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ABSORBED RATION, RESPIRATORY COSTS AND RESULTANT SCOPE FOR GROWTH IN THE MUSSEL *AULACOMYA ATER* (MOLINA) FED ON A DIET OF KELP DETRITUS OF DIFFERENT AGES

V. STUART

Department of Zoology, University of Cape Town, Rondebosch, Republic of South Africa

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SUMMARY

Analysis of sea-water samples from the vicinity of a mussel bed of *Aulacomya ater* (Molina) revealed that approximately 85% of the particulate matter consisted of detritus particles and only 15% of phytoplankton cells, with an annual mean dry mass of particulate matter of 3.28 mg $\cdot l^{-1}$ being recorded. An energy budget was calculated for *A. ater* fed on a diet of kelp debris derived from the macrophyte *Laminaria pallida* (Grev.). The scope for growth for all size classes were found to increase with ration level, yielding maximum values at the highest concentrations. This was compared with the scope for growth of mussels fed on a diet of algal cells, and the significance of the observed discrepencies discussed. Age of detritus was also found to affect the scope for growth, the optimum age being 2.8 days, which can be related to the probable age of detritus in the natural environment.

Key words: *Aulacomya ater*, scope for growth, kelp detritus, age of detritus.

INTRODUCTION

In studies on the growth and energetics of bivalve molluscs the difference between net energy gain from the environment and energy losses through excretion and metabolism has often been expressed as the 'scope for growth' (see Warren and Davis, 1967; Thompson and Bayne, 1974; Griffiths and King, 1979a; Buxton et al., 1981). Laboratory experiments using suspensions of cultured algal cells to calculate filtration rates and absorption efficiencies have lead to a greater understanding of how the overall growth rate of an organism is affected by factors such as food ration level, body size and temperature (Foster-Smith, 1975a, b; Bayne et al., 1976; Widdows, 1978).

However, recent investigations into the natural food available for mussels have revealed that high concentrations of pure algal cells are seldom experienced in the field, and the major component of the diet of filter feeding bivalves consists of particulate organic matter (Widdows et al., 1979; Griffiths, 1980) or mixtures of

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algal cells with varying ammounts of resuspended bottom material (Kiørboe et al., 1980). Growth rates and absorption efficiencies using this type of food have been found to be much higher than those obtained with pure algal cultures, especially at increased ration levels (Widdows et al., 1979; Kiørboe et al., 1980, 1981). Thus extrapolation of data from laboratory experiments using algal monocultures to field conditions should be performed with caution, and laboratory experiments should be made to simulate natural food conditions as closely as possible.

In a previous study (Stuart et al., in press) it was observed that particulate debris derived from the kelp plant *Laminaria pallida* was absorbed by *Aulacomya ater* with an efficiency of approximately 50%, and this was not significantly affected by increasing ration level. In the present study the relationship between food ration level, body size, age of detritus and overall scope for growth of *A. ater* has been examined simultaneously using a multivariate approach (see Alderdice, 1972; Widdows, 1978). This approach has the advantage that it is possible to obtain a broader understanding of the effects of each factor, and it provides information on interaction between variables.

MATERIALS AND METHODS

Field sampling

An estimate of the levels of food naturally available to filter feeding organisms in the kelp bed at Oudekraal on the west coast of the Cape Peninsula, South Africa (34°S:18°E) was obtained by sampling the water column at intervals throughout the year. On each occasion 20–40 l of water were collected in large plastic bags by SCUBA divers from a depth of 20 m directly above a mussel bed. Two 500 ml aliquots were filtered through pre-ashed, weighed 25 mm glass fiber filters (Whatman GF/C) and rinsed with an isotonic ammonium formate solution. Dry mass of particulate material was estimated after oven drying at 70°C for 2 days, while the organic content was obtained by difference after ashing at 480°C for 3 h. Particulate material was collected by filtering up to 40 l of water onto a 0.45 μm Millipore filter (142 mm diameter). After rinsing with distilled water to remove all salts, the residue was scraped from the paper and washed into a crucible. A small amount of this material was filtered onto a 1 μm Nucleopore filter and the mean number of detrital particles and phytoplankton cells were estimated from 20 random microscope fields. The amount of detrital material in each sample was then expressed as a percentage of the total number of particles. The remaining residue in the crucible was dried in an oven at 70°C for 3–4 days, pulverized in a 'Wig-1-bug' (Crescent Dental Instruments) and the energy values of 3 replicate samples measured with a Phillipson microbomb calorimeter. Carbon and nitrogen content of the dried particulate materials was measured by combustion in a Heraeus CHN analyser (Model EA415-50) fitted with an integrator to give peak area.

Experimental procedure

A. ater were collected at weekly intervals by SCUBA divers from a depth of 10–20 m at Oudekraal. Encrusting organisms were scraped off the shells, care being taken to retain the byssus attachements of the mussels to a neighbouring shell. Kelp fragments from the macrophyte *L. pallida* were used as a food source to simulate the detrital particles which characterize the water column near to mussel beds. These were prepared by freeze-drying the aging tips of *L. pallida* fronds, which were then ground and sieved to obtain particles with a diameter of <37 μm. A microbial community was allowed to colonize these particles by incubating the kelp debris in fresh sea water for periods of up to 18 days (see Linley and Newell, 1981; Linley et al., 1981; Lucas et al., 1981; Stuart et al., 1981, 1982). Experiments were carried out at 12.5°C on both freshly powdered kelp debris and on material which had been colonized by a microbial community.

