27.719	15.763	0.068	11.887	1.0	76.467	31.351	15.763	0.068	15.523
1.2	63.666	31.196	17.977	0.087	13.132	1.2	87.257	35.775	17.977	0.087	17.711

growth efficiencies (*P*/*Ab*) were approximately 10 percentiles higher at high tide, ranging from 49% for juveniles to 53% for adult clams compared to a corresponding range of 37 to 42% at low tide. This increase, together with the behaviour of extending the siphons and valve gape, indicates the successful and immediate exploitation of the tidally induced improvement in food supply.

DISCUSSION

Venerupis corrugatus attained a positive potential for growth and reproduction (*P*) when maintained in the laboratory in unfiltered seawater collected from its natural rock-pool habitat. Furthermore, when feeding on particulates in water collected at high tide, energy gain was significantly greater than on a diet of low-tide particles; for instance a clam of 1 g dry wt increased its positive energy balance by 30.6%. This coincided with an overall rise in the food source from 6.7 to 9.6 mg dry wt l^{-1} between low and high tide or, in energy terms, from 39.7 to 49.5 J l^{-1}.

It is of interest to place *P* data (J h^{-1}) within the timetable of the 13 h spring tidal cycle described by Stenton-Dozey & Brown (1992) for the rock pool at Bloubergstrand. The cycle over which particle concentrations were measured involved an initial 4 h low-tide period followed by flooding of the pool for the next 5 h, and then isolation for a further 4 h. During this 13 h

cycle we can estimate energy gain, based on *P* data, at low tide as 11.9 J h^{-1} g^{-1} × 8 and at high tide, 15.5 J h^{-1} g^{-1} × 5: this amounts to 172.7 J, or if extrapolated to 24 h (× 1.85), 318.8 J d^{-1} g^{-1}. This represents a percentage change in body energy d^{-1} of 1.86% based on 17.14 kJ g^{-1} body dry wt (unpubl. data). This is a moderate estimate which falls within the range calculated for other bivalves fed natural diets (Stuart 1982, Stenton-Dozey 1989).

While it is clearly evident that the potential for growth and reproduction in *Venerupis corrugatus* is enhanced in the short period between tides, it is the mechanism by which this is achieved that needs addressing. In balancing energy gain and loss, it is the former which changed significantly between tides principally because at high tide, food intake increased when clearance rates doubled without a significant change in rates of respiration and excretion. When clearance rates increased, the siphons of *V. corrugatus* extended fully and the siphon aperture and valve gape increased to a larger degree than among clams feeding on low-tide particulates. This reaction has earlier been described by Riisgård & Randløv (1981) and Riisgård (1991). According to Jørgensen et al. (1988) and Jørgensen (1990) the degree of valve gape and area of siphon aperture vary with pumping rates from zero to a maximum rate characteristic of the fully open state. The maximum clearance rate of *V. corrugatus* compared favourably with that of *V. pullastra* when stimulated into the fully open state on a diet of algae (Møh-

lenberg & Riisgård 1979). Furthermore, Jørgensen (1990) states that environmental conditions that are compatible with the fully open state may be characterised as optimal. In this context conditions at high tide may be considered optimal for short-term exploitation of *V. corrugatus* growth potential.

Jørgensen (1990) disputes the widely held concept that water processing is energetically expensive and thus, to conserve energy, is physiologically controlled to ensure a constant intake of food over a wide range of particle concentrations (see references on p. 67 & 68 in Jørgensen 1990). Rather, pumping rates are considered to constitute physical consequences of the interfilament distances that are loosely coupled with valve gape. In this study the postural changes that accompanied clearance rate increases in *Venerupis corrugatus*, together with no significant increase in respiration rates, support Jørgensen's interpretation.

Clearance rate increases on the flood tide were associated with a 10 % increase in the rock-pool silt load, a 25 % rise in overall particle concentration and a shift in the particle size spectrum from a maximum diameter of 12 µm at low tide to 23 µm at high tide (Stenton-Dozey & Brown 1992). Clearance rate increase was significantly linked to this shift in the size spectrum so that larger particles (8 to 13 µm) were cleared at maximum rates (3 to 4 l h^{-1} g^{-1}) at high tide compared to smaller particles (5 to 9 µm) being filtered at top rates of 2 to 3 l h^{-1} g^{-1} at low tide. This, however, does not imply preferential clearance of larger particles. According to the principles of fluid mechanics (Jørgensen 1990), when water processing increases in response to denser suspensions, the shear forces between ciliary currents intensifies and particles most plentiful in these currents are indiscriminately directed towards the mouth. Nonetheless the end result was a 65 % increase in gross ingestion. At the same time pseudofaeces production doubled so that in net terms, ingestion increased by 39 %.

Even though more pseudofaeces was released at high tide in response to an increase in particle concentration and silt content, the proportion of nutritious material (% organics) filtered but then rejected differed little between tides, any variation being more a function of clam size than food quantity or quality (31 to 37 % at low tide, 29 to 46 % at high tide). Consequently particle sorting efficiency, derived from the proportions of organics in filtered and rejected material, also showed no marked differences between tides. Thus the process of organic enrichment of filtered material, i.e. pre-ingestive selection, does not appear to be influenced by the amount of material that has the potential for rejection. This is probably set by morphological constraints, such as the structure and size of the labial palps, food grooves and gills rather than physiological parameters. Indeed Jørgensen (1990) suggests that it is the nature of the spatial and temporal relationships between the surface currents along the gill filaments and the mucus strings across the filaments that determine the selective rejection of particles from mixed suspensions, the particle concentration of which exceeds the capacity of the digestive tract.

Material entering the digestive tract was absorbed with an efficiency of 49 % at low tide and 41 % at high tide, a small difference that was nonetheless significant. However, since the net ingested ration was 1.2 times that at low tide, the amount absorbed (*IR* × absorption efficiency), and ultimately *P*, were significantly greater at high tide. The intertidal change in absorption efficiency was thus insufficient to affect *P*, further demonstrating that particle clearance rate has primary influence on short-term growth potential.

Over the last decades filter feeding in bivalves has been considered to be physiologically regulated so as to secure a more or less constant ingestion rate at varying concentrations of suspended food particles (Winter 1978, Bayne & Newell 1983). This aspect has recently been elaborated whereby feeding, metabolism and growth are seen to constitute controlled processes based on endogenous rhythms of gut fullness, gut passage time and absorption efficiency that are, in turn, correlated with the seasons (Hawkins et al. 1983, 1985, Bayne et al. 1984, 1987, Hawkins & Bayne 1984, 1985). Jørgensen, in his recent review (1990) disputes these concepts, recognising that water processing is an autonomous process reflecting physical properties of the filter pump that are not subject to physiological regulation. Particle retention is viewed as being determined by the capacity of the pump and the ambient water quality and food concentration. Data in this paper are insufficient to support convincingly either argument although indirect evidence is in favour of Jørgensen's approach. Nonetheless it is important to realise that in future research the filter pump activity must be measured at full capacity to determine a bivalve's maximum growth potential before introducing variations in the environment (season, silt load, particle concentration) that may change this capacity.

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