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## **Low-density particles as potential nitrogenous foods for benthos**

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and Susan Trumbore<sup>5</sup>

### **ABSTRACT**

The demonstrated bias of both macrobenthos and fluids to mobilize low-density particles leads to their potential importance as nutritional materials in benthic systems. We fractionated sediments from three coastal regions into low- and high-density separates, and examined both their organic geochemical characteristics and effects on ingestion rates of a deposit feeder. The low-density separates were highly enriched in total organic matter relative to the high-density phases. Enzymatically hydrolyzable protein concentrations in low-density separates were as much as 57-fold higher than the corresponding high-density separates, though some samples from Puget Sound and the Mediterranean Sea showed no enrichment at all. Low-density phases without nutritional enrichments were usually composed of woody debris. In spite of the organic richness of the low-density phase, it makes up no more than a minor fraction of either total sedimentary organic matter or its nutritional component. Addition of anomalously high concentrations of low-density materials to sediments caused a deposit-feeding spionid polychaete to reduce ingestion rates.

### **1. Introduction**

Marine sediments consist largely of minerals and water, to which organic matter generally adds but a few percent of the mass. Much of this organic matter is in turn rather indigestible (Lopez and Levinton, 1987), so that many animals living in sediments have evolved mechanisms to select relatively nutritious components of the organic matter present. It is not yet completely predictable which characteristics of potential food particles will be used in selection, but both chemical and physical properties are candidates. One of the physical attributes of potential food particles likely to provide a basis for selection by deposit feeders is particle density. Such selectivity has been inferred in a number of experimental and field investigations

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(Hylleberg and Galucci, 1975; Sibuet *et al.*, 1982; Brown, 1986) and documented experimentally (Self and Jumars, 1978, 1988; Jumars *et al.*, 1982).

Deposit feeders share this selective ability with overlying fluids. At small particle Reynolds numbers, particle movement in fluids is described by Stokes Law, in which both the size and density of particles are important terms. Because organic particles are of lower density than mineral grains, organic particles behave hydrodynamically like finer-grained mineral particles. Hence we might expect spatial correlations between sediment grain size and concentrations of low-density, organic particles based on this hydrodynamic equivalence. Hydrodynamic sorting of mineral- and organic-rich particles has been observed in flume experiments and can benefit benthic suspension feeders (Muschenheim, 1987a) or deposit feeders (Yager *et al.*, 1993).

The incentive for selection of low-density particles—their potentially high nutritional value—has received little attention. Here we examine low-density particles found in nearshore marine sediments, with emphasis on their proteinaceous components as indicators of nutritional quality. This focus on protein results from the presumed importance of nitrogen in deposit-feeder nutrition (Tenore, 1981, 1983; Rice and Rhoads, 1989; Taghon and Greene, 1990). Certainly proteinaceous materials dominate the identified portion of metabolizable detritus in marine sediments (Khripunoff and Rowe, 1985; Cowie, 1990).

## 2. Methods and materials

Samples were collected by box cores or Smith-MacIntyre grabs from vessels, or by hand-held cores in intertidal or SCUBA depths. Samples were obtained from estuarine and nearshore sites (0–200 m depth) in mid-coastal Maine and Puget Sound (Washington), U.S.A., and shelf and slope sites (44 and 2500 m depth) in the northwest Mediterranean Sea. Except for two cores described in this study, all samples represent the top 1–2 cm at the sediment-water interface. Samples were frozen immediately after collection and then freeze-dried.

Density separations were performed on freeze-dried sediments by suspending 10 g sediment in 25 ml of saturated CsCl solution ( $\rho = 1.9 \text{ g ml}^{-1}$ ), shaking, and centrifuging. The  $< 1.9 \text{ g ml}^{-1}$  fraction was recovered by aspirating the material floating on top of the supernatant with an eyedropper and placing the suspensions onto 0.4- $\mu\text{m}$  Nuclepore filters. These filters were rinsed with deionized water to remove CsCl. The amounts of low-density material recovered were determined by weighing the filter before and after scraping off the material. The high-density fractions were washed in a 1:10 seawater:deionized water solution to remove CsCl.

