Marine Biology 50, 195-207 (1979)

MARINE BIOLOGY

Relationships between Seston, Available Food and Feeding Activity in the Common Mussel *Mytilus edulis*

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Abstract

The feeding and metabolic rates of *Mytilus edulis* L. of different body sizes were measured in response to changes in particle concentrations ranging from 2 to 350 mg l^{-1}. Rates of oxygen consumption were not significantly affected by changes in seston concentration, whereas clearance rates gradually declined with increasing particle concentration. Pseudofaeces production was initiated at relatively low seston concentrations (<5 mg l^{-1}). Marked seasonal changes were recorded in the composition of suspended particulates (seston) in an estuary in south-west England. Total seston was sampled at frequent intervals throughout an annual cycle and analysed in terms of: particle size-frequency distributions, total dry weight (mg l^{-1}), inorganic content, chlorophyll *a*, carbohydrate, protein and lipid. The particulate carbohydrate, protein and lipid content provided an estimate of the food content of the seston. The results are discussed in terms of the "food available" to a non-selective suspension feeder, such as *M. edulis*, during a seasonal cycle. The effect of inorganic silt in suspension was mainly to limit by "dilution" the amount of food material ingested rather than to reduce the amount of material filtered by the mussel. In winter, the food content of the material ingested was 5%, and this increased to 25% during the spring and summer.

Introduction

Recent laboratory studies have shown that ration is one of the most important factors determining the estimated "scope for growth" (Thompson and Bayne, 1974; Widdows, 1978a, b) and measured growth (Winter and Langton, 1976) of the common mussel *Mytilus edulis*. But the literature on the chemical composition of suspended particulates in the sea (reviews by Riley, 1970; Strickland, 1972; Parsons and Takahashi, 1973) contains little comprehensive information on seasonal changes in the food available to estuarine suspension feeders. The majority of such studies have been concerned with quantifying either a specific component of the seston, such as phytoplankton from chlorophyll measurements, or the total suspended organic material, measured in terms of carbon. The former is only a small component of the food available, whereas the latter includes both utilisable food material and non-utilisable organic detritus and therefore overestimates the true ration.

There is also a paucity of data on the feeding behaviour of bivalve molluscs under natural conditions. Our present understanding of the effects of food concentration on the feeding of bivalves has been derived mainly from laboratory experiments using unicellular algal suspensions as the food source (Davids, 1964; Winter, 1969, 1973; Thompson and Bayne, 1974; Foster-Smith, 1975; Schulte, 1975; review by Bayne *et al.*, 1976). Although these studies have provided valuable information, the relationships between feeding activity and particle concentration appear to be affected by the type of algal cell or inorganic particle used (Foster-Smith, 1975). Furthermore, the algal cell concentrations, usually presented as either number of cells or dry weight of cells per unit volume, are difficult to relate to the conditions encountered in the estuarine and nearshore environments where inorganic silt forms a considerable and a variable component of the total seston.

In considering the effects of particle concentration on ingestion rate, as

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opposed to clearance rate, it is important to identify the rate of pseudofaeces production (i.e., material that is filtered but rejected by the gills and palps). Most laboratory studies have maintained bivalves at food concentrations below those necessary to produce pseudofaeces.

In a study by Foster-Smith (1975), clearance rate and pseudofaeces production by 3 bivalves (*Mytilus edulis, Cerastoderma edule* and *Venerupis pullustra*) were measured in response to increasing concentrations of different particles in suspension (*Platymonas suecica, Phaeodactylum tricornutum, Isochrysis galbani,* and grades of graphite and alumina). He showed that both clearance rate and pseudofaeces production were dependent on the concentration and the nature of the particulate material in suspension. The effects of food concentration on the feeding and biodeposition (production of faeces and pseudofaeces) rates of several bivalves (*Mytilus edulis, Crassostrea virginica, Mercenaria mercenaria*) have also been determined under artificially controlled conditions by Tenore and Dunstan (1973). In a field study by Haven and Morales-Alamo (1966), the seasonal changes in biodeposition by oysters (*C. virginica*) were measured at ambient particulate concentrations, but they gave no details of the clearance rate or of the available food.

An understanding of the production and bioenergetics of bivalves in their natural environment, therefore, requires not only an assessment of the food available in the water but also a measure of the total amount of food material filtered out of suspension and the amount of potentially utilisable food lost through rejection as pseudofaeces.

The objectives of this study were (a) to determine the nature and chemical composition of suspended particulates in an estuarine environment; (b) to estimate the food available to suspension feeders; (c) to study the feeding and biodeposition rates of *Mytilus edulis* in the field under different concentrations of suspended particulate material, and (d) to examine the relationships between food availability, total suspended particulates, and the feeding behaviour of *M. edulis*.

Materials and Methods

Effect of Particle Concentration on Feeding and Metabolic Rate

Mytilus edulis L. were collected from a population in the Lynher estuary, a tributary of the River Tamar in south-west England. Individuals were immediately cleaned of any epibiotic growth and placed in experimental chambers (volume 500 ml) on board a research vessel (R.V. "Jane" or R.V. "Squilla"). They were left undisturbed for at least 60 min before physiological measurements were started. Sea-water was pumped from directly over the mussel bed into a header tank and thence through the experimental chambers.

The rates of oxygen consumption were measured by isolating the chamber from the flowing water for a period of 45 to 60 min and monitoring the decline in oxygen tension in the chamber with a Radiometer oxygen electrode coupled to a chart recorder (for details see Bayne *et al.*, 1977).

The clearance rate, defined as the volume of water cleared of particles >3 µm per unit time, was estimated by monitoring the removal of suspended particles as the water passed through the 6 experimental chambers containing individual mussels (for details see Bayne *et al.*, 1977). Mussels were left undisturbed for 60 min before the particle concentration of water flowing into and out of the chambers was measured by a Coulter Counter Model ZB.

The effect of particle concentration on the clearance rate was determined in January (8°C), May (12°C) and July (16°C), and the effect on oxygen consumption was studied in July. The effects of particle concentration on both the rate of oxygen uptake and filtration by *Mytilus edulis* were studied by adding fine surface sediments, collected from nearby mudflats, to the sea-water in the header tank. It is this material that is resuspended during storms and at times of high fresh-water input into the estuary. The mussels experienced different particle concentrations (mg l^{-1}) in a random manner and were allowed at least 60 min to respond to changes in concentration before measurements were started. The relationship between clearance rate and particle concentration was determined for 3 size classes (3 cm, 5 cm and 7 cm shell length). These shell lengths are equivalent to approximately 0.2, 0.7 and 1.5 g dry tissue weight, respectively.

