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ASPECTS OF BIODEPOSITION BY OYSTERS AND OTHER INVERTEBRATE FILTER FEEDERS[1]

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ABSTRACT

Quantities of suspended matter removed by oysters (*Crassostrea virginica*) and deposited as feces or pseudofeces varied seasonally, reaching maxima in September. Below 2.8C, measurable quantities were not produced. At certain seasons, levels of suspended solids influenced quantities of biodeposits. Laboratory studies indicated that the oysters on 0.405 hectare of an estuarine bottom may produce up to 981 kg of feces and pseudofeces weekly. Of the particles, 95% were under 3 μ in diameter. All types of algal cells present in the surrounding water were represented. The deposits contained 77–91% inorganic matter, mostly illite, chlorite, and mixed-layer clays, 4–12% organic carbon, and 1.0 g/kg phosphorus. Biodeposits of filter feeders such as barnacles, tunicates, and other lamellibranchs were similar to those of oysters. Filter feeders may influence deposition, transport, and the composition of suspended sediments in estuaries. A possible relationship between the removal from suspension and the subsequent deposition of radionuclides associated with particles of clay, silt, or planktonic algae and feces or pseudofeces is suggested.

INTRODUCTION

Filter-feeding marine animals are important in initiating sedimentation of fine suspended matter. These animals filter the material from the water, combine it into aggregates, and void it as feces or pseudofeces. These fecal strings or pellets have characteristic shapes and vary in length from less than 1 mm to 4 mm or more (Moore 1931*a*). Feces and pseudofeces that settle to the bottom are termed *biodeposits*; the processes involved in production of these biodeposits, that is, filtration of seston, compaction within the animal, and subsequent deposition, are included under the term *biodeposition.*

Biodeposition may influence sediment transportation rates and it may be important in initiating sedimentation of particles in the 1 to 3 μ range (Damas 1935; Verwey 1952; Jørgensen and Goldberg 1953; Jørgensen 1960). Lund (1957) demonstrated that volumes of feces and pseudofeces produced by laboratory oysters were eight times greater than those of control sediments that settled by gravity.

Commonly occurring marine filter feeders may produce large quantities of biodeposits. In the Clyde Sea, fecal pellets from *Calanus* sp. and euphausiids are deposited in spring at a weekly rate approaching 33.4 mg/cm^2 (Moore 1931*b*). Damas (1935) stated that in certain coastal areas of France a single *Cardium* produced about 648 mg (wet weight) of fecal material daily. Using this value, Verwey (1952) calculated that in the Waddenzee this species deposits 100,000 metric tons (dry weight) of suspended matter in one year. From the data of Blegvad (1915), Fox and Coe (1943), and Kamps (1950), Verwey also calculated that in the Waddenzee, *Mytilus* would annually remove from suspension between 25,000 and 175,000 metric tons (dry weight) of suspended matter. In Japanese waters, a single oyster weighing 90 g produced a minimum of 0.03 g (dry weight) feces daily (Ito and Imai 1955); these authors calculated that a raft of oysters 60 m square would annually produce 0.6 to 1.0 metric tons (dry weight) of fecal material. Lund (1957), the first to study biodeposition quantitatively in the laboratory, calculated that if oysters covered an acre of bottom, they would deposit 7.58 metric tons of fecal material (dry weight) in 11 days.

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The increasing possibility of contamination of estuarine waters with fission products gives added importance to the process. If radionuclides are introduced into marine waters, many would occur in particulate form and additional quantities would become incorporated into living tissue of planktonic organisms; others would become adsorbed on silts, clays, or detritus, and much of this particulate matter and its associated radionuclides would be removed from suspension by filter feeders and voided as compacted biodeposits. As a consequence, the final distribution of radioactive material in the marine environment does not depend solely on physical and chemical factors or hydrographic conditions but is profoundly influenced by activity of filter-feeding animals.

The present investigation was initiated in 1960 to measure seasonal rates of biodeposition of the oyster *Crassostrea virginica* and other invertebrates in relationship to ecological conditions and to determine the physical and chemical characteristics of biodeposits. This basic study is necessary for a better understanding of dispersal and accumulation of biodeposits in the marine system because their transport, breakdown, rate of sedimentation, influence on bottom enrichment, and association with radionuclides will be determined by their physical and chemical properties and the quantities produced.

Appreciation is expressed to Mr. John J. Norcross of this institute for assistance in the statistical aspects of trough design and in the statistical analysis of weekly deposition rates. Thanks are also given to Dr. Morris L. Brehmer for analysis of samples for total phosphorus. X-ray diffraction determinations were made by Dr. Bruce Nelson, Virginia Polytechnic Institute, and the resulting curves were analyzed by Dr. Seymour Greenberg, Virginia Geological Survey.

