

SOME QUANTITATIVE ASPECTS OF FEEDING IN SABELLID AND SERPULID FAN WORMS

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INTRODUCTION

It is apparent, from Jørgensen's recent review (1955) of quantitative aspects of filter feeding in invertebrates, that virtually nothing is known of the rate of filtering in polychaete suspension feeders, of which the sabellid and serpulid fan worms are perhaps the most important.

There seems to be little variation in the filter-feeding mechanism in different sabellid and serpulid polychaetes. The most detailed account of the feeding mechanism of these worms is that of *Sabella* published by Nicol (1930) with a résumé of earlier work on sabellids and serpulids. Some information on feeding and the anatomy of the crown in other genera may be found in the works of Soulier, 1891 (*Serpula*, *Hydroides*, *Protula*, *Branchiomma*, *Spirographis* and *Myxicola*), Johansson, 1927 (*Serpula* and *Pomatoceros*) and Thomas, 1940 (*Pomatoceros*). That the crown arises as a paired structure from the prostomium was shown by Wilson (1936) in *Branchiomma*. In adults, the crown may retain a clearly divided form, as in many serpulids such as *Pomatoceros*, or form an almost continuous single cone as in *Myxicola* or *Salmacina*. It is not, however, the purpose of the present paper to describe these variations in morphology, but to present some quantitative data on the filtering process. The species investigated were those which could be obtained in sufficient quantity at Plymouth. The results of experiments on the sabellids, *Myxicola infundibulum* (Rénier) and *Sabella pavonina* Savigny, and on the serpulids, *Pomatoceros triqueter* (L.), *Hydroides norvegica* (Gunnerus), *Spirorbis borealis* Daudin, and *Salmacina dysteri* (Huxley) are presented here.

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METHODS

The total volume of water strained, not the actual quantity of particles ingested, has been measured. Suspensions of 'Aquadag', a colloidal graphite suspension in water supplied by Acheson Colloids Ltd., London, was used. The method depends on the assumption that all the particles in the water filtered are removed from suspension, and those remaining are evenly distributed. The removal of particles from a closed system is exponential and as the filtering rate in fan worms was found not to vary with density, the volume and initial density of suspension could be adjusted to any convenient value. Both Jørgensen (1949), working with *Mytilus*, and Ballantine & Morton (1956), working with another lamellibranch, *Lasaea*, have found graphite suspensions to give variable results. Nevertheless, all the worms investigated fed and behaved normally in 'Aquadag' suspensions, and the values for filtering rates obtained here were consistent for each species. The suspensions were made up in the following way. A knife-point of the graphite paste was shaken vigorously in a test-tube with distilled water for 1-2 min, and then poured into a small beaker. After 5 min the resulting suspension was carefully decanted into a bottle, made up to 50 ml. with distilled water and allowed to stand a further 5 min. Such freshly made-up suspensions were used for each experiment and were found to give even suspensions consisting of particles almost entirely 1-2 μ in size, with a few larger particles up to 4-5 μ . In distilled water such dilutions are stable for at least some days. For the experiments, 1-2 ml. of this stock suspension was added to about 250 ml. of sea water. After 4 h all the particles were less than 10 μ and most 1-2 μ across. After 12 h, aggregates up to 50-60 μ had appeared; 18 h afterwards, 100 μ aggregates had formed, and after 24 h the aggregates rapidly sedimented. The optical density decreases during this aggregation process, but not materially during the first 4 h after preparing the sea-water suspension. The density of the suspension and the number of animals used in each experiment was therefore adjusted to give an easily measurable value in 2-3 h. The rate of filtering was calculated from the formula used by Jørgensen (1943) from measurements of the decrease in optical density of the suspension by means of an absorptiometer. Jørgensen (1949) found a change in feeding rate during the experiments using colloidal graphite with *Mytilus*. This may have been due to the suspensions being initially uneven, rather than to more rapid aggregation of small particles. Only by following the shaking and decanting process described here was it found possible to obtain even and stable suspensions. In some test experiments with *Myxicola*, estimation of filtering rate using suspensions in sea water, 12 and 18 h old, did not give values significantly different from those obtained with freshly made suspensions. While much of the graphite was ingested by the worms in all experiments, some was rejected, probably owing to the rather dense sus-

pensions used. As all the particles caught on the pinnules become entangled in mucus, however, the fall in optical density of the suspension gives a measure of the volume strained through the crown. Probably under natural conditions, where the density of small particles in suspension is much less, the majority of suitable particles would be ingested, so that the filtering rate becomes equivalent to the feeding rate.

