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Theodore J. Smayda

Limnology and Oceanography, Vol. 14, No. 4 (Jul., 1969), 621-625.

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SOME MEASUREMENTS OF THE SINKING RATE OF FECAL PELLETS¹

A "rain" of dead plankton and their fecal material has long been suggested as an important source of food to abyssal communities (*see* Menzies 1962). There is increasing evidence that fecal pellets may represent an even more quantitatively significant food source, at least in nearshore benthic areas, than previously realized (*see* Frankenberg, Coles, and Johannes 1967). The availability of zooplankton fecal pellets as food is related in part to the depths to which they can sink. Moore (1931a) detected zooplankton fecal pellets in nearshore sediments to depths of 166 m and followed their production and sinking characteristics during a spring phytoplankton bloom. Osterberg, Carey, and Curl (1963) gave an average sinking rate for *Euphausia pacifica* fecal pellets. However, we have little such information, which is needed to assess the role of fecal pellets in nutrition, in influencing the vertical distribution of radionuclides (Osterberg et al. 1963) and trace elements, and in contributing to sedimentary oozes of phytoplanktonic remains (Smayda 1969). The purpose of this investigation was to determine the sinking rates of fecal pellets collected from seawater. I wish to acknowledge the technical assistance of Miss B. J. Boleyn during this study.

MATERIAL AND METHODS

Fecal pellets were collected from Narragansett Bay (Rhode Island) in No. 25 net tows (vertical) made during November and December 1967 off the laboratory pier where the high-water depth is about 7 m. The pellets were dark brown and usually of a shape similar to that depicted in Figs. 1 and 5a in Moore (1931b), that is, parallel-sided with rounded ends and circular in cross section. A few ovoid pellets were also collected. The surfaces were smooth and regular. The width ranged from 53 to 173 μ and the length from 93 to 266 μ . *Although the pellets were collected from*

the water column, it cannot be excluded that they were produced by the benthos and roiled into suspension.

Shortly after collection, individual fecal pellets were isolated from the unpreserved sample using Boleyn's (1967) apparatus. Firm, noncontaminated (i.e., without visible "Aufwuchs") material of various sizes was selected, transferred to a vial containing filtered seawater of about 32‰ salinity and stored at 2C for several days until used.

A Nessler tube 37.5 cm tall and 2 cm in diameter served as a settling chamber. The height of the water column through which sinking speed was measured was 29.6 cm. In all experiments, the chamber was clamped to a leveled ringstand, filled to within a few centimeters from the top with 34.4‰ water at 15C, and kept in a 15C constant temperature room. The fecal pellets were kept at 15C for several hours before use. Suitable indirect lighting was arranged to permit observation of the sinking pellets without magnification. Only firm, intact pellets without apparent signs of breakage from handling were chosen (few were rejected). The pellets were carefully transferred to a watchglass, placed under a dissecting microscope, measured, and reisolated with the Boleyn apparatus. The capillary tube of the apparatus was then inserted just below the surface of the medium in the settling chamber and the fecal pellet gently expelled without bubbling. A second person was in front of the settling chamber to detect and track the sinking pellet. The pellet was permitted to sink untimed for about 5 cm primarily so that it could be detected. When it reached the 100-ml mark scored into the chamber wall 29.6 cm above bottom, two stop watches were started. One timed the descent to the 50-ml level (scored 14.8 cm above bottom), while the other recorded the time to reach bottom. Various sized pellets were used to assess the influence of size on sinking rate. The smallest pellets that could be

¹ This work was supported by National Science Foundation Grant GB-5366.

TABLE 1. *Sinking rates of 41 fecal pellets at 15C and 34.4‰ salinity*

Size (μ) (width \times length) No.	Sinking rate (m/day)
53 \times 106 2	100; 36
53 \times 120 1	47
53 \times 133 2	117; 98
60 \times 133 1	96
67 \times 120 1	152
67 \times 133 4	141; 136; 120; 109
67 \times 146 2	93; 117
67 \times 160 6	140; 110; 134; 141; 160; 188
67 \times 173 3	134; 180; 118
67 \times 186 1	206
80 \times 160 1	141
80 \times 173 8	173; 222; 185; 188; 139; 149; 167; 203
80 \times 186 3	185; 207; 309
93 \times 186 2	187; 147
93 \times 200 2	252; 169
120 \times 200 1	240
173 \times 266 1	376

detected with the unaided eye (with difficulty) were 53 μ wide; several were lost. In some instances, the sinking rate of these and slightly wider pellets could be clocked only from the 50-ml level to the bottom (14.8 cm). The sinking rate of each pellet was determined only once. In all, successful experiments were made for 41 of the 44 pellets used.

