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ENERGY RESOURCE ALLOCATION IN *MULINIA LATERALIS* (SAY), AN OPPORTUNISTIC BIVALVE FROM SHALLOW WATER SEDIMENTS

SANDRA E. SHUMWAY [1,2] & RICHARD C. NEWELL[3]

[1]Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11974, U.S.A.

[2]Present address: Department of Marine Resources, West Boothbay Harbor, Maine 04575, U.S.A.

[3]Royal Society Senior Research Fellow, c/o Institute for Marine Environmental Research, Prospect Place, Plymouth PL1 3DH, U.K.

ABSTRACT

The coot clam, *Mulinia lateralis*, is an inhabitant of soft, salt-clay substrata and shows high rates of growth and reproduction followed by episodic mass mortality. An analysis of the effects of body size, temperature and starvation on the major components of energy balance in this bivalve suggests that it has a relatively high energy demand of approximately $10 \cdot 66$ cal $\cdot$ day^{-1} ($\sim$44.66 joules $\cdot$ day^{-1}) estimated for a 7 mg dry tissue mass individual at 20°C. Since the absorption efficiency is 63 %, a daily ration of 16.87 cal ($\sim$70.67 joules) is required to meet the consumption requirements of this bivalve. This could be met by the filtration rate of 572 ml $\cdot$ day^{-1} in a phytoplankton cell density of $3 \cdot 10^5$cells $\cdot$ ml^{-1}, such as occurs during bloom conditions in coastal waters or when phytoplankton is supplemented by natural seston at the sediment-water interface.

The relative allocation of energy in *Mulinia lateralis* shows that 54.6 % of the absorbed ration is channelled into growth (P_g) with a rather small component of 1 % becoming incorporated into shell matrix (P_{shell}), and with 16.1 % of the absorbed ration being channelled into gamete production (P_r). Total production (P) thus amounts to 70.8 % of the absorbed ration, with approximately 28.6 % losses through respiration (R) and only 0.6 % through ammonia excretion (U). The relative allocation of resources in the coot clam therefore do not differ sharply from other molluscs despite the opportunistic nature of this bivalve. Instead, *Mulinia lateralis* appears to be primarily adapted to exploit the high concentrations of phytoplankton and natural seston which occur at the sediment-water interface, and is likely to achieve high growth and reproductive rates provided that the available ration exceeds 17 cal $\cdot$ day^{-1}. The possibility that food resources may seasonally fall below this value, and the apparent inability of *Mulinia lateralis* to catabolize protein during prolonged periods of starvation, may account for the episodic mass mortalities which are characteristic of this species.

INTRODUCTION

The distribution and population biology of the coot clam, *Mulinia lateralis*, has been described by several authors who have shown that it is a widely distributed 'opportunistic' species (see MacArthur 1960) whose numbers are characterized by major spatial and temporal variability (Sanders 1956, Stickney & Stringer 1957, Rhoads 1976, Parker 1975, Holland *et al.* 1977, Santos & Simon 1980). It lives primarily in soft silt : clay substrata and, unlike most bivalves, maintains a high level of feeding, shell valve and locomotory activities under anoxia which may allow the clam to escape short-term periodic burial in unstable oxygen-deficient sediments (Shumway *et al.* 1983). Its high fecundity, short generation time (approximately 60 days from egg to egg) and gametogenic activity which occurs over much of the year (Calabrese 1969, 1970) may also allow rapid colonization of unstable sediments (see also Levinton 1970, Levinton & Bambach 1970). Santos & Simon (1980), for example, reported that *M. lateralis* achieves densities of as much as $74000 \cdot m^{-2}$ prior to annual summer mass mortalities which appear to be associated with low oxygen levels and high temperatures.

Apart from the work of Ansell & Sivadas (1973) on *Donax vittatus*, a series of studies by Bayne and co-workers on the mussel, *Mytilus edulis*, (for reviews, see Bayne 1976, Bayne & Newell 1983), and a more recent study by Shumway (1983) on *Mulinia lateralis*, there have been few attempts to interpret either the mass mortalities or the fecundity and rapid growth of opportunistic bivalves in terms of the basic physiological energetics of the individual. Assuming steady state conditions, the net energy exchange in an individual organism may be described by the well-known expression:

$$C = P + R + F + U \qquad (1)$$

where ingested ration (or consumption, C) is the energy equivalent of food intake, (P) is the sum of energy incorporated as growth (P_g) plus reproductive products (P_r), (R) is the energy equivalent of metabolic heat losses, (F) is the energy equivalent of faeces and (U) is the energy content of urine and mucus (see Winberg 1956, Ricker 1968, Petrucewicz & MacFadyen 1970, Crisp 1971, Grodinski *et al.* 1975, Conover 1978, Brett & Groves 1979).

Ansell & Sivadas (1973) found, for example, that the metabolic rate of *Donax vittatus* shows an exaggerated increase in response to a rise of temperature within the normal environmental range. They suggested that this may represent an exploitative strategy provided that sufficient environmental food resources are available as temperatures rise during the summer months. In this, and other bivalves, however, if food availability is insufficient to support the metabolic rate, mass mortalities may occur when the lipid and carbohydrate reserves have been utilized (see also Johnson 1968). Shumway (1983) has recently studied factors affecting oxygen consumption in *Mulinia lateralis* in

response to a variety of intrinsic factors (including body size, gill surface area and activity) and extrinsic variables (including temperature, salinity, oxygen concentration and food) and has shown that apart from the effects of body size, metabolic energy expenditure is strongly affected by salinity and exposure temperature. Since there is little evidence of compensation for long-term changes in environmental temperature (Shumway 1983), *Mulinia lateralis* also appears to be a bivalve which is adapted to exploit seasonal increases in temperature, even though this increases vulnerability to starvation and subsequent mortality at high temperatures if food availability falls below that required to sustain the metabolic energy demands.