Total organic carbon and nitrogen (TOC, TN) were measured on a Carlo Erba 1106 CHNOS Analyzer, after vapor-phase acidification to remove carbonate minerals (precision, as average SE on duplicates, = 1% for TOC and 2.5% for TN). Enzymatically hydrolyzable protein (hereafter termed “protein”) was analyzed by

the method of Mayer *et al.* (1986), which assays those polypeptides (with at least 7–15 amino acid residues) susceptible to proteolytic enzyme hydrolysis (typical SE = 15% on quadruplicates). Total acid-hydrolyzable amino acids (THAA) were extracted under N<sub>2</sub> by 6 N HCl at 100°C for 24 h, and measured by cation exchange HPLC (model 2000, St. John Associates), with postcolumn OPA derivatization and fluorometric detection. Sediment specific surface area was determined, after removal of organic matter by a mixture of hydrogen peroxide and sodium pyrophosphate, by the one-point BET adsorption method, using N<sub>2</sub> gas with a Quantachrome Monosorb analyzer (Mayer *et al.*, 1988; precision on duplicates, 1%). Surface area was used in this study as a surrogate for grain size measurements, and shows excellent correlation with many traditional grain size measures (Mayer and Rossi, 1982). Stable carbon and nitrogen isotopic ratios were determined on cryogenically purified gases following a 900°C combustion conducted under vacuum in quartz tubing for 1 h. Analyses of the gases (CO<sub>2</sub> or N<sub>2</sub>) were conducted on a VG PRISM and are reported in standard delta notation relative to PDB for δ<sup>13</sup>C and atmospheric N<sub>2</sub> for δ<sup>15</sup>N (typical SE = salinity ‰). Radiocarbon analyses were performed on samples by combustion at 900°C to form CO<sub>2</sub> which was then cryogenically purified and converted to graphite by cobalt-catalyzed reduction in the presence of H<sub>2</sub> (Vogel *et al.*, 1987). These graphite targets were then analyzed on the Accelerator Mass Spectrometer at Lawrence Livermore National Laboratory by the method of Davis *et al.* (1990).

*a. Feeding experiments.* As a bioassay, we fed various sediment treatments to a surface deposit-feeding polychaete. *Streblospio benedicti* individuals were collected from Lowes Cove, coastal Maine, and held in natural sediments at the adjacent Darling Marine Center for three days before experiments began. Individual worms were accommodated in vials to facilitate experimental manipulation and retrieval. Four sediment treatments were sequentially provided to the same individuals. First, surficial (top 5 cm) sediment from Lowes Cove was sieved (0.5 mm) and then fed to the animals. Second, this sieved sediment was separated by the CsCl method described above and the high-density fraction, washed copiously with seawater to remove all traces of CsCl, was then fed to the animals. Third, pellets from *S. benedicti* individuals that had fed on the first treatment sediments were disaggregated and then provided to the animals. Fourth, 10 mg of the separated low-density phase, also washed copiously, was added to 350 mg of the high-density separate and then provided to the animals. The low-density phase contained 38 mg g<sup>-1</sup> protein; while the protein content of the high-density separate was unfortunately not determined, our extensive experience with sediments from this locality (Mayer and Rice, 1992) indicates protein contents of no more than 2.5 mg g<sup>-1</sup>. The low-density material added was more than ten times the amount normally present in this sediment, and probably increased the protein content of the mixture by at least 50% (and likely as much as 100%) relative to whole, unfractionated sediment. Feeding experiments