RESULTS AND DISCUSSION

The slowest sinking rate was 36 m/day obtained with the smallest fecal pellet (53 \times 106 μ) successfully monitored; another pellet of this size sank 100 m/day (Table 1). The fastest sinking rate was 376 m/day obtained with the largest pellet (173 \times 266 μ). These results reflect the general tendency for the rate of sinking to increase with pellet size. This trend is especially evident when *mean* sinking rates are calculated for the various sizes of width and length encountered (Table 2). The influence of pellet surface area was as observed for volume (Fig. 1).

TABLE 2. *Mean sinking rate of fecal pellets of various widths and lengths*

Width			Length		
Size (μ)	No.	Mean rate (m/day)	Size (μ)	No.	Mean rate (m/day)
53	5	80	106	2	68
60	1	96	120	2	100
67	17	140	133	7	117
80	12	189	146	2	105
93	4	189	160	7	145
120	1	240	173	11	169
173	1	376	186	6	207
			200	3	220
			266	1	376

The two largest pellets were more ovoid than the others, which were of similar shape although varied in size (Table 1). Shape can be expected to influence sinking rate. Lack of material prevented replicate runs with the largest pellets. These facts make it somewhat uncertain whether a curvilinear or linear relationship normally exists between sinking rate and pellet size when plotted on semilogarithmic paper (Fig. 1). Where more frequent replication was possible, as when size was expressed as pellet length, a linear relationship appeared to hold.

The mean sinking rates calculated for pellets within the various widths and lengths encountered suggest several general trends (Table 2). A fecal pellet of a given *width* sinks approximately twice as fast as one having an equivalent *length*. The responses of the 120- and 173- μ categories, the only sizes where a direct comparison is possible in these data, illustrate this. Second, the mean sinking rate of pellets of a given width is similar to that for pellets twice as long. For example, the mean sinking rate of pellets 53 μ wide is 80 m/day and is 68 m/day for pellets 106 μ long, and so on. Finally, a doubling of width approximately doubles sinking speed, whereas a doubling of length approximately triples it. In most instances, the fecal pellets sank straight down. On occasion, a sinusoidal descent occurred.

Osterberg et al. (1963) reported that the mean sinking rate of *Euphausia pacifica*

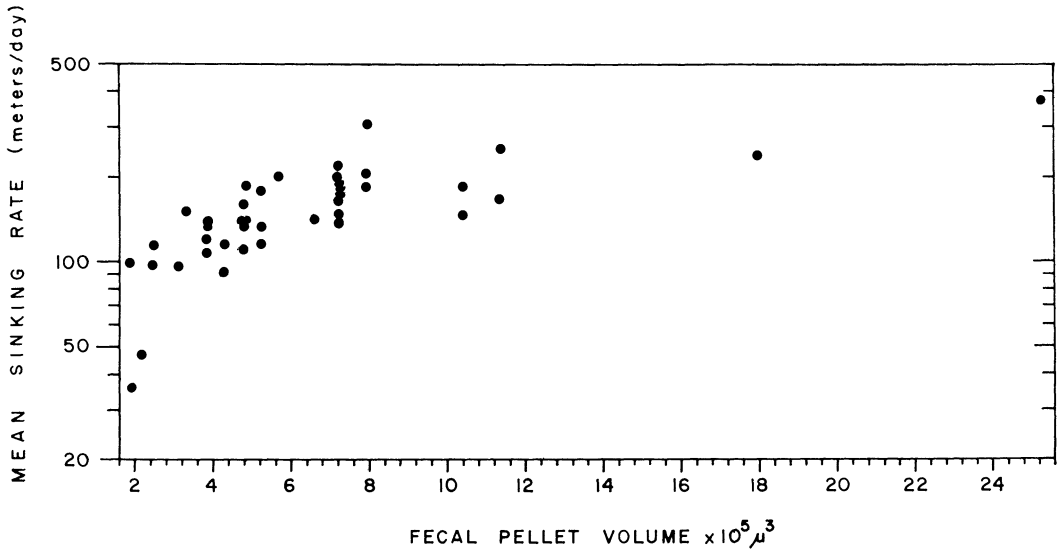


FIG. 1. The relationship between mean sinking rate of fecal pellets and their volume.

