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Evidence for food-resource partitioning by kelp-bed filter feeders

V. Stuart[1] and D. W. Klumpp[2]

[1] Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa
[2] Biologische Anstalt Helgoland, Notkestraße 31, D-2000 Hamburg 52, Federal Republic of Germany

ABSTRACT: Particle-size selection was studied in 3 species of suspension feeding bivalves, an ascidian and a sponge, using a direct and an indirect technique. All 3 bivalve species retained particles > 4 μm with 100 % efficiency, while the retention of 0.6 μm cells dropped to approximately 20 %. In contrast, sponges showed the highest retention for the smallest particles and a declining efficiency for larger particles, suggesting an effective food resource partitioning on the basis of particle size between these 2 groups of animals. The ascidians, however, retained all particles > 0.6 μm with approximately 100 % efficiency. The sponges, were able to meet their entire carbon requirements by utilization of particles < 1 μm in diameter. This size fraction could only meet 5 to 21 % of the bivalves', and 17 % of ascidian carbon requirements, while free-living bacteria at a concentration of 0.5×10^6 ml^{-1}, provided 1 to 4 % of the bivalves' carbon requirements, 17 % of the sponges' and approximately 3 % of the ascidians' carbon requirements.

INTRODUCTION

Numerous studies have been undertaken on the retention of different-sized particles by various taxonomic groups of suspension feeding invertebrates, in an attempt to quantify the amount of particulate material utilized by these organisms. Most bivalve species have been found to retain completely all particles greater than 4 μm, while smaller particles are retained with a reduced efficiency (Jørgensen, 1966; Haven and Morales-Alamo, 1970; Vahl, 1972a, b 1973; Møhlenborg and Riisgård, 1978; Winter, 1978; Palmer and Williams, 1980). Similar results have been recorded for pelagic tunicates and ascidians, with particles greater than 1 to 4 μm in diameter being completely retained (Jørgensen and Goldberg, 1953; Harbison and McAlister, 1979; Randløv and Riisgård, 1979), whereas several species of sponges were found to retain very small particles (i.e. bacteria) with the greatest efficiency (Claus et al., 1967; Reiswig, 1971, 1975; Frost, 1978). In recent years there has been a continuing debate as to the significance of bacteria and other small particles as a food resource for marine animals, since small naturally occurring particles may dominate the particulate matter in coastal waters and bacterial numbers in the region of 10^5 ml^{-1} are commonly recorded (Jørgensen, 1966; Ferguson and Rublee, 1976; Sieburth, 1976; Linley and Field, 1982). Even though this fraction of the suspended material may be inefficiently retained by many suspension feeding organisms, it may nevertheless constitute an extremely large fraction of the food ingested. Studies on several suspension feeding invertebrates have shown that a significant proportion of their organic carbon could be obtained from the utilization of bacteria or small particles less than 1.5 μm in diameter (Reiswig, 1971, 1975; Sorokin, 1973; Simmons, 1979; Wright et al., 1982).

In many environments a large number of different suspension feeders occur in the same habitat, such as coral-reef communities, fouling communities or kelp-bed communities which may result in competition for specific-sized food particles. As might be anticipated from Gause's principle (1934) which states that no 2 species can occupy exactly the same niche, various co-occurring species have been found to partition their food resources in different ways. Fenchel et al. (1975) reported that 2 co-occurring deposit feeders, the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*, reduced competition by partitioning their food resources on the basis of the particle size frequency ingested, while Caine (1977) demonstrated that closely related species of filter-feeding amphipods

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do not utilize the same particles as a food resource, but either feed on different sized particles or filter at different heights from the substratum.

Apart from a preliminary study by Mook (1981) on the removal of suspended particles by an entire fouling community, little is known about the partitioning of resources by benthic filter-feeding communities. In the kelp-bed communities along the west coast of South Africa, the standing stocks of suspension feeders dominate the fauna and may represent up to 72 % of the total faunal biomass (Newell et al., 1982). The principle filter-feeding organisms are the mussel *Aulacomya ater,* the ascidian *Pyura stolonifera* and several species of sponges, all of which have overlapping zones of distribution (Velimirov et al., 1977). Intertidally, the mussel population is more diverse with species of *Choromytilus meridionalis, Perna perna* as well as *A. ater,* all occurring in similar habitats. The present study was therefore undertaken to investigate to what extent particle-size selection is implicated in the partitioning of the available food resources by the suspension-feeding invertebrates which characterize kelp-bed and adjacent intertidal communities, and whether under natural conditions, the carbon resources available in each of the size fractions selected are sufficient to meet the estimated consumption requirements of the filter-feeding community.

MATERIAL AND METHODS

Collection of animals

All 3 species of mussel were collected intertidally from a reef at Bloubergstrand, in Table Bay near Cape Town on the west coast of South Africa, and transported to the laboratory where they were kept in flowing seawater at 12 °C for up to 1 wk. Their shells were cleaned of all encrusting organisms, care being taken to retain the byssus attachments of each mussel to a neighbouring shell, which was subsequently sacrificed.