In July, when the seston concentration was minimal (2.5 mg l^{-1}), observations were made to determine the particle concentration which initiated pseudofaeces production in 4 size classes of mussels (1.7, 3.5, 5.5 and 7 cm shell length). This threshold was established by carefully observing 5 actively filtering mussels in each size class and gradually increasing the concentration

of suspended matter until a slow but continuous stream of pseudofaeces was produced along the ventral side of the septum dividing the inhalent from the exhalent siphon. The particle concentration was then determined and expressed as mg l^{-1}.

The relationship between pseudofaeces production (g $mussel^{-1}$ h^{-1}) and particle concentration (mg l^{-1}) was also determined by weighing the amount of pseudofaeces collected from 6 mussels (7 cm length) after a period of time at different particle concentrations.

Analysis of Seston

Suspended particulate material was sampled from the water above a mussel population situated in the mouth of the Lynher estuary. The annual sea-water temperature ranged from 8°C in February to 19.5°C in August 1976. Salinity was maintained between 29 and 33‰ for most of the year, except during the autumn and winter when there were periods of reduced salinity (fluctuations between 7 and 25‰ S over a tidal cycle have been recorded) following heavy rainfall.

Initial experiments in March and June 1975 compared the composition of suspended particulates in the water pumped from the surface and from the bottom, within 0.25 m of the mussel bed.

Routine sampling of suspended particulate material was carried out from a research vessel anchored in the mouth of the Lynher estuary. Water was pumped from a depth of between 1 and 2 m and particulate samples collected at approximately 2-h intervals over a tidal cycle on several days each month throughout 1976.

Several aspects of the composition of suspended particulate matter (seston) were studied:

(1) Total Seston Concentration. The weight of suspended particulate matter per litre of sea-water was determined by the method described by Strickland and Parsons (1972). A known volume of sea-water was filtered through a washed, ashed and pre-weighed glass-fibre filter (pore size 0.45 µm). The filters were then dried at 90°C and ashed at 450°C to determine the dry weight and ash weight of suspended matter per litre.

(2) Size-Frequency Distribution of Suspended Particles. The size distribution of particles above 2.9 µm (equivalent spherical diameter) was analysed by a Coulter Counter (Model ZB) using 140 and 280 µm orifice tubes (as described by Sheldon and Parsons, 1967).

Particulate material was also sampled for chlorophyll *a*, carbohydrates, protein and lipid analysis. Measured aliquots of the water sample were filtered through glass-fibre filters coated with magnesium carbonate and these filters were then stored at -25°C prior to analysis.

(3) Chlorophyll. Photosynthetic pigments were extracted with 90% acetone and chlorophyll *a* determined from absorption spectra measured on a Pye Unicam SP 8000 spectrophotometer (Strickland and Parsons, 1972). Account was taken of phaeopigments.

(4) Carbohydrates. Particulate carbohydrate determination was based on the anthrone method described by Strickland and Parsons (1972).

(5) Protein. Protein was determined by converting the nitrogen in the particulate matter to ammonia by Kjeldahl digestion with sulphuric acid. After diluting and neutralising, the resulting ammonia was then determined spectrophotometrically by the phenol-hypochlorite method of Solórzano (1969). The protein value was obtained by multiplying the nitrogen value by 6.25.

(6) Lipid. Lipid was extracted with chloroform and methanol and then determined by the method of Marsh and Weinstein (1966) using tripalmitin as a standard. Details of extraction and analysis are given by Holland and Gabbott (1971) and Holland and Hannant (1973).

Results

Effect of Suspended Particulates on Rate of Oxygen Consumption

Table 1 shows the rate of oxygen uptake by individuals of *Mytilus edulis* of different body sizes at several seston concentrations. There was no effect of particle concentration on the rate of oxygen uptake by *M. edulis* (correlation coefficient = 0.16).

Effect of Suspended Particulates on Clearance Rate

Data collected in January, May and July showed that the clearance rate of *Mytilus edulis* was independent of seasonal temperature. This confirms the results of previous laboratory studies (Widdows, 1978a) in which clearance rates of acclimated mussels were found to be temperature-independent. Consequently, the clearance rate data were pooled for each size class. The relationships between clearance rate and particle concentration for 3, 5 and 7 cm individuals are

Table 1. *Mytilus edulis*. Effect of seston concentration on weight-specific rate of oxygen consumption ($\bar{V}_{O_2}$)

Individual	Shell length (cm)	Body weight (g)	Seston concentration (mg l^{-1})	$\bar{V}_{O_2}$ (ml O_2 g^{-1} h^{-1})
1	7	2.066	10	0.716
			200	0.759
			280	0.811
2	7	1.572	10	0.666
			200	0.739
			280	0.675
3	6	1.361	3	0.417
			50	0.494
			100	0.364
4	6	1.290	3	0.637
			50	0.679
			100	0.567
5	4	0.575	5	0.810
			100	0.507
			160	0.677
6	4	0.438	5	0.825
			100	0.752
			160	0.736
7	3	0.211	12	0.717
			180	0.717
8	3	0.307	12	0.770
			100	0.614
9	3	0.297	12	0.711
			100	0.695

illustrated in Fig. 1 and are described by the following equations:

Shell length	Regression equation
3 cm	Clearance rate = 1.356 (SD ± 0.087) − 0.00546 (SD ± 0.0007)W (r = −0.73)
5 cm	Clearance rate = 2.416 (SD ± 0.007) − 0.0086 (SD ± 0.0005)W (r = −0.85)
7 cm	Clearance rate = 2.300 (SD ± 0.099) − 0.0061 (SD ± 0.0005)W (r = −0.82),

where clearance rate is expressed in terms of 1 h^{-1} and particle concentration (w) in mg l^{-1}.

There was a negative correlation between clearance rate and particle concentration. Previous laboratory studies (Thompson and Bayne, 1974; Foster-Smith, 1975; Widdows, 1978a), however, have not recorded a significant effect of particle concentration on clearance rate. This may be due to the high variance in the clearance rate data (caused by individual variation) masking the slight effect of particle concentration over the narrower range of concentrations studied in laboratory experiments.

