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Filtration, Respiration and Assimilation in the Black Mussel *Choromytilus meridionalis*

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Abstract: Filtration rates, respiration rates and assimilation efficiences of *Choromytilus meridionalis* (Kr.) fed on *Dunaliella primolecta* were examined. No seasonal or tidal changes in filtration rate were recorded. Filtration rates were variable within and between individuals but were independent of algal concentration over the range 0.4 – 50 x 10^6 cells l^{-1}. Below 0.4 x 10^6 cells l^{-1} the filtration rate increased with declining ration. Respiration rate was not affected by ration level but increased with rising temperature. Assimilation efficiencies were high, averaging 80 % between 0.5 and 8 x 10^6 cells l^{-1}, but declined to zero at 30 x 10^6 cells l^{-1}. The effects of starvation on the filtration rate, respiration rate and assimilation efficiency were also studied. Following starvation, filtration rates increased at all cell concentrations while the curve for assimilation efficiency showed translation to the left so that efficiency declined to zero at 20 x 10^6 cells l^{-1} instead of 30 x 10^6 cells l^{-1}. The net result was a shift of the zone of positive scope for growth into a region of lower cell concentrations. *C. meridionalis* may co-exist with the bivalve *Aulacomya ater* in the field. Assimilation efficiency and scope for growth were compared in the two species. The greater scope for growth in *C. meridionalis* may be related to its higher filtration rate; it was more than twice that of *A. ater*. However, *A. ater* obtained a positive scope for growth over a wider range of algal ration levels.

INTRODUCTION

The use of cultured algal species as a food source has proved valuable in obtaining data on the filtration rates, respiration rates and assimilation efficiencies of filter feeders. The use of monocultures has the further advantage of facilitating comparison between data from different species fed on the same or similar diets. This technique has been applied to the study of bivalves in particular, and a considerable body of information is presently available. Much of this has been summarised by Bayne et al. (1976) with special reference to the European mussel *Mytilus edulis*.

Griffiths and King (1979a) have obtained data on the filtration and respiration rates of the South African bivalve *Aulacomya ater* when fed on *Dunaliella primolecta*. However, due to a paucity of information on local or southern hemisphere species, their data could only be compared with that of northern hemisphere bivalves. In order to obtain further data on local species and permit future comparison of the eco-physiology of the different bivalve species, the filtration rates, respiration rates and assimilation efficiency of *Choromytilus meridionalis* are investigated. *D. primolecta* monoculture was used as a food source to obtain data comparable with that on *A. ater*.

Of the three common rocky littoral and sublittoral mytilid bivalves found on the coast of South Africa, *Aulacomya ater* and *Choromytilus meridionalis* have similar distributions around the southwestern Cape Province, while *Perna perna* is dominant in the warmer waters of the east coast. Comparative data on the reproductive cycles, growth and population dynamics of *C. meridionalis* (Griffiths, 1977; Griffiths, in press) and *P. perna* (Berry, 1978) show that these species have considerably faster maturation times and growth rates than *A. ater* (Griffiths and King, 1979b) and hence would be more suitable to commercial cultivation. However, little is known of the metabolic requirements for maintenance of a positve energy balance in the laboratory or field.

MATERIALS AND METHODS

Mussels were collected at low water spring tide (L.W.S.) level from the shore at Bailey's Cottage, False Bay, South Africa (34°06'S 18°28'E). They were housed in a recirculating aquarium (3500 l capacity) at ambient sea temperature (12 °C in winter, 18° in summer). Except for experiments on the effect of laboratory storage, when mussels were maintained for 3 weeks,

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all individuals were used within 3 d of collection, usually on the same day. Mussels were cleaned of epibiotic growth and the byssus threads remained intact unless discarded by the animal.