METHODS

Seasonal aspects of biodeposition were investigated in two long-term experiments during 1961 and 1962. Both were based on quantities of biodeposits accumulated during one week. Additional short-term studies were conducted in 1962 and 1963, when materials were collected daily.

In 1961, oysters were held in rectangular, acrylic plastic troughs, 10.2 cm square and 46 cm long, subdivided into eight compartments, each holding a single oyster, similar to the unit designed by Lund (1957). Water flowed over the oysters at 1.75 liters/min, and feces and pseudofeces accumulated on separate sides of each compartment. During 1962 and 1963, oysters were held in specially designed, 30-cm diameter circular troughs, subdivided into eight wedge-shaped compartments, each containing a single 5- to 8-cm oyster (Haven and Morales-Alamo 1965*b*). A division on the bottom of each compartment separated feces from pseudofeces. Each oyster received a flow of about 202 ml/min. Rates of flow were determined in preliminary studies and were such that the volumes of feces and pseudofeces produced were not limited and shell growth equaled that of controls grown under optimum conditions in the York River. Water was pumped from the York River 150 m offshore at 0.5 m from the bottom into a shallow, constantly overflowing, overhead supply trough; from there it was siphoned to the experimental oysters. Salinity was measured daily with a hydrometer, and temperature was recorded continuously.

Feces and pseudofeces were removed from the compartments with a suction pipette. Feces from each unit of eight oysters were combined into one sample; pseudofeces were similarly combined into a single sample. Biodeposits were washed free of salt by decanting, dried at 87C and weighed to the nearest 0.01 g; results were expressed as total deposition in each trough in g/week or g/day. Seston settling out by gravity in a control trough where single oyster shells were substituted for living oysters was collected and treated the same as biodeposits. Weight of this seston (control sediment) was subtracted from biodeposit weights. Five or 10 troughs were run simultaneously, making possible statistical comparison by "*t*" tests between weekly or daily deposition rates.

Oysters used in the studies were selected for uniformity of weight and placed randomly in compartments. At intervals, each animal was weighed to the nearest 0.1 g. In certain supplemental studies, tissue weights were determined; tissues were removed from the shell, dried at 87C, and weighed to the nearest 0.01 g.

For three periods in 1963, daily fecal production by soft clams (*Mya arenaria*), barnacles (*Balanus eburneus*), tunicates (*Molgula manhattensis*), and ribbed mussels (*Modiolus demissus*) was compared with that of the oyster. Animals were held in the circular troughs under flows which did not limit deposition rates, and biodeposits were treated as outlined for oysters.

A series of tests related the quantity of feces and pseudofeces produced by oysters to size of the animals. Groups of eight oysters were selected in four weight groups, and these were placed in rectangular troughs under flows of 3 to 5 liters/min.

The composition and size of components of oyster feces, pseudofeces, and control sediments were determined microscopically. Samples collected from an experimental trough, representing a week's accumulation, were dispersed by shaking for 10 min with 3 drops of sodium hexametaphosphate solution (0.6 g/liter) on a mechanical shaker. After dilution, counts were made with a hemocytometer and measurements of the longest axis of each particle were made with a calibrated eyepiece reticule. Contents of each of the 24 samples were classified into two categories: 1) algal cells and recognizable fragments of algae and, 2) particulate matter not recognizable as an algal cell or fragment ("particles").

Total organic and inorganic matter was determined for representative samples of biodeposits and control sediments collected in the 1962 seasonal study. Dried samples, treated with 10% HCl to remove carbonates, were ashed at 600C and the two fractions calculated on the basis of weight loss, which included loss of water of hydration. Organic carbon content of biodeposits and control sediments was determined with a LECO carbon analyzer (Laboratory Equipment Corp., St. Joseph, Michigan). Organic carbon content was similarly determined in bottom sediments of the lower York River. Cores were taken in two transects, one at Gloucester Point and the second 7.2 km upriver, from the shore zone and across to the other side. Analysis was made on subsamples from the top 1-cm layer of each core.

Total phosphorus was determined daily in feces, pseudofeces, and control sediments during part of 1962 using a modified colorimetric molybdate method (American Public Health Association 1960) after digestion with perchloric acid (Jackson 1958). Mineral composition of biodeposits was determined by x-ray diffraction analysis of a representative series of 45 samples collected during the 1961 seasonal study.

Total seston in the water supplying the experimental animals was measured daily for several periods by filtration through membrane filters with a pore size of 0.45 μ. The inorganic fraction (abioseston) of the material retained on the filter was determined as the fixed residue after ignition at 600C. Water samples analyzed represented a composite collection over a 24-hr period. A small pump operating for 30 sec out of every 12 min pumped about 150 ml of water from the supply trough into a storage carboy kept at 0C to suppress bacterial and chemical activity. After 24 hr, a subsample from the carboy was collected for analysis, and the carboy was emptied and washed prior to the start of a new collection period.