The clearance rate is equivalent to ventilation (or pumping) rate when all suspended particles are removed from the ventilation current by the gill with 100% retention efficiency. Recently,

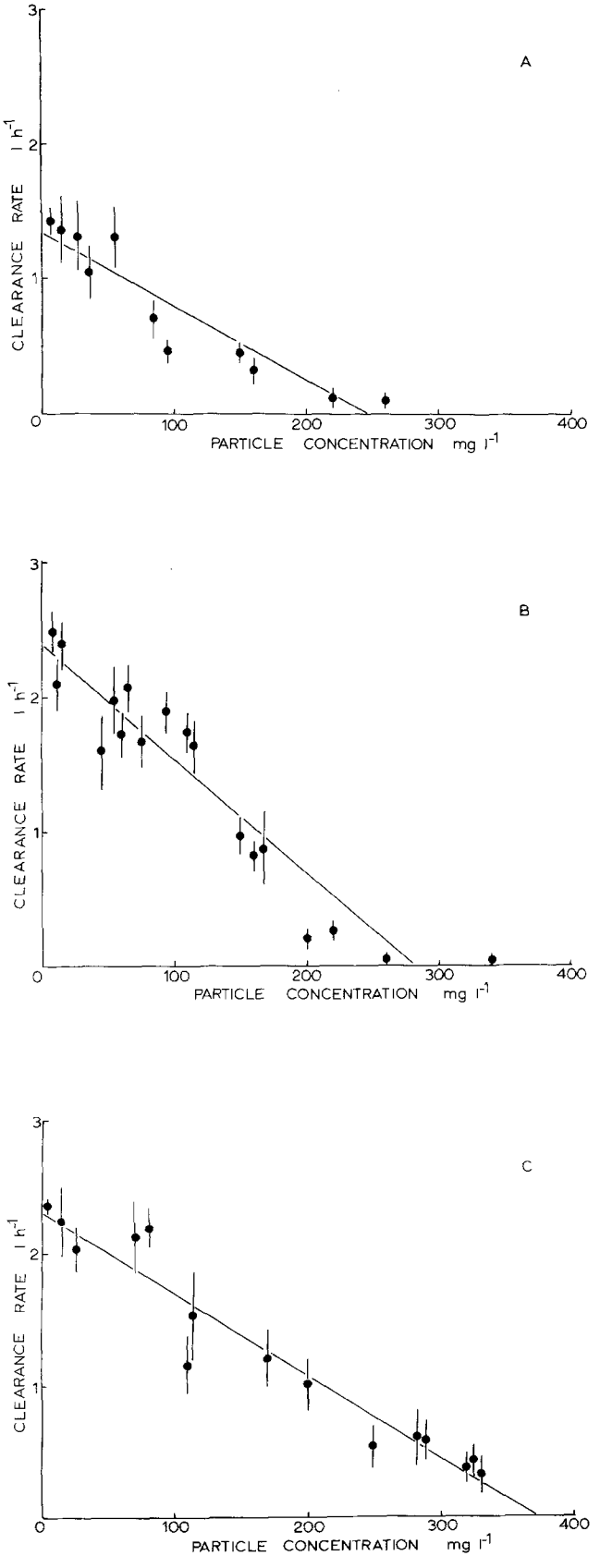

Fig. 1. *Mytilus edulis*. Effect of particle concentration on clearance rate of (A) 3 cm, (B) 5 cm, and (C) 7 cm mussel. Values are means ± standard errors

Bayne *et al.* (1977) studied particle selection by *Mytilus edulis* in the estuarine environment and showed that all particles greater than 2 to 5 µm are filtered with 100% efficiency. Therefore, the clearance rate measured in this study also represents the ventilation rate of *M. edulis*.

Clearance rate declined with increasing particle concentration, and resulted in a minimal feeding and pumping activity at approximately 220, 260 and 330 mg l^{-1} for mussels 3, 5 and 7 cm in length, respectively (Fig. 1). Mussels may not completely close their valves at these very high particulate levels, but maintain a minimum water flow over the gills in order to meet their oxygen requirement.

The response of clearance rate (or ventilation rate) to changes in particle concentrations was reflected in the oxygen extraction efficiency (i.e., the oxygen consumed per hour as a percentage of the oxygen made available to the mussel per hour by the ventilation current). Fig. 2 illustrates the relationship between oxygen extraction efficiency and particle concentration for a 7 cm mussel at 16°C. As the ventilation rate declined with increasing particle concentration, there was a decrease in the amount of oxygen delivered to the gills per unit time. In order to maintain a constant metabolic rate independent of seston concentration, the extraction efficiency has to increase exponentially with increasing particle concentration. *Mytilus edulis* has been shown to maintain a constant metabolic rate up to concentrations of at least 280 mg seston l^{-1} (Table 1) by increasing the percentage extraction efficiency to 25%. Fig. 2 predicts that the oxygen extraction efficiency will increase rapidly above this seston concentration, but it is unknown whether these high extraction efficiencies can be maintained. If not, the rate of oxygen uptake must decline.

The quantity of particulate material filtered out of the water per hour by mussels of different size has been calculated from the relationship between clearance rate (l h^{-1}) and particle concentration (mg l^{-1}). This is subsequently termed the filtration rate (g h^{-1}). Three curves are presented in Fig. 3 to demonstrate the filtration rate of 3, 5 and 7 cm mussels over particle concentrations ranging from 0 to 370 mg l^{-1}. The filtration rate increased with higher particle concentrations until a maximum rate was reached, after which the filtration rate declined with further increases in particle concentration. Both the maximum rate and the concentration at which it occurred increased as a function of body size.

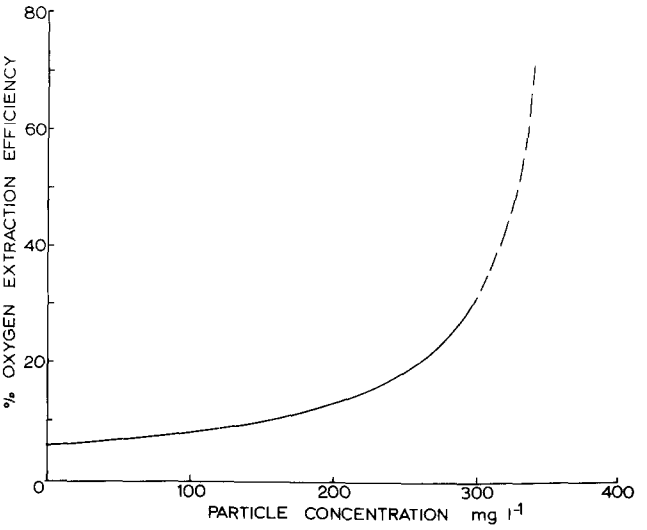

Fig. 2. *Mytilus edulis*. Relationship between oxygen extraction efficiency and particle concentration for a 7 cm mussel at 16°C. (Date interpolated from Table 1 and Fig. 1C. Dashed line represents predicted efficiency of oxygen extraction if metabolic rate is maintained constant above 280 mg l^{-1})