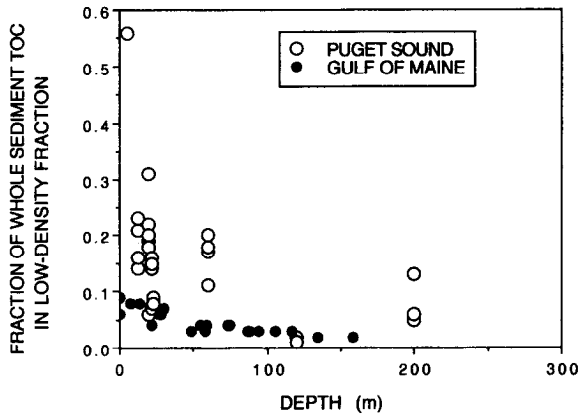


Figure 1. Fraction of whole sediment organic carbon contained in low-density separate (LD-TOC:WS-TOC) vs. depth, for Puget Sound and Gulf of Maine surface sediment samples.

consisted of providing, by pipet, a layer of sediments surrounding experimental worms. This layer was thick enough to prevent feeding on underlying sediments. Each worm was observed for 1 h. Feeding rate of the animals was monitored by noting the elapsed time between production of successive fecal pellets. The size of the pellets did not vary among treatments, so that the average elapsed time between pellets was related inversely to volumetric feeding rate.

### 3. Results

We chose CsCl solutions after trials with several other high-density aqueous solutions, such as sodium iodide, zinc chloride, and sodium metatungstate. CsCl solutions provided the highest recovery of total organic matter in the low- and high-density separates relative to the unfractionated whole sediment. Average recovery efficiencies, defined as the ratio of the sum of the amounts in the low- and high-density separates to the concentration in the unfractionated sediment, were 97% for TOC ( $n = 54$ ) and 96% for TN ( $n = 53$ ).

*a. Fractions of material in the low-density separates.* The total amounts of low-density separates obtained by the method used here were low, ranging from 0.3 to 30 mg separate (g unfractionated sediment)<sup>-1</sup> among the three geographic areas. The proportions of unfractionated sediment organic matter contained in the low-density separates were also low (Fig. 1). In Gulf of Maine sediments the low-density fraction contained generally less than 10% of the TOC of the total sediment. Puget Sound sediments showed greater contributions, but almost all samples were still below 30%. Those samples with particularly high fractions of TOC in the low-density phase were observed to contain wood chips. Low-density proportions of TOC were strongly

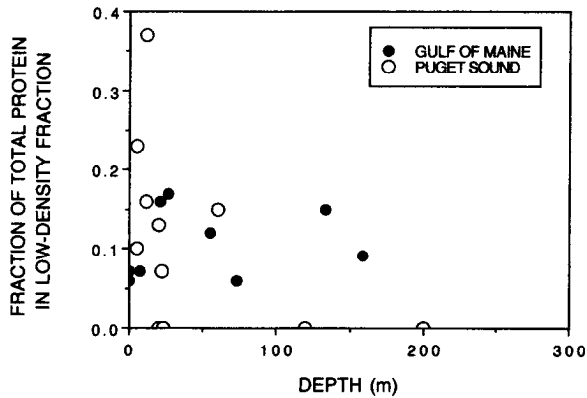


Figure 2. Fraction of whole sediment protein contained in low-density separate vs. depth, for Puget Sound and Gulf of Maine surface sediment samples.

correlated inversely with water depth in both areas ( $p < 0.01$ ). The two Mediterranean samples each had 10% of the TOC in the low-density fraction.

Minor amounts of protein were also found in the low-density fraction. This fraction contained a somewhat greater proportion of the protein in Maine sediments, relative to TOC or TN (Fig. 2). Sediments from Puget Sound were variable, with some sediments containing essentially no protein in the low-density fraction and others containing significant fractions of protein in this phase (Fig. 2). The depth relationships of this parameter were more ambiguous than those of TOC, with no evident relationship in the Gulf of Maine sediments. The Puget Sound samples showed an inverse relationship, perhaps due to the fact that shallow water samples from this area had generally lower total protein concentrations than deeper samples. The two Mediterranean samples contained  $< 1\%$  of their protein in the low-density fraction. THAA were distributed among the density fractions in a similar fashion as protein.