Numerous species of sponges occur subtidally in the kelp beds at Oudekraal on the west coast of the Cape Peninsula, just south of Cape Town (34°S, 18°E), among which is the common encrusting demosponge *Haliclona anonyma,* which was selected for experimentation on account of its abundance as well as its large exhalent oscula. These sponges are commonly attached to the rocks by means of corraline algae (octocorralia) which grow through the sponge matrix. Specimens were collected from a depth of approximately 10 m, by carefully severing the coralline algae attaching small isolated communities to the rocks using a broad flattened scraper, ensuring that no damage was done to the sponge tissue during removal. Specimens were transferred into a container underwater, which was subsequently surrounded by crushed ice to maintain the water temperature at approximately 12 °C. Sponges were then returned to the laboratory where they were kept in flowing seawater for no longer than 2 d before being used for experimentation.

Ascidians were collected from the same locality at Oudekraal by carefully removing the tests from the substratum with a broad scraper. The animals were returned to the laboratory where they were kept in flowing seawater supplied with 10×10^6 *Dunaliella primolecta* cells for at least 1 d before being used in experiments. MacGinitie (1939) and Jørgensen and Goldberg (1953) have shown that in undisturbed ascidians, the straining of particles was performed by continuous sheets of mucus produced by the endostyle, but when disturbed, the ascidians cut off the secretion of the mucus sheet with the result that only larger particles were filtered by the ostia. Preliminary experiments with *Pyura stolonifera* showed that small particles only were efficiently retained at least 1 d after collection, indicating that by this time continuous mucus sheets were being secreted.

Particles in the field

Total concentration and size distribution of suspended particulate material in the water column at Oudekraal vary a great deal with wave action and upwelling conditions (Field et al., 1980), and can be measured by analysing water samples after periods of upwelling (S.E. winds) or downwelling (N.W. winds). On each occasion, water samples collected by SCUBA divers from the vicinity of a bed of suspension feeders, were counted on a Coulter Counter (Model TA II) using both the 70 and 280 µm aperture orifice tubes. Total dry mass of suspended material was obtained by filtering 1 l of seawater through a pre-ashed GF/C filter and drying in an oven at 70 °C for 2 d. Bacterial numbers were estimated using the acridine orange direct count (AODC) technique after Linley et al. (1981); bacterial biomass was calculated assuming a mean bacterial volume of 0.2 μm^3 (Linley, pers. comm.).

Carbon and nitrogen content of the different size fractions of the particulate material were obtained by filtering up to 10 l of seawater through a series of 63, 30, 20 and 10 µm sieves and by backwashing the particulate material collected on each sieve onto a pre-ashed GF/C filter with 0.2 µm filtered distilled water. For the smaller size fractions, water samples were filtered onto a series of 5, 3, 1 and 0.4 µm Nuclepore

polycarbonate membrane filters, which were subsequently rinsed in 0.2 μm filtered distilled water to remove particulate material, and the water filtered onto a GF/C filter. The filters were dried in an oven at 70 °C for 2 d, after which the carbon and nitrogen content of triplicate 4.7 mm discs punched from each filter were determined on a Carlo Erba elemental analyser (Model 1106), using a cyclohexanone standard. Corrections for dissolved organic carbon were made by subtracting the carbon content of a blank disc punched from the perimeter of each filter. Sample volume and filter area were used to calculate the total carbon and nitrogen concentration of each size fraction.

Particles used in experiments

Particle size distributions in the water column range from small bacterial cells (0.5 μm) to particles up to 125 μm in diameter, with the greatest volume of material always being recorded in the 10 to 20 μm diameter range (p. 30). Since over 80 % of all particulate material (by volume) falls in the size range 0.5 to 20 μm, experimental particles were chosen to cover this range. Four different species of spherical algal cells covered a broad size range of diameters, from 1.6 to 16 μm, while 2 strains of coccoid bacteria were used to include the smaller size range of particles from 0.5 to 1.6 μm (Table 1). Bacterial cells of approximately 1 μm in diameter (M1-01) were isolated from decomposing kelp debris and cultured at 20 °C in a seawater broth consisting of 1 g yeast extract and 5 g peptone l^{-1}; freeze-dried *Micrococcus lysodeikticus* cells (SIGMA) were used to represent particles of approximately 0.6 μm in diameter. Stock solutions were prepared by suspending 60 mg freeze-dried cells in 1 ml 0.06 M phosphate buffer (pH 6.4). A large proportion of these cells were in a state of division, ensuring rapid identification during microscopic counting, as well as a range of sizes from 0.5 to 0.8 μm in diameter.

Table 1. Particles used for size-selection experiments, with minimum and maximum diameters (μm) for each species

Particle	Range of diameters (μm)
BACTERIA	
Micrococcus lysodeikticus	0.5– 0.8
M1–01	0.9– 1.6
ALGAE	
Chlorella sp.	1.6– 2.5
Pseudoisochrysis paradoxa	2.5– 4
Dunaliella primolecta	4.0– 6.35
Tetraselmis chuii	8.0–16

Experimental procedure

Particle-size selection by filter feeders can be measured both directly, by comparing the size distribution of particles in the inhalent and exhalent currents, or indirectly by measuring the relative changes in proportions of different sized particles after a fixed period of time in a closed system. Since the direct method avoids the problem of proportional changes in different sized particles due to filtration by experimental animals, the results obtained may be more reliable, although this method may be unsuitable for some suspension feeders due to difficulty in isolating the inhalent and exhalent currents. The direct method of measuring particle retention efficiency was tested on the ascidian, the sponge and the mussel *Choromytilus meridionalis*. Animals were repeatedly rinsed in 0.45 μm filtered seawater to remove all particulate debris, and then allowed to acclimate overnight in filtered seawater at 12 °C. During this time, 2 glass tubes were positioned over the animals' exhalent siphon and in the path of the inhalent current. In the case of the sponge and ascidian, the glass tube had a diameter of 5 mm which was widened at the end to 15 mm to fit neatly over the animals' exhalent osculum or siphon. In the case of the mussel, a 4 mm diameter glass tube was used, which was flattened at the end to 10 × 4 mm to fit over the exhalent aperture. Flexible plastic tubing was connected to each glass tube to enable water samples to be carefully siphoned off.