Filtration rate

The shell substratum to which the mussels were attached, was fastened to a mesh covered grid suspended in a beaker containing 1.5 l to 0.45 μm filtered sea water circulated with a magnetic stirrer. After an equilibration period of 2 h, detrital material was added to give the desired concentration, and the decline in particle numbers was measured at 15 min intervals using a model TA II Coulter Counter and 280 μm aperture. Further detrital material was added at intervals to maintain the concentration to within 20% of the desired concentration. Experiments were conducted at ration levels from 0.5 to 6.0 $mg \cdot l^{-1}$ (dry mass) because preliminary experiments showed that no pseudofaeces were produced over this range, although the dry mass of particulate matter in the natural environment may reach higher values. A control vessel was set up with each run to monitor the rate of settlement of particles in suspension, which was obtained from the following equation:

$$a = \frac{\log_e \mathrm{conc}_0 - \log_e \mathrm{conc}_t}{t},$$

where a = rate of settlement of particles; conc_0 = initial concentration at time 0; conc_t = concentration after time t in hours. Filtration rates were calculated for each 15 min period according to the standard formula:

$$\text{filtration rate } (l \cdot h^{-1}) = \left(\frac{\log_e N_1 - \log_e N_2}{t} - a\right) \times V,$$

where N_1 = cell concentration at time t_1; N_2 = cell concentration at time t_2; t = elapsed time in hours, V = volume of vessel in liters; a = rate of settlement of particles. Three to six readings were used to obtain a mean filtration rate for each individual or group.

Absorption efficiency

The relationship between age, concentration of kelp particles and absorption efficiency was investigated using a ^{14}C: ^{51}Cr twin tracer method, which is described in a previous paper (Stuart et al., in press), the results of which have been used in the present study.

Oxygen consumption

Respiration rates of mussels feeding at different concentrations of detrital material were measured using sealed vessels fitted with YSI P_{O_2} probes connected with a switch–gear mechanism to a Beckman multi-channel chart recorder. The volume of the vessels ranged from 180 ml to 1 l according to the size of experimental animals, and more than one animal per chamber was used in the case of the very small mussels. The water in each container was maintained in rapid circulation by means of a magnetic stirrer. After 1 h equilibration time concentrated food material was injected directly into the chambers, and the decline in oxygen tension was recorded for the next 10 min. The oxygen probes were calibrated at the start of each experiment using Winkler titrations (Strickland and Parsons, 1968), and the dry flesh mass of each experimental animal was obtained after oven drying at 70°C for 3–4 days.

Filtration activity and oxygen consumption was tested mainly in 3 size classes of *A. ater* (shell lengths 15, 50 and 75 mm, each ± 2 mm) but several experiments on animals of an intermediate size were performed to obtain the mass exponents for filtration and respiration. The standard dry flesh mass of the 3 size classes was taken to be 0.022, 0.54 and 1.91 g, respectively (after Griffiths and King, 1979a), and filtration and oxygen consumption rates were corrected to a standard mussel mass for each size class using the equation:

$$V_s = \frac{(W_s)^b}{W_e} \cdot V_e,$$

where V_s = standard mussel filtration or O_2 consumption rate; W_s = standard dry flesh mass of each size class of mussel; b = mass exponent of filtration or respiration; W_e = dry flesh mass of experimental animal; and V_e = experimental filtration of respiration rate.

Modelling methods

The response surface technique (Box and Wilson, 1951) was used to analyse the interrelationships between absorbed ration (RA), ration level (RL), oxygen consumption (OC), body size (DW) and age of food (FA). The absorbed ration is a product of filtration rate, food concentration and adsorption efficiency and the

scope for growth can be calculated by subtracting energy lost through respiration from the energy value of the absorbed ration. Multiple regression equations were obtained by stepwise multiple linear regression analysis (Allen, 1973) using the computer program 'STEPREG 1' (STATJOB, Madison Academic Computing Center, U.S.A.). Energy values for adsorbed ration and oxygen consumption were entered as dependent variables while body size (animals over the entire size range), food concentration (6 food levels) and age of kelp debris (5 different ages) acted as independant variables. Second to fourth degree terms as well as interaction terms between the independent variables up to the 4th power (i.e. 16 terms) were used to describe the curvilinear relationship.

All 16 terms were included in a stepwise fashion at the 95% confidence level, to give an equation combining the fewest terms with the best overall coefficient of determination (r^2). These multiple regression equations were then entered into a computer program called 'GRAPHUNCTION' which was written for the purpose of generating a three dimensional plot of two independant variables versus a response (i.e. dependent variable). This program also allowed two surfaces to be substracted from one another, the resulting surface being plotted as a new response. This function was used to generate a response surface for the 'scope for growth', which was obtained from the difference between the energy gained from the absorbed ration and that lost through metabolic energy expenditure. This type of analysis had also been used by Buxton et al. (1981) for examining the combined effects of exposure and acclimation temperatures on the scope for growth of the oyster *Ostrea edulis* (L.).

RESULTS

Sea-water analysis

Analysis of sea-water samples revealed that only 15% of the particulate matter in water samples above a mussel bed consisted of phytoplankton cells (Table I), which are therefore not the principal food resource available under natural conditions, while the remaining 85% was comprised of detrital material derived largely by

TABLE I

Mean annual total dry mass, energy values, organic content, percent detrital material and C:N ratios of particulate matter in the water column above a mussel bed at Oudekraal.