The contribution of low-density particles to organic matter (as TOC or protein) in the whole sediment did not change markedly downcore at an intertidal site in the Gulf of Maine (Fig. 3b), despite downcore decreases in concentrations of the various organic fractions (Mayer and Rice, 1992). At a shelf site (Fig. 3a) there was a decrease between 3 and 23 cm depth, but no further change in deeper horizons. For this latter core, we used a lower-density ( $1.4 \text{ g ml}^{-1}$ ) CsCl solution for separation, attempting to separate a more organic-rich fraction. This attempt was unsuccessful; TOC concentrations in the low-density phase averaged  $82 \text{ mg g}^{-1}$  (compare to Fig. 4), indicating that organic matter made up less than 20% of the low-density fraction by weight. We also found this lack of change in downcore contribution of low-density organic matter to the total organic matter in a number of cores separated with sodium metatungstate ( $\rho = 1.9 \text{ g ml}^{-1}$ ; data not shown).

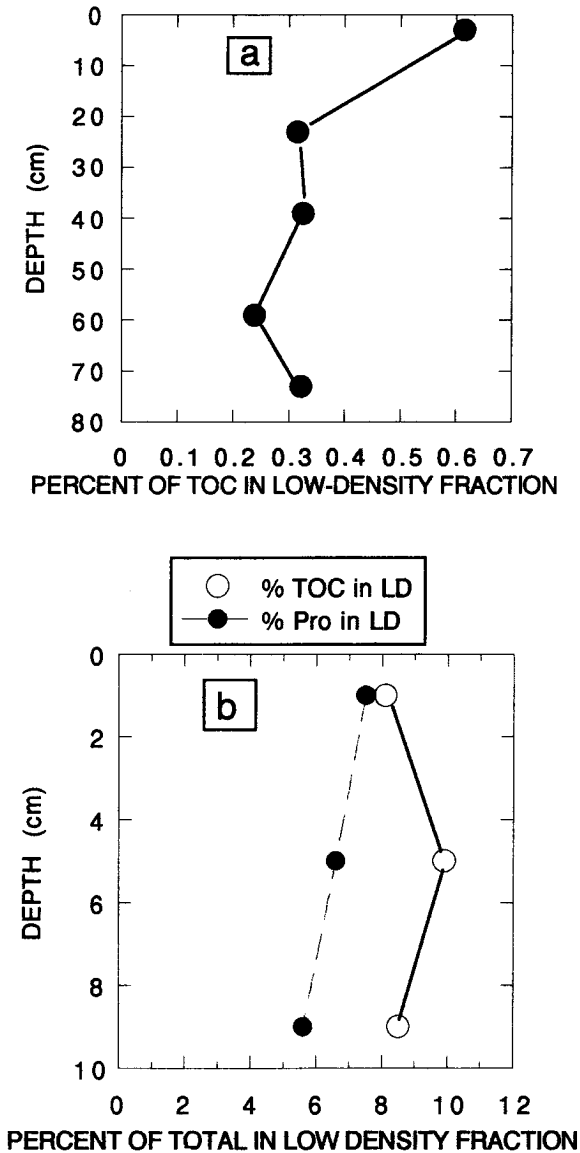


Figure 3. Fraction of whole sediment organic carbon (TOC) and protein (Pro) contained in low-density separate, in cores from Gulf of Maine shelf (a) and intertidal (b) sites.

*b. Compositional variations.* The low-density fraction was highly enriched in organic carbon (range = 82 – 499 mg-OC g<sup>-1</sup>) relative to the whole sediment or high-density fractions (range = 1 – 33 mg-OC g<sup>-1</sup>). Enrichments were lower in finer-grained (i.e., higher surface area) sediments (Fig. 4). While certainly enriched in organic matter, these low-density fractions were not pure organic materials; in some