RESULTS

Quantities of solids deposited

The seasonal variations in biodeposition by oysters were similar in 1961 and 1962 and are illustrated by the data for 1962 from the circular troughs (Fig. 1). The deposition of feces and pseudofeces always greatly exceeded the deposition of solids by gravity (control sediments) which, during 1962, averaged 14.3% of the combined weight of feces and pseudofeces. The bio-

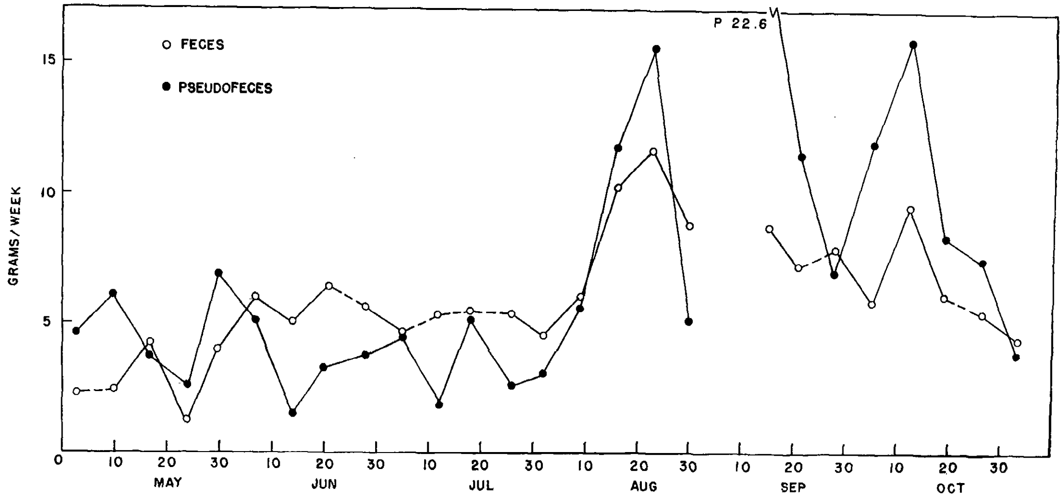

Fig. 1. Mean weekly rates of biodeposition for groups of eight oysters, 1962. Points connected by solid lines differ statistically; those connected by dotted lines show no evidence of a statistical difference.

deposition in 1962 was characterized by abrupt changes, but nearly all differences between weekly values were significant (Fig. 1). For the entire period, the mean total weight of biodeposits (feces plus pseudofeces) for individual oysters averaged 1.62 g/week with a maximum of 3.92 g/week. Daily biodeposition rates were obtained from 10 July to 22 August 1962 in a concurrent experiment (Fig. 2). These data emphasize the variability of biodeposition because the daily fluctuations exceeded the weekly and monthly changes observed in the seasonal study; the more regular weekly rates may result from the averaging of the daily values.

There was wide variation in the daily production of biodeposits from species to species. Size differences of animals among the groups and variability in the shell weight to tissue relationships made total weight an unsuitable index for comparing relative rates of biodeposition, so the mean dry weight of tissue for each group was used (Table 1). The tunicate *M. manhattensis* produced more solids per unit of tis-

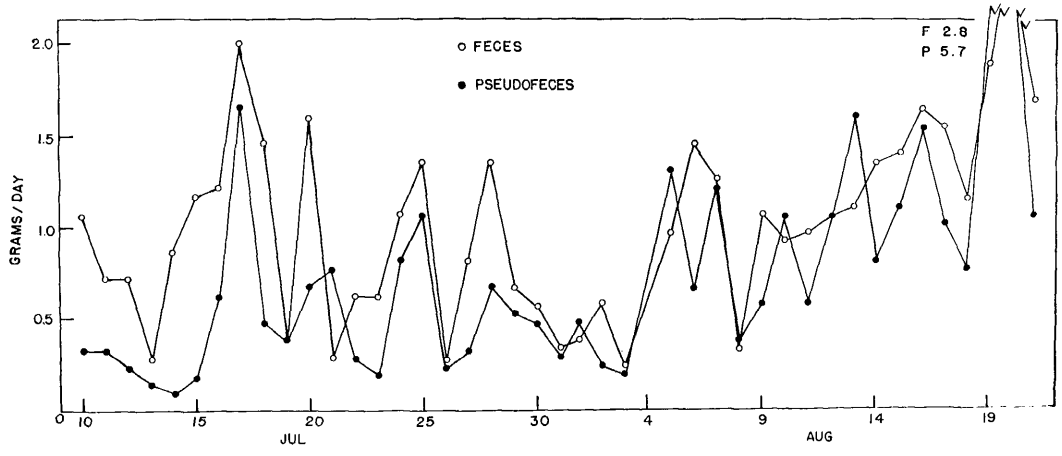

Fig. 2. Daily rates of biodeposition for oysters, 10 July to 22 August 1962.

