

Particle size, flow velocity, and suspension-feeding by the erect bryozoans *Bugula neritina* and *B. stolonifera*

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Abstract

Patterns of feeding by the erect bryozoans *Bugula neritina* and *B. stolonifera* were studied by assessing ingestion rates of mixtures of polystyrene particles of three sizes present in equal densities at two ambient water-flow velocities. Particle size was found to influence feeding by *B. neritina*, while feeding by *B. stolonifera* was influenced by an interaction between particle size and flow velocity. Large and medium-sized particles were ingested at rates disproportionate to their numerical abundance, and small particles were always ingested in low numbers. Disproportionate feeding did not appear to be due to the greater likelihood of directly intercepting or of detecting particles of larger sizes, but may be explained by other size-dependent particle behaviors, active selection or rejection by the bryozoans, and/or the utilization of different feeding techniques. Comparison with a parallel study indicated that patterns of feeding on single-sized suspensions cannot be used to predict patterns of feeding on mixed suspensions. This is one of the few studies to test the combined influence of variation in both suspended particulate matter and in properties of the fluid medium. Such investigations will provide more realistic views of suspension-feeding performance.

Introduction

The influence of variation in suspended material on patterns of suspension-feeding has been the focus of many investigations. Particular emphasis has been placed on patterns of feeding selectivity in response to such particle characteristics as: size (e.g. Miller 1984, Schröder 1987, Johnsen and Borsheim 1988), taste (Poulet and Marsot 1978, Rassoulzadegan et al. 1984, DeMott 1986), motility (Gilbert and Bogdan 1981), food value (Newell and Jordan 1983, Shumway et al. 1985, Thorpe et al. 1986) and concentration (Berman and Richman 1974, Richman et al. 1977), and surface chemistry (LaBarbera 1978, Gerritsen and Porter 1982).

The influence of variation in characteristics of the fluid medium on suspension-feeding has received substantially less investigation. The wide range of flow regimes associated with tides, ambient currents, and waves is a particularly striking source of variation experienced by many suspension-feeders. The effect of flow on suspension-feeding by benthic organisms has been the focus of recent investigation (Okamura 1984, 1985, 1987, Patterson 1984, McFadden 1986, Braimah 1987, Leonard et al. 1988, Hunter 1989). However, the combined influence of variation in flow and in the composition of suspended material on patterns of suspension-feeding has received scanty attention. For exceptions see Muschenheim's (1987a, b) studies of spionid polychaete feeding-responses to variation in particle quality arising from differential flows within the boundary layer and Leonard's (1989) study showing the importance of the interaction between particle concentration and current velocity in crinoid feeding. The purpose of the present study was to investigate the combined influence of variation in the size of suspended particles and in fluid flow on suspension-feeding performance of bryozoans. Specifically, I quantified feeding under two ambient flow-velocities on mixtures of polystyrene particles of varying size by the two co-occurring, arborescent bryozoans, *Bugula neritina* and *B. stolonifera*.

Bryozoans feed by means of a ciliated crown of tentacles, the lophophore. Feeding currents produced by cilia on the tentacles of the lophophore enter the lophophoral region from above and exit near the base of the tentacles. Many bryozoans appear to utilize several feeding techniques. Purely ciliary feeding involves local ciliary reversals that redirect particles towards the mouth at the base of the tentacles (Strathmann 1982). At very high particle concentrations, bulk ingestion of small particles in incoming feeding currents may be important (Best and Thorpe 1983). In addition, varying degrees of tentacular activity appear to be involved with feeding. These can range from individual tentacular flicks directing particles to the mouth, to engagement of larger particles by all the tentacles of the lophophore (Winston 1978, Okamura 1987).

Materials and methods

Colonies of the arborescent cheilostomes *Bugula neritina* and *B. stolonifera* are common fouling organisms. In Florida (USA) colonies are found on seagrasses, oyster shells, docks, canal walls, floats, rotting wood, algae, coastal rock ledges, and inlet breakwaters (Winston 1982). Both species are widespread. *B. stolonifera* is the smaller species in both colony and zooid dimensions (Ryland and Hayward 1977, Winston 1982), and is often found attached and growing within *B. neritina* colonies. In this study, colonies of *B. neritina* and *B. stolonifera* were collected from the floating docks of the Harbor Branch Oceanographic Institution at Link Port, Florida, from February to early June 1986.