	Total dry mass ($mg \cdot l^{-1}$)	$kJ \cdot g^{-1}$ dry	Percent organic material	Percent detritus	C:N ratio
$\bar{X}$	3.28	6.04	48.57	85	7.1:1
SD	2.40	2.50	9.90	14	0.98
n	22	20	21	22	11

TABLE II

Data used for the calculation of scope for growth at 12.5°C of 3 size classes of *Aulacomya ater* fed on kelp particles aged for 6 days at 12.5°C. Filtration and respiration rates for each size class were corrected to the corresponding standard dry flesh mass of mussel, and the following conversion factors were used to calculate energy equivalent: 1 ml O_2 = 19.85 J (Griffiths and King, 1979a); kelp particles (aged 6 days) = 9.7 J · mg^{-1} dry.

Size class (mm)	Ration (mg · l^{-1} dry)	Filtration rate (l · h^{-1})		Absorbed ration (J · h^{-1})	Respiration (μlO$_2$ · h^{-1})			(J · h^{-1})	Scope for growth (J · h^{-1})	Growth efficiency	
		$\bar{x}$ (± SD)	n		$\bar{x}$ (± SD)		n			K_1	K_2
15	0	–		–	19.03	(5.99)	7	0.38	– 0.38	–	–
(= 0.022 g)	0.5	0.10(0.06)	4	0.27	19.38	(4.18)	3	0.38	– 0.11	−0.23	−0.41
	1.0	0.08(0.02)	4	0.50	24.62	(10.12)	3	0.49	– 0.01	−0.01	−0.02
	1.5	0.08(0.02)	4	0.66	31.39	(16.53)	5	0.62	+ 0.04	+0.03	+0.06
	3.0	0.17(0.02)	7	2.54	28.45	(13.83)	4	0.56	+ 1.98	+0.40	+0.78
	4.5	0.16(0.05)	5	3.01	31.83	(13.05)	4	0.63	+ 2.38	+0.34	+0.79
	6.0	0.14(0.06)	4	3.35	21.20	(5.42)	3	0.42	+ 2.93	+0.36	+0.87
50	0	–			104.31	(18.69)	6	2.07	– 2.07	–	–
(= 0.54 g)	0.5	0.92(0.31)	8	2.56	216.95	(72.25)	3	4.31	– 1.75	−0.39	−0.68
	1.0	0.71(0.19)	7	4.44	231.27	(22.50)	5	4.59	– 0.15	−0.02	−0.03
	1.5	1.01(0.15)	3	8.39	210.95	(26.52)	4	4.19	+ 4.20	−0.29	+0.50
	3.0	1.01(0.22)	8	15.08	234.97	(68.25)	3	4.66	+10.42	+0.35	+0.69
	4.5	1.25(0.39)	9	23.53	206.14	(64.48)	3	4.09	+19.44	+0.36	+0.83
	6.0	1.16(0.10)	7	27.75	224.87	(66.08)	5	4.46	+23.29	+0.35	+0.84
75	0	–		–	281.14	(28.44)	6	5.58	– 5.58	–	–
(= 1.91 g)	0.5	2.03(0.66)	4	5.62	463.93	(57.38)	5	9.21	– 3.59	−0.37	−0.64
	1.0	1.93(0.45)	6	12.08	448.73	(25.12)	3	8.91	+ 3.17	+0.17	+0.26
	1.5	1.80(0.39)	3	15.00	434.12	(60.15)	5	8.62	+ 6.38	+0.24	+0.42
	3.0	2.29(0.76)	6	34.19	538.79	(71.35)	3	10.69	+23.50	+0.35	+0.69
	4.5	2.31(0.57)	4	43.51	387.71	(91.55)	5	7.70	+35.81	+0.36	+0.82
	6.0	2.96(0.35)	4	70.82	491.22	(38.54)	4	9.75	+61.07	+0.35	+0.86

erosion of kelp fronds (Field et al., 1977, 1980). However, it must be noted that these estimates may be biased as it was not possible to collect samples during extremely rough conditions such as experienced during the winter months (June and July). The mean dry mass of particulate material was 3.28 $mg \cdot l^{-1}$ of which approximately 48% was organic (Table I). It is also of interest to note that the mean C:N ratio of the particulate material is similar to that of decomposing kelp debris (Stuart et al., 1982), confirming that the experimental material closely resembles the particulate matter found in the field.

Effect of body size and ration on scope for growth

Data for the calculation of scope for growth for three size classes of *A. ater* corrected to a standard mass of mussel is shown in Table II. Absorbed ration is a product of absorption efficiency, filtration rate and food concentration while the scope for growth is calculated by subtraction of energy lost through respiration from energy gained through the absorbed ration. It is noticeable that at low ration levels the scope for growth has a negative index, indicating that respiratory costs exceed the energy value of the food absorbed. Scope for growth first becomes positive at 1.5 $mg \cdot l^{-1}$ dry mass of food for 15 and 50 mm animals and 1.0 $mg \cdot l^{-1}$ for the large size class of mussels, with progressively greater values being obtained with increasing ration levels.

It is also of interst to obtain a measure of the efficiency with which the food is converted into animal body tissue in order to compare data from different size classes of mussels fed a range of ration levels. This can be done by calculating the gross growth efficiency (K_1) which is the efficiency with which an animal utilizes the ingested ration (= filtration rate × food concentration), or the net growth efficiency (K_2) which gives an estimate of how the absorbed ration is utilized (Thompson and Bayne, 1974; Bayne, 1976). These efficiencies are also presented in Table II. It is apparent from these data that the maximum gross growth efficiency (K_1) in the smallest size class of mussels is achieved at 3.0 $mg \cdot l^{-1}$ while in the larger animals this only occurs at 4.5 $mg \cdot l^{-1}$. In other words the optimum ration at which growth is most efficient is an increasng function of body mass, and at low ration levels small animals are most efficient in converting food into body tissue. These optimum rations compare favourably with the mean annual dry mass of particulate matter found in the natural environment (see Table I), indicating that the mussel population is well adapted to gain maximum benefit from available resources. It is also noteworthy that the maximum overall growth efficiency is dependent on body size, with the greatest values being obtained by smaller mussels.