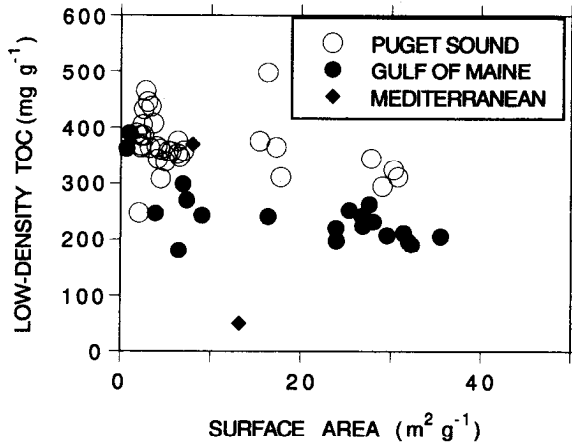


Figure 4. Total organic carbon (TOC) concentration in low-density separates (per g low-density separate) vs. surface area of whole sediment, for Puget Sound, Gulf of Maine and Mediterranean samples. Assuming organic matter to contain 50% organic carbon, these TOC values can be doubled to obtain organic matter content.

of the Maine sediments, for example, organic matter made up as little as one-third of the mass by weight, and a deep (2500 m) Mediterranean sample had only ca. 10% organic matter.

Visual observations of the low-density fraction indicated prevalence of amorphous material and marine biotic remains in the Maine sites, while wood chips were commonly observed in the Puget Sound samples. These observations were borne out by C:N ratios, which were much higher in the low- relative to the high-density fractions in Puget Sound and usually the opposite in the Maine sites (Fig. 5). Stable carbon isotope measurements further corroborate these trends (Fig. 6). Whole-sediment  $\delta^{13}\text{C}$  values show typically marine values at all five sites analyzed, while low-density fractions show typically terrestrial  $\delta^{13}\text{C}$  values of ca.  $-25$  per mil in the Puget Sound sites and more normal marine values in the Maine sites (Fig. 6a). The nitrogen isotope data also show typically marine values for the whole sediment at all sites (Fig. 6b), but with some influence of terrestrial source in the low-density fraction of the Puget Sound sites. These observations of terrigenous low-density material are consistent with a variety of other organic geochemical data on low-density materials from the Washington continental shelf (Prah and Carpenter, 1983; Ertel and Hedges, 1985). The Maine sediments showed no marked nitrogen isotope differences between the density separates. One of the Maine sites (ME 7) showed a high  $\delta^{15}\text{N}$  typical of macroalgal organic matter from this area (Mayer *et al.*, 1988).

Radiocarbon measurements were made on the various fractions from the Maine shelf core. These assays were performed in order to test if the low-density fraction showed significantly younger  $^{14}\text{C}$  ages consonant with their apparently more nutritious, and hence perhaps "fresher," status. As noted above, the density separations



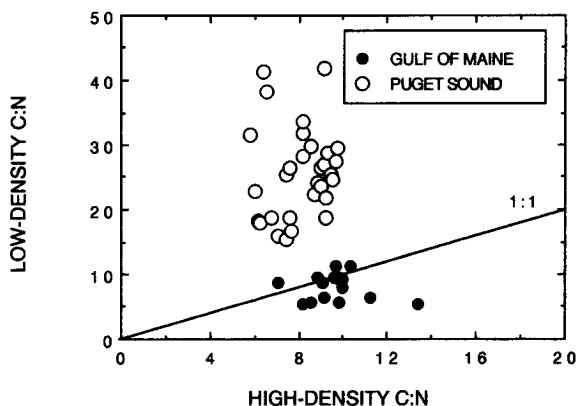


Figure 5. C:N ratios (wt/wt) of low- vs. high-density separates of samples from Puget Sound and Gulf of Maine. Points above the 1:1 line indicate higher C:N ratio in low- vs. high-density separate, and vice-versa.

at  $1.4 \text{ g ml}^{-1}$  were unsuccessful in yielding a more organic-rich phase. The  $^{14}\text{C}$  contents of these low-density fractions were lower than the high-density fractions or whole sediments, indicating greater ages for the low-density phases at almost every horizon (Fig. 7). It is not clear why the low-density fraction consisted of older material. One possibility is the occurrence of fossil fuel fragments; we occasionally observed black particles in low-density separates suggestive of fossil fuel materials.