The following work was undertaken simultaneously with the oxygen consumption studies which, because of the large volume of experimental data, have been reported in a separate publication by Shumway (1983). It allows us to establish a full balanced energy equation for *Mulinia lateralis* in which all components except growth have been determined at the same time and on the same experimental animals and to compare the relative allocation of energy in this opportunistic species with values obtained for other bivalves.

We are grateful for the technical assistance of T. Scott and for the provision of animals by A. Ducharme. E.F. DePew kindly advised on the excretion experiments, and P. Almeda made growth measurements. We also acknowledge the field assistance and stimulating discussions with L. Deaton. This work was funded by USPMS Grant #GM21133 to R.K. Koehn who provided laboratory facilities at the State University of New York, Stony Brook.

MATERIALS AND METHODS

Experimental animals

Specimens of *Mulinia lateralis* (Say) were collected from Port Jefferson Harbor, New York and were also supplied by the University of Delaware Marine Laboratory, Lewes, Delaware. The clams were held at 10, 20, and 30°C in recirculating seawater (salinity 28‰) and either fed a mixture of *Thalassia maculata, Monochrysis lutheri* and *Isochrysis galbana* for at least 3 weeks prior to use, or were starved at each of the three acclimation temperatures (see also Shumway 1983). All experiments were conducted on clams of a size range from 3-20 mm shell length and the results expressed as regressions on tissue weight following oven drying at 60°C for 24 h.

Ammonia excretion (U; equation 1)

Individual clams were placed in a measured volume of 2.5 or 5.0 ml Millipore-filtered seawater and the ammonia determined colorimetrically by the method of Solorzano (1969) after 60-90 minutes depending on the size of the animal.

Ammonia excretion as a function of body size and acclimation temperature was then expressed as mg $NH_4N \cdot h^{-1}$ and the data converted to calories using a value of $5.94 \cdot 10^{-3}$ cal $\cdot \mu g^{-1}$ for the heat of formation of ammonia (see Elliot & Davison 1975). The atomic ratio of oxygen consumed to amonia nitrogen excreted (O:N ratio) was calculated from equations relating the oxygen consumption ($\dot{V}O_2$, $\mu l\ O_2 \cdot h^{-1}$; Shumway 1983) and the experimental data for ammonia excretion ($\dot{V}NH_4N$; mg $\cdot$ day^{-1}) in relation to body size.

Absorption efficiency ($Ab = [(C - F)/C] \cdot 100$; equation 1)

Absorption efficiency was estimated by the method of Conover (1966), and although originally termed 'percentage assimilation', a distinction has been made here between the absorbed ration ($C - F$; see equation 1) or absorption efficiency ($[C - F/C] \cdot 100$) to which the Conover ratio more properly refers, and assimilation efficiency in accordance with International Biological Programme teminology (see Crisp 1971). No distinguishable pseudofaeces were produced at the ration available to the experimental animals during acclimation. Because of the low rate of faecal production and the small size of the clams, experimental animals were left for periods of 12-24 h before a measurable amount of faecal material could be collected. The faeces were then filtered onto GF/C membranes which had been pre-ashed at 450°C for 6 h, and were dried at 60°C for 12 h prior to ashing at 450°C for at least 12 h. They were then weighed on a Cahn microbalance and the data expressed as absorption efficiency (%) in relation to dry tissue weight.

Egg and sperm production (P_r)

Eggs and sperm were stripped from 'ripe' females and males, counted, rinsed in ammonium formate solution, and dried to constant weight at 60°C for up to 24 h. The samples were then ashed at 400°C for 6 h and reweighed. Results were then expressed as number or dry weight $\cdot$ mg dry tissues of parent^{-1}, and converted to calories using a calorific equivalent of 6 Kcal $\cdot$ g of eggs^{-1} (Crisp 1971; Rodhouse 1978; Perron 1981; Vahl 1981).

Production as growth (P_g)

The relation between shell dry weight and ash-free dry weight of shell was determined by ashing pre-weighed shells at 400°C and was used to estimate organic production channelled into shell production.

Some measurements were made of the mean specific growth rate (G, see Crisp 1971) of *Mulinia* from the increase in length ($\mu m \cdot day^{-1}$) over a period of 10 days using the laser diffraction pattern technique of Strömgren (1975).*

*These data were kindly made available by P. Almeda from measurements made on animals transported to the NERC Unit Marine Science Laboratories, Menai Bridge, North Wales.