On examination of the various factors contributing to the scope for growth of a 50 mm *A. ater* fed on kelp debris, it is evident that the absorbed ration increases asymptotically with increase in the ration level (Fig. 1a). However, similar sized animals fed on a diet of *Dunaliella primolecta* (Butch) cells (data from Griffiths and

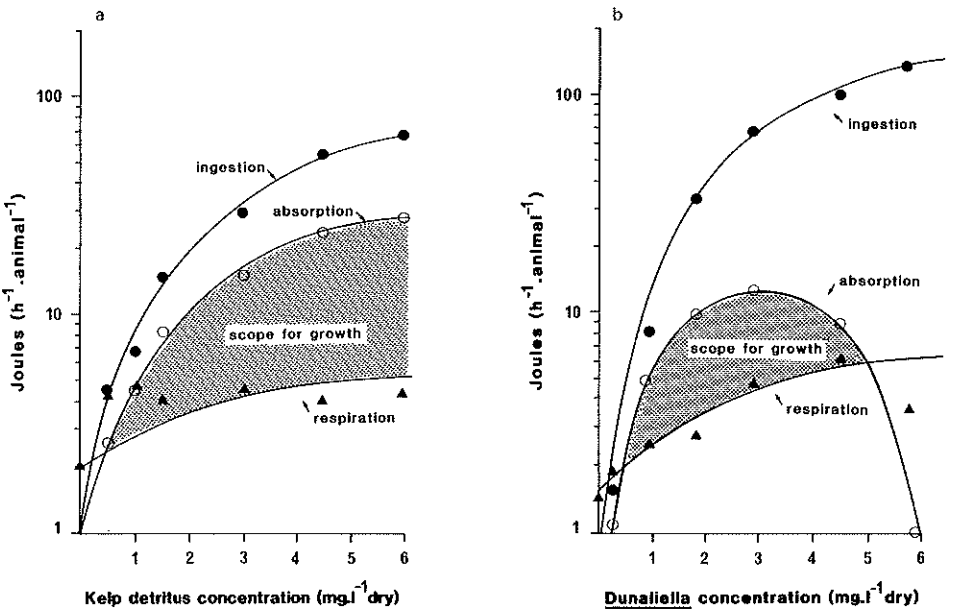

Fig. 1. Ingested ration, absorbed ration, respiration and scope for growth in 50 mm *Aulacomya ater*, as a function of increasing rations of (a) kelp material (data derived from Table I) and (b) *Dunaliella primolecta* cells. (Data derived from Griffiths and King, 1979a.)

King, 1979a) showed a steep decline in the absorbed ration beyond a cell concentration equivalent to approximately 2 mg · l^{-1} dry mass (Fig. 1b), resulting in a negative scope for growth at concentrations above 4.5 mg · l^{-1}. This trend can clearly be seen in all size classes of *A. ater* fed on *D. primolecta* cells compared to the same size classes of mussels fed on kelp debris (Fig. 2).

The maintenance of a positive scope for growth at high ration levels is also evident in the growth efficiencies plotted against increasing dry mass of particulate material (Fig. 3). The growth efficiencies increase with food concentration, attaining maximum values of 0.3 to 0.4 for gross growth efficiency (K_1) and 0.8 to 0.9 for net growth efficiency (K_2). These figures compare closely with those of *Mytilus edulis* (L.) fed on natural detritus where growth efficiencies were found to increase towards asymptotic values of 0.4 (K_1) and 0.8 (K_2) (Bayne and Widdows, 1978; Bayne and Newell, in press), unlike results obtained using pure algal cultures in which growth efficiencies decline at high ration levels (Thompson and Bayne, 1974). However, recent investigations have shown that the net growth efficiencies of mussels fed algal diets mixed with suspended silt, increased with increasing algal concentration, approaching a maximum level of about 0.7 (Kiøboe et al., 1981), which is also comparable to the present study.

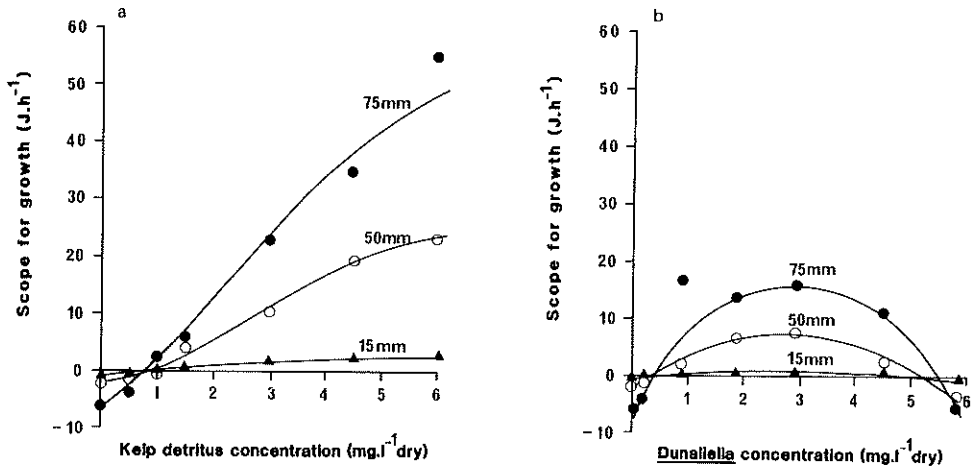

Fig. 2. Scope for growth (J · animal^{-1} · h^{-1}) as a function of ration level of (a) kelp material and (b) *Dunaliella* cells (after Griffiths and King, 1979a) for mussels of 3 different shell lengths.