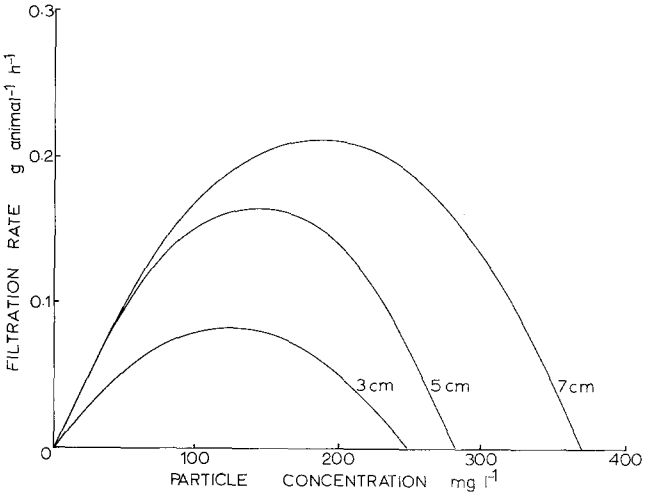

Fig. 3. *Mytilus edulis*. Effect of particle concentration on filtration rate of three size classes (3, 5 and 7 cm shell length)

Effect of Suspended Particulates on Pseudofaeces Production

The rate of pseudofaeces production (g h^{-1}) for a 7 cm mussel was measured over a range of seston concentrations from 12 to 280 mg h^{-1} (Fig. 4). The production of pseudofaeces increased with particle concentration, reached a maximum at ap-

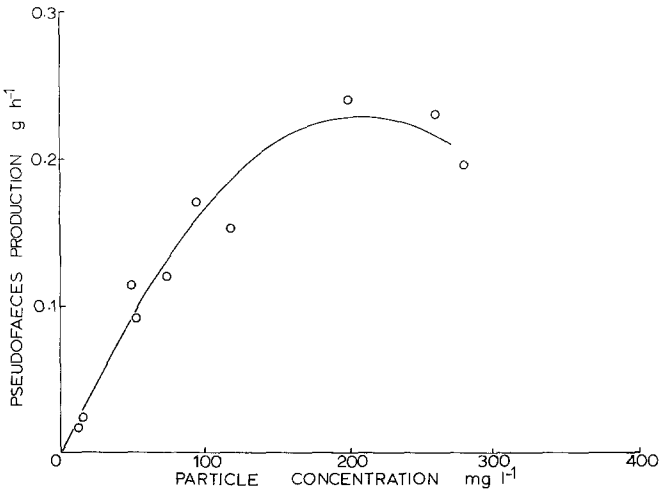

Fig. 4. *Mytilus edulis*. Effect of seston concentration on rate of pseudofaeces production for 7 cm mussel. Curve fitted by eye

Table 2. *Mytilus edulis*. Relationship between body size and seston concentration at which pseudofaeces production was initiated

Shell length (cm)	Seston concentration (mg l^{-1})
1.7	2.6
3.5	4.3
5.5	4.6
7.0	5.0

Table 3. Comparison of particle size distribution at surface and at 2 m depth in Lynher estuary. (Relative volume 10 = 5.455 x 10^5 μm^3 per ml)

Diameter (μm)	Surface (0 m)		Bottom (2 m)	
	Relative volume	Cumulative %	Relative volume	Cumulative %
2.9	66	6.8	66	6.7
3.8	108	18.0	115	18.0
4.7	141	32.7	145	33.0
5.9	146	47.8	152	48.5
7.5	135	61.8	132	61.9
9.4	119	74.2	111	73.1
11.9	91	83.6	90	82.3
15.0	61	89.9	75	89.8
19.0	50	95.1	60	95.9
31.0	24	97.6	20	97.9
39.0	13	99.0	12	99.1
49.0	10	100.0	8	100.0
Seston concentration (mg l^{-1})	15.20		13.84	

proximately 200 mg l^{-1} and then began to decline at higher particle concentrations. This measured rate of pseudofaeces production shows a close agreement with the filtration rate for a similar sized mussel (Fig. 3).

The particle concentrations at which pseudofaeces were first produced are recorded in Table 2. However, the technique used does not allow an estimate of variance to be made. The threshold concentration occurred at approximately 4.5 to 5.0 mg l^{-1} for individuals larger than 5 cm.

Seston Analysis

Effect of Depth on Composition of Suspended Particulates

Initial studies examined the effect of depth on the composition of suspended particulate material in the Lynher estuary. Table 3 compares the particle size distribution, expressed in terms of relative volume and cumulative percent, in the sea-water sampled from the surface and from the bottom within 0.25 m of the mussel bed. The size of suspended particles falls mainly in the range of 3 to 50 μm, and there is no difference in the size distribution of particles in surface- and bottom-water samples. In addition, a *t*-test using the method of paired comparisons showed that neither the total weight nor the composition of particulate material was significantly affected by depth (Table 4).

The routine seasonal sampling of suspended particulates was therefore carried out from a depth of between 1 and 2 m.

Seasonal Changes in Suspended Particulates

Total Seston Concentration. The weight and composition of suspended particulates

Table 4. Comparison of suspended particulates in surface and bottom waters (depth 2 to 3.5 m and within 0.25 m of mussel bed). NS: not significant

Date (1975)	Time (hrs)	Total particulates (mg l^{-1})		Carbohydrate, protein and lipid content (as percentage of seston)	
		Surface sample	Bottom sample	Surface sample	Bottom sample
14 Mar.	10.45	13.00	13.28	10.7	11.91
	13.00	13.84	15.20	11.25	10.00
	15.15	11.06	14.00	12.05	10.9
5 June	10.15	2.84	3.18	42.01	38.40
	12.15	3.38	3.29	50.36	49.84
	14.15	4.41	3.52	32.45	36.50
	16.15	4.61	4.36	37.14	29.20
t-test using method of paired comparisons:					
Total particulates				t = 1.086, NS	
$\frac{\text{Carbohydrate + protein + lipid}}{\text{seston}} \times 100$				t = 0.971, NS	

were analysed and the data grouped on a monthly basis to show seasonal changes in the seston composition. The seasonal cycle in the weight of particulates is illustrated in Fig. 5A. The particle concentration was maximal in the autumn and winter when the fresh-water input and river flow were high. The level of particulates then declined in the spring and was minimal during the summer. The percent ash content followed a similar seasonal cycle (Fig. 5B). During the autumn and winter the ash content was 88% due to the high silt load, and declined to 52% in the summer when there was minimal river flow and the percentage organic content was maximal.