Clams were fed 5-6 cells · μl^{-1} of *Pavlova lutheri* at approximately 300 $\mu l \cdot min^{-1}$ in seawater at 15°C and 32‰. Estimates of somatic growth (P_g) were also made from clams held at 20°C and 28‰ maintained on a diet of *Thalassiosira maculata* and *Isochrysis galbana*. After a period of 5 months under this somewhat higher temperature regime at the Delaware Laboratory, the clams had attained lengths of approximately 20-25 mm (A. Ducharme, University of Delaware Marine Laboratory, Lewes, Delaware; pers. comm.). Final estimates of production as somatic growth were converted to dry tissue from measurements of the shell length and dry tissue weight of *M. lateralis* which yielded the equation:

$$DW_{mg} = 0.0025\, L_{mm}^{3.45} \qquad (r^2 = 0.771;\ n = 494) \qquad (2)$$

RESULTS AND DISCUSSION

Excretion

Protein catabolism leads to the formation of ammonia which comprises 60-90% of the total nitrogen excretion in a variety of bivalves (for review, see Bayne 1976). In the gastropod, *Thais lapillus*, a common exponent of 0.610 ± 0.05 was reported by Stickle & Bayne (1982) whilst exponents of between 0.711 and 0.872 have been reported for *Polinices alderi* by Mace & Ansell (1982). The relation between ammonia excretion rates and body size can, however, be variable in molluscs depending among other factors on the relative contribution of carbohydrate and protein catabolism at different seasons of the year and under differing nutritional conditions. Bayne & Scullard (1977a), for example, found the value of the weight exponent (b) to vary between 0.482 and 1.480 in *Mytilus edulis*, small individuals having an increased reliance on carbohydrates rather than protein for metabolism during the winter and spring compared with larger individuals. A seasonal variation in ammonia excretion has also been noted in *Mytilus edulis* by Hawkins (1983).

Values for the ammonia excretion rates ($\dot{V}NH_4N$; mg · day^{-1}) as a function of dry tissue weight (mg) in *Mulinia lateralis* are shown in Fig. 1. The equations for the regressions for starved and fed clams at 10, 20, and 30°C are summarized in Table 1. It is evident that ammonia excretion rates in *M. lateralis* are affected by an interaction between body size, temperature and nutritional conditions, much as has been described for several other molluscs (see Ansell & Sivadas 1973; Bayne & Scullard 1977a; Mace & Ansell 1982; Stickle & Bayne 1982). In *Mulinia lateralis*, the value for the weight exponent (t) in the allometric equation $\dot{V}NH_4N = pW^t$ ranged from 0.476-0.622 (mean = 0.535 ± 0.053) increasing somewhat with temperature from 10 to 30°C in fed clams.

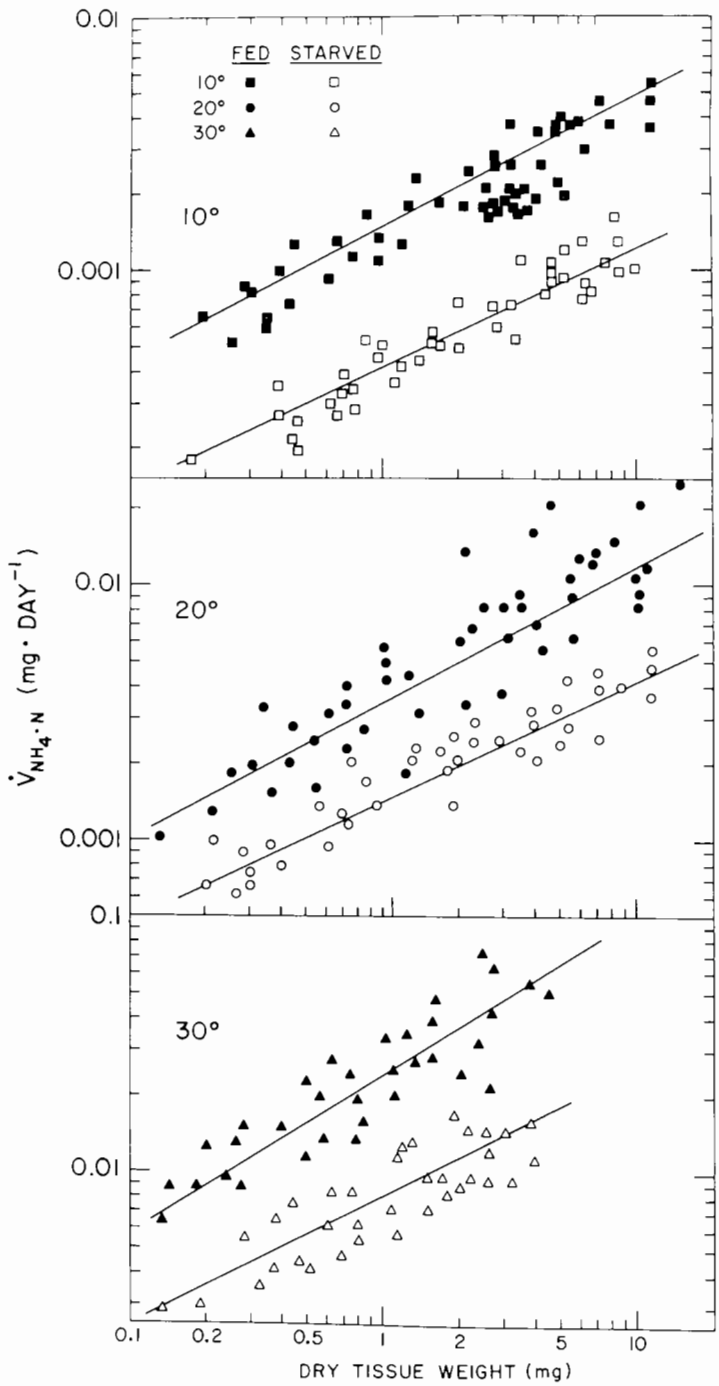

FIG. 1. Ammonia excretion rates ($\dot{V}NH_4N$; mg · day^{-1}) in relation to body size (W; mg dry tissue · wt) in *Mulinia lateralis* acclimated to 3 temperatures. Data for fed and starved individuals; regression data are given in Table 1.