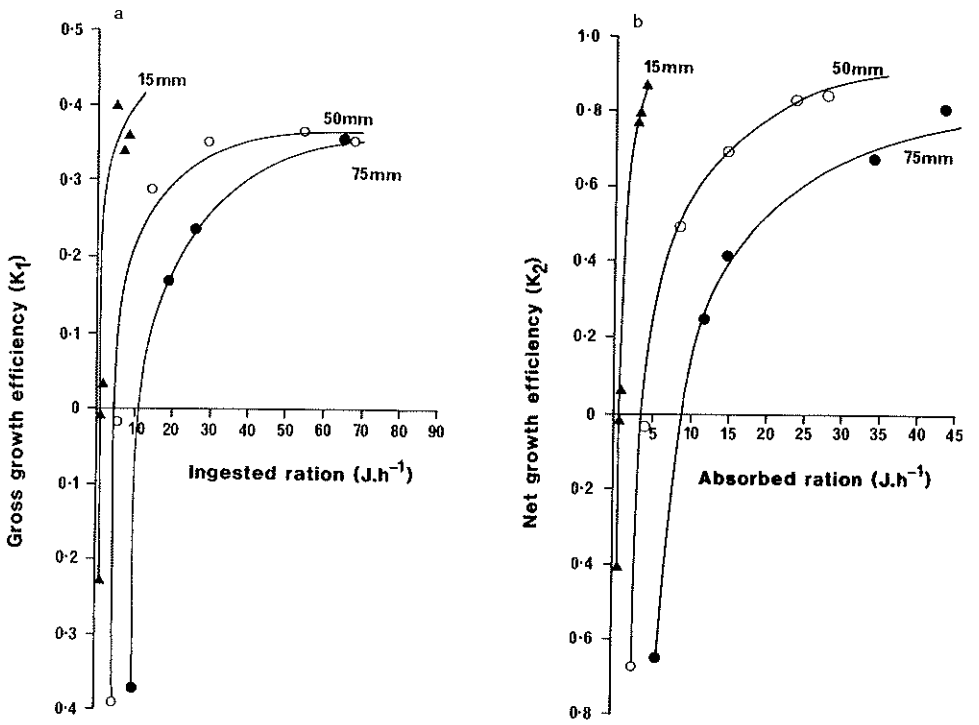

Fig. 3. (a) Gross growth efficiency (K_1) of *Aulacomya ater* in relation to ingested ration of kelp material and (b) net growth efficiency (K_2) in relation to absorbed ration of kelp material for mussels of three different size classes.

TABLE III

Multiple regression equations relating absorbed ration and respiratory costs of *Aulacomya ater* (0.005–2.1 g dry flesh mass) at 12.5°C fed different ration levels of kelp particles (0.5–6.0 mg·l^{-1} dry mass) aged for 6 days. All terms in the equations are ranked according to their partial correlation coefficients and expressed as J·h^{-1}.

$$RA = 1.89 + 8.66\,DW \cdot RL^2 - 2.37\,DW \cdot RL^3 - 5.10\,DW^3 \cdot RL + 1.94\,DW^4 \cdot RL + 0.20\,DW \cdot RL^4 + 1.61\,DW^2 \quad (n = 119;\ r^2 = 0.88) \quad (1)$$

$$OC = 0.35 + 5.81\,DW + 1.71\,DW \cdot RL - 0.18\,DW \cdot RL^3 + 0.024\,DW \cdot RL^4 - 1.67\,DW^2 \quad (n = 91;\ r^2 = 0.88) \quad (2)$$

RA = absorbed ration, OC = oxygen consumption, DW = dry flesh mass, and RL = ration level.

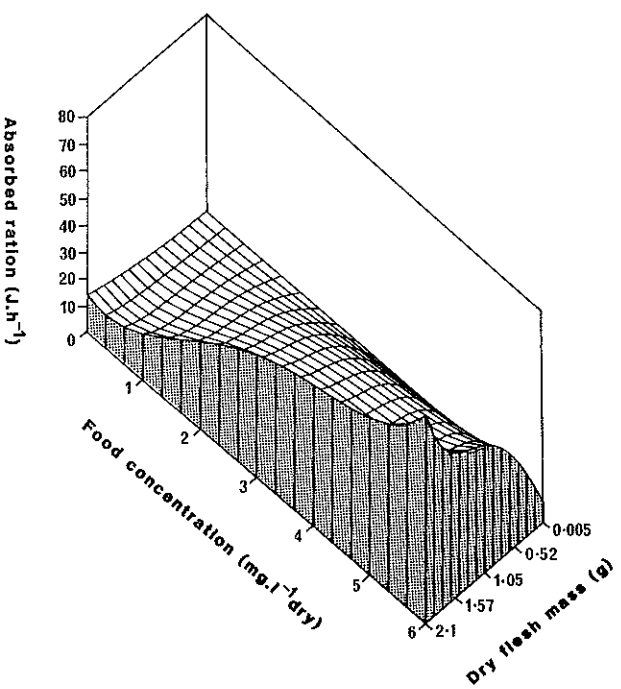

Fig. 4. Response surface relating absorbed ration of *Aulacomya ater* fed on kelp particles aged for 6 days to ration level and dry flesh mass (generated from Eqn. 1).