TABLE 1. *Biodeposition rates for several species of invertebrates*

Species	No. animals	Mean wt whole animal (g)	Mean dry wt tissue (g)	Mean deposition (g animal^{-1} week^{-1})	Mean deposition / Mean tissue weight
		14 April to 26 April 1963			
Crassostrea virginica	16	14.7	0.48	0.98*	2.0
Mya arenaria	16	18.0	1.82	0.19	0.1
Modiolus demissus	4	12.2	0.72	0.90	1.2
Balanus eburneus	53	3.4	0.09	0.03	0.3
		19 June to 14 July 1963			
Crassostrea virginica	16	36.0	1.41	1.32*	0.9
Mya arenaria	8	33.5	0.99	0.16	0.2
Molgula manhattensis	16	5.7	0.24	0.56	2.3
Balanus eburneus	39	5.4	0.08	0.02	0.2
		15 August to 29 August 1963			
Crassostrea virginica	8	30.7	1.14	1.56*	1.4
Modiolus demissus	8	19.0	0.58	0.86	1.5
Molgula manhattensis	8	2.1	0.11	0.28	2.5

* Feces and pseudofeces combined.

sue weight than the other animals; oysters ranked second, while barnacles produced the least. Values shown for the soft clam may be minimal because these animals were not held in their usual substrate.

Factors influencing biodeposition

Oyster weight A possible relationship between oyster size and production of biodeposits was suggested by the 1962 seasonal study data. Coincidental with an upward trend in the weekly deposition curve (Fig. 1), mean weight of oysters increased from 10.9 g to 33.4 g between 30 April and 2 October (a similar weight increase was shown by a control group cultured in the York River). However, these observations extending over six months were made under varying environmental conditions and only suggest that growth and deposition were related.

From 16 to 26 October, the deposition by four weight groups of oysters was determined. Oysters were chosen to fall within 2 g of selected weights covering a wide range; mean weights of each group were 6.6, 11.0, 33.0, and 73.3 g. Biodeposits were collected daily from each group and averaged to give mean weekly rates (Fig. 3). The largest group deposited relatively less per unit of weight than the three smaller groups. The 11.0- and 33.0-g groups were comparable in weights to initial and final weights of oysters used in the 1962 weekly deposition study (Fig. 1). Within this range, the larger group produced about twice as much feces as the smaller group and four times more pseudofeces. Consequently, part of the gradual upward trend in production of feces and pseudofeces for laboratory oysters shown in Fig. 1 may be attributed to increases in weight.

Temperature Low water temperatures reduced oyster biodeposition rates. During early December 1961, when temperatures decreased to 6.7C, there was an 85% decrease in weight of biodeposits. Later in the same month when water temperatures ranged between 2.8 and 5.3C, feces and pseudofeces were still being produced by some of the oysters but in amounts less than 0.05 g/week. At temperatures lower than 2.8C in January and February 1962, measurable quantities of feces and pseudofeces were not produced. Loosanoff (1958) obtained similar results and found that at temperatures between 2.0 and 3.0C, 1.1% of 90 Long Island oysters expelled feces and only 15% expelled pseudofeces.

Suspended solids Comparison of biodeposition rates with quantities of seston in the water at weekly or daily intervals gave

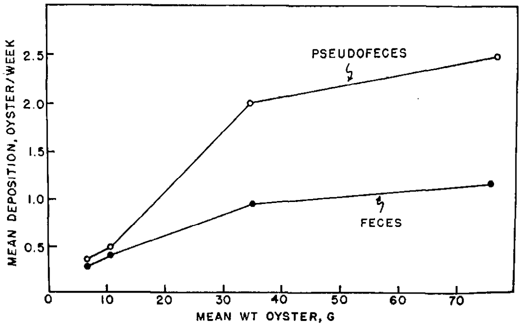

FIG. 3. Relationship between biodeposition rates and mean weight of oysters, 16 October to 26 October 1962.

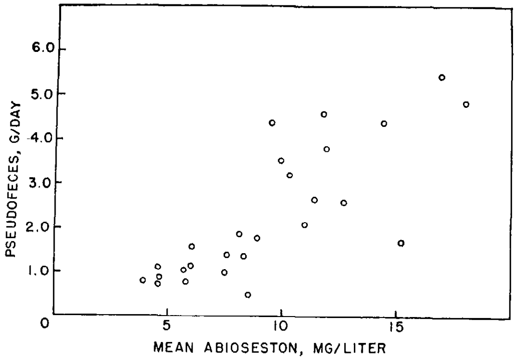

FIG. 5. Daily rate of pseudofecal production in relationship to abioseston, 13 September to 23 October 1962.

varying results. The weekly rates obtained during the 1962 seasonal study (Fig. 1) were compared with mean weekly seston values. To facilitate comparison with other studies, the season was divided into three periods: 30 April to 8 July, 9 July to 25 August, and 27 August to 7 November. No relationship was found during these intervals between total seston and production of feces or pseudofeces.