Particle Size-Frequency Distribution. The seasonal variation in particle size distribution is presented as cumulative percent curves in Fig. 6A. The four curves are representative of winter, spring, summer and autumn particle size distributions. At all times the majority of particles were less than 40 µm (spherical diameter).

Cumulative curves for February and November illustrate the dominance of the smaller silt particles during autumn and winter, whereas in the spring and summer there was an increase in the relative importance of larger particles (8 to 30 µm), resulting in a shift in the curves to the right. The dominance of these larger particles then declined during the summer (Fig. 6B).

Chemical Composition. There were marked seasonal changes in the chlorophyll *a* content of suspended particulates in the Lynher estuary (Fig. 7). Chlorophyll *a* was not present in detectable amounts in the autumn and winter (October to February), but increased in the spring and attained maximum values in the summer (June to August). The seasonal changes in the chemical composition of suspended particulates was analysed in terms of the main constituents of food material, namely carbohydrate, protein and lipid (Fig. 8A). Protein, which formed the major component, occurred at a maximum concentration in the winter (1.35 mg l^{-1}). A similar seasonal variation in particulate protein has recently been recorded by Maita and Yanada (1978) in Funka Bay, Japan. Carbohydrate showed a similar but less marked seasonal variation with winter values (0.6 mg l^{-1}) three times the summer concentration (0.2 mg l^{-1}). Lipid content was smaller (ca. 0.15 mg l^{-1}) and did not demonstrate any marked seasonal cycle. The "food material" in the total seston, as represented by the sum of carbohydrate, protein and lipid concentrations (mg l^{-1}), is maximal in the

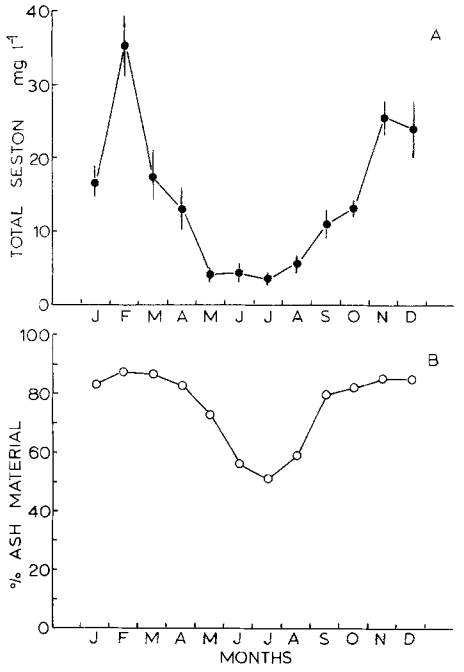

Fig. 5. Seasonal variation in (A) total seston (values are means ± standard errors) and (B) proportion of ash material in the seston

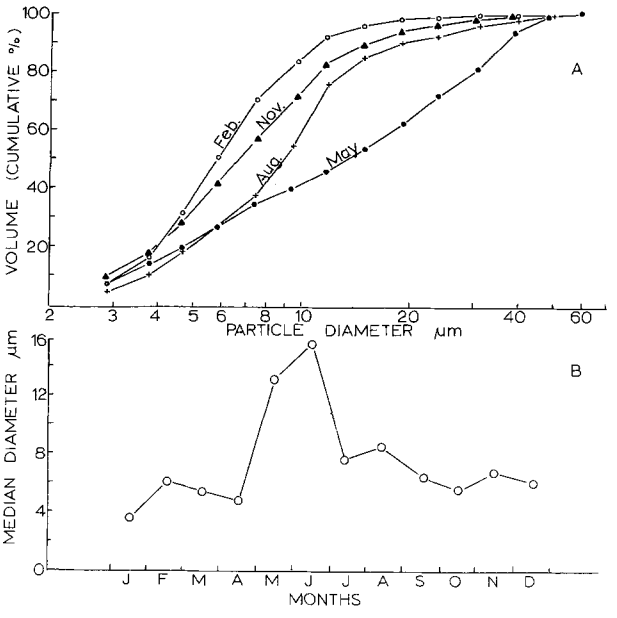

Fig. 6. (A) Cumulative curves of suspended particle volume against particle diameter for February, May, August and November; (B) seasonal variation in median particle diameter of total seston

winter and minimal in the summer. However, the "food material", when expressed as a percentage of the total seston, shows the reverse relationship (Fig. 8B). In winter the food material forms a small percentage (ca. 6%), and

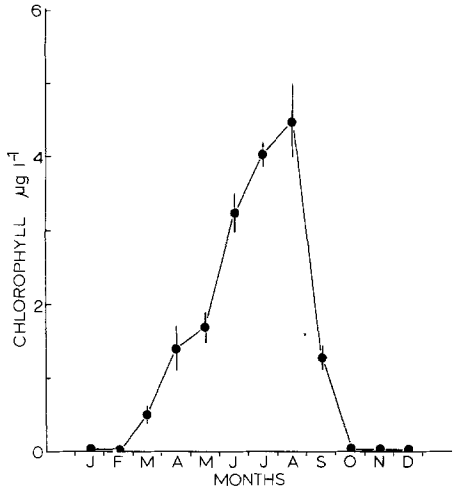

Fig. 7. Seasonal cycle in chlorophyll *a* content of suspended particulate matter. Values are means ± standard errors

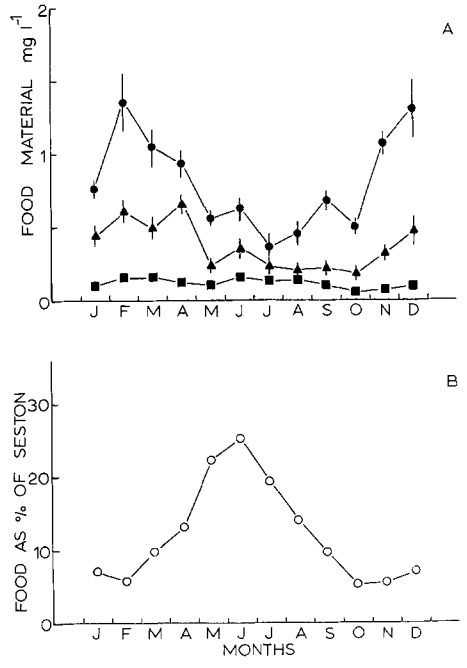

Fig. 8. (A) Seasonal changes in carbohydrate (triangles), protein (circles) and lipid (squares) composition of suspended particulates (values are means ± standard errors); (B) seasonal variation of food material in total seston (particulate carbohydrate, protein and lipid combined as percentage of seston)

in the summer it rises to ca. 25% of the total seston. The proportion of food in the seston therefore follows a seasonal cycle similar to that recorded for "percentage ash-free material" (i.e., the inverse of percent ash material in Fig. 5B) and chlorophyll *a* (Fig. 7).