Filtration Rate

Filtration rates were determined by measuring the rate of decline of a suspension of *Dunaliella primolecta* employing a Model TA II Coulter Counter with a 70 μm aperture. Each mussel was attached to a fine mesh-covered grid with a rubber band so that it was maintained in a natural upright position. The grid was suspended in a glass beaker containing a magnetic stirrer bar and 2 l of 0.45 μm filtered seawater. Faecal strands eliminated during the experiment became trapped on the mesh and were removed immediately with a pipette. Algal concentrate was added to give the desired concentration and the decline in algal numbers measured at 10 or 15 min intervals. Further algal concentrate was added at intervals to maintain the concentration. Unavoidable fluctuation in cell concentration occurred in this system but efforts were made to contain this within 20 % of the desired concentration by frequent addition of culture.

Filtration rate was calculated according to the standard formula:

$$\text{Filtration rate (l h}^{-1}) = \left(\frac{\log_e N_1 - \log_e N_2}{T}\right) \times V$$

where N_1 = cell concentration at time t_1; N_2 = cell concentration at time t_2; T = time elapsed between readings in h; V = volume of solution in litres. Six readings were obtained from each individual tested.

Winter (1969) and Bayne et al. (1976) have reviewed the numerous methods employed by authors to measure the filtration rates of bivalves. The disadvantage of the above method is the constant fluctuation in cell count experienced by the animal and the short duration of the experiments. This may obscure changes in filtration rate with cell concentration and give a slight overestimate of filtration rate until the animal has adjusted to the experimental conditions. However comparison of this method with results obtained from a recirculating constant flow apparatus using 20 l of water containing algal cells, showed that reliable results may be obtained with *Choromytilus meridionalis*.

Respiration

The respiration rate of mussels feeding at different concentrations of algal culture was measured using a Gilson Differential respirometer and constant pressure respirometers (Davies, 1966). Mussels were placed in 0.45 μm filtered seawater and respiration measured at 10 min intervals for 1 h. The oxygen consumption was then measured for a further 10 min interval following injection of known concentrations of algal culture into the water.The flasks were subsequently opened and a suitable time interval allowed for utilisation of the remaining algae, before more concentrate was injected and another reading taken. In this manner 6 continuous readings of respiration rate before feeding, and 6 intermittent readings during feeding, were obtained.

Table 1 *Choromytilus meridionalis*. Effect of tide on filtration rate of 40 mm mussels collected from sublittoral and 0.85 m above L.W.S. (high-shore)

Zone	Mean filtration rate and standard error			
	Low tide	n	High tide	n
Sublittoral	0.94 ± 0.05	22	0.87 ± 0.06	24
High-shore	1.16 ± 0.06	22	1.10 ± 0.11	10

Respiration rates at different temperatures were measured using the Gilson respirometer for mussels of 10-44 mm shell length. For mussels 30-110 mm, 6 YSI pO_2 probes connected via a switch gear mechanism to a multichannel chart recorder were used. The switch-gear maintained constant potential across all electrodes while monitoring each probe for 5 s every 1.25 min. Mussels were attached to perspex grids with the aid of rubber bands and inserted into 500 ml perspex containers which were sealed with oxygen probes placed centrally in the lids. Water was maintained in rapid circulation with a magnetic stirrer. Each chamber lid contained inlet and outlet pipes (clamped shut when not in use) enabling replenishment of the water at intervals. The volume of oxygen in the water at the start of each experiment was determined by replicate Winkler analysis (Strickland and Parsons, 1968).

Assimilation Efficiency

Assimilation efficiency was determined according to the method of Conover (1966). Assimilation of *Dunaliella primolecta* cells was measured simultaneously with filtration studies. Mussels were maintained in the laboratory for 24 h prior to use, allowing evacuation of sand from the gut. Preliminary studies showed that approximately 1 h elapsed between onset of feeding and the appearance of algal cells in the faeces. Faeces produced within the first 1.5 h were thus discarded and all subsequent faeces over a 4-5 h period collected for analysis. Faecal strands and replicate 10 ml volumes of algal concentration of known cell concentration, were filtered onto pre-ashed, weighed 25 mm diameter GFC

filters. Each sample on the filter was flushed with ammonium formate isotonic with seawater. Filters were dried, weighed and ashed at 450 °C for 3 h, and weighed again. The ratios of the ashfree dry weight of food and faeces were used in the Conover ratio. An electronic microbalance was used for weighing filters (readability 1 µg).