At the initiation of each experiment, density and mean cell volume of each algal culture were measured on the Coulter Counter. An equal concentration (by volume) of each algal species, and approximately 10^6 ml^{-1} bacteria, was added to the experimental vessels at a final concentration of approximately 3 mg l^{-1} (dry mass), which is equivalent to the annual mean dry mass of particulate matter in the seawater at Oudekraal (Stuart, 1982). After an equilibration period of 5 min, 50 ml water samples were siphoned off at a rate of 3 to 5 ml min^{-1}, and the particle size distribution of inhalent and exhalent samples was recorded on the Coulter Counter using a 70 μm aperture tube. Samples for bacterial analysis were preserved in 2.5 % glutaraldehyde, and cell numbers were estimated using the AODC technique. Corrections were made for production of particles, by placing the animals in 0.45 μm filtered seawater and recording any increase of particles in the exhalent current. The fraction of each size class retained was then calculated using the formula $1–C_e/C_i$ (Palmer and Williams, 1980), where C_e = concentration of particles in the exhalent current; C_i = concentration in the inhalent current. In all experiments with mussels and ascidians, maximal retention was attained with *Dunaliella primolecta* cells (4 to

6.35 μm); it was assumed therefore that retention of larger cells was constant, and *Tetraselmis chuii* cells were not used in these experiments. However, due to a declining retention with particle size in the sponge experiments, the larger algal cells were included in the food source. The retention efficiency for each size class was then expressed relative to the particles which showed maximal retention (i.e. *D. primolecta cells* for mussels and ascidians, and *Micrococcus lysodeikticus* cells for sponges).

Experiments on the sponges, as well as on all 3 species of mussel, were repeated using the indirect technique, due to difficulties in isolating the exhalent current. For these experiments, each animal was placed on a mesh-covered grid suspended in 1.5 l 0.45 μm filtered seawater circulated with a magnetic stirrer, and allowed to equilibrate at 12 °C overnight. Appropriate volumes of algal cells and bacteria were then added, and samples were removed for Coulter Counter analysis and bacterial counts. Successive samples were removed at 30 min intervals, and the decline in particle numbers recorded. Results were corrected for settling and division of cells using control beakers containing food only, while beakers containing animals in filtered seawater were used to correct for any production of particles by the animals.

RESULTS

Particles in the field

Variation in particle-size distribution of water samples collected from Oudekraal under different environmental conditions are shown in Fig. 1. Results have been expressed in ppm by volume (obtained from the product of the geometric mean volume and particle numbers) and plotted against the $\log_{10}$ of the mean particle diameter for each channel (Strickland and Parsons, 1972).

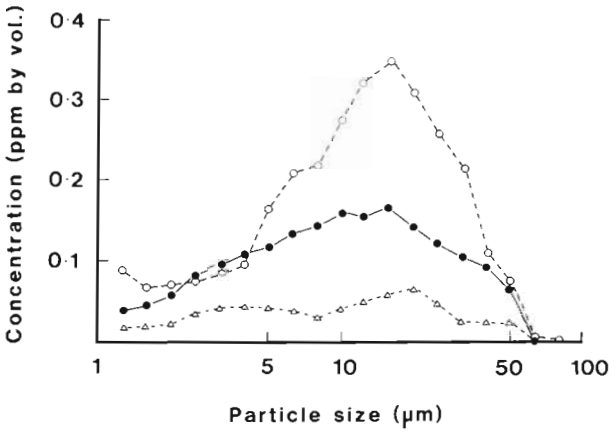

Fig. 1. Particle-size distribution of suspended particulate material in the water column at Oudekraal under different environmental conditions (△ after SE wind, 0.95 mg l^{-1} dry mass, bacteria = 0.14×10^6 ml^{-1}; ● after NW wind, 2.74 mg l^{-1} dry mass, bacteria = 0.34×10^6 ml^{-1}; ○ after rough seas, 7.33 mg l^{-1} dry mass, bacteria = 3.00×10^6 ml^{-1})

Carbon and nitrogen concentrations (μg l^{-1}) of the different size fractions of suspended particulate material, obtained from a water sample containing 7.33 mg l^{-1} dry mass are shown in Table 2. The total carbon and nitrogen concentration for a sample containing 2.74 mg l^{-1} dry mass suspended material, which is representative of the average annual concentration of particulate matter at Oudekraal (Stuart, 1982), is also indicated.