Table 5. Seasonal changes in chemical composition and energy value of "suspended food material"

Months	% composition			Energy value	
	Carbohydrates	Protein	Lipid	(cal mg^{-1})	(J mg^{-1})
J	35.0	57.5	12.7	5.88	24.64
F	28.7	63.6	7.7	5.50	23.05
M	28.9	61.1	10.0	5.58	23.38
A	39.0	53.4	7.5	5.33	22.33
M	26.8	61.8	11.3	5.66	23.72
J	31.7	53.4	14.9	5.72	23.97
J	32.9	48.9	18.2	5.83	24.43
A	26.2	55.9	17.9	5.92	24.80
S	22.8	68.2	8.9	5.63	23.59
O	27.8	68.9	4.2	5.43	22.75
N	23.3	71.9	5.0	5.49	23.00
D	24.8	68.6	6.6	5.52	23.13

Seasonal changes in the relative proportions of carbohydrates, proteins and lipids in the "food material" are presented in Table 5. Protein values ranged from 49 to 72% for the total food content. Carbohydrate varied from 23 to 39%, whereas lipid, the smallest component, had the most marked seasonal cycle ranging from 4.2% in the autumn to 18.2% in the summer. Calculated energy values showed that this seasonal variation in percentage lipid had relatively little effect on the total energy value of the food, which varied between 22.3 and 24.8 J per mg (Table 5).

Discussion

There is an abundance of data in the literature on the influence of particle or food concentration on the clearance rate of *Mytilus edulis* and other bivalve molluscs (Loosanoff, 1962; Davids, 1964; Winter, 1969, 1973; Thompson and Bayne, 1972, 1974; Foster-Smith, 1975; Schulte, 1975; Bayne *et al.*, 1976). Fewer studies have examined the effect of particle concentration on the biodeposition and ingestion rates of bivalves (Haven and Morales-Alamo, 1966; Tenore and Dunstan, 1973; Foster-Smith, 1975). In laboratory studies, a variety of unicellular algal suspensions and inorganic suspensions has been used and, as a result, different relationships between clearance rate, biodeposition and particle concentration have been recorded. For example, Davids (1964), Winter (1973) and Schulte (1975) observed a decrease in the clearance rate of *M. edulis* in dense suspensions (>10^7 cells l^{-1}) of *Phaeodactylum tricornutum*, *Dunaliella marina* and *Platymonas suecica*. In contrast, Thompson and Bayne (1974), Foster-Smith (1975) and Widdows (1978a) recorded remarkably constant clearance rates by *M. edulis* fed with *Platymonas suecica* (<2 x 10^6 to 2 x 10^7 cells l^{-1}), *Phaeodactylum tricornutum* or *Isochrysis galbani* (<2 x 10^7 to 7 x 10^8 cells l^{-1}). Foster-

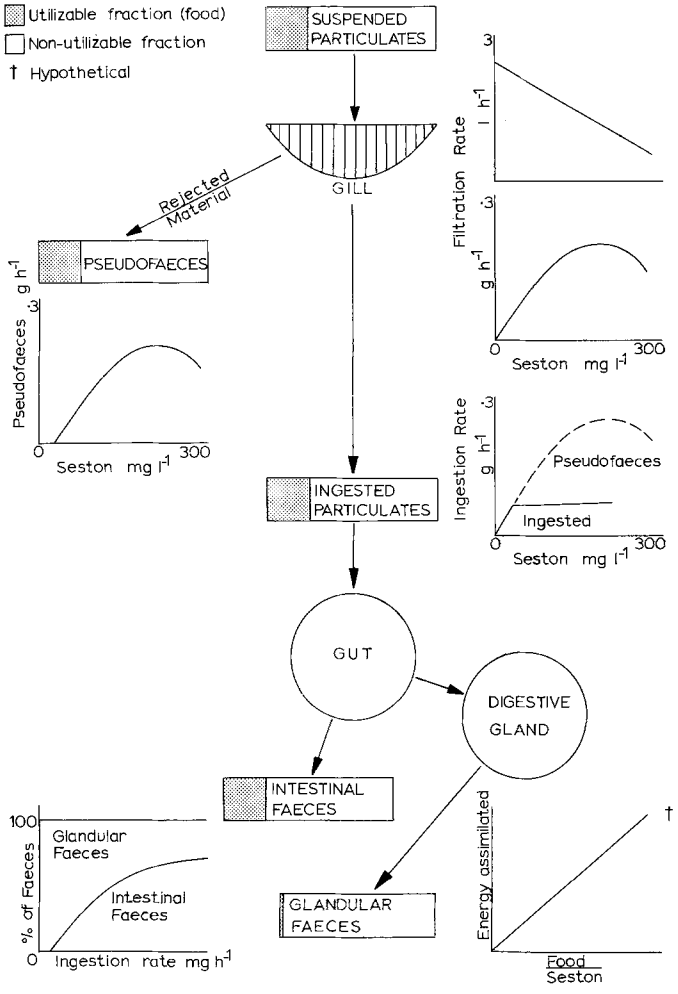

Fig. 9. *Mytilus edulis*. Schematic diagram summarising effect of particle concentration on feeding and digestive system

Smith (1975) noted that the effect of particle concentration on the rate of feeding and pseudofaeces production of 3 bivalve species (*M. edulis, Cerastoderma edule* and *Venerupis pullustra*) varied with the type of algal cell and inorganic suspensions.