The problem was studied by comparing daily values of total seston (and on one occasion abioseston) with daily biodeposition during three separate periods. One study compared biodeposition with total seston for the period 16 July to 22 August 1962. In this interval, quantities of pseudofeces varied over wide limits with a mean of 1.5 g/day. Fecal production had a mean of 1.1 g/day, and total seston concentrations ranged from 4.7 to 29.0 mg/liter with a mean of 10.0 mg/liter. Correlation analysis showed no relationship between total seston and pseudofeces or feces.

From 13 September to 23 October 1962, daily biodeposition values were compared with total seston as well as with abioseston. Total seston concentration was similar to that for the preceding July and August period; abioseston ranged from 3.9 to 18.0 mg/liter, with a mean of 9.0 mg/liter. Correlation analysis suggested a positive relationship between pseudofeces and total seston (correlation coefficient, $r = 0.59$) and with abioseston ($r = 0.80$) (Figs. 4 and 5). Fecal production was at levels similar to

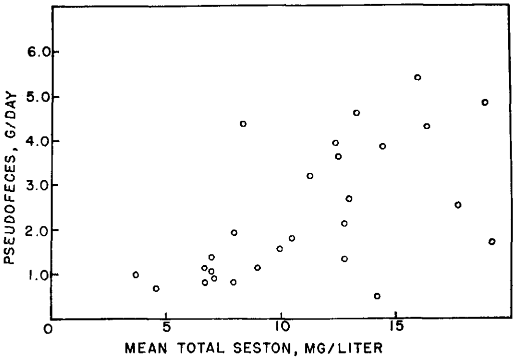

FIG. 4. Daily rate of pseudofecal production in relationship to total seston, 13 September to 23 October 1962.

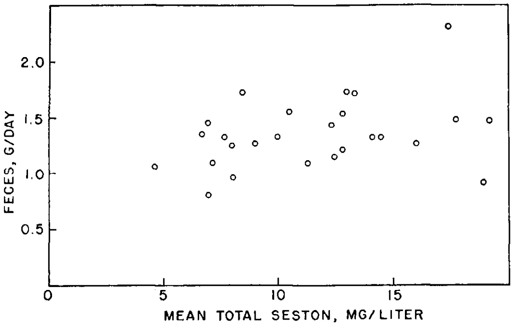

FIG. 6. Daily rate of fecal production in relationship to total seston, 13 September to 23 October 1962.

the preceding July and August period, with no apparent relationship between feces and total seston or abioseston (Figs. 6 and 7).

Daily seston was again compared to biodeposition from 11 to 27 April 1963. Seston levels were similar to the preceding periods, with a mean of 10.7 mg/liter. The mean value for pseudofecal deposition per trough was 1.4 g/day, and correlation analysis suggested a positive relationship between pseudofeces and total seston ($r = 0.52$). Feces production was low, averaging 0.5 g/day, but correlation analysis suggested a negative relationship ($r = -0.51$) with total seston.

Physical and chemical characteristics of oyster biodeposits

Gross appearance Freshly deposited oyster feces consist of short green or brown segments from about 1 to 5 mm long. In cross section, they are thickened filaments about 1 mm across with recurved edges and a low median longitudinal ridge. Under certain laboratory conditions, production of fecal ribbons was continuous, but production of short segments was most frequent. Pseudofeces were similar in color but were ejected as clumps loosely aggregated with mucus and occasionally as a continuous string without definite form.

Nature of particles Dispersed samples of feces, pseudofeces, and gravitationally settled sediments collected from 10 April to 8 May 1961 were examined microscopically. The material classed as "particles" included sand grains, particles of silt and clay, fragments of detritus, bacteria, sponge spicules, and many unrecognizable fragments. These occurred in large numbers, necessitating high dilutions before counts could be made in the hemocytometer cell. Twenty-four samples were examined and cumulative percentage frequencies computed. Size ranges of particles in feces, pseudofeces, and control sediments were essentially the same, ranging from less than 0.8 to about 13 μ size, with at least 80% under 2 μ and approximately 95% less than 3 μ. Many particles in the 0.8-μ range or lower were observed, but as these were beyond the resolving power of the microscope, their nature is unknown and counts and measurements are unreliable.