Length-Weight Relationships

Data on length-weight relationships of different body components and their calorific values are taken from Griffiths (in press).

RESULTS AND DISCUSSION

Filtration Rates

Preliminary experiments showed no difference in filtration rates in mussels whose byssal threads were attached to the substrate, detached or absent, although such differences have been noted in *Mytilus edulis* (Theede, 1963 quoted by Winter, 1969). In *Choromytilus meridionalis* byssal production appears to occur regularly throughout life, particularly in areas where continuous deposition and erosion of sand occurs. Individuals in the laboratory show considerable mobility and facility of byssal production.

Age of *Dunaliella primolecta* culture was found to affect filtration and assimilation. Filtration rates were higher and assimilation efficiency lower on young culture in the exponential growth phase than on culture which had passed the peak growth phase by several days. Consequently only cultures in the latter stage of the exponential growth phase and immediately about the peak were used in experiments.

No pseudofaeces were produced in the experiments. A minimum concentration of 50 to 60 x 10^6 cells l^{-1} being required before this occurred. Once pseudofaeces production is initiated the filtration rate no longer equals ingestion rate. Foster-Smith (1975) quantified pseudofaeces production in *Mytilus edulis*. The amount of food rejected rose rapidly with increasing concentration from 50-100 x 10^6 cells l^{-1}. An interesting and inexplicable feature in *Choromytilus meridionalis* was that pseudofaeces production was initiated at a concentration well above that at which the assimilation efficiency on algal cells fell to zero (see below).

Variability in filtration rate is a common feature in bivalves (Winter, 1969; Schulte, 1975). *Choromytilus meridionalis* was no exception and Figure 1 demonstrates the fluctuation in high and low filtration rates which may occur with some regularity. This may reflect digestive gland activity, e.g. saturation and reduction of the filtration rate until this has cleared. However, digestive gland phasic activity has hitherto been reported over a longer time cycle, usually associated with tidal exposure (Owen, 1974; Morton, 1977).

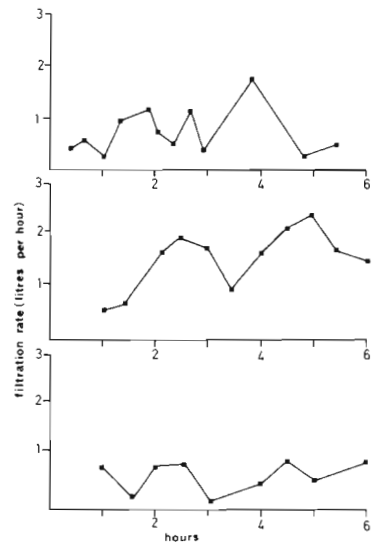

Fig. 1. *Choromytilus meridionalis*. Changes in filtration rate over time in three 40 mm individuals fed 10 x 10^6 cells *Dunaliella primolecta* l^{-1} 12 °C. (Filtration rates slightly depressed due to use of aged algal culture)

The controversy of tide-induced rhythms in filtration rate has been reviewed by Winter (1969) who found existing data inconclusive. There was no evidence of tidal rhythmicity in *Mytilus edulis*. The filtration rates of *Choromytilus meridionalis* (40 mm, ambient sea temperature 12 °C) was measured during 2 h periods corresponding to high and low water spring tide in the field. Mussels were collected at the appropriate state of tide from the sublittoral and 0.85 m above L.W.S. (highshore) immediately prior to measurement in the laboratory. Figure 2 and Table 1 show that there was no significant difference in filtration rate at times corresponding with high or low tide. However, the rate of filtration was slightly higher in highshore mussels compared with sublittoral individuals. This may be a consequence of aerial exposure.