Experimental protocol

Feeding experiments were performed by submerging colonies in a recirculating flow-tank (Vogel and LaBarbera 1978) in which currents of known velocities could be created in the working section (13 cm × 13 cm × 13 cm). The flow-tank contained suspensions of polystyrene particles of varying sizes (polystyrene divinylbenzene calibration particles; Duke Scientific Corporation, Palo Alto, California). These are non-ionic, chemically inert particles, and thus present no surface charge that might influence capture success (LaBarbera 1978, Gerritsen and Porter 1982). Initial observations indicated that the bryozoans would ingest these particles in large numbers. The mean diameters of particles employed were 14.6 (SD = 1.0), 19.1 (SD = 1.1), and 9.6 (SD = 0.5) μm . Feeding was assessed on mixed suspensions in which particles of all three sizes were present in equal numbers. The total concentration of particles was set at 100 particles/ml at the outset of experiments by adding appropriate volumes of stock suspensions of known concentrations to a known volume of filtered seawater in the flow tank. High turbulence in the return pipes of the flow tank provided homogeneous mixing of the three particle sizes. A concentration of 100 particles/ml lies well within the range of natural concentrations of flagellates which are thought to be important components of bryozoan diets (e.g. Jørgensen 1966, Bullivant 1968). The size range of flagellates is approximately 8 to 20 μm .

Feeding was assessed at two freestream flow velocities; a relatively slow flow (1 to 2 cm/s) and a relatively fast flow (10 to 12 cm/s). Flow velocities in this range have been measured in the field at the level of the branch tips of *Bugula stolonifera* with an electromagnetic flow meter (Marsh McBirney No. 523) (Okamura 1984). The actual flow velocities at bryozoan feeding-surfaces were not measured. Measuring flows in the vicinity of organisms requires using equipment that was unavailable (e.g. heated-bead thermistor probes or laser doppler flow meters).

Portions of colonies (approximately 1.5 to 2.0 cm in length and with 8 to 15 branch tips) were used in all experiments. Clipping colonies does not affect feeding activity (Okamura 1984). Colonies were suspended in the flow tank

from a thin wooden stick (2 mm diam), with their distal branches facing down (an orientation of many colonies in nature). Colonies were allowed to feed for 20 min (two replicate colonies per run), and were then removed from the flow tank and placed in dilute sodium hypochlorite to dissolve the organic contents and facilitate counting the particles ingested by individual zooids during experiments. There was no evidence that treatment of colonies resulted in regurgitation of pellets; however, there was occasional information loss when gas bubbles formed during dissolution in dilute sodium hypochlorite suddenly broke through zooid frontal membranes entraining ingested particles in the process. Only zooids that ingested particles were sampled, since it could not be determined whether non-feeding zooids were senescent, immature, unsuccessful in feeding, or did not attempt to feed. Previous work has indicated that when per zooid ingestion rates increase, the proportion of feeding zooids per colony also increases (Okamura 1985). The first 100 zooids encountered per colony that had ingested particles were sampled. In each case, numbers of particles of each size were recorded. If fewer than 100 zooids had fed, all zooids with particles were sampled.

Analysis of data

Data collected as numbers of particles ingested per zooid were summarized in feeding categories representing the frequencies of zooids that had consumed different numbers of particles of varying size when feeding from the two flow regimes. Log-linear analysis of these frequency data was used to develop statistical models that best describe the multidimensional categorical data. This procedure, analogous to analysis of variance, allows testing of the importance of main effects (i.e., particle size, flow velocity) and interaction effects by assessing the *G*-statistic for goodness-of-fit provided by the various models (Feinberg 1970, Bishop et al. 1975, Sokal and Rohlf 1981). To avoid analyzing feeding on different particle sizes by the same zooids, equal numbers of zooids in each colony were randomly assigned to one of three groups, and zooids in each group were sampled for feeding on a specific particle size. Data from each group were pooled with group data from other colonies for log-linear analysis. A potential problem in applying analysis of frequencies is recognized, since zooids from the same colonies may not represent independent data points. However, zooids were deemed to be functionally independent because: (1) within colonies a range of ingestion rates was observed; (2) only portions of colonies were used, thus interference by upstream regions of colonies was not occurring (Okamura 1984); (3) the volume of the suspension was so large that concentration depletion would be insignificant.