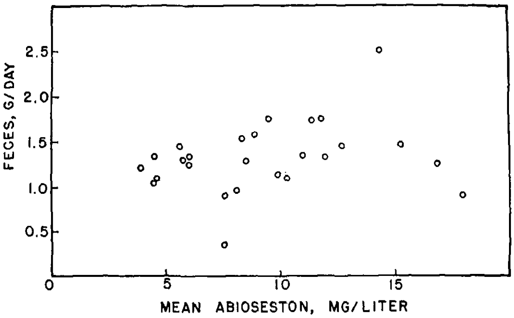

FIG. 7. Daily rate of fecal production in relationship to abioseston, 13 September to 23 October 1962.

Examination of algal cells and cell fragments seen in feces, pseudofeces, and control sediments showed almost every type observed in York River phytoplankton at the time, but the most common were species of *Cyclotella, Peridinium, Prorocentrum, Cocconeis, Melosira,* and *Coscinodiscus.* The smallest identifiable cell was about 3 μ, while the largest was a *Nitzschia* cell about 146 μ long. Size ranges of the algal cells most frequently seen were *Cyclotella,* 10–80 μ; *Peridinium,* 16–32 μ; and *Cocconeis,* 8–30 μ.

Mineral composition X-ray diffraction analyses of samples of feces, pseudofeces, and control sediments collected between April and September 1961 showed their mineral content to be similar. The major constituents (about 70 to 90% of each of the samples) were illite, chlorite, and mixed-layer clay. Quartz, feldspar, and montmorillonite formed the minor minerals. These minerals are typical of sediments in the Rappahannock River, a representative part of the Chesapeake Bay estuary (Nelson 1960). Both the diffraction analyses and the loss on ignition reported below indicated the high inorganic content of sediments—those collected in 1962 contained from 77 to 91%.

Organic matter Organic content of oyster biodeposits and control sediments was determined in two studies. In the first, sam-

TABLE 2. *Range and mean total organic matter expressed as per cent dry weight in oyster biodeposits, control sediments, and seston, 1962*

Source	Range	Mean
Monthly, 30 April–7 November		
Feces	12.0–19.7	15.0
Pseudofeces	14.0–19.3	15.7
Control sediments	10.4–16.9	14.8
Daily, 13 September–16 October		
Feces	9.0–22.1	13.7
Pseudofeces	9.5–17.9	12.3
Control sediments	9.0–22.6	14.3
Seston	2.2–51.2	23.4

TABLE 3. *Range and mean total organic carbon expressed as per cent dry weight in biodeposits from five species of filter feeders, 1963*

	29 April–9 May		25 September–30 September	
	Range	Mean	Range	Mean
Crassostrea virginica				
Feces	5.0–6.9	6.1	4.0–5.1	4.6
Pseudofeces	4.1–6.9	5.9	4.1–7.8	5.4
Balanus eburneus	4.7–6.2	5.5	6.2–7.5	6.8
Mya arenaria	4.3–6.9	5.3		
Modiolus demissus	4.3–6.8	5.6	4.0–4.7	4.4
Molgula manhattensis			4.4–6.4	5.4

ples of biodeposits and control sediments were collected from 30 April to 7 November 1962; each sample represented one week's accumulation. In a second study, 13 September to 16 October 1962, the organic content of oyster biodeposits and control sediments collected daily was compared with that of the seston in the water supplying the oysters. The biodeposits and control sediments contained similar quantities of organic matter, and there was no evident seasonal trend (Table 2). In the last period, the range in daily values of organic matter in the seston was wider than that of biodeposits, and the mean value was about 40% higher.

Total organic carbon There were distinct seasonal trends in the total organic carbon content of both feces and pseudofeces in the 1961 seasonal study, and there were apparent differences between the feces and pseudofeces (Fig. 8). During April and May, the organic carbon content of the pseudofeces gradually increased, while that of the feces decreased. There were significant differences in the total organic carbon content of the feces, pseudofeces, and control sediments. From 3 April to 5 June, the feces contained 44% more carbon than the pseudofeces (the feces averaged 8.3%, the pseudofeces 4.5%), but from 5 June to 29 August they were similar, averaging 6.4% and 6.2%, respectively. From October through December, when water temperatures began to decrease, the feces contained an average of 4.6%, while the pseudofeces contained 4.0%, a difference of 13%. Throughout the year, the control sediments contained less organic carbon than feces or pseudofeces, the average being 4.0%.

The total organic carbon content of feces, pseudofeces, and control sediments collected from 7 May through 27 August 1962 during the weekly study was essentially the same as in the comparable period in 1961, averaging 5.3% in all three. Samples collected daily from 24 September to 16 October 1962 had organic carbon contents that agreed with those from the comparable period in 1961 (Fig. 9). Feces consistently contained more organic carbon, averaging 5.0%, than pseudofeces, which averaged 4.2%, while the control sediments averaged 5.2%. The organic carbon contents of biodeposits collected from other species between 29 April and 9 May 1963 and from 25 to 30 September 1963 (Table 3) were similar to those of oyster feces and pseudofeces.