fecal pellets produced when fed *Skeletonema costatum* and ranging in size from $100 \times 1,000 \mu$ to $500 \times 3,000 \mu$ was 43 m/day. This is twofold to ninefold lower than the mean rates found for the various pellet sizes used in my experiments (Table 2); it is comparable with the lowest observed absolute rate of 36 m/day. From the apparent influence of size on pellet sinking rate, the euphausiid fecal pellets might be expected to sink faster than even the largest pellets studied here. However, these pellets appear to differ in at least two respects, which may account for the apparent differences in sinking rates: diet residue and geometry. The *Skeletonema* food provided to *Euphausia* differed from the phytoplankton diet present in Narragansett Bay² when the pellets were col-

lected. The compaction, size, and coloration of zooplankton fecal pellets vary with diet (Marshall and Orr 1955). Different foods also leave different waste residues that might influence the fecal pellet density and, hence, sinking rate. The *Euphausia* pellets had a length:width ratio of from 6:1 to 10:1, while those from Narragansett Bay ranged from 1.5:1 to 2:1 (Table 2). The elongate euphausiid pellets would be expected to offer greater resistance to sinking than the more spherical pellets used in my experiments. Some planktonic copepods also produce elongate pellets (Moore 1931b; Marshall and Orr 1955), whereas the pellets collected from Narragansett Bay were similar in shape to those produced by at least some benthic animals (Moore 1931b). The source of the pellets in my studies is unknown; if they were produced in the benthos, especially by a deposit feeder, the ingestion of sedimentary material might lead to their having a greater density than those produced by plankton. Such pellets would be expected to have a greater sinking rate than similar-sized or more elongate pellets containing the wastes of a herbivorous or carnivorous animal.

² The surface phytoplankton population during early November and December amounted to 3.8×10^6 and 4×10^6 cells/liter, respectively. Microflagellates comprised about 85% of the total population as numbers in both instances. *Asterionella japonica* (380,000 cells/liter) dominated a mixed diatom and dinoflagellate community in which *Skeletonema costatum* and *Rhizosolenia delicatula* were important during both months, together with *Chaetoceros curvisetus*, *Nitzschia seriata*, and *Thalassionema nitzschioides* in November, and *Thalassiosira decipiens* in December.

TABLE 3. Comparison of fecal pellet sinking rates with some rates obtained for dead marine protozoans, fish eggs, zooplankton, and living and dead phytoplankton, as reported in the literature

Group	Rate (m/day)	No. of species used	Source*
Fecal pellets	36-376	—	here, 1
Fish eggs	215-400	2	2
Phytoplankton			
1. Living	0-30	~25	3
2. Palmelloid stages†	~5-6,150	1	4
3. Dead	<1-510	~10	3, 5
Protozoans‡			
1. Foraminifera	30-4,800	—	6
2. Radiolarians	~350	—	6
Zooplankton			
1. Amphipoda	~875	1	2
2. Chaetognatha	~435	1	2
3. Cladocera	~120-160	2	2
4. Copepoda	36-720	14	2, 5, 8
5. Heteropoda	~1,400	1	5
6. Ostracoda	400	1	2
7. Pteropoda	760-2,270	5	2, 5
8. Salpa§	165-253	2	2
9. Siphonophora	240	1	2
10. "Animal plankton"	~225-500	?	7

* 1 = Osterberg et al. 1963; 2 = results of sinking experiments conducted at 16.4C and 35.31‰ salinity as reported by Apstein 1910; 3 = Smayda 1969; 4 = Bernard 1963; 5 = Vinogradov 1961; 6 = Kuenen 1950; 7 = Seiwel and Seiwel 1938 for "animal plankton (chiefly copepod)" after being dead for 2 hr; 8 = Gardiner 1933.

† These are the aggregated cell masses formed by the coccolithophorid *Cyclococcolithus fragilis*.