TABLE 1. Regression data for ammonia excretion rate ($\dot{V}NH_4N$; $mg \cdot day^{-1}$) in relation to body size (W; mg dry tissue) in *Mulinia lateralis* acclimated to three temperatures. Data for fed and starved animals were fitted to the equation: $\dot{V}NH_4N = pW^t$ where p is the intercept ($mg \cdot day^{-1}$) and t is the weight exponent. n is the number of determinations; r is the correlation coefficient.

Acclimation conditions		p	t	n	r
10°C	Fed	0.0015	0.541	53	0.531
	Starved	0.0004	0.498	43	0.932
20°C	Fed	0.0038	0.564	49	0.810
	Starved	0.0014	0.476	41	0.810
30°C	Fed	0.0245	0.622	32	0.900
	Starved	0.0008	0.511	39	0.832

Clearly, the values for the weight exponent recorded here for ammonia excretion by *M. lateralis* fall within the range reported for other molluscs. The similarity of the slopes for starved and fed clams at each of the three acclimation temperatures suggests in addition that in this bivalve, there is little size-dependence in the relative significance of protein and carbohydrate as a metabolic substrate. Because the levels of the regression lines for starved clams are lower than those for fed clams, the results suggest that protein is not mobilized as a major metabolic substrate even after as much as 3 weeks of starvation. These results resemble those of Crisp *et al.* (1981) who observed a decline in the rate of ammonia excretion by *Nassarius* during starvation. A decrease in ammonia excretion following starvation during the summer has also been reported by Bayne & Scullard (1977a) for *Mytilus edulis*.

Oxygen : nitrogen ratio

The ratio of atomic equivalents of oxygen consumed to nitrogen excreted (O : N ratio) has been widely used to indicate the proportion of protein which is catabolized relative to carbohydrates and lipids in planktonic crustacea (Corner & Cowey 1968; Conover & Corner 1968), prawns (Snow & Williams 1971, Regnault 1981), isopods (Wieser 1972) and in molluscs (Bayne & Scullard 1977a; Mace & Ansell 1982; Stickle & Bayne 1982).

The relationship between the O : N ratio and dry tissue weight in *Mulinia lateralis* is shown in Fig. 2 and has been calculated from simultaneous measurements of $\dot{V}O_2$ ($\mu l \cdot h^{-1}$) reported by Shumway (1983) and the ammonia excretion rates $\dot{V}NH_4N$ ($\mu g \cdot day^{-1}$) reported here. Although, as has been shown above, the absolute values for ammonia excretion increase with temperature

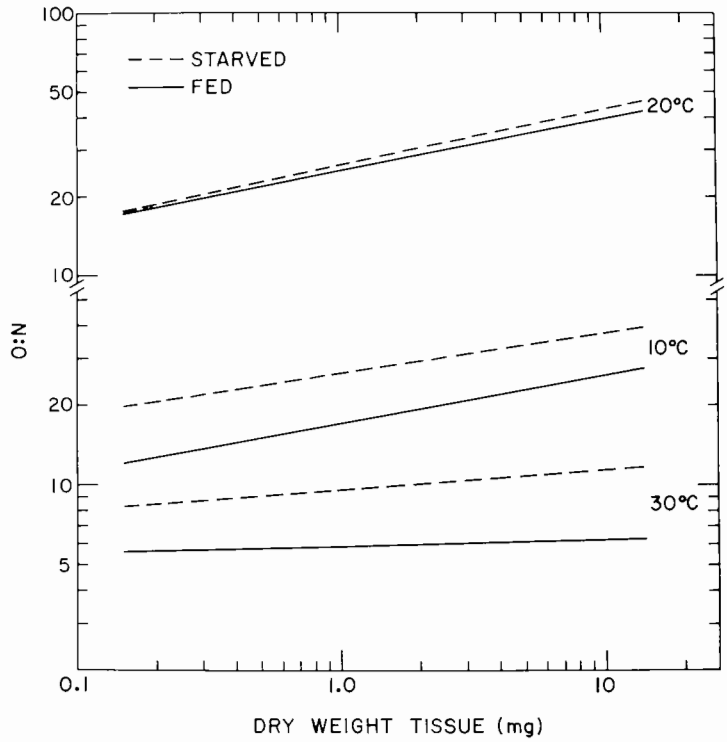

FIG. 2. The relationship between the atomic ratio of oxygen consumed to ammonia-nitrogen excreted and tissue dry weight in *Mulinia lateralis* acclimated to three temperatures. Data for fed and starved animals; regression data are given in Table 2.

from 10 to 30°C (see Fig. 1 and Table 1), it is evident from Fig. 2 that the proportion of oxygen consumed to nitrogen excreted falls steeply at 30°C. This reflects the decline in oxygen consumption which occurs under conditions of heat stress and implies an increased significance of proteins as a catabolic substrate during heat stress. It closely resembles the results for *Donax vittatus* in which Ansell & Sivadas (1973) recorded an increase in the O:N ratio from 26 to 36 between 10 and 15°C followed by a decline in the ratio to approximately 16 at 20°C.