Parallel studies of feeding on particles of the same sizes but made available as single-sized suspensions were carried out concurrently. Results from these studies are considered here to determine whether patterns of feeding on single-sized suspensions can be used to predict patterns of feeding on mixed suspensions. The observed total numbers of particles

of each size ingested from mixtures was compared with the expected numbers as predicted by feeding on single-sized suspensions. Expected numbers were generated by considering the relative number of particles of each size ingested by 300 zooids feeding on single-sized suspensions. As the total concentration of particles in single-sized and mixed suspensions was the same (100 particles/ml), the actual number of particles of each size available in mixed suspensions was one-third that of particles in single-sized suspensions. The expected numbers were therefore divided by three. It should be noted that there is a potential confounding factor if concentration of particles influences feeding. However, *Bugula stolonifera* shows similar patterns of feeding from different flow velocities on single-sized suspensions that vary by an order of magnitude in concentration (Okamura 1984 and present study). This suggests that concentration has little influence on feeding patterns.

Results

Feeding patterns

Bugula neritina

Feeding by *Bugula neritina* is summarized in Table 1. Results of log-linear analysis indicate a significant effect of particle size on feeding rate ($G=726.63$, $DF=21$, $p<0.001$), but little effect of flow on feeding rate ($G=11.47$, $DF=7$, $p>0.05$). Significance of treatment effects can be tested by assessing the difference in G -values for models that include and leave out the term of interest (Sokal and Rohlf 1981). Large and medium-sized particles were ingested at much greater rates than were small particles in experiments in both

flow velocities. This can be clearly seen by comparing the percentages of zooids in the category of zero particles ingested.

Bugula stolonifera

Feeding by *Bugula stolonifera* is summarized in Table 2. In this case there was a significant interaction such that, while feeding rate was associated with particle size the relationship was also dependent on velocity ($G=54.70$, $DF=12$, $p<0.001$). Again, large and medium-sized particles were ingested at greater rates than small particles. However as flow increased, large particles were ingested at greater rates while ingestion of medium-sized and small particles decreased. As for *B. neritina*, this is clearly seen by comparing the percentages of zooids in the first category of zero particles ingested.

Mechanisms resulting in disproportionate feeding

If particle size had no influence on feeding rates, then particles of varying size should have been ingested in equal numbers, as in all other respects particles were identical. This did not occur, and is reflected in the significant influence of particle size on feeding. Disproportionate feeding on particles of certain sizes may arise actively through selection or passively as a consequence of direct interception or likelihood of detection. Larger particles have a greater likelihood of capture since they occupy more space and/or have thicker associated boundary layers (Vogel 1981, LaBarbera 1984) that may be detected by mechanoreceptors in the low Reynolds-number environment at suspension-feeding sur-

Table 1. *Bugula neritina*. Frequency (and %) of zooids that ingested varying numbers of large (L, 19.1 μm), medium (M, 14.6 μm), and small (S, 9.6 μm) particles in slow (1 to 2 cm s^{-1}) and fast (10 to 12 cm s^{-1}) flow. Number of colonies sampled is indicated in each case. Model of best-fit is (PI) ($G=726.63$, $DF=21$, $p<0.001$)

Flow velocity (F) and particle size (P)	No. of particles ingested (I)							
	0	1	2	3	4	5	6	≥ 7
Slow (7 colonies)								
L	32 (20.5)	42 (26.9)	30 (19.2)	21 (13.5)	17 (10.9)	6 (3.9)	5 (3.2)	3 (1.9)
M	37 (23.7)	30 (19.2)	28 (18.0)	19 (12.2)	10 (6.4)	6 (3.9)	13 (8.3)	13 (8.3)
S	69 (44.2)	37 (23.7)	21 (13.5)	8 (5.1)	5 (3.2)	7 (4.5)	4 (2.6)	5 (3.2)
Fast (8 colonies)								
L	40 (21.6)	50 (27.0)	36 (19.5)	20 (10.8)	8 (4.3)	13 (7.0)	11 (6.0)	7 (3.8)
M	51 (27.6)	50 (27.0)	34 (18.4)	21 (11.4)	10 (5.4)	7 (3.8)	6 (3.2)	6 (3.2)
S	99 (53.5)	41 (22.2)	24 (13.0)	11 (6.0)	3 (1.6)	4 (2.2)	2 (1.1)	1 (0.5)