Figure 3 shows the filtration rates of 20-100 mm long mussels at 10 x 10^6 cells l^{-1} during summer (ambient sea temperature 18 °C) at 18° and 12 °C, and during winter at ambient sea temperature of 12 °C. The regression equations for these data and the pooled data (no significant difference between slopes and intercepts) are given in Table 2. There was no change in filtration rate with ambient temperature change. Schulte (1975) and Widdows (1978) have shown that acclimation of the filtration rate to temperature change

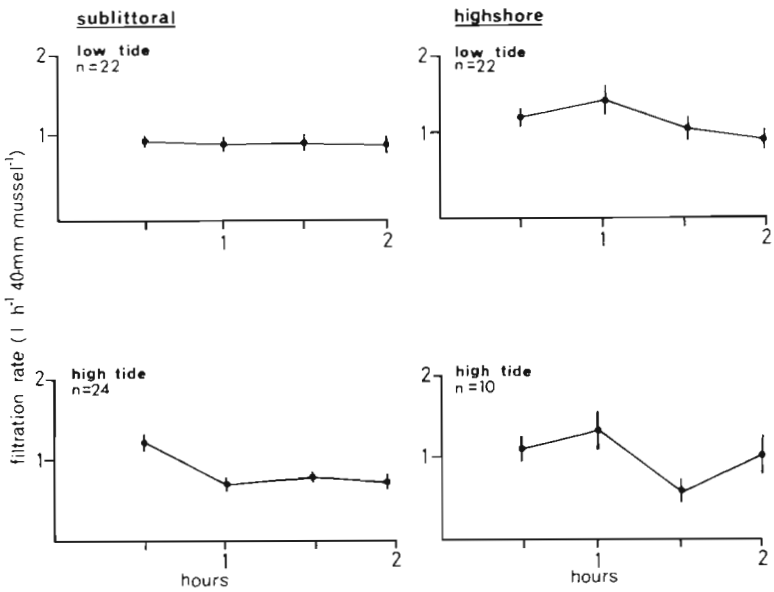

Fig. 2. *Choromytilus meridionalis*. Mean filtration rate and one standard error of 40 mm mussels over 2 h period during low and high tide at L.W.S. Mussels collected from sublittoral and 0.85 m above L.W.S.; fed 10 x 10^6 algal cells l^{-1} 12 °C. (Filtration rate slightly depressed due to use of aged algal culture)

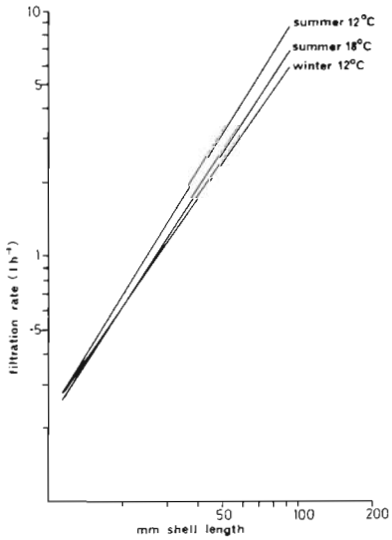

Fig. 3. *Choromytilos meridionalis*. Filtration rate of different sized mussels fed 10 x 10^6 algal cells l^{-1}; in summer at 18 °C (ambient sea temperature) and 12 °C, in winter 12 °C (ambient sea temperature). Regression equations given in Table 2

Table 2. *Choromytilus meridionalis*. Filtration and respiration rates at different seasonal sea temperatures and respiration rate at different algal concentrations. Equations in the form $y = ax^b$, where y = filtration rate in l h^{-1}, or respiration rate in $\mu l\ h^{-1}$, or dry flesh weight in g; x = mm shell length

	a	b	r^2	n
Filtration rate				
Summer 12 °C	0.00478	1.66	.89	27
Summer 18 °C	0.00565	1.57	.86	18
Winter 12 °C	0.00755	1.47	.76	19
Pooled data	0.00644	1.58	.85	64
Respiration rate				
Summer 18 °C	0.2900	1.78	.89	69
Summer 25 °C	0.6516	1.74	.86	22
Winter 12 °C	0.1751	1.83	.91	12
18 °C : no food	0.2900	1.78	.89	69
250 cells ml^{-1}	0.6138	1.60	.74	35
1000 " "	0.1778	1.94	.76	44
10000 " "	0.1306	2.03	.71	33
20000 " "	0.2742	1.81	.88	28
40000 " "	0.2483	1.81	.89	21
Dry flesh wt	1.251×10^{-5}	2.65	.98	116

may be expected within the normal environmental range.