Table 2. Mean carbon and nitrogen concentration (± S.D.) of different size fractions of suspended particulate material in the water column at Oudekraal, obtained from a sample containing a total dry mass of 7.33 mg l^{-1}. Total carbon and nitrogen concentration of the sample before size fractionation, as well as that of a sample containing 2.74 mg l^{-1} dry mass, which is similar to the annual mean concentration of particulate material (Stuart, 1982), is also shown

Particle-size fraction (μm)	μg C l^{-1} (± S.D.)	μg N l^{-1} (± S.D.)	C : N (± S.D.)
< 0.4	69.84 (± 20.38)	11.38 (± 2.24)	6.06 (± 0.74)
0.4– 1	111.16 (± 12.07)	15.11 (± 1.59)	7.34 (± 0.46)
1 – 3	112.24 (± 10.67)	19.38 (± 2.73)	5.77 (± 0.30)
3 – 5	73.44 (± 4.41)	9.79 (± 1.03)	7.58 (± 1.44)
5 – 10	165.19 (± 5.23)	25.81 (± 0.90)	6.40 (± 0.03)
10 – 20	115.97 (± 1.48)	17.37 (± 0.44)	6.68 (± 0.09)
20 – 30	79.81 (± 2.16)	10.20 (± 0.04)	7.79 (± 0.17)
30 – 63	175.98 (± 8.94)	17.69 (± 1.08)	9.95 (± 0.22)
63 –125	143.89 (± 37.52)	12.44 (± 3.20)	11.61 (± 1.05)
Unfractionated sample (7.33 mg l^{-1} dry mass)	1091.07 (± 45.32)	129.47 (± 9.42)	8.45 (± 0.31)
Unfractionated sample (2.74 mg l^{-1} dry mass)	416.04 (± 21.39)	61.51 (± 4.57)	6.77 (± 0.25)

Retention of different-sized particles by bivalves

The apparent retention of different sized particles by the bivalve *Choromytilus meridionalis,* determined by using both the direct and indirect technique, and expressed relative to the retention of *Dunaliella primolecta* cells, is shown in Fig. 2. The direct technique yielded a 42 to 94 % retention of *D. primolecta* cells, lower values indicating incomplete separation of the exhalent current in some experiments, and thus contamination of these samples by cells in the surrounding water. It should be noted, however, that the results of the two techniques are nevertheless comparable.

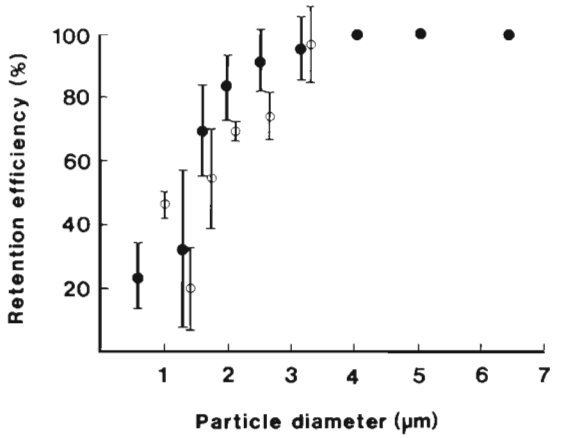

Fig. 2. Retention efficiency (%) of different-sized particles by the mussel *Choromytilus meridionalis* expressed relative to the retention of *Dunaliella primolecta* cells (4 to 6.35 μm), and measured using direct (●) and indirect (○) techniques. Bars: standard deviation of each measurement

Retention efficiencies for the bivalves *Aulacomya ater* and *Perna perna,* measured by using the indirect technique, are illustrated in Fig. 3 and 4. Under these food conditions all 3 bivalve species exhibit very similar trends, retaining particles greater than 4 μm with an apparent efficiency of 100 %, while the retention of the smallest bacterial cells (0.6 μm) dropped to approximately 20 %. Similarly, most other bivalve species retain 100 % of particles greater than 4 μm, and may retain up to 50 % of particles 1 μm in diameter (Haven and Morales-Alamo, 1970; Vahl, 1972a, b, 1973; Jørgensen, 1975; Møhlenberg and Riisgård, 1978), although the bivalve *Geukensia demissa* retains bacterial cells in the size range 0.4 to 0.6 μm with an efficiency of 86 % (Wright et al., 1982).

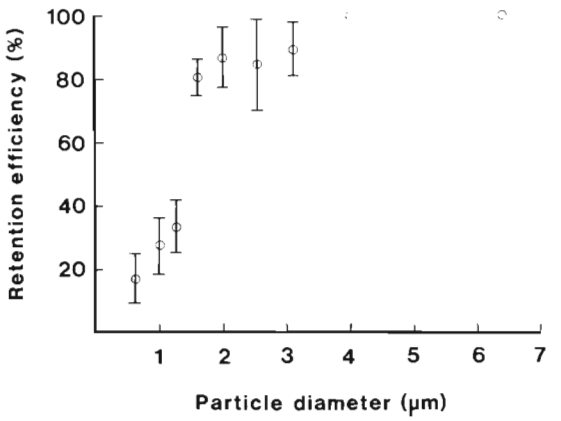

Fig. 3. Retention efficiency (%) of different-sized particles by the mussel *Aulacomya ater* expressed relative to the retention of *Dunaliella primolecta* cells (4 to 6.35 μm) and measured using the indirect technique. Bars: standard deviation of each measurement