The carbon content of surface sediments from the York River was compared with that of biodeposits. At Gloucester Point, sediments from 6-, 12-, and 18-m depths contained about 10% sand and had organic carbon contents ranging from 2.0 to 2.8%; sediments from 3.6 m were about 85% sand and contained from 0.4 to 0.7% organic carbon. At the station 7.2 km upriver, sediments from 1.8- to 12-m depths contained 20 to 73% sand and 0.9 to 2.5% organic carbon. It is evident that oyster feces, oyster pseudofeces, and biodeposits from

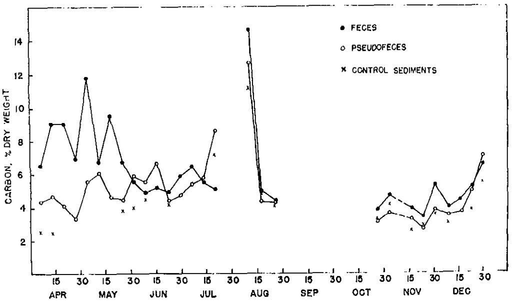

FIG. 8. Per cent total organic carbon in oyster feces, pseudofeces, and control sediments collected weekly from laboratory troughs, April 1961 to January 1962.

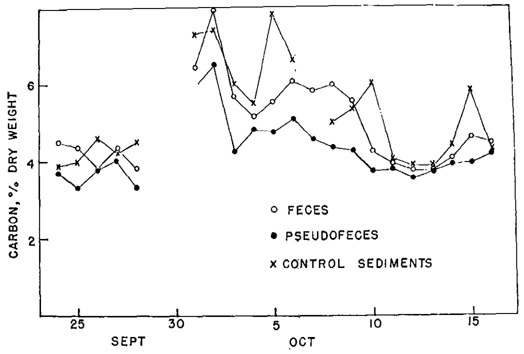

FIG. 9. Per cent total organic carbon in oyster feces, pseudofeces, and control sediments collected daily from laboratory troughs, 24 September to 16 October 1962.

other invertebrates contained significantly more organic carbon than the surface sediments. This was true for sediments from the shore zone to mid-channel and for sediments ranging from mostly sand to largely silts and clays.

Total phosphorus The total phosphorus contents of samples collected daily between 25 September and 16 October 1962 fluctuated between 0.3 and 1.7 g/kg with a mean of 1.0 g/kg. There were no discernible seasonal trends or differences in the phosphorus content of feces, pseudofeces, and control sediments.

DISCUSSION

Our results show that in the laboratory oysters may filter seston from the water and deposit it as feces or pseudofeces about seven times faster than it would settle by gravity. Consequently, it is pertinent to establish the magnitude of biodeposition as it may occur in the estuary. Data from the trough studies show that individual oysters deposited 1.62 g/week with a September maximum of 3.92 g/week. In the lower York River, commercial oyster growers frequently plant to an acre (0.405 hectare) about 250,000 small oysters similar in size to those used in the trough study. From April through October these would deposit about 405 kg (dry weight)/week of solids with a maximum of 981 kg/week; larger oysters would produce greater quantities. Biodeposition rates for other common species of invertebrates may equal or exceed that of the oyster, and when the abundance of these animals is considered, the magnitude of the process becomes evident. Barnacles literally cover many wharfs and pilings in the intertidal zone as well as rocks and shells on the bottom. Tunicates compete for space on the same objects, and many hundreds may be found in 0.1 m^2. Soft clams and ribbed mussels occur in the shallow intertidal zone and their densities may be as high as several hundred on a square meter.

The quantities of feces or pseudofeces produced by oysters and other filter feeders are determined by the physiological responses of the animals to environmental stimuli, and particle filtration is the most important of these responses. From 0 to 90% of the solids filtered from suspension may be retained on the oyster's gills, depending on particle size and concentration, algal species, temperature, salinity, and other environmental factors (Korringa 1952; Jørgensen 1960; and others), while particle selection in the ciliated tracts or grooves on the oyster's gills and palps determines the relative fractions of feces or pseudofeces (Nelson 1938; Yonge 1949; Korringa 1952).

In the laboratory, oysters produced no measurable quantities of feces or pseudofeces at water temperatures lower than

2.8C. Nelson (1923) stated that between 4 and 5C there is a sharp decrease in ciliary activity in oysters and that almost no food is taken at temperatures below 4C. Galtsoff (1964) obtained similar values for New England oysters, indicating that ciliary activity ceases at 5 to 7C. The temperature studies show the seasonal nature of biodeposition by oysters in Chesapeake Bay. Thermograph records from 1953 through 1962 show that water temperatures in the York River estuary are seldom higher than 7C between 15 December and 1 March, and during January and February, periods of two or three weeks commonly occur when maximum temperatures do not exceed 5C (Virginia Institute of Marine Science 1959). These data indicate that oysters in the York River will produce little, if any, biodeposits during the winter months.