Table 2. *Bugula stolonifera*. Frequency (and %) of zooids that ingested varying numbers of large (L), medium (M), and small (S) particles in slow and fast flow (particle sizes and flow rates as in legend to Table 1). Number of colonies sampled is indicated in each case. Model of best-fit is (PFI) ($G = 54.70$, $DF = 12$, $p < 0.001$)

Flow velocity (F) and particle size (P)	No. of particles ingested (I)						
	0	1	2	3	4	5	≥6
Slow (8 colonies)							
L	57 (26.5)	55 (25.6)	48 (22.3)	30 (14.0)	8 (3.7)	14 (6.5)	3 (1.4)
M	58 (27.0)	49 (22.8)	43 (20.0)	23 (10.7)	20 (9.3)	12 (5.6)	10 (4.7)
S	98 (45.6)	47 (21.9)	33 (15.4)	23 (10.7)	5 (2.3)	5 (2.3)	4 (1.9)
Fast (8 colonies)							
L	36 (15.5)	64 (27.6)	62 (26.7)	30 (12.9)	9 (3.9)	11 (4.7)	20 (8.6)
M	82 (35.3)	70 (30.2)	45 (19.4)	13 (5.6)	11 (4.7)	5 (2.2)	6 (2.6)
S	145 (62.5)	47 (20.3)	12 (5.2)	14 (6.0)	13 (5.6)	0 (0)	1 (4.3)

Table 3. *Bugula neritina* and *B. stolonifera*. Results from goodness-of-fit tests under the hypotheses that particle volume and particle radius determine feeding rates. Expected frequencies based on total number of particles ingested in the experiments (see "Results – Mechanisms resulting in disproportionate feeding" for further discussion)

Flow velocity	G-value	DF	p
Volume			
<i>B. neritina</i>			
slow	70.93	2	<0.001
fast	11.68	2	<0.005
<i>B. stolonifera</i>			
slow	197.41	2	<0.001
fast	3.01	2	NS
Radius			
<i>B. neritina</i>			
slow	28.64	2	<0.001
fast	4.65	2	NS
<i>B. stolonifera</i>			
slow	53.06	2	<0.001
fast	28.08	2	<0.001

faces [see Koehl and Strickler (1981) for discussion of suspension-feeding and low Reynolds number].

To ascertain what aspect of particle size might influence feeding, I compared the observed total numbers of particles ingested with expected numbers predicted by particle volume and diameter (see Table 3). In only one of the four cases (*Bugula stolonifera* feeding from fast flow) were feeding patterns consistent with those expected if volume determined feeding rates. In other cases, zooids tended to feed less on large particles and more on medium-sized and small particles than particle volumes would predict. Similarly, there was only one case (*B. neritina* feeding from fast flow) in

which feeding patterns were consistent with the hypothesis that particle radius influences feeding. In other cases there were no consistent trends in whether zooids tended to feed more or less than predicted by their radii.

Feeding on mixed vs single-sized suspensions

The frequencies of particles of varying sizes ingested by both bryozoans when feeding from mixed suspensions were significantly different than those predicted on the basis of their feeding from single-sized suspensions (Fig. 1). This was true for feeding from both flow velocities. Furthermore, in three of the four cases the orders of preference (as determined by ranking the particle sizes according to greatest total ingestion) were dissimilar (the exception being *Bugula stolonifera* feeding from fast flow).

Discussion and conclusions

Interpretation of feeding patterns

This study is one of only a few to explicitly test how the combined influence of variation in some particle attribute (size) and in the fluid medium (flow rate) can affect suspension feeding. Both *Bugula neritina* and *B. stolonifera* were found to ingest particles of each size in slow and fast flow; however, rates of feeding depended on particle size and for *B. stolonifera* varied with flow. In all cases, small particles were ingested in relatively low numbers. In slow flow, particles of large and intermediate size were ingested at fairly similar rates by *B. stolonifera*. In fast flow, feeding-patterns shifted, and *B. stolonifera* fed at higher rates on large particles.