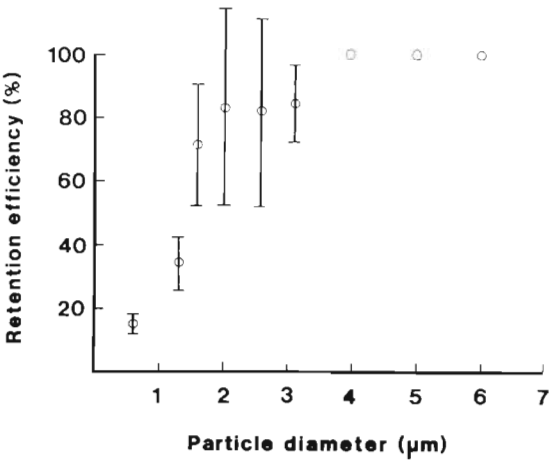

Fig. 4. Retention efficiency (%) of different-sized particles by the mussel *Perna perna* expressed relative to the retention of *Dunaliella primolecta* cells (4 to 35 μm) and measured using the indirect technique. Bars: standard deviation of each measurement

On the basis of particle size alone, it would appear that all 3 bivalve species would be competing for the same food resource; such competition might be minimized in the field where the species are generally spatially separated, with *Aulacomya ater* occurring mostly subtidally, and *Perna perna* and *Choromytilus meridionalis* intertidally.

Retention of different-sized particles by ascidians

Maximal retention efficiencies were obtained by *Pyura stolonifera* with *Dunaliella primolecta* cells (94 to 99 % retention using the direct method), although the retention of all other particle sizes was also very high (Fig. 5). Fiala-Médioni (1978) also recorded relatively high filtering efficiencies (65 to 90 %) with 3 species of benthic ascidians fed on the algae *Monochrysis lutheri,* although the results may have been underestimated due to the technique used. From Fig. 5 it can be seen that *P. stolonifera* is a non-selective filter

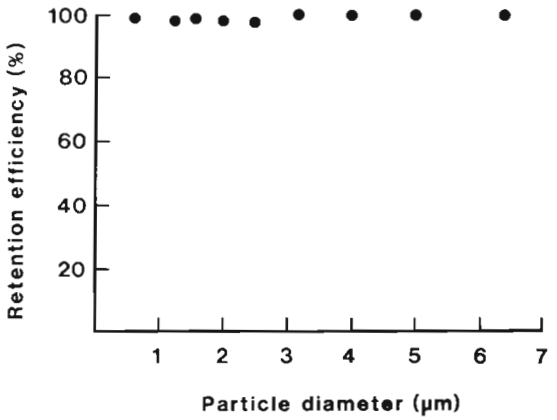

Fig. 5. Retention efficiency (%) of different-sized particles by the ascidian *Pyura stolonifera* expressed relative to the retention of *Dunaliella primolecta* cells (4 to 6.35 µm) and measured using the direct technique. In all cases, standard deviations were smaller than the size of the dots

feeder, removing all particles very efficiently even down to the smallest bacterial cells. As is well known, ascidians trap particles using a continuous mucus sheet (Jørgensen, 1966); this would explain the non-selective nature of feeding and the high retention efficiencies recorded. Harbison and McAlister (1979) found that pelagic tunicates could remove particles of approximately 4 µm and larger with 100 % efficiency, while Randløv and Riisgård (1979) reported that particles 2 to 3 µm in diameter were completely retained by 4 different species of ascidians. However, they recorded lower retention efficiencies for smaller particles than in *P. stolonifera*. This suggests that *P. stolonifera* is capable of producing a much finer, and therefore more efficient mucus mesh than other species of ascidians.

Retention of different-sized particles by sponges

Haliclona anonyma showed the greatest retention for *Micrococcus lysodeikticus* cells with efficiencies ranging from 85 to 99 %, measured by using the direct method. Similarly, numerous investigators have reported that other species of marine and freshwater sponges are capable of efficiently filtering out bacterial cells from the water column (Claus et al., 1967; Madri et al., 1967; Reiswig, 1971, 1975). Retention of different-sized particles by *H. anonyma*, expressed relative to the retention of *M. lysodeikticus* cells, is shown in Fig. 6. There is a sharp decline in retention efficiency for particles 2 to 4 µm in diameter, after which efficiencies increased again. This phenomenon was observed in all experiments (n = 20) using both direct as well as indirect techniques. These results suggest either a selection of particles < 2 µm and

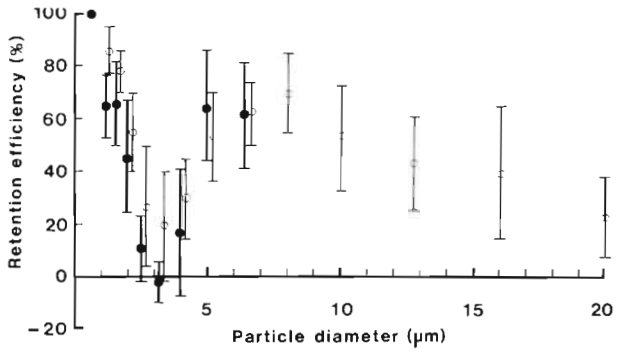

Fig. 6. Retention efficiency (%) of different-sized particles by the sponge *Haliclona anonyma* expressed relative to the retention of *Micrococcus lysodeikticus* cells (0.6 µm) and measured using the direct (●) and indirect (○) techniques. Bars: standard deviation of each measurement

> 4 µm, or a production of particles in the 2 to 4 µm size range, which would have the effect of reducing the apparent retention efficiency in this size range.