A schematic diagram (Fig. 9) is used to integrate all the available data and summarise the results of this present study. The mechanism by which the lamellibranch gill filters suspended particles from the water pumped through the mantle cavity has been recently reviewed by Jørgensen (1975b) and by Bayne *et al.* (1976). *Mytilus edulis* is a non-selective filter-feeder, its gills retaining all particles greater than 2 to 5 µm with 100% efficiency (Davids, 1964; Vahl, 1972; Jørgensen, 1975a; Bayne *et al.* 1977). The filtered material is then transferred to the food grooves (ciliary tracts) on the gills and thence to the labial palps. The function of the labial palps is the continuous removal of materials from the lamellar food tracts, whether to be ingested as food or to be rejected as pseudofaeces (Foster-Smith, 1974).

At very low particle concentrations, probably >0.25 mg l^{-1} (derived from laboratory experiments by Thompson and Bayne, 1974; Widdows, 1978a), all suspended particulate material (>2 µm diameter) is filtered by the gill, ingested through the mouth, and transported to the digestive gland for digestion. Following food assimilation, the remaining unassimilated matter is rejected as glandular faeces (Thompson and Bayne, 1972, 1974).

As the seston concentration increases, the digestive gland cannot digest and assimilate all the material entering the stomach. This excess material, after bypassing the digestive gland, is transported through the gut undigested and rejected as intestinal faeces (Van Weel, 1961). The ratio of intestinal to glandular faeces, therefore, increases with increasing ingestion rate (mg h^{-1}) and this is reflected in a decline in assimilation efficiency (Thompson and Bayne, 1972, 1974; Widdows, 1978a).

Ingestion rate increases with increasing particle concentration until a threshold is reached, above which further material filtered by the gills is carried away from the mouth by rejection tracts on the labial palps and deposited as pseudofaeces (Foster-Smith, 1974). No size-selection of particles has been observed on the palps and it is difficult to envisage any such mechanism since the particles are bound in mucous strings. Bernard (1974) studied the labial palps of *Crassostrea gigas* and concluded that their main function was to reduce mucus volume prior to ingestion and to reject excess material.

At the threshold concentration of pseudofaeces production, the amount of material filtered per hour will be equivalent to the maximum ingestion rate before any rejection occurs. This threshold concentration increases with body size (Table 2). For a mussel of 1 g dry weight, the onset of pseudofaeces production occurs at a seston concentration of 5 mg l^{-1}, and therefore the maximum ingestion rate is approximately 11 mg of particulate material per hour (i.e., 2.2 l h^{-1} x 5 mg l^{-1}). Increasing particle concentrations up to 180 mg l^{-1} results in an increase in the total amount of material filtered out of suspension, but the majority of this is rejected as pseudofaeces (Fig. 4). There

is a close agreement between the pseudofaeces production and the filtration rate of *Mytilus edulis* at the higher seston concentrations (>50 mg l^{-1}), suggesting that ingestion rate is small relative to the filtration rate and that it does not increase significantly after the onset of pseudofaeces production. This relationship between pseudofaeces production and ingestion rate with increasing seston levels has also been demonstrated in *Crassostrea virginica* by Haven and Morales-Alamo (1966). Their data show (a) that pseudofaeces production begins at seston concentrations of approximately 4 mg l^{-1}, (b) a positive correlation between pseudofaeces production and total seston above 4 mg l^{-1}, and (c) no increase in faeces production (essentially equal to ingestion rate when inorganic content is high) with increasing seston concentrations above 4 mg l^{-1}.

There is also good agreement between the ingestion rates of *Mytilus edulis* measured in laboratory experiments by Foster-Smith (1975) and those presented in this paper. Foster-Smith recorded a maximum ingestion rate of 100 x 10^6 *Phaeodactylum tricornutum* cells h^{-1} by a mussel of 4.5 to 5.2 cm shell length, with a clearance rate of 1.4 l h^{-1}. When converted into dry weight of algal cells (0.07 mg day weight = 10^6 *P. tricornutum* cells; Widdows, 1978a) this gives a maximum ingestion rate of 7 mg h^{-1}.

As clearance rate (l h^{-1}) declines with increasing particle concentration (Fig. 1), the filtration rate (i.e., the amount of material filtered per hour) increases to a maximum rate and then declines with further increases in the seston (Fig. 3). The maximum filtration rate occurs at higher seston concentrations with increasing body size. For a mussel of 7 cm length or 1.5 g weight, filtration rate (0.21 g h^{-1}) occurs at a concentration of ca. 180 mg l^{-1}.

The results of this study indicate that the amount of food available to *Mytilus edulis* cannot be simply assessed as the concentration of particulate food material in the water, because a large proportion of this may be "unobtainable" and rejected as pseudofaeces. The amount of utilisable food ingested by a non-selective filter-feeder, such as *M. edulis*, is determined by the total particulate concentration and the proportion of non-utilisable organic and inorganic material present in the seston. The effect of inorganic silt in suspension is mainly to limit by "dilution" the amount of food material ingested rather than to reduce the amount of material filtered by the mussel. For a mussel weighing 1 g, clearing 2.2 l h^{-1}, material begins to be rejected as pseudofaeces at relatively low seston concentrations (ca. 5 mg l^{-1}). The filtration rate of 11 mg h^{-1} at this concentration represents an upper limit for ingestion rate and, as the concentration of seston increases, progressively more material is rejected by the gills and palps.

In winter, the total seston concentration in the Lynher estuary is high (20 to 35 mg l^{-1}) and the amount of particulate food in suspension is 1.5 to 1.9 mg l^{-1} (Fig. 8A). This relatively high food concentration is probably caused by the periphytic micro-organisms associated with the large surface area provided by the suspended particles, since Fenchel (1970) demonstrated that the number of micro-organisms on detrital particles was approximately proportional to the total surface area. However, food accounts for only 6% of the total particulates at this time of year. A maximum of 5 mg of seston is ingested from each litre of water filtered by the gills, the remainder being rejected as pseudofaeces. The amount of food material ingested can, therefore, be considered either as 0.66 mg h^{-1} or as 0.3 mg l^{-1} filtered (February, Table 6).