Animals were acclimatized for some days to the experimental vessels kept under circulation before measurement of filtering rate. Care was taken to see that the animals were filtering and behaving normally before each experiment. Most species, especially *Sabella*, were found to become much less sensitive to shock if the vessels containing the animals were handled repeatedly for a day or so before the experiment. This was done so that the supernatant water could be sampled for measurement of optical density without causing retraction of the worm and interruption of feeding. Momentary, and apparently spontaneous, retractions take place, but the recovery and resumption of filtering is more prompt than after a shock reaction. *Hydroides* was found the most sensitive to experimental conditions. The *Sabella* (in their own tubes), were arranged individually, in small specimen tubes cemented to the bottom of the vessel, so that the crowns could be expanded and twirled without obstruction. *Myxicola* was allowed to secrete new tubes in the bottom of the vessel before being used in an experiment. Vessels with a capacity of 750 ml. were used for these large sabellids, with 1-3 worms in each. For the experiments on *Pomatoceros*, animals were selected with their tubes cemented to pebbles of convenient size, and these scraped clean of other filter-feeding animals before being acclimatized to vessels of 250-300 ml. capacity. *Hydroides*, growing on *Pecten* and *Buccinum* shells, were placed in 100 ml. vessels; pieces of *Salmacina* colony, and *Spirorbis* growing on *Fucus*, were placed in 10 ml. vessels for measurement of their filtering rates.

The worms used in the experiments were dried on filter paper and weighed; the larger species individually. *Spirorbis* and *Salmacina* were weighed in batches. Ten worms were placed on a cover-slip, the crowns dissected off, and surplus moisture drained off with filter paper; the whole process being performed under a binocular microscope. After weighing, the crowns were removed, and the cover-slip weighed again; the difference was taken as the weight of the crowns. Weighing was performed on an aperiodic microchemical balance with a sensitivity of 0.01 mg. In serpulids, the operculum and its stalk were dissected off, and, while included in the total body weight, are excluded from the weight of the crown. The extreme values for the weights of *Salmacina* and *Spirorbis* (Table 1, column 4) represent the means of ten of the largest and ten of the smallest selected from those used in the experiments.

TABLE 1. RESULTS OF EXPERIMENTS ON FILTERING RATES USING COLLOIDAL GRAPHITE SUSPENSIONS

(The figures in parentheses represent the number of animals or experiments from which each calculation is derived)

	1	2	3	4	5	6	7
	Total number of animals used	Total number of experiments	Arithmetic mean of total (fresh) weight (g)	Extreme total (fresh) weights (g)	Temperature range of experiments (° C)	Arithmetic mean filtering rate/animal (l./h)	Standard deviation of mean filtering rate/animal
<i>Myxicola infundibulum</i>	137	45	2.695 (65)	1.410-4.360	17-20	0.28600 (120)	0.06323
<i>Sabella pavonina</i>	150	50	0.187 (45)	0.043-0.236	18-20	0.07300 (150)	0.04266
<i>Pomatoceros triqueter</i>	42	45	0.0185 (42)	0.0117-0.0273	16-17	0.02700 (42)	0.01557
<i>Hydroides norvegica</i>	41	44	0.0123 (41)	0.0081-0.0235	16-17	0.01116 (44)	0.04908
<i>Spirorbis borealis</i>	2500	99	0.00024 (75)	0.000089-0.00052	17-19	0.00023 (2475)	0.00016
<i>Salmacina dysteri</i>	340	50	0.00014 (56)	0.00012-0.00015	17-18	0.00029 (340)	0.00012
	8	9	10	11	12	13	
	Arithmetic mean filtering rate/unit total (fresh) weight (l./h/g)	Mean crown weight (g)	Standard deviation of crown weight	Arithmetic mean filtering rate/unit crown weight (l./h/g)	Ratio of total weight to weight of crown	Standard deviation of ratio	
<i>Myxicola infundibulum</i>	0.10 (120)	0.323 (24)	0.1118	0.842 (48)	7.99 (21)	0.905	
<i>Sabella pavonina</i>	0.39 (150)	0.0195 (47)	0.00486	3.620 (48)	9.48 (48)	5.400	
<i>Pomatoceros triqueter</i>	1.40 (42)	0.004 (36)	0.000415	5.400 (42)	4.62 (42)	0.832	
<i>Hydroides norvegica</i>	0.90 (41)	0.00256 (41)	0.000806	2.300 (41)	4.81 (41)	0.976	
<i>Spirorbis borealis</i>	0.95 (75)	0.00008 (50)	0.000003	5.320 (75)	2.99 (50)	0.279	
<i>Salmacina dysteri</i>	2.09 (56)	0.00005 (50)	0.0000038	5.860 (56)	2.80 (50)	0.235	