Monitoring the decline in total particle number with time (Fig. 7) reveals a gradual increase in particles in

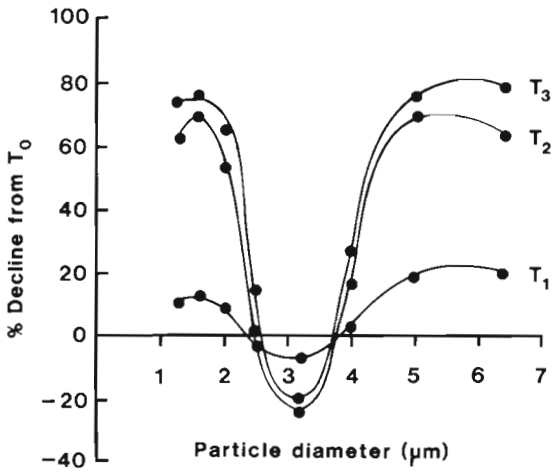

Fig. 7. Percentage decline (from T_0) in particle numbers of different sizes as a result of filtering activity by the sponge *Haliclona anonyma*, measured at 3 consecutive time intervals. Negative results indicate production of particles by the sponge

the 2 to 4 µm range, with a corresponding decrease in particles < 2 µm and > 4 µm, indicating a production of 2 to 4 µm particles by the sponge. This was verified in a single experiment in which a sponge fed a high concentration of bacterial cells ceased all filtration activity (Ankel, 1949), but there was a noticeable increase in particles in the 2 to 4 µm size range (Fig. 8). Microscopic analysis of exhalent water samples revealed numerous detrital particles, probably breakdown products of digestion, which could be the source of these particles. Reiswig (1971) also found a net

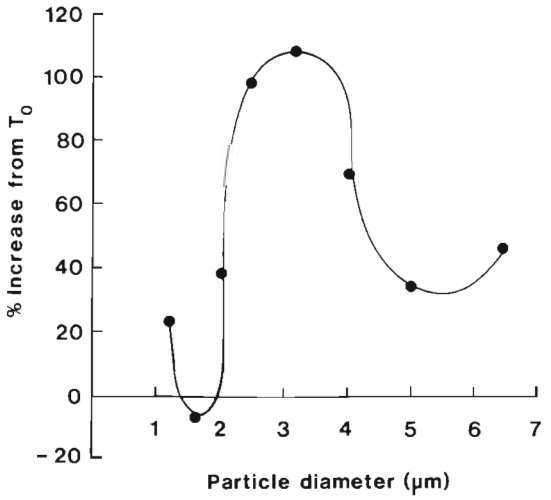

Fig. 8. Production of particles of different sizes by the sponge *Haliclona anonyma*, expressed as percentage increase from T_0

production of detrital particles, mainly in the 2.5 to 4.5 μm size range, by 3 species of marine demosponges. Retention efficiency of particles between 2 and 4 μm by *Haliclona anonyma* can therefore be obtained by extrapolation of results between these points in order to avoid the problem of particle production.

Retention efficiencies by *Haliclona anonyma* suggest that these sponges can efficiently retain small particles less than 1 μm in diameter, while larger particles are less efficiently retained. Johnston and Hildemann (1982) have shown that there are potentially 4 structural levels at which the marine demosponge *Callyspongia diffusa* could discriminate between suspended particulate matter on the basis of particle dimension. There is an upper limit of 50 μm for particles entering the sponge, reduced canal diameter (25 μm) then restricts larger particles, while particles down to approximately 1 μm are filtered from the feeding current by the bases of the choanocytes, and finally the microvilli of each choanocyte collar filter particles down to 0.1 μm. Fig. 6 suggests that the choanocyte filtering system is the major method used by *H. anonyma* to capture food particles. Similarly, Reiswig (1971) showed that the choanocyte capture system supplied approximately 81.4 % of the total particulate organic carbon in the diet of marine demosponges.

Since *Haliclona anonyma* relies mainly on small particles (< 1 μm) for its diet, this implies that the sponges are not competing directly with the mussels for their food. It is also of interest to note that the detrital particles produced by the sponges fall in the size range which can be utilized efficiently by the mussels, suggesting that it might be mutually beneficial for these 2 species to have overlapping zones of distribution.

Estimation of filtration rates by sponges

Filtration rates can be calculated from the decline in cell numbers with time, using the standard formula:

$$\text{Filtration rate } (\text{l h}^{-1}) = \frac{\log_e N_o - \log_e N_1}{t} \times V \quad (1)$$

where N_o = number of particles at t_o; N_1 = number of particles at t_1; t = time in hours; V = volume of container in litres.

Sponge filtration rates were calculated using bacterial cells (since these were retained with approximately 100 % efficiency); the rates at different bacterial concentrations are shown in Fig. 9. There is an

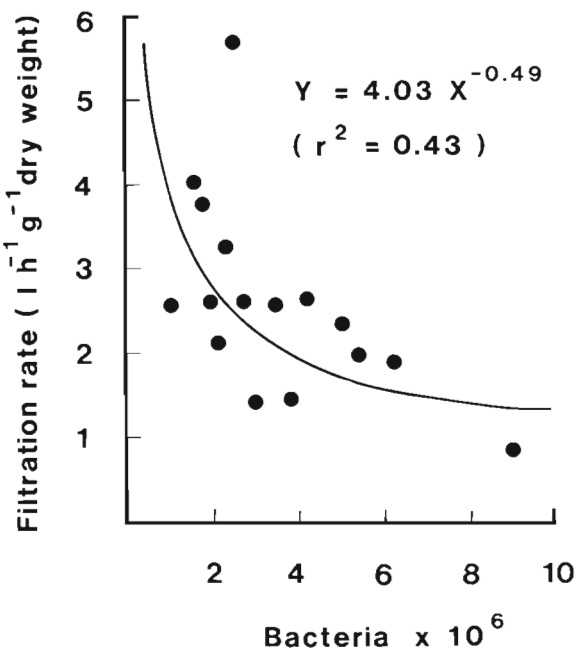

Fig. 9. Filtration rate (l h^{-1} g^{-1} dry weight) of the sponge *Haliclona anonyma* at different bacterial concentrations