Bayne et al. (1976) have summarised the weight exponents found in relating filtration rate to size in different bivalve species. These vary from negative values to 0.76. The significance of this is difficult to interpret, particularly where filtration rate may vary with experimental technique and ration level. Comparison between published data is further complicated because the weight exponent has been found to vary with the size of individuals sampled. It is generally higher in experiments including small individuals and low (e. g. 0.38 in Widdows, 1978) when mostly large individuals are used. The equation for *Choromytilus meridionalis* was:

$$l\ h^{-1} = 5.3676 \times [\text{g dry flesh weight}]^{0.5959}$$

and included a large size range of 15-110 mm (0.02 – 3.2 g dry flesh wt).

Measurements from *Choromytilus meridionalis* and *Aulacomya ater* (Griffiths and King, 1979a, b) were obtained under similar experimental conditions and the filtration rate of 50 mm individuals at 10 x 10^6 cell l^{-1} at 12 °C may be compared. Measurement of the gill area of a size range of live individuals (unpublished data) has shown no difference in filtration area in the two species. A 50 mm *C. meridionalis* (dry flesh mass 0.39 g) filtered at 3.1 l h^{-1} compared with 1.26 l h^{-1} in the same sized *A. ater* (dry flesh mass 0.54 g). The filtration rate in *A. ater* increases with ration level, however the maximum rate measured in a 50 mm mussel was 1.6 l h^{-1} at 32 x 10^6 cells l^{-1}. Thus a 50 mm *A. ater*, which is nearly twice the weight of *C. meridionalis*, filters, and grows, at a considerably slower rate.

The effect of increasing cell concentration on filtration rate has been examined in several bivalve species. Experiments on *Mytilus edulis* show conflicting results. Thompson and Bayne (1974), Foster-Smith (1975) and Widdows (1978) have shown no effect of concentration on the feeding rate of *M. edulis*, while Winter (1969) and Schulte (1975) demonstrated declining filtration rates with high cell concentrations. The filtration rate of 45 mm *Choromytilus meridionalis* was measured at different concentrations of *Dunaliella primolecta* (Fig 4a). No threshold concentration for the onset of filtration was recorded as in *M. edulis* (Thompson and Bayne, 1972) and *Aulacomya ater* (Griffiths and King, 1979a). The filtration rate remained constant at 1.82 l h^{-1} between 0.4 and 50 x 10^6 cells l^{-1} and increased with declining ration below 0.4 × 10^6 cells l^{-1}. These data were compared with those obtained from starved (45 mm) mussels maintained in the laboratory for 3 weeks. During this time the organic material in the water was approximately half that recorded in the field (1.07 mg AFDW• l^{-1} in aquarium, 2.65 mg AFDW l^{-1} in natural seawater). Reduced ration resulted in a marked rise in filtration rate (Fig. 4b), particularly at low cell concentrations. The variation in rate displayed by individuals increased as indicated by the standard deviations in Fig. 4b. These data indicate that although compensation to lower ration levels does not occur in the short term, *C. meridionalis* may adjust the filtration rate when subject to limited food availability over 2 to 3 weeks. However, under conditions of prolonged starvation it may be expected that a marked decline in filtration rate would occur. Starvation usually results in a decline in the metabolic rate to a basal level (Bayne, 1973; Bayne et al. 1976).