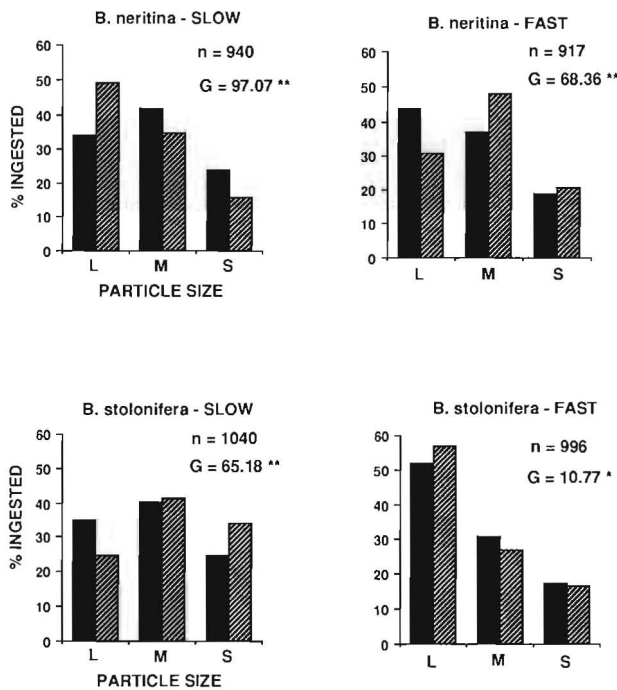


Fig. 1. *Bugula neritina* and *B. stolonifera*. Comparison of observed (filled bars) and expected (hatched bars) percentages of particles ingested from mixtures under slow- and fast-flow conditions. Expected percentages were generated from feeding rates on single-sized suspensions (see "Materials and methods - Experimental protocol"). L: large; M: medium-sized; S: small particles; n: total number of particles ingested from mixed suspensions. * $p < 0.005$; ** $p < 0.001$

Since particles varied in size but were otherwise identical, these patterns of disproportionate feeding should reflect a response to size alone. However, these feeding patterns cannot be adequately explained as a direct consequence of the greater likelihood of intercepting or detecting larger particles. It is possible that more complicated size-dependent particle behaviors may be important (e.g. residence times in downstream eddies) or that the bryozoans actively select or reject particles by size. In addition, there is the possibility that feeding may occur via ciliary currents or tentacular activity depending on particle size and flow velocity (Winston 1978, Okamura 1987). Observations of both particle behavior and lophophore behavior will be necessary to ascertain which mechanism(s) best explains disproportionate feeding. Regardless of the mechanism(s) involved, this investigation provides evidence that bryozoans can display variation in feeding on particles of different size and that the patterns of feeding are influenced by fluid flow.

Patterns of feeding of some predators seem to be adequately assessed by single-prey experiments (e.g. Greene et al. 1986). However, for bryozoans, patterns of feeding on single-sized suspensions cannot be used to make even qualitative predictions of patterns of feeding on mixtures. Rather, the proportion and rank-order of particle sizes ingested vary with suspension type. Jumars et al. (1982) similarly found feeding to depend upon the nature of the mixture presented to deposit-feeding polychaetes. Colton (1987)

demonstrated the failure of one-predator/one-prey experiments to predict correctly the one-predator/two-prey functional responses of damselfly naiads preying on copepods and cladocerans. Chesson (1989) has demonstrated that the presence of one prey type can influence the handling time of another, thereby affecting the functional response of notonectids. It therefore appears that for many organisms, single-prey experiments that systematically vary prey characteristics may be useful in assessing the inherent vulnerabilities associated with those characteristics and may provide insight as to mechanisms of prey capture (Brahmah 1987, Okamura 1987). However, in nature, suspension-feeders are exposed to a heterogeneous array of potential food items, and patterns of feeding on such mixtures by many suspension-feeders will probably be a complex function of the inherent vulnerabilities of the suspended particles and the responses of suspension-feeders to resource heterogeneity.

Importance of environmental variation

Food resources of suspension-feeders are highly variable in time, space, and composition. In addition, waves, ambient currents, and tidal flux produce variation in the movement of suspended particles through the habitats of many suspension-feeders. Many studies of suspension-feeding ignore the effects of moving water and offer homogeneous food or a mixture of food items differing in a variety of traits. In the present study, food items differed only in size, allowing the role of particle size to be tested explicitly. The results demonstrate that particle vulnerability can be determined not only by size, but also by the velocity of ambient currents. Other untested properties of suspended particles may influence feeding patterns as well. For instance, motility, diffusibility, charge, and density may affect suspension-feeding success (see Rubenstein and Koehl 1977). However, the present study demonstrates an important point: variation in the physical environment (e.g. water flow) can significantly influence ingestion of different particle types by suspension-feeders. The interaction of environmental variation and particle characteristics and its significance to patterns of suspension-feeding deserves further investigation.

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