inverse relation between cell concentration and filtration rate, which may be caused by the contraction of some of the flagellated chambers at high food concentrations, to protect against over-feeding (Ankel, 1948). The average filtration rate of 5.66 l h^{-1} g^{-1} dry weight by *Haliclona anonyma* at a bacterial concentration of 0.5×10^6 ml^{-1}, which is similar to the mean concentration recorded at Oudekraal (Linley and Field, 1982), falls well within the range of values reported for other sponge species (Frost, 1978). It is noteworthy that filtration rates calculated using the decline in the larger algal cells with time were substantially lower than those recorded using bacterial concentrations, which may be attributed to the lower retention efficiencies of these cells.

DISCUSSION

A generalized model of the relative proportion of different-sized particles retained by the 3 major groups of suspension-feeding organisms, derived from all direct and indirect experiments, is shown in Fig. 10. It

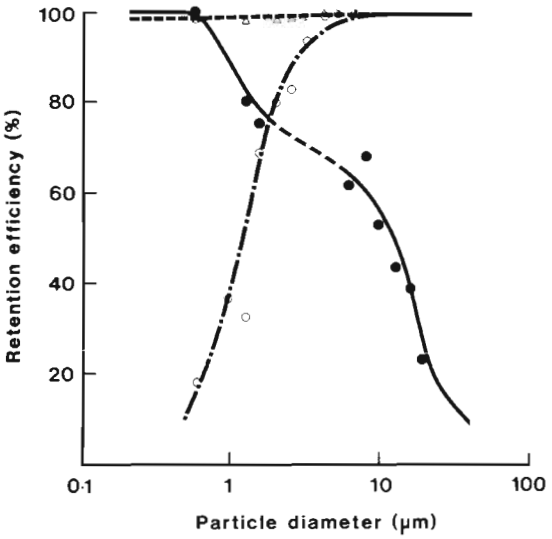

Fig. 10. Comparative retention efficiencies (%) of different-sized particles by the 3 mussels (○), the sponge (●) and the ascidian (△) calculated from mean results of direct and indirect measurements for each group of animals. For the sponge, results have been extrapolated between 2 and 5 μm because of the production of particles in this size range

is evident that there is little overlap in the size of particles retained by bivalves and sponges, suggesting an effective food-resource partitioning between these 2 groups of animals, thus reducing competition in areas with high densities of both species. Furthermore, particles released by the sponges are in a size range which may be subsequently available as a food source for the mussels (p. 32), indicating that a mixed assemblage of sponges and bivalves may be able to utilize the suspended material more efficiently than a single-species population, due to recycling of some of the food particles. It is also apparent that the ascidians are capable of effectively removing all size fractions of the particulate material and thus appear to compete directly with both bivalves and sponges. However, interspecific competition may be minimized in the field due to general spatial separation of ascidians from the other groups of suspension feeders, since *Pyura stolonifera* is largely confined to exposed areas with strong currents and turbulence, while the bivalves and sponges are often found in more protected areas.

Taking into account the retention efficiencies of different-sized particles by the experimental animals (Fig. 10), it is now possible to estimate the amount of carbon and nitrogen ingested from each size fraction of suspended particulate material in the field, using the data in Table 2. Assuming the relative proportion of carbon and nitrogen in each size fraction remains constant, the values presented in Table 2 for a sample containing 7.33 mg l^{-1} dry mass can be adjusted to that of a sample containing 2.74 mg l^{-1} dry mass, which is representative of the annual mean concentration of suspended particulate material at Oudekraal (Stuart, 1982). The carbon and nitrogen concentrations thus obtained, multiplied by the retention efficiency (Fig. 10) and filtration rate for a standard animal of 1 g dry mass (Table 3) are presented in Table 4. These values can now be compared to the minimum amounts

Table 3. Filtration (1 h^{-1} g^{-1} dry weight) and respiration rates (ml O_2 h^{-1} g^{-1} dry weight) of experimental animals

Animal	Filtration rate (1 h^{-1} g^{-1})	Conditions	Source	Respiration rate (ml 0_2 h^{-1} g^{-1})	Conditions	Source
Aulacomya ater	1.82	12 °C: 3 mg l^{-1} (d.wt.) kelp particles	Stuart (1982)	0.30	12 °C	Stuart (1982)
Perna perna	8.85	20 °C	Schleyer (1980)	0.37	18 °C	Schleyer (pers. comm.)
Choromytilus meridionalis	5.37	12 and 18 °C, 10×10^6 cells ml^{-1}	Griffiths (1980)	0.43	12 °C	Griffiths (1980)
Pyura stolonifera*	0.49	13 °C	Klumpp (unpubl.)	0.14	13 °C	Klumpp (unpubl.)
Haliclona anonyma	5.66	12 °C; 0.5×10^6 cells ml^{-1} (bacteria)	Present study	0.27	–	Jørgensen (1966)