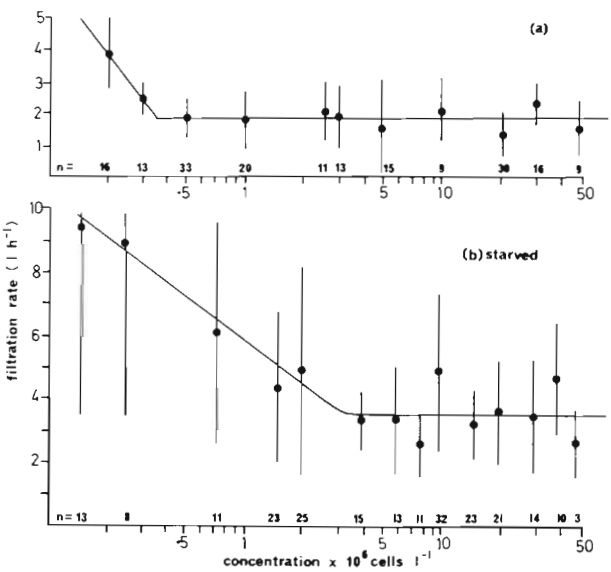

Fig. 4. *Choromytilus meridionalis*. Filtration rate of 45 mm individuals at different algal cell concentrations. 18 °C. (a) Mussels unstarved, (b) starved for 3 weeks. n = number of individuals used for each data point; vertical bars: one standard deviation

Respiration

Preliminary experiments showed that the rate of oxygen consumption was not influenced by detachment or removal of byssal threads or state of tide.

The respiration rate of a size range of mussels was measured at ambient sea temperature during summer (18 °C) and winter (12 °C) and is shown in Figure 5 and Table 2. Oxygen consumption was also measured at 25 °C in summer. Although *Choromytilus meridionalis* in False Bay seldom experience sea conditions in excess of 20 °C, individuals on the south-east coast of Cape Province are subject to warmer sea temperatures. The respiration rate showed no seasonal acclimation to temperature change and increased with rising tempe-

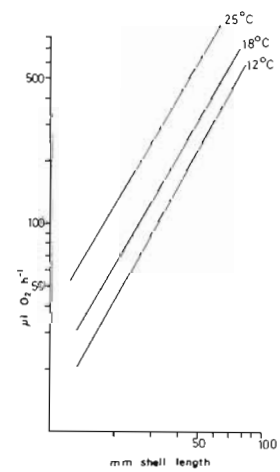

Fig. 5. *Choromytilus meridionalis*. Respiration rate of individuals measured during summer at 18 °C and 25 °C and winter at 12 °C

• AFDW = ash-free dry weight

rature. Q_{10} values for a 45 mm mussel in the ranges 12°–18 °C and 18°–25 °C were 1.69 and 2.55, respectively. This is equivalent to the routine rate of oxygen consumption and is similar to the response measured in other mytilids (Bayne et al., 1976). The routine rate may not only be affected by temperature but by state of gametogenesis. Bayne and Thomson (1970) and Bayne (1973) found that the respiratory rate in *Mytilus edulis* was higher in late winter during active gametogenesis and lower during the gonad resting stage in late summer. In *C. meridionalis*, however, gametogenesis is almost continuous with extended spawning peaks in summer and winter (Griffiths, 1977) and unlikely to produce seasonal change in respiratory rate.

For comparison of respiration with that of other species, oxygen consumption in *Choromytilus meridionalis* may be expresed as a function of dry flesh weight in g. At 18 °C, 'a' = 0.576 ml 0_2 h^{-1} and 'b' = 0.673; at 12 °C, 'a' = 0.430 ml 0_2 h^{-1} and 'b' = 0.692. Both the intercepts and weight exponents compare favourably with those obtained for routine rates of oxygen consumption in other bivalve species (summarised by Bayne et al., 1976). However, the respiratory rate in *Aulacomya ater* is considerably lower than that in *C. meridionalis*, and Griffiths and King (1979a) report that 'a' = 0.17 ml 0_2 h^{-1}.

Thompson and Bayne (1974) working on *Mytilus edulis* and Griffiths and King (1979a) on *Aulacomya ater* have demonstrated increasing oxygen consumption with increasing ingestion ration. At 18 °C, respiration rates of *Choromytilus meridionalis* (10–100 mm) were measured at 250, 1000, 10 000, 20 000 and 40 000 cells ml^{-1}, and compared with the rate measured in the absence of food. Table 2 presents the regression equations for these data. There was no significant difference between the slopes and intercepts. Oxygen consumption in *C. meridionalis* is not influenced by ration level.

Although filtration rate increased, respiration rate of mussels starved in the aquarium for 3 weeks did not differ from that of unstarved mussels, indicating that the level of stress was not severe. Starvation in *Mytilus edulis* and *M. californianus* is usually accompanied by a decline in filtration and respiration rate, the time taken for this to occur varying with gametogenic state (Bayne, 1973; Bayne et al., 1976.