It will also be noted that the O:N ratio for starved *Mulinia lateralis* is generally higher than that for fed clams. Thus, the absolute values of ammonia excretion are depressed following starvation (see Fig. 1 and Table 1) reflecting a decline in overall utilization of metabolic reserves during starvation and the O:N ratio suggests in addition that the relative significance of protein as a catabolic substrate remains small. These results differ from those for several other molluscs in which an increase in the relative significance of nitrogen excretion during starvation has been recorded as protein is catabolized to sup-

TABLE 2. Regression data for the O : N ratio and tissue dry weight in *Mulinia lateralis* acclimated to 3 temperatures. Data were fitted to the equation $O:N = kW^m$ (from data in Figs 1 & 2 for animals at 28‰ salinity).

Acclimation conditions		k	m
10 °C	Fed	17.11	0.189
	Starved	25.83	0.164
20 °C	Fed	25.32	0.165
	Starved	26.17	0.217
30 °C	Fed	5.941	0.011
	Starved	9.529	0.084

port maintenance metabolism (Stickle & Bayne 1982; for reviews see Bayne 1976; Bayne & Newell 1983) although they resemble those for the bivalve *Donax vittatus* (Ansell & Sivadas 1973).

The equations for the regressions relating the O : N ratio to dry tissue weight are summarized in Table 2. There is some evidence of a size-dependence in the O : N ratio, especially at 10 °C ($b = 0.189$ for fed and $b = 0.164$ for starved individuals) and 20 °C ($b = 0.165$ for fed and $b = 0.217$ for starved individuals) whereas under heat-stressed conditions at 30 °C the O : N ratio is almost independent of tissue weight. The mean value for starved and fed *Mulinia lateralis* at 10 and 20 °C is 0.184 ± 0.025 indicating a small size-dependence for the O : N ratio in the coot clam and a somewhat increased importance of protein as a catabolic substrate compared with carbohydrates and lipids in small individuals. In both *Polinices alderi* (Mace & Ansell 1982) and *Thais lapillus* (Stickle & Bayne 1982), the O : N ratio is independent of body size. That is, there is no change in the relative contribution of proteins and carbohydrates or lipids with size. In *Mytilus edulis*, however, the O : N ratio varies considerably with size, and, as in the results reported here for *Mulinia lateralis*, there is an interaction with both ration and temperature as well as season (Bayne & Scullard 1977a; see also Hawkins 1983).

Absorption efficiency (Ab)

The values for the absorption efficiency of bivalves feeding on natural foods have been reviewed by Bayne (1976), Winter (1978), Widdows *et al.* (1979a), Vahl (1980) and more recently for molluscs in general by Bayne & Newell (1983; see also Conover 1978). Although efficiencies may be as high as 80%

for suspension-feeders utilizing living algal cells (Bayne 1976; Winter 1978), values of 30-60% are more typical of natural seston, especially when this is diluted with inorganic materials (Widdows *et al.* 1979; Bayne *et al.* 1979; Vahl 1980). The absorption efficiency of suspension-feeding bivalves is also commonly reported to decline rapidly in high concentration of living algal cells (Thompson & Bayne 1974; Widdows 1978; Griffiths 1980a), but this decline is not shown in the presence of natural particulate material (Bayne & Widdows 1978; Stuart *et al.* 1982), the absorption efficiency then averaging approximately 40° at ration levels from 3-18 mg · l^{-1} in the mussel *Choromytilus meridionalis* (Griffiths 1980b). There also appears to be little effect of body size on absorption efficiency. Ansell (1981) estimated absorption efficiencies of 28-50% in the carnivorous gastropod *Polinices alderi* and reported no significant dependence on either body size or temperature.

Absorption efficiency was determined as a function of dry tissue weight in *Mulinia lateralis* held at 20°C in the presence of 10^4 cells · ml^{-1} *Thalassia maculata, Monochrysis lutheri* and *Isochrysis galbana*. The results are shown in Fig. 3 which indicates an absorption efficiency of 50-60% at that ration level

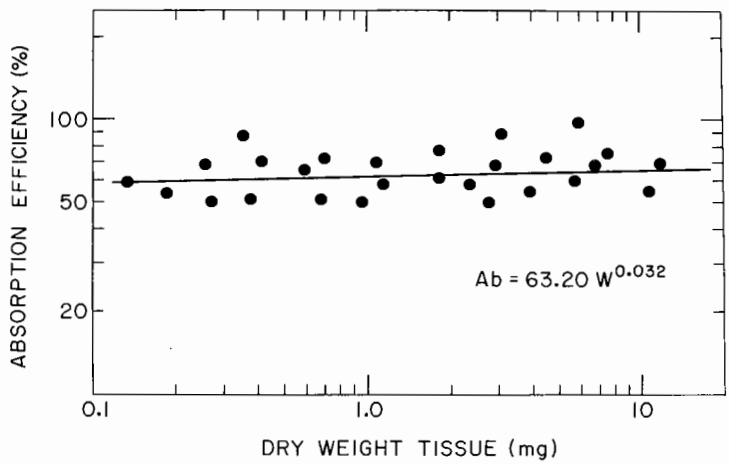

FIG. 3. Absorption efficiency (*Ab* %) by *Mulinia lateralis* in relation to body size (*W*; mg dry tissue).

with little dependence on body size. The absorption efficiency (Ab) is related to body size by the following equation:

$$Ab = 63.20\, W^{0.032} \qquad (3)$$

where Ab is the absorption efficiency (%) and *W* is the dry tissue weight in mg.