‡ These rates appear to have been calculated after assuming a diameter of 0.02 and 0.5 mm for planktonic foraminifera and 0.5 mm for radiolarians.

§ Moseley 1892 reported shipboard experiments which suggested that a dead salp about 50 mm long would sink about 1,000 m/day; the salps in Apstein's experiments ranged from 4 to 10 mm.

Sinking rates for fecal pellets through nonturbulent liquid have been calculated using Stokes' equation:

$$V = \frac{2}{9} gr^2 \frac{\rho - \rho_0}{\eta},$$

where V is the velocity in cm/sec, r is the pellet radius in cm, g is the acceleration due to gravity (980 cm/sec²), ρ is the density of the pellet, ρ_0 is the density of the medium at 15C and 34.4‰ salinity

(1.025 g/cm³), and η is the viscosity of the medium at 15C and 34.4‰ salinity (0.012 g cm⁻¹ sec⁻¹—Sverdrup, Johnson, and Fleming 1942). Dillon's (1964) mean value for fecal pellet density ($\rho = 1.19$ g/cm³), based on pellets collected from sediments, was used. Stokes' equation is valid primarily for spherical particles. This condition is not wholly satisfied by the pellets used—the dimensions of the smallest and largest ones being $53 \times 106 \mu$ and $173 \times 266 \mu$. Therefore, the diameter of these pellets was considered to be the mean of their width and length, or 80 and 220 μ for the smallest and largest. The calculated sinking rates are about 40 m/day for the smallest and about 305 m/day for the largest. These agree reasonably well with observed rates of 36 and 376 m/day for pellets of this size (Table 1).

The fecal pellet sinking rates are compared with those reported for various plankton groups in Table 3; an exhaustive literature search was not attempted. Rates for dead material were emphasized (1) to place into perspective the magnitude of the observed pellet rates, and (2) to compare the potential capability of fecal pellets vis à vis dead plankton to sink to depth. The latter is especially interesting since Johannes and Satomi (1966) have suggested that the rate of production of organic matter as feces probably exceeds that as tissue in marine planktonic herbivores.

Fecal pellets sink faster than living and dead phytoplankters in general. The maximum rate of 510 m/day for dead cells is that reported by Vinogradov (1961) for the giant (1.5 to 1.75 mm in diameter) diatom, *Ethmodiscus rex*—a size and rate hardly representative of phytoplankton in general (Smayda 1969). The next highest rate reported, for example, is about 10-fold lower (Apstein 1910) and for the smaller (though quite large) diatom, *Coscinodiscus concinnus*. Similarly, the formation of palmelloid stages is apparently restricted to certain coccolithophorids, and the associated high sinking rates cannot therefore be ascribed to phytoplankton in general.

At the other extreme, the range in fecal

pellet sinking rates is considerably lower than those reported for heteropods, pteropods, larger foraminifera, and amphipods. This may reflect the large size (8–9 mm long) of the single amphipod studied (*Parathemisto obliqua*) and the occurrence of shells in the others. Otherwise it is apparent that these fecal pellet sinking rates are not appreciably different from most of those reported for dead representatives of groups common in the zooplankton. This limited comparison suggests, then, that a fecal pellet may not generally represent a more rapid means of transport of organic matter to depth than would occur in the form of an intact, but dead, zooplankton, contrary to expectations. In fact, it might be a fairly slow mechanism should the value of Osterberg et al. (1963) of about 40 m/day be more representative of zooplankton fecal pellets than my values.

The sinking speed of dead zooplankton decreases with the characteristic reduction in size accompanying decomposition and breakage (Seiwell and Seiwell 1938). Plankton fecal pellets are more friable than those produced by benthic animals (Moore 1931a), and a 50% reduction in carbon content may occur within several days after pellet formation (Johannes and Satomi 1966). Vinogradov (1961) observed that even very fast sinking pteropods are generally devoid of organic matter below 500 m, presumably because density discontinuity layers significantly reduce sinking rate from that expected from experimental data.

Thus, it is still an open question whether fecal pellets represent a significant transport mechanism and source of organic matter to deep water, despite the apparently significant, seasonal incorporation of organic matter into this form in the upper layers.

THEODORE J. SMAYDA

Graduate School of Oceanography,
University of Rhode Island,
Kingston 02881.

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