Assimilation Efficiency

The assimilation efficiencies of 45 mm mussels fed on various concentrations of *Dunaliella primolecta* are shown in Figure 6a. Efficiency was slightly reduced at low cell concentrations, but maintained 80 % between 0.5 x 10^6 to 8 x 10^6 cells l^{-1} before declining to zero between 30-40 x 10^6 cells l^{-1}. No pseudofaeces were produced over this range. High assimilation efficiencies were also found in *Mytilus edulis* (Thompson and Bayne, 1972) and *Aulacomya ater* (Griffiths and King, 1979a); in both these species there is a decline to zero between 20 and 30 x 10^6 cells l^{-1}.

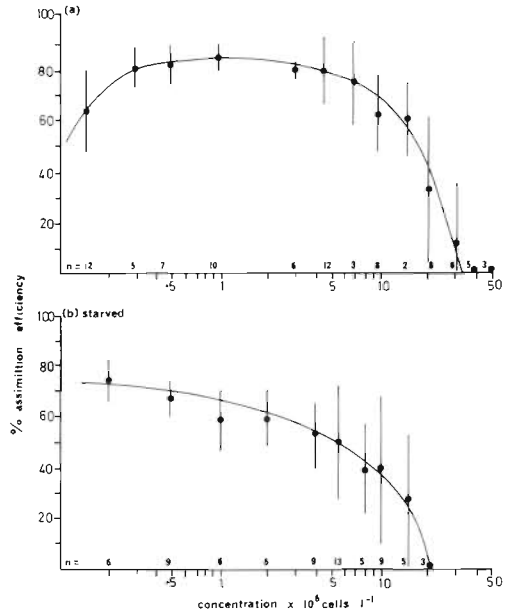

Fig. 6. *Choromytilus meridionalis*. Assimilation efficiency of 45 mm mussels fed different algal rations. Vertical bars: one standard deviation; n = number of individuals used for each data point. (a) Mussels unstarved, (b) starved for 3 weeks

Starvation for 3 weeks (see filtration section) resulted in a lateral shift of the assimilation efficiency curve to the left so that efficiency declined to zero at about 20 x 10^6 cells l^{-1} (Fig. 6b). The effect of increased filtration rate and lateral shift of the assimilation efficiency curve on the assimilated ration and scope for growth is presented in Figure 7. Calculated values are shown in Table 3. The assimilated ration and scope for growth curves are displaced to the left when compared with unstarved mussels. It would appear that metabolic effort was concentrated on obtaining a positive energy balance from a lower ration level, the optimum being reduced from 20 x 10^6 cells l^{-1} to 10 x 10^6 cells l^{-1}.

The assimilation efficiency and scope for growth of *Choromytilus meridionalis* have been compared with that of *Aulacomya ater* (from Griffiths and King, 1979a) in Figure 8. Assimilation efficiencies in *A. ater* are similar to those in *C. meridionalis* but remain positive at considerably higher ration levels. However, because of the lower filtration rate the maximum assimilated ration in *A. ater* is less than half that of *C. meridionalis* and the scope for growth considerably reduced. Data from Griffiths and King (1979b) show that *A. ater* has a slower growth rate and heavier flesh mass than compa-

Table 3. *Choromytilus meridionalis*. Calculation of assimilation ration and scope for growth in starved and unstarved 45 mm mussels