The absorption efficiency of *Mulinia lateralis* thus accords well with estimates for many other molluscs. There is little evidence that temperature affects absorption efficiency in *Mytilus* (Bayne 1976) or in *Polynices* (Ansell 1981). It

seems likely, therefore, that a value of approximately 63% is typical of the absorption efficiency of *Mulinia lateralis* both over a range of sizes and at different exposure temperatures.

Production (P)

Production (P) represents the sum of the energy equivalent of somatic growth (P_g), the energy investment in the organic content of shell and the energy equivalent of gamete production (P_r).

Because growth rate studies are difficult to carry out over the same time scale of hours, few investigators have incorporated the value (P) into an energy budget estimation. They have instead expressed the net energy gain as 'scope for growth' (see Bayne 1976) over the time span of the experiment. The values for both (P_g) and (P_r) in the balanced energy equation can, however, be estimated for the population on a daily basis and incorporated into the equation to arrive at a realistic estimate of energy requirements without the assumptions which are inherent in converting a 'scope for growth' value into real values for (P).

Somatic (tissue) growth (P_g). The growth rate of *Mulinia lateralis* was estimated from increases in shell length and converted to dry tissue weight from equation 2. An estimate of the growth rate of specimens in the breeding tanks at Lewes, Delaware, which were held at 20°C, suggests a growth rate of approximately 1.11 mg dry tissue · day^{-1} including all stages from juvenile to breeding adults. In other experiments on adults only and at lower temperatures, using the laser diffraction pattern technique (Strömgren 1975), rather lower growth rates were obtained. For the purposes of overall energy resource estimates including both juvenile and adult *Mulinia lateralis*, we have assumed that the growth in the breeding tanks at 20°C approaches that found under local conditions and have used a value of 1.11 mg · day^{-1} for estimates of P_g.

Organic content of the shell (P_{shell}). The organic content of the shell represents a component of energy resource allocation which requires to be added to somatic (tissue) growth to arrive at P_g. The amount of organic matter incorporated into shell growth can be estimated from the daily shell length increments and the following equations relating shell length to shell ash-free dry weight, (equation 4) and shell dry weight to ash-free dry weight (equation 5):

$$\text{ash}W_{shell} = 0.200\ (\text{length mm})^{2.5} \qquad (n = 189;\ r^2 = 0.839) \qquad (4)$$

$$DW_{shell} = 1.203\ (AFDW_{shell})^{0.970} \qquad (n = 45;\ r^2 = 0.999) \qquad (5)$$

Daily shell growth amounted to approximately 0.114 mm · day^{-1} in the breeding tables, which yields 1.812 mg ashW_{shell} · day^{-1} (equation 4). From equation (5) the daily increment corresponds to 3.930 mg DW_{shell} · day^{-1} so that the

daily organic production incorporated into the shell is 3.930-1.812 = 2.118 mg · day^{-1}. Hughes (1970) showed that the energy equivalent of organic matrix in the shell of *Scrobicularia plana* was 20.88 joules · mg^{-1} whilst that in *Crassostrea* is 21 joules · mg^{-1} (Dame 1972). This yields a calorific equivalent of approximately 5.0 cal · mg^{-1} (1 joule ~ 0.239 cals) for these bivalves. The energy equivalent of organic matter in the shell of *Mulinia lateralis* is thus 0.0004264 · 5 = 0.00213 cal · day^{-1}.

Gamete production (P_r). The relationship between dry weight of eggs (F, mg) and dry tissue weight (W, mg) in *Mulinia lateralis* is shown in Fig. 4. It will be noted that we were able to obtain accurate measurements on gonad weight on

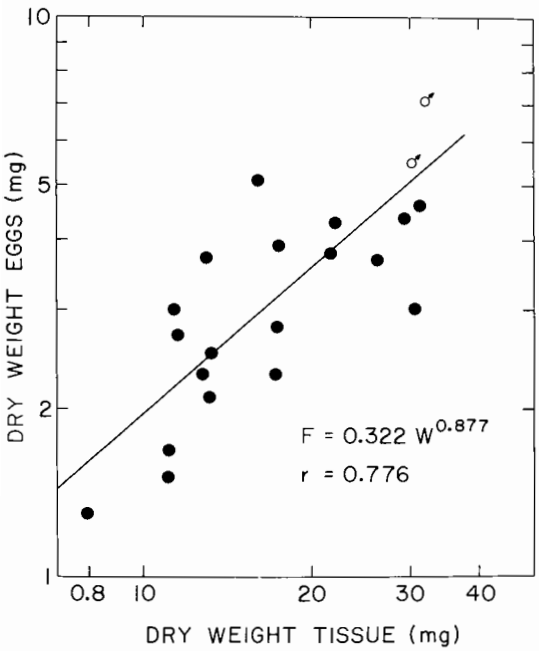

FIG. 4. The relationship between dry weight of eggs (F; mg) and tissue dry weight (W; mg) in *Mulinia lateralis*. Also shown is dry weight of sperm for two individuals (♂).