There was no statistical correlation between quantities of oyster feces or pseudofeces collected at weekly intervals with mean values for total seston obtained over a similar period. When deposits were collected daily, pseudofeces seemed to be positively correlated with suspended solids when temperatures were at mid-range but not during the warmest period in midsummer. Possible reasons for these relationships are not apparent. Daily studies relating fecal production to seston indicated a negative correlation in one instance, and oysters were apparently producing maximum quantities at the lowest levels of total seston. The data give no indication of a maximum rate of removal of seston as pseudofeces. Seston levels included in these studies were essentially the same as in the York River at the inlet of the pump, 0.5 m above the bottom in inshore waters. In regions of this estuary where turbidities are higher, deposition of pseudofeces may reach higher levels than shown by our data.

Limited studies by several authors have estimated quantities of feces or pseudofeces produced by oysters in relationship to substances added to the water, and their results partially agree with ours. Lund (1957) added varying quantities of ground *Ulva* to water flowing over oysters and showed a positive correlation for feces and pseudofeces. Loosanoff and Engle (1947), using a continuous flow system, added *Chlorella* suspensions to seawater and estimated quantities of feces and pseudofeces produced; pseudofeces were approximately proportional to concentrations of the added materials, while feces production decreased with increasing concentrations. A difference between these studies and ours is that the former were for short periods and substances were added to the water; our program involved naturally occurring particles.

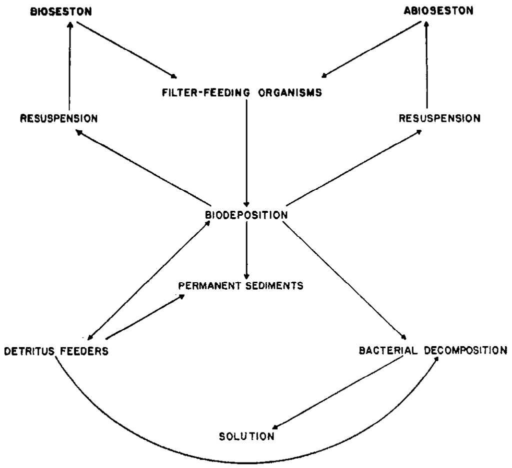

FIG. 10. Theoretical biodeposition cycle in the estuary.

The organic contents of feces, pseudofeces, and control sediments were nearly equal, but the water that supplied these animals contained nearly twice as much. An explanation for this wide difference is not apparent, but it is possible that the oysters were not able to filter all the available organic matter and that a portion occurred as particles too small to be filtered from suspension. Mullin (1965) showed that the organic carbon content of seston particles between 1 and 10 μ is appreciably higher than that of all larger sizes combined. Jørgensen and Goldberg (1953) showed that *Crassostrea virginica* could retain 2- to 3-μ particles but that a large percentage of particles smaller than 1–2 μ passed through the gills. Unpublished data from size retention studies by the present authors are similar to those of Jørgensen and Goldberg.

The organic carbon content of biodeposits varied between 4 and 12%, but the results suggest maximum quantities during spring and fall. The higher level of carbon in feces than in pseudofeces during spring and fall is probably the result of particle sorting by the oyster after the solids are filtered from suspension by the oyster's gills as outlined by Nelson (1938) and Galtsoff (1964). Oysters probably ingest carbon-rich particles and reject poorer particles as pseudofeces. A second possibility is that the less compacted pseudofeces may, on standing, lose carbon faster than the more compacted feces. However, differences in the carbon content of week-old feces and pseudofeces were essentially the same as in those collected daily.

Biodeposits of oysters and other invertebrates contained more organic carbon than bottom sediments collected from the shore zone to mid-channel; therefore, in estuaries such as the York River, accumulation of oyster feces and pseudofeces on the bottom would tend to enrich the existing sediments with carbon as outlined by Ito and Imai (1955). Control sediments sometimes had about the same organic carbon content as biodeposits, so accumulation of the former would also enrich the bottom with carbon. However, biodeposits accumulate faster than seston settling under gravity alone.

Recent studies show that biodeposits from oysters are mixed into sediments adjacent to their site of production (Haven and Morales-Alamo 1965*a*, 1966). The extent to which they would modify the physical and chemical characteristics of existing sediments would depend on the quantities deposited, the nature of the existing sediments, composition of the benthic populations, and hydrographic features such as currents (which could resuspend and transport the biodeposits). Thus, biodeposition in an estuary is an extremely complex process involving many groups of animals and physical and chemical factors. A tentative illustration of the entire process is shown in Fig. 10.

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