Multiple regression equations relating absorbed ration and oxygen consumption to body size and ration level for animals over the entire size range are presented in Table III. In both cases these equations explain 88% of the total variation in

experimental data. Individual factors are ranked according to their partial correlation coefficients and it is evident that interaction terms between dry flesh mass and food ration level are important in controlling the absorbed ration, whereas dry flesh mass alone appears to be the most important factor affecting oxygen consumption. The response surface generated from Eq. (1) relating absorbed ration to dry flesh mass and food concentration is shown in Fig. 4. It is apparent that the maximum absorbed ration is achieved with the largest mussels (2.1 g dry flesh mass) at the highest food ration level (6.0 $mg \cdot l^{-1}$ dry mass). The corresponding response surface for respiratory costs derived from Eq. (2) is shown in Fig. 5, where maximum metabolic rates were recorded for the largest experimental animals at a food ration level of 2.21 $mg \cdot l^{-1}$ dry mass. Respiratory costs of smaller experimental animals were not affected by changes in ration level to the same extent. Resultant scope for growth derived from the difference between the absorbed ration and respiratory costs has been expressed in the form of a response surface (Fig. 6a) and a contour diagram (Fig. 6b). Maximum scope for growth ($J \cdot animal^{-1} \cdot h^{-1}$) is again achieved at the highest ration level for all size classes of mussels, with a region of negative scope for growth being obtained at food concentration below 1 $mg \cdot l^{-1}$, where respiratory costs exceed the amount of energy gained from the food. It is evident that in contrast to the results obtained with pure algal cultures, the scope for

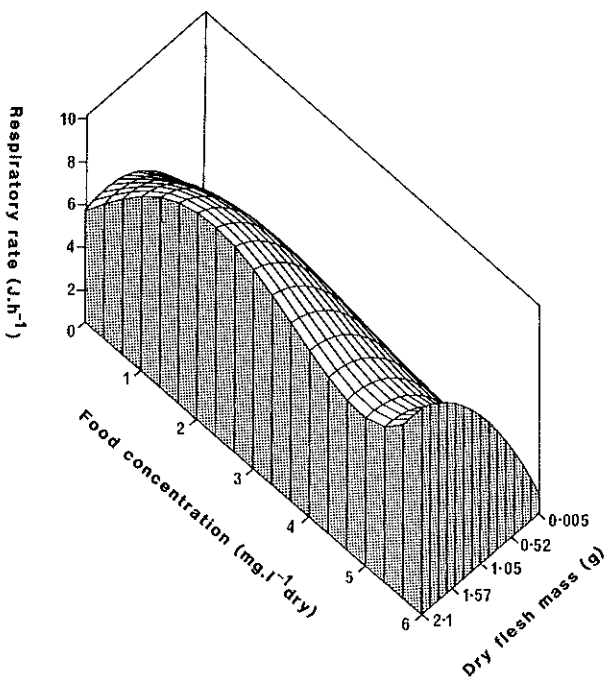

Fig. 5. Response surface relating oxygen consumption of *Aulacomya ater* fed on kelp particles aged for 6 days, to ration level and dry flesh mass (generated for Eqn. 2).

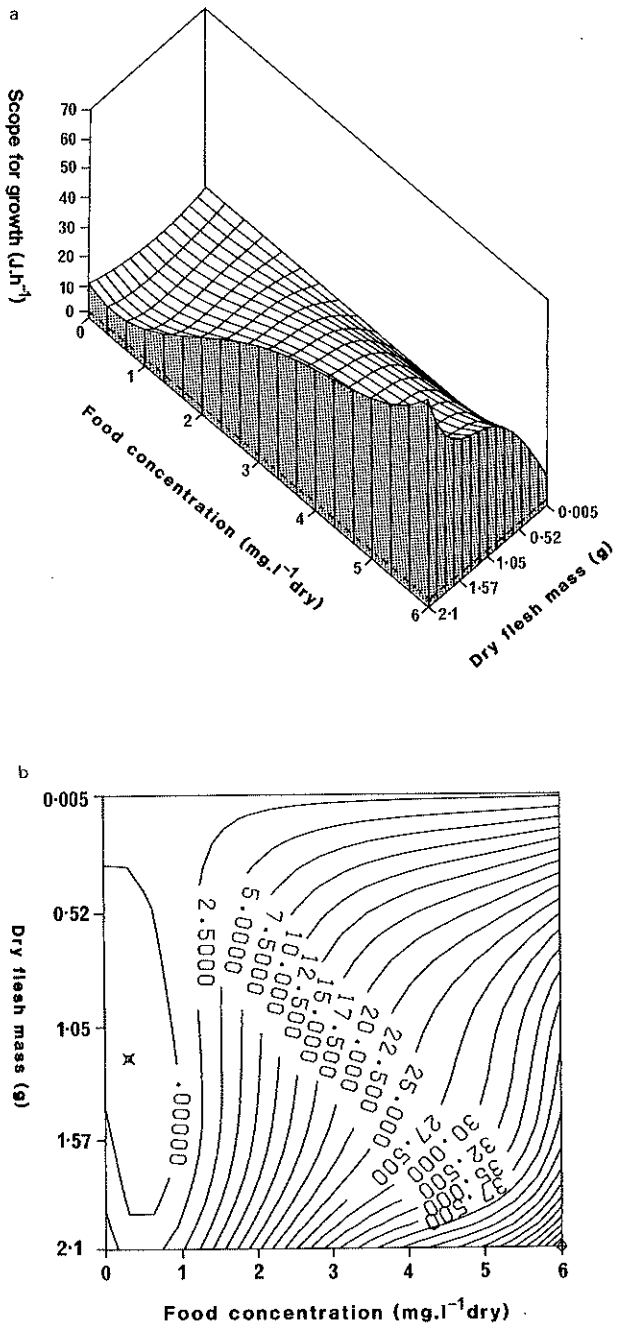

Fig. 6. (a) Response surface and (b) contour diagram relating scope for growth of *Aulacomya ater* fed on kelp material aged for 6 days to ration level and dry flesh mass (generated from Eqns. 1 and 2).