specimens which were of a rather larger size than those used for other components of the balanced energy equation. Nevertheless, the size range covers the 7-8 mg dry tissue weight used in other experiments and the regression suggests that the data can be validly applied to smaller individuals. The dry weight of eggs (F) is related to dry tissue weight (mg) by the expression:

$$\text{Dry weight of eggs} = 0.322\,W^{0.877} \qquad (n = 20;\ r^2 = 0.776) \qquad (6)$$

The number of eggs produced is related to dry tissue weight (mg) by the expression:

$$\text{Number of eggs} = 1.98 \cdot 10\,W^{0.878} \qquad (n = 20;\ r^2 = 0.682) \qquad (7)$$

It will be noted from Fig. 4 that the dry weight of sperm of two individuals conformed with the regression for eggs. We have no further data for males, but these data for two specimens suggest that (P_t) may be independent of sex in *Mulinia lateralis* (see also Vahl & Sundet 1984).

The effects of temperature

The effects of temperature, body size and nutrition on the major components of the balance energy equation for *Mulinia lateralis* are summarized in Table 3. Data for oxygen consumption and filtration rate are based on data in Shumway (1983). It can be seen that over the temperature interval 10-20°C, oxygen consumption increases steeply with temperature in both fed and starved *M. lateralis* whilst ammonia excretion increases at a similar rate, the Q_{10} for both processes ranging from 2.5-3.7. This applies over a broad range of sizes of clams since the values for the slopes all indicate little size-dependence in the Q_{10}

TABLE 3. Q_{10} values for oxygen consumption ($\dot{V}O_2$; from Shumway 1983), ammonia excretion ($\dot{V}NH_4N$), filtration rate (C_w; from Shumway 1983), and the O:N ratio plotted against body size (dry tissue; mg) in *Mulinia lateralis* which had been fed or starved for 3 weeks at 10, 20 and 30°C. Data fitted to the equation: $Q_{10} = aW^b$; pW^t; cW^d or kW^m for $\dot{V}O_2$, $\dot{V}NH_4N$, C_w and O:N respectively.

Temp. range, °C		$\dot{V}O_2$		$\dot{V}NH_4N$		C_w		O:N	
		a	b	p	t	c	d	k	m
10-20	Fed	3.798	−0.001	2.533	0.023	2.163	0.013	1.480	−0.024
	Starved	3.543	0.258	3.450	−0.022	–	–	1.013	0.053
20-30	Fed	1.513	−0.097	6.447	0.058	1.446	0.200	0.235	−0.154
	Starved	2.064	−0.096	0.571	0.035	–	–	0.364	−0.133
10-30	Fed	5.748	−0.049	16.544	0.0405	1.768	0.107	0.347	−0.089
	Starved	7.313	−0.035	1.970	0.0065	–	–	0.369	−0.040

values. The O:N ratio consequently shows relatively little effect of temperature (Q_{10} = 1.0-1.5) over the interval 10-20°C. In contrast, the rate of increase of filtration increases more slowly (Q_{10} = 2.16) than either oxygen consumption or ammonia excretion and has a value similar to that recorded for many other molluscs (for reviews, see Bayne 1976; Newell 1979; Bayne & Newell 1983). It seems likely, therefore, that as temperatures increase during the spring months, metabolic and dissolved losses increase rather more rapidly than filtration and that increasing availability of food is necessary for a positive 'scope for growth' (see Bayne 1976; Bayne & newell 1983) to be sustained.

Over the interval 20-30°C, marked differences in the effects of temperature on oxygen consumption and ammonia excretion occur. From Table 3, it is clear that the Q_{10} for oxygen consumption by starved *Mulinia lateralis* is higher than

that of fed ones. Ammonia excretion, on the other hand, increases dramatically with a Q_{10} of as much as 6.4 in fed clams but declines (indicated by a $Q_{10}<1.0$) in individuals which had been starved for 3 weeks. Values of only 0.235-0.364 for the Q_{10} of the O:N ratio show that the O:N ratio also decreases with temperature in both fed and starved *Mulinia*, indicating that protein catabolism plays an increasing role in supporting metabolism at high temperatures.

The values for the Q_{10} suggest, therefore, that over the temperature range 10-20°C, oxygen consumption, nitrogen excretion and filtration rate remain approximately coupled with a Q_{10} of 2-3 and with little temperature dependence of the O:N ratio in all size classes. At higher temperatures of 20-30°C, however, there is evidence of increasing nitrogen mobilization under conditions of heat stress, although in *Mulinia lateralis*, starvation for as much as 3 weeks at 30°C appears to result in little increase in protein catabolism compared with well-fed clams.

CONCLUSIONS

The results which have been summarized above allow some estimates to be made of the allocation of energy resources in *Mulinia lateralis*, and of the environmental food availability which would be required to support the energy demands of the individual.