DISCUSSION OF THE RESULTS

The results of all the experiments using colloidal graphite suspensions are summarized in Table 1. The detailed results need not be given here; measurements and calculations of general interest are included in the table, and the consistency of the values obtained may be judged from the standard deviations given, bearing in mind the random selection of the animals and their size range. About fifty experiments were performed on each species.

It is not surprising that the largest species, *Myxicola infundibulum*, should have the highest individual filtering rate (286 ml./h), which is over 1000 times that of *Salmacina* and *Spirorbis* (0.23–0.29 ml./h). On the other hand, the size range within the group is very great; the weight of *Myxicola* is over 25,000 times that of *Salmacina*. Thus the largest species have lower filtering rates per unit of weight than the smallest. This is in accordance with the general dictum that larger animals have lower metabolic rates than smaller ones within a phylogenetic series. The respiration rates of the smaller serpulids have not been measured, but Wells (1952) found the respiration rate of *Myxicola* to be 0.035 ml. O₂/g fresh weight/h, and *Sabella* about 0.05 ml. O₂/g/h, a similar value for *Sabella* having been found also by Ewer & Fox (1940). It is of interest to note also that, as far as is known, the larger species with lower filtering rates have a longer life span than the smaller. *Spirorbis borealis* lives for a few months only, *Pomatoceros* for at least two or three years (Robertson & Pantin, 1938), and a single *Sabella* has been recorded as living in the Plymouth Aquarium for at least ten years (Wilson, 1949).

If the filtering rate is expressed as a function of the crown weight alone, it is found that the rates are not significantly different in any of the species studied. The higher filtering rates per unit total weight in the smaller species are therefore not attained by crowns which for some structural reason are more efficient—that is, capable of straining a larger quantity of water per unit weight and time—than those of larger species, but rather of having relatively larger crowns. In *Spirorbis*, the crown represents a third of the total weight, in *Hydroides* about a fifth, in *Sabella* only a ninth. Conversely, the greater apparent complexity of the crown in *Myxicola* must be related to other factors. While both *Myxicola* and *Sabella* are found at the mouths of estuaries in mud banks, *Sabella* builds a tube projecting well above the surface, so that when the crown is expanded it is held away from the bottom. The slimy tubes of *Myxicola* are completely buried, so that the expanded crown only just projects from the surface. The inter-filamentary membranes probably prevent the crown from becoming clogged, the current bearing the finer suspended particles on which the worms feed entering from the rim. As Wells (1952) noticed, the pinnules are somewhat rotated so that the ventro-lateral cilia have a stronger longitudinal, as opposed to transverse, component with

reference to the axis of the filament. The high standard deviation of the ratio of crown to total body weight (Table 1, column 13) in *Sabella* is due to some of the animals having partially regenerated crowns.