* Filtration and respiration rates are independent of food concentration

Table 4. Concentration of carbon and nitrogen ingested by experimental animals (standard dry mass of 1 g) from different size fractions of particulate material up to 20 μm. Data for each experimental animal were obtained from the sum of filtration rate (Table 3), retention efficiency (Fig. 10) and carbon and nitrogen concentrations (Table 2), assuming a total dry mass of suspended material of 2.74 mg l^{-1}

Particle-size fraction (μm)	μg carbon and nitrogen ingested (h^{-1} g^{-1} dry weight)									
	A. ater		*C. meridionalis*		*P. perna*		*P. stolonifera*		*H. anonyma*	
	C	N	C	N	C	N	C	N	C	N
< 0.4	2.42	0.49	7.15	1.45	11.78	2.39	12.65	2.57	150.72	30.62
0.4– 1	19.29	3.27	56.90	9.63	93.78	15.88	20.39	3.45	220.73	37.39
1 – 3	54.53	11.73	160.88	34.61	265.14	57.03	20.74	4.46	181.69	39.10
3 – 5	49.94	8.29	147.37	24.48	242.86	40.34	13.72	2.28	110.94	18.42
5 –10	114.64	22.31	338.25	65.85	557.45	108.52	30.86	6.00	217.48	42.33
10 –20	80.48	15.01	237.47	44.32	391.34	73.03	21.67	4.04	100.11	18.68
Total (μg h^{-1})	321.30	61.10	948.02	180.34	1562.35	297.19	120.03	22.80	981.67	186.54

of carbon required by each animal to cover normal metabolic and growth costs. According to Jørgensen (1955), the food requirements of various suspension feeders during optimal growth are 3 to 4 times greater than indicated by the metabolic rate, so the respiration rates presented in Table 3 have been multiplied by a factor of 3 to cover the amount of food needed for growth (Table 5).

It can be seen that the carbon requirements of all the animals examined can be adequately met by the utilization of particles up to 20 μm in diameter, although it should be borne in mind that only a portion of this carbon may become available to the organisms since some of the particulate material (e.g. detritus) may be difficult to digest. The mussel *Aulacomya ater* absorbs approximately 50 % of kelp detritus (Stuart et al., 1982) while preliminary experiments on *Pyura stolonifera* indicate that only 34 % of kelp detritus can be absorbed (Klumpp, unpubl.). It is interesting to note that the entire carbon requirements of the sponge *Haliclona anonyma* may be potentially met by utilization of the size fraction < 1 μm in diameter, which can be attributed to the high retention efficiencies of these particles (Fig. 10). It is further evident that since only 6 to 20 % of the mussels' carbon requirements can be met by this size fraction due to their low retention efficiency, these animals would have to rely on the presence of larger particles to balance energy costs.

Some indication of the importance of free-living bacteria as food source for suspension-feeding animals can be obtained by using a mean bacterial concentration of 0.5×10^6 ml^{-1} (Linley and Field, 1982), a mean volume of 0.2 μm^3 (Linley, pers. comm.) and assuming the carbon content of bacteria to be 50 % of their dry biomass (Sorokin and Kadota, 1972). Under these conditions free-living bacteria can only provide 1 to 3.6 % of the mussels' and ascidians' carbon requirements, and 17 % of the sponges' carbon requirements (Table 5). Therefore free-living bacteria do not appear to be a major carbon source for most groups of suspension feeders. However, during periods of high bacterial numbers (e.g. 3×10^6 ml^{-1}; Fig. 1), free-living bacteria alone could potentially meet the entire carbon requirements of sponges and up to 30 % of that of the mussels and ascidians.

Few data are available on the utilization of nitrogen by these animals, and their actual requirements are difficult to assess since they vary greatly with season as

Table 5. Carbon requirements of experimental animals (1 g standard dry mass) obtained from metabolic rates (Table 3) multiplied by a factor of 3 for optimal growth (Jørgensen, 1955), using a conversion of 1 ml O_2 = 458 μg Carbon (Jørgensen, 1955). Carbon obtained from free bacteria at a concentration of 0.5×10^6 ml^{-1} is indicated, assuming a carbon content of 50 % of the dry mass (Sorokin and Kadota, 1972), and a mean bacterial volume of 0.2 μm^3 (Linley, pers comm.). The percentage of C requirements met by free bacteria and the size fraction < 1 μm are also shown

Requirements	*A. ater*	*C. meridionalis*	*P. perna*	*P. stolonifera*	*H. anonyma*
C required (μg h^{-1} g^{-1})	412.20	590.82	508.38	192.36	368.23
% requirements met by < 1 μm fraction	5.27	10.84	20.76	17	100
C from bacteria 0.5×10^6 ml^{-1} (μg h^{-1} g^{-1})	3.72	10.99	18.11	5.28	62.26
% requirements met by bacteria	0.90	1.86	3.56	2.70	16.91

well as growth and reproductive conditions (Bayne and Widdows, 1978). However, it is evident that the smaller particles are richer in nitrogen (Table 2), suggesting that suspension feeders could optimize their nitrogen uptake by retention of particles less than 20 μm in diameter.

In summary, particle size appears to play an important role in the partitioning of food resources between at least 2 of the major groups of suspension-feeding organisms in the kelp bed environment, while spatial separation can be an important factor in reducing competition between species which are able to utilize overlapping size fractions of particulate material.

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