growth of mussels fed on a natural detrital diet increases with ration level in all size classes with maximum values being obtained at the highest ration levels.

Effect of age of detritus on scope for growth

Kelp debris aged for up to 18 days was fed to an entire size range of mussels at a concentration of 3 $mg \cdot l^{-1}$ dry mass. Equations relating filtration and respiration rates to dry flesh mass are summarized in Table IV. It is evident that the filtration rate is somewhat depressed by increasing age of detrital material (decreasing *a*-values) although the respiratory activity is held at a relatively constant level. The absorbed ration for each animal was calculated using the following energy equivalents of aged kelp material (±SD): 0 day = 8.93 $J \cdot mg^{-1}$ (±0.25); 3 days = 10.02 $J \cdot mg^{-1}$ (±0.06); 6 days = 9.70 $J \cdot mg^{-1}$ (±0.07); 12 days = 9.42 $J \cdot mg^{-1}$ (±0.25); 18 days = 8.55 $J \cdot mg^{-1}$ (±0.23); and these data were used to generate multiple regression equations relating metabolic respiratory costs and absorbed ration to dry flesh mass and age of kelp particles (Table V). As to be

TABLE IV

Regression equations relating filtration (F) and respiration (OC) rates to dry flesh mass (DW) of mussels fed 3 $mg \cdot l^{-1}$ dry mass of kelp debris aged for up to 18 days.

Age of food (days)	Filtration rate ($l \cdot h^{-1}$)			Oxygen consumption ($ml \cdot h^{-1}$)		
	Equation	*n*	r^2	Equation	*n*	r^2
0	$F = 1.50\ DW^{0.54}$	18	0.89	$OC = 0.28\ DW^{0.69}$	14	0.94
3	$F = 1.82\ DW^{0.56}$	12	0.94	$OC = 0.30\ DW^{0.60}$	16	0.91
6	$F = 1.59\ DW^{0.59}$	32	0.94	$OC = 0.31\ DW^{0.62}$	12	0.92
12	$F = 1.20\ DW^{0.62}$	11	0.85	$OC = 0.28\ DW^{0.65}$	10	0.90
18	$F = 1.29\ DW^{0.64}$	13	0.90	$OC = 0.24\ DW^{0.70}$	15	0.87

TABLE V

Multiple regression equations relating oxygen consumption, absorbed ration and dry flesh mass of *Aulacomya ater* (0.005 to 2.1 g) fed on 3 $mg \cdot l^{-1}$ dry mass of kelp material aged for up to 18 days. All terms are ranked according to their partial correlation coefficients and expressed in $J \cdot h^{-1}$.

$$RA = -0.4108 + 62.3625\ DW^2 - 53.8016\ DW^3 + 13.2174\ DW^4 + 49.8924\ FA - 86.0779\ FA^2 + 47.7177\ FA^3 - 8.4125\ FA^4 - 0.7964\ DW \cdot FA^2 \quad (3)$$

$$(n = 86;\ r^2 = 0.89)$$

$$OC = 0.4630 + 6.1105\ DW - 0.4811\ DW^3 + 1.2066\ DW \cdot FA^4 - 4.8407\ DW \cdot FA^3 + 4.3055\ DW \cdot FA^2 \quad (4)$$

$$(n = 67,\ r^2 = 0.90)$$

RA = absorbed ration, OC = oxygen consumption, DW = dry flesh mass and FA = age of food.