	Ration × 10^6 (cells l^{-1})	Ration (J l^{-1})	Filtration rate ($l\ h^{-1}$)	Ingestion ration (J h^{-1})	Assimilation efficiency (%)	Assimilation ration (J h^{-1})	Respiratory cost (J h^{-1})	Scope for growth (J h^{-1})	Scope for growth (% body kJ d^{-1})
Starved	0.2	0.4359	8.7	3.792	72	2.731	215.5 ml O_2	− 1.620	−0.36
	0.5	1.0898	7.3	7.955	68	5.410	= 4.351 J	+ 1.059	+0.24
	1.0	2.1795	5.9	12.859	65	8.358		+ 4.007	+0.89
	5.0	10.8976	3.6	39.449	49	19.330		+14.979	+3.33
	10.0	21.7952	3.6	78.899	36	28.403		+24.052	+5.34
	20.0	43.5904	3.6	157.797	0	0		− 4.351	−0.97
	30.0	65.3856	3.6	236.695	0	0		− 4.351	−0.97
	50.0	108.9760	3.6	394.490	0	0		− 4.351	−0.97
Unstarved	0.2	0.4359	3.8	1.656	72	1.193	254 ml O_2	− 3.935	−0.87
	0.5	1.0898	1.8	1.983	79	1.567	= 5.128 J	− 3.561	−0.79
	1.0	2.1795	1.8	3.967	84	3.332		− 1.796	−0.40
	5.0	10.8976	1.8	19.834	77	15.272		+10.144	+2.25
	10.0	21.7952	1.8	39.667	68	26.974		+21.846	+4.85
	20.0	43.5904	1.8	79.334	40	31.734		+26.606	+5.91
	30.0	65.3856	1.8	119.002	3	3.570		− 1.558	−0.35
	50.0	108.9760	1.8	198.336	0	0		− 5.128	−1.14

Conversion: 10^6 cells *Dunaliella primolecta* = 0.112 mg dry wt; 1 mg *D. primolecta* = 19.46 J; 1 ml O_2 = 4.83 cal = 20.19 J. 45 mm *C. meridionalis* = 10804.2 J

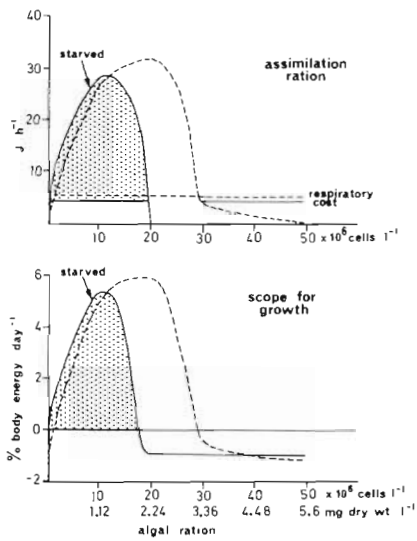

Fig. 7. *Choromytilus meridionalis*. Assimilation ration and scope for growth of starved and unstarved 45 mm mussels at different algal concentrations

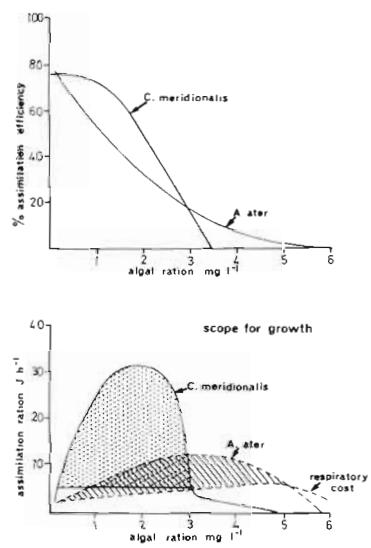

Fig. 8. *Choromytilus meridionalis* and *Aulacomya ater*. Comparison of assimilation efficiencies and scope for growth (*A. ater* data from Griffiths and King, 1979a). Food: *Dunaliella primolecta*

rable sized *C. meridionalis*. *A. ater* reaches breeding condition at 15 mm in the third year of growth, while *C. meridionalis* reaches the reproductive size of 20 mm within the first year (Griffiths, in press). Comparison of data in Figure 8 also shows that the optimum scope for growth occurs at different ration levels in the different species. Positive scope for growth in *C. meridionalis* feeding on *Dunaliella primolecta* varies from 0.2 – 3 mg l^{-1} with a peak at 2 mg l^{-1}, compared with a range of 0.2 – 5 mg l^{-1} in *A. ater* with peak at 3 mg l^{-1}. The different physiological responses and growth strategies in *C. meridionalis* and *A. ater* are interesting in view of the fact that these species frequently occur as adjacent populations, and occasionally may be completely intermingled, in both the littoral, and sublittoral zones.

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