With the larger species it was not found practicable to measure the filtering rate with algal cultures owing to the very large volume which would be required. A few experiments using *Phaeodactylum tricorutum* Bohlin with *Myxicola*, and a number using cultures of *Phaeodactylum*, *Isochrysis galbana* Parke, and *Chromulina pusilla* Butcher, were made with *Spirorbis*. These three species of algae were selected, not only because of their availability at the Plymouth Laboratory, but because of their size differences: *Phaeodactylum* cells are 20–40 μ ; *Isochrysis*, 5–6 μ ; *Chromulina*, 1–2 μ in length. All the fan worms avoided dense suspensions of *Phaeodactylum* and *Isochrysis*, and even when much diluted the filtering rates were very small compared with those obtained with colloidal graphite. *Myxicola* and *Spirorbis* both removed *Phaeodactylum* from suspension at less than a tenth of the rate recorded with colloidal graphite. The other fan worms would not keep their crowns expanded in dense suspensions of these algae. This is certainly not merely a matter of size. *Myxicola* in 18 h old 'Aquadag' suspensions filtered at the same rate as in freshly made suspensions in which the majority of the particles were less than 2 μ , and which had a greater density than the *Phaeodactylum* suspensions used. *Chromulina* are closely similar to such fresh graphite particles in size, but dense suspensions of this alga produced repeated retractions of the crown in *Spirorbis*. The *Spirorbis* would remain with the crown expanded in more dilute cultures, but the filtering rate was negligible. One can only conclude that these algae can escape from the pinnules which are thus only capable of filtering inert particles of detritus from suspension. This is perhaps one explanation of the abundance of fan worms at the mouths of estuaries where there is much fine detritus in suspension.

During the present work a few experiments were made on *Chaetopterus*, using 'Aquadag' suspensions. Using seventeen different animals in their own tubes in groups of 1–3, allowing 1.5 l. of suspension for each group, and measuring the filtering rate over a 2 h period, it was found that at 16° C the mean filtering rate was 0.3 l./h./animal (standard deviation 0.183 l./h). The mean fresh weight of these animals was 6.0 g, giving a value of 0.05 l./h/g. Jørgensen (1955) calculated the filtering rate as 0.96 l./h from data given by Wells (Wells & Dales, 1951), but this was based on a calculation of the flow through the tube of one worm on a single occasion. The highest value obtained here over the 2 h period was 0.75 l./h, in a vessel containing a single animal. It is known from the work of MacGinitie (1939) and Wells (Wells & Dales, 1951) that *Chaetopterus* may both irrigate the burrow without feeding and feed without secreting a complete mucus bag such as might be expected to retain all the graphite particles in the water strained. It is also known that such activities are discontinuous. The value for the 'filtering rate' given here

may, therefore, bear little relation either to the feeding rate or the total volume of water passed, and is not comparable with the values for fan worms which filtered more or less continuously during the course of an experiment. It is impossible to observe the activity of the animals in their own tubes as these are opaque.

The values obtained for the fan worms (Table 1) are all low compared with known values for other invertebrates. For example, from the information given by Jørgensen (1955), derived from various sources, *Ostrea virginica* filters at the rate of about 0.5 l./h/g, *Mytilus edulis* at 1.6 l./h/g and *Ciona intestinalis* at 0.23 l./h/g, at comparable temperatures. *Ciona* has much the same fresh weight as *Myxicola*, which strains at less than half this rate (0.1 l./h/g). Clearly the fan worms are less efficient than other suspension-feeding invertebrates, both in the volume of water they are capable of straining, and in the kind of particles which can be retained. While some sorting according to size occurs in *Sabella* (Nicol, 1930) and in other fan worms, this is crude compared with sorting mechanisms in some other suspension-feeding invertebrates.

SUMMARY

The rate of filtering has been examined in a series of sabellids and serpulids of widely different size, using suspensions of colloidal graphite and algal cultures. The filtering rates have been expressed as individual rates, as the volume strained per unit fresh weight, and per unit weight of the crown. It may be concluded that the smaller fan worms filter at a relatively higher rate than the larger. This is achieved partly by the relatively larger crown. Free swimming algae escape through the crown; only inert particles down to 1–2 μ are retained, implying that fan worms depend on suspended detritus alone. The filtering rates are briefly compared with those of *Chaetopterus* and some other filter-feeding invertebrates.