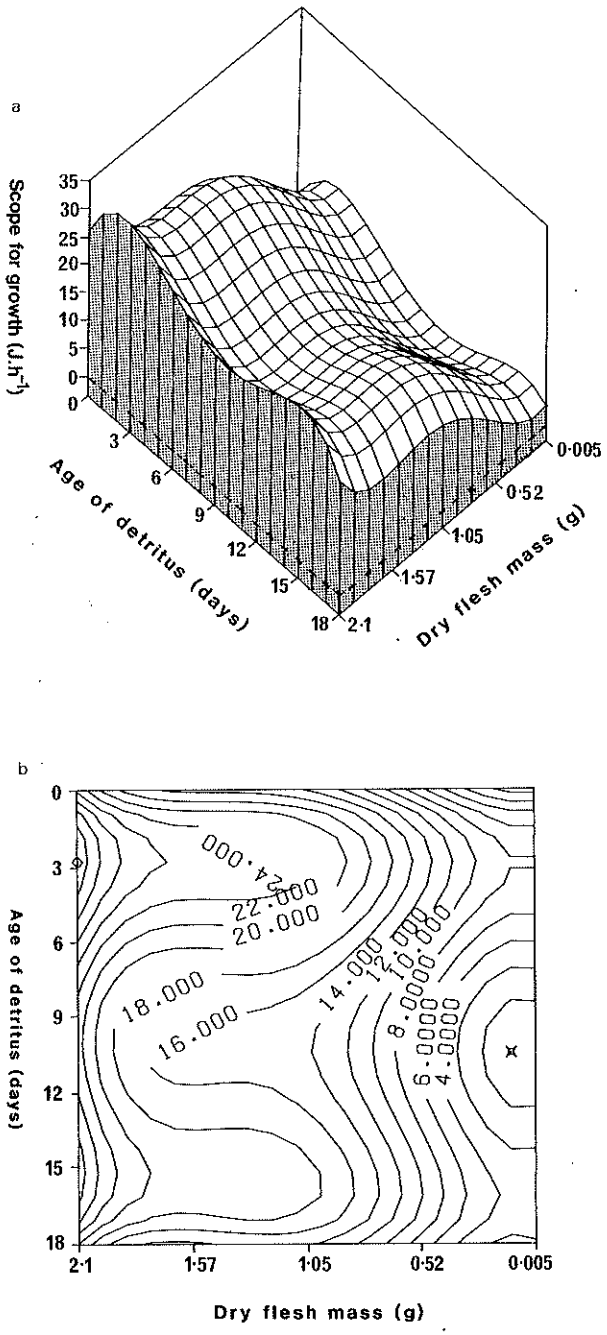

Fig. 7. (a) Response surface and (b) contour diagram relating scope for growth of *Aulacomya ater* fed on 3 mg·l^{-1} dry mass of kelp material, to age of kelp particles and dry flesh (generated from Eqns. 3 and 4).

expected, both the dependent variables (i.e. oxygen consumption and adsorbed ration) are influenced primarily by dry body mass, although age of kelp material nevertheless has some influence on these factors. The resultant scope for growth is shown in Fig. 7a, while a contour diagram of the relationship is presented in Fig. 7b.

DISCUSSION

It is evident that the overall scope for growth of *A. ater* increases with body size and ration level with maximum values being attained by the largest animals at the highest ration level (see Fig. 6). However, the maximum gross growth efficiency is attained by the smallest mussels (see Fig. 3), suggesting that they are more efficient in converting food into body tissue. Similarly, Thompson and Bayne (1974) found that the relationship between growth efficiency and ration in *M. edulis* was partly determined by the weight of the mussel. In large mussels up to 80% of the total production (or scope for growth, Bayne and Worral, 1980) may be spent on gonad production (Griffiths and King, 1979b) whereas in smaller animals gonad output is very low, so all the energy may be channelled into somatic growth.

In contrast to the extremely low or even negative scope for growth attained by mussels fed high ration levels of pure algal cultures (see Thompson and Bayne, 1974; Griffiths and King 1979a).

A. ater was able to maintain a large positive scope for growth at all concentrations of particulate kelp material (see Fig. 6a). This suggests that *A. ater* is able to digest kelp material more readily than *D. primolecta* cells, which appear to be more resistant to digestion, live cells being observed often in the faeces of mussels fed high ration levels (C.L. Griffiths, pers. comm.). Clearly, the quality of the food as well as its quantity influences the overall scope for growth of filter feeding organisms. Numerous laboratory experiments on bivalves presented with a variety of phytoplankton diets have failed to obtain the maximum growth rates observed in the field (Tenore et al., 1973; Winter and Langton, 1976). However, Kiørboe et al. (1981) have recently demonstrated that the presence of resuspended bottom material in the food allows the mussel to fully exploit its clearance potential and reach the maximum growth rates observed in nature. Similarly, *A. ater* may depend upon the presence of particulate material derived from macrophytes to increase its growth potential and to maintain a positive scope for growth at high ration levels.

It is evident from Fig. 7 that maximum scope for growth was attained by the largest mussels with food aged for 2.8 days while the smallest mussels (0.005–0.25 g) achieved a negative scope for growth with 10-day-old food. General trends suggest a decrease in scope for growth with age of food after approximatly 3 days, which is a function of the declining energy content of the food with age, as well as filtration rates being depressed by aged food cultures (see Table IV). In other words, filter feeders in the natural environment obtain maximum benefit from fragments eroded off kelp fronds in the earlier stages of decomposition, before most of the energy rich

compounds such as mannitol, sugars and alginates are utilised by micro-heterotrophic metabolism (see Lucas et al., 1981). Independent calculations based on the filtration rate of *A. ater* have revealed that the entire water column near a mussel bed is filtered approximately once every 3–4 days (C.L. Griffiths, pers. comm.), which coincides well with the age of detritus from which the consumer organisms are able to gain maximum benefit.

It is interesting to note that detritus derived from the vascular salt marsh plants *Spartina foliosa* and *Salicornia virginica* provides little nourishment for immature *M. edulis*, which lost soft tissue weight in laboratory experiments when supplied with this food source (Williams, 1981). However, Tenore (1981) has suggested that because vasculr plants contain a high percentage of unavailable energy, this can only be utilised after microbial decomposition and energy enrichment, whereas detritus from seaweed is already high in nitrogen so the available energy may be utilised directly. Decomposing kelp detritus used in the present experiments was found to have C:N ratios ranging from 5.8: 1 to 8.6:1 depending on the age of the detrital material (Stuart et al., 1982) which covers the same range as natural detritus (see Table I), whereas salt marsh plants have a much lower nitrogen content with C:N ratios ranging from 24:1 to 73:1 (see Haines and Hanson, 1979). Material derived from the erosion of macrophytes thus appears to be of major importance in the kelp bed system, where it may be directly absorbed by the filter feeding organism, meeting a substantial fraction of their carbon energy requirements.

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