In the summer, when the total seston and total food concentrations decline to ca. 4.5 mg l^{-1} (Fig. 5A) and 1.1 mg l^{-1}, respectively, the food material can represent as much as 25% of the total seston. At this seston concentration no pseudofaeces are produced and the food ingestion rate reaches a maximum value of 2.35 mg h^{-1} or 1.1 mg l^{-1} filtered (Table 6). The latter values of food ingested per litre filtered provide an estimate of food availability that is comparable with algal food concentrations used in laboratory experiments where all material filtered was ingested (Widdows, 1978a, b). Under laboratory conditions (15°C), the maintenance ration for a mussel of 1 g dry flesh weight was calculated to be 0.28 mg algal cells ingested per litre. The food available to mussels in the Lynher estuary in winter closely approximates this estimated maintenance ration. From October to February, the amount of food material ingested is ca. 0.3 mg from each litre filtered (Table 6). In the winter, *Mytilus edulis* enters a period either of zero growth (B.L. Bayne and C.M. Worrall, unpublished data), when the available food is equivalent to the maintenance ration, or of negative growth and utilisation of body reserves (Dare and Edwards, 1975), when the available food is less than the maintenance ration. The ration level required to maintain a mus-

Table 6. *Mytilus edulis*. Seasonal changes in food content (carbohydrates + protein + lipid) of material ingested by a 1 g mussel. Maintenance ration, established in laboratory experiments (Widdows, 1978b) = 0.28 mg organic matter l^{-1}

Months	mg food material ingested per litre filtered	mg food material ingested per hour
J	0.37	0.81
F	0.30	0.66
M	0.50	1.10
A	0.67	1.47
M	0.90	1.98
J	1.07	2.35
J	0.68	1.50
A	0.70	1.54
S	0.47	1.03
O	0.27	0.59
N	0.29	0.64
D	0.36	0.79

Table 7. Seasonal changes in food value of phytoplankton fraction. Carbon content = chlorophyll a x 54 (Riley, 1970); organic matter = carbon x 2.14. Maintenance ration, established in laboratory experiments (Widdows, 1978b) = 0.28 mg organic matter l^{-1}

Months	Chlorophyll *a* (µg l^{-1})	Carbon (µg l^{-1})	Organic matter (mg l^{-1})	Algal organic matter as % of total utilisable food material
J	0	0	0	0
F	0	0	0	0
M	0.5	27.0	0.06	3.3
A	1.4	75.6	0.16	9.6
M	1.7	91.8	0.19	22.0
J	3.2	172.8	0.37	34.5
J	4.0	216.0	0.46	68.0
A	4.5	243.0	0.52	64.0
S	1.3	70.2	0.15	14.0
O	0	0	0	0
N	0	0	0	0
D	0	0	0	0

sel increases with body size (Thompson and Bayne, 1974; Widdows, 1978b), so that there may be enough food available in winter to support small individuals, but insufficient to prevent the utilisation of body reserves in larger mussels. In the summer, the maximum ingestion rate (2.35 mg h^{-1}) greatly exceeds the maintenance ration and provides an energy excess for growth and the production of gametes. This summer value for food availability (1.1 mg of food per litre filtered) corresponds to the optimum ration, that is, the ration at which maximum growth efficiency (K_1) occurs, as determined in laboratory experiments (Widdows, 1978a, b).

The conversion of particulate chlorophyll *a* values (Fig. 7) into carbon and organic matter equivalents (Table 7) provides an assessment of the relative importance of phytoplankton material in the natural food of *Mytilus edulis*. Phytoplankton are not present in any measurable quantities during the autumn and winter (October to February). From May to August there is a marked increase in phytoplankton to ca. 0.52 mg organic matter l^{-1}. At these concentrations, it is estimated that phytoplankton amount to 68% of the total utilisable particulate food material in the Lynher estuary. However, phytoplankton concentrations are only significantly above the calculated maintenance ration of 0.28 mg algal cells per litre during the summer (June to August). This suggests that the phytoplankton alone cannot meet the food requirements of *M. edulis* in the Lynher estuary. The additional particulate food material is probably detrital or bacterial in origin, especially in the autumn and winter.

It should be noted that the food material (carbohydrates, protein and lipid) forms a variable component (32 to 83%) of the ash-free material (often referred to as "particulate organic matter"). This confirms the results of several previous studies (Menzel and Ryther, 1970; Holm-Hansen, 1972; Strickland, 1972) in which a large proportion of the particulate organic matter was found to be refractory and not utilised as an energy substrate by heterotrophic organisms.

The relationship between particle concentration and feeding activity established in this present study complements the earlier work of Haven and Morales-Alamo (1966) on biodeposition by oysters in the natural environment. However, there is little agreement between these experiments involving naturally occurring particulates and those experimental studies using artificially controlled food concentrations (Loosanoff and Engle, 1947; Tenore and Dunstan, 1973; Winter, 1976). Winter (1976) recorded very low clearance rates (ca. 0.08 l h^{-1}) for small mussels (19 mm shell length), and this may explain the lack, in his study, of pseudofaeces production at particle concentrations consisting of 12.5 mg of organic-free silt per litre added to algal cells (*Dunaliella marina*) at concentrations from 0.53 to 2.14 mg l^{-1}. The ingestion rate and growth rate of the mussels also increased in response to the addition of silt to the algal cells. However, Winter recorded an extremely high mortality when mussels were fed at a high ration level (3.21 mg of *D. marina* per litre), and this may reflect the abnormal feeding conditions. These differences suggest that the results of laboratory feeding experiments, involving artificial particulates at high concentrations, should be applied to the natural environment with caution.

Extrapolation of the results presented in this paper indicate that high seston concentrations may limit the growth and distribution of *Mytilus edulis*, either by restricting the amount of food ingested or by reducing pumping rate and thereby oxygen availability (Fig. 2). In estuarine waters with a high silt content, the food availability (measured in terms of food as a percentage of the seston) and consequently growth rate is likely to be inversely proportional to the particle concentration. The limit of distribution will therefore occur at seston concentrations where the food available over the year is below the maintenance requirement. The effect of seston concentration on oxygen availability is also a possible factor limiting a species distribution. An increase in the particle concentration reduced the filtration or ventilation rate of *M. edulis*, and therefore the amount of oxygen delivered to the gills per unit time. In order to maintain a constant rate of metabolism the oxygen extraction efficiency must rise (Fig. 2). At concentrations above 280 mg l^{-1}, the oxygen extraction efficiency of a mussel of 1 g flesh weight increases rapidly to very high levels which are unlikely to be maintained in the natural environment.

Acknowledgements. We thank Dr. B.L. Bayne for helpful discussions and critically reading the manuscript. We are also indebted to the crews of the R.V. "Jane" and R.V. "Squilla" for their valuable assistance. This work forms part of the estuarine and nearshore research programme of the Institute for Marine Environmental Research, a component of the Natural Environment Research Council. It was commissioned in part by the Department of the Environment (Contract No. DGR 980/97).

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Date of final manuscript acceptance: October 6, 1978. Communicated by J. Mauchline, Oban