From p. 111, we have estimated somatic (tissue) production (P_g) at 20°C of 1.11 mg · day^{-1}. This yields a calorific equivalent of 5.82 cal · day^{-1} at a mean value of 5.24 cal · mg^{-1} (Thayer *et al.*1973). The equivalent organic content of the shell (P_{shell}) is 2.118 mg · day^{-1} which yields 0.0106 cal · day^{-1} using a calorific equivalent of 5.0 cal · g^{-1} organic matrix. A median sized *Mulinia lateralis* of 7 mg dry tissue weight corresponds with an age of 7/1.11 = 6.306 days at a growth rate of 1.11 mg · day^{-1}. Egg production by a 7 mg dry tissue coot clam is 1.81 mg (equation 6) which corresponds with a daily rate of 1.81/6.306 = 0.287 mg · day^{-1}. This is equivalent to 1.72 cal · day^{-1} at a calorific equivalent of 6 cal · mg^{-1} (Crisp 1971; Rodhouse 1978; Perron 1981; Vahl 1981). Total production (P) thus equals (P_g and P_{shell}) + P_r = (5.82 + 0.0106) + 1.72 = 7.55 cal · day^{-1} (31.6 joules · day^{-1}).

From the data of Shumway (1983), respiratory losses (R) (VO_2; $\mu l \cdot h^{-1}$) for a 7 mg dry tissue *Mulinia lateralis* at 20°C are 26.47 μl · h^{-1} or 3.048 cal · day^{-1} (12.8 joules · day^{-1}) at an oxycalorific equivalent of 4.8 cal · ml^{-1} (Crisp 1971). Similarly, from the data cited on p. 105, ammonia losses (U) amount to 11 μg NH_4N · day^{-1} for a 7 mg dry tissue individual. This is equivalent to 0.065 cal · day^{-1} (0.27 joules · day^{-1}) at a calorific equivalent of 5.94×10^{-3} cal · g^{-1} (Elliot & Davison 1975).

The estimated energy demands by a 7 mg dry tissue *Mulinia lateralis* is thus $(P = 5.82 + 0.0106 + 1.72) + (R = 3.05) + (U = 0.065) = 10.66$ cal · day^{-1}

TABLE 4. The major components of the balanced energy equation $A = P + R + U$ (where A = consumption − faeces) for the coot clam, *Mulinia lateralis*. All values expressed for an individual of 7 mg dry tissue weight at 20°C. Data for respiration (R) taken from Shumway (1983).

	Raw value	Energy equivalent		% of absorption requirements
		Cal · day^{-1}	J · day^{-1}	
Production as somatic growth (P_g)	1.11 mg · day^{-1}	5.82	24.39	54.61
Production as shell organic matter (P_{shell})	2.118 mg · day^{-1}	0.0106	0.044	1.00
Production as gametes (P_r)	0.29 mg · day^{-1}	1.72	7.21	16.14
Total production (P)	1.400 mg · day^{-1}	7.54	31.60	70.76
Respiration (R)	0.635 ml · day^{-1}	3.05	12.78	28.62
Ammonia (U)	11 μg NH_4N · day^{-1}	0.065	0.27	0.60
Absorption requirements (A)	–	10.66	44.66	100.00
Consumption requirements (C) at absorption efficiency of 63.2%	–	16.87	70.67	–

(= 44.66 joules · day^{-1}; Table 4). The filtration rate of a 7 mg dry tissue coot clam is 23.83 ml · h^{-1} or 572 ml · day^{-1} at 20°C (Shumway 1983) and the absorption efficiency is 63.2%. Each 572 ml water filtered by the coot clam must therefore contain at least 10.66/0.632 = 16.87 cal (~70.67 joules) to meet the estimated consumption requirements at 20°C. This corresponds with rather high cell densities, such as are likely to occur under bloom conditions in shallow coastal waters, or where the phytoplankton is supplemented by a detrital supply. Since 10×10^6 cells is equivalent to approximately 1 cal (Malouf 1977), the consumption requirement of 16.87 cal · day^{-1} is equivalent to 168.7×10^6 cells. At a filtration rate of 572 ml · day^{-1} at 20°C this daily requirement could be met by a cell concentration of $168.7/572 \times 10^6 = 2.95 \times 10^5$ cells · ml^{-1}.

The relative allocation of energy in *Mulinia lateralis* is also shown in Table 4. This shows some interesting features in relation to the high growth rates which have commonly been recorded for the coot clam. It will be noticed that the net growth efficiency (P_g/A) is approximately 54.6% with a rather small component of 1% becoming incorporated into shell matrix (P_{shell}), and with 16.1% of the absorbed ration being channelled into gamete production (P_r). Total production (P) thus amounts to 70.8% of the absorbed ration, with approximately 28.6% losses through respiration (R) and only 0.6% through ammonia excretion (U). These values are quite similar to those recorded for many other bivalves in which respiratory losses commonly approach 33%, whilst urinary losses amount to 3-7% of the absorbed ration (A) (Bayne & Newell 1983).

The relative allocation of resources in the coot clam, therefore, do not differ sharply from other molluscs despite the opportunistic nature of this bivalve. Instead, *Mulinia lateralis* appears to be primarily adapted to exploit the high

concentrations of phytoplankton and natural seston which is available at the sediment-water interface in caostal environments, and is likely to achieve high growth and reproductive rates provided that the ration available in the water is at a relatively high value of 17 cal · day^{-1}. Although we have no data on seasonal variations in available food which occur under natural conditions, it is likely that the combined phytoplankton and detrital supply may seasonally fall below this value. The apparent inability of *Mulinia lateralis* to catabolize protein during prolonged periods of starvation may then account for the episodic mass mortalities which are characteristic of this species.

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