REFERENCES

- BALLANTINE, D. & MORTON, J. E., 1956. Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra*. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 241–74.
- EWER, R. F. & FOX, H. M., 1940. On the function of chlorocruorin. *Proc. roy. Soc. B*, Vol. 129, pp. 137–53.
- JOHANSSON, K. E., 1927. Beiträge zur Kenntnis der Polychaeten-Familien Hermedilidae, Sabellidae und Serpulidae. *Zool. Bidr. Uppsala*, Bd. 11, pp. 1–183.
- JØRGENSEN, C. B., 1943. On the water transport through the gills of bivalves. *Acta physiol. scand.*, Vol. 5, pp. 297–304.
- 1949. The rate of feeding by *Mytilus* in different kinds of suspension. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 333–44.
- 1955. Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.*, Vol. 30, pp. 391–454.
- MACGINITIE, G. E., 1939. The method of feeding of *Chaetopterus*. *Biol. Bull., Woods Hole*, Vol. 77, pp. 115–18.

- NICOL, E. A. T., 1930. The feeding mechanism, formation of the tube, and physiology of digestion in *Sabella pavonina*. *Trans. roy. Soc. Edinb.*, Vol. 56, pp. 537-98.
- ROBERTSON, J. D. & PANTIN, C. F. A., 1938. Tube formation in *Pomatoceros triquetus* (L.). *Nature, Lond.*, Vol. 141, pp. 648-9.
- SOULIER, A., 1891. Études sur quelques points de l'anatomie des Annélides tubicoles de la région de Cette. *Trav. Inst. Zool. Univ. Montpellier*, T. 2, pp. 1-310.
- THOMAS, J. G., 1940. *Pomatoceros, Sabella and Amphitrite*. *L.M.B.C. Memoirs*, No. 33, 88 pp. Liverpool: University Press.
- WELLS, G. P., 1952. The respiratory significance of the crown in the polychaete worms *Sabella* and *Myxicola*. *Proc. roy. Soc. B*, Vol. 140, pp. 70-82.
- WELLS, G. P. & DALES, R. P., 1951. Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *J. mar. biol. Ass. U.K.*, Vol. 29, pp. 661-80.
- WILSON, D. P., 1936. The development of the sabellid *Branchiomma vesiculosum*. *Quart. J. micr. Sci.*, Vol. 78, pp. 543-603.
- 1949. Notes from the Plymouth Aquarium. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 345-51.

SUMMARY

The rate of filtering has been measured in a series of sabellid and eurythoeid worms using different sized suspensions of colloidal graphite and silver chloride. The filtering rates have been expressed as individual rates, as the volume retained per unit fresh weight, and per unit weight of the crown. It may be concluded that the smaller the worms filter at a relatively higher rate than the larger. This is achieved partly by the relatively larger crown. The swimming cilia escape through the crown, only inert particles down to 1-2 μ are retained, implying that the worms depend on suspended detritus alone. The filtering rates are briefly compared with those of Chaetopterus and some other tube-building invertebrates.

REFERENCES

- BRANCHIOMMA, D. & MONTAGU, J. E., 1927. Filtering, feeding, and digestion in the invertebrates. *London notes J. mar. biol. Ass. U.K.* Vol. 22, pp. 247-72.
- BRANCHIOMMA, D. & MONTAGU, J. E., 1928. On the function of the crown in the Sabellidae. *J. mar. biol. Ass. U.K.* Vol. 23, pp. 117-22.
- BRANCHIOMMA, D. & MONTAGU, J. E., 1927. Beiträge zur Kenntnis der Polychaeten-Tubicoles. *Archiv für Naturgeschichte und Zoologie*, Bd. 11, pp. 1-121.
- BRANCHIOMMA, D. & MONTAGU, J. E., 1927. On the water transport through the gills of invertebrates. *Proc. roy. Soc. B*, Vol. 2, pp. 297-302.
- 1928. The rate of feeding by Sabellidae in different kinds of suspension. *J. mar. biol. Ass. U.K.* Vol. 23, pp. 222-24.
- 1927. Quantitative aspects of tube feeding in invertebrates. *Phil. Mag.*, Vol. 12, pp. 101-112.
- BRANCHIOMMA, D. & MONTAGU, J. E., 1928. The method of feeding of Chaetopterus. *Phil. Mag.*, Vol. 12, pp. 112-15.