Proteinaceous materials, as protein or THAA, were generally also much richer in the low-density fraction relative to the unfractionated sediment or high-density phase (Fig. 8). Protein enrichments (defined as the ratio of the protein concentrations in the low- relative to the high-density fraction) ranged up to 57-fold, and were highest in sediments from Maine. While most sediments from Puget Sound also showed enrichments, some showed little enrichment and even depleted protein in several samples. The Mediterranean samples showed similar lack of enrichment in the low-density phases.

These protein enrichments in the low-density phase of the Maine sediments were not due simply to higher overall organic matter contents in the low-density fraction. The proportion of low-density TN present as protein was also higher than for the whole sediment (Fig. 9a,b). In the Puget Sound samples, on the other hand, these ratios were usually lower in the low-density separate than in the whole sediment. Again, THAA trends were similar to those of protein.

Compositions of the acid-hydrolyzable amino acids in the various separates were generally similar to one another and to compositions reported in Mayer *et al.* (1988). In the Maine sediments, the low-density fractions often showed elevated glycine and tyrosine relative to the whole sediment, consistent with the inshore enrichments of these amino acids relative to offshore compositions (Mayer *et al.*, 1988).

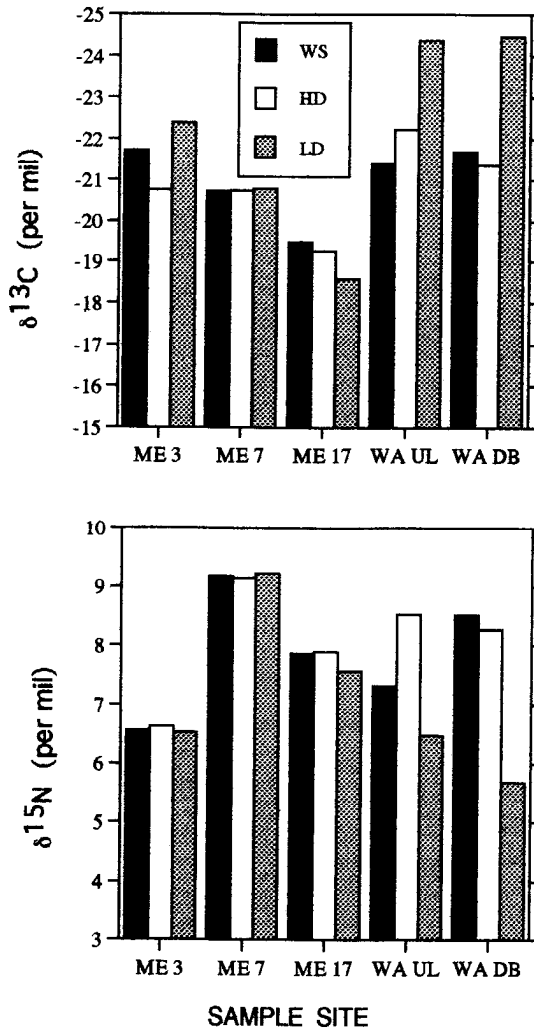


Figure 6.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of whole sediment (WS), high-density (HD) and low-density (LD) fractions of sediments from Gulf of Maine (ME 3, 7, and 17) and Puget Sound (WA UL and DB) sites.

*c. Feeding experiments.* The rate of ingestion of various sediment treatments by *Streblospio benedicti* was similar in all treatments except the case where excess low-density material was added to a high-density separate, with its consequent probable enrichment of protein content by at least 50% (Fig. 10). Feeding rate on the enriched sediment was 26–77% lower than on the other sediments. The worms' feeding rate on the high-density fraction was indistinguishable from both the untreated whole sediment and disaggregated pellets, indicating that residual CsCl did not remain after the washing to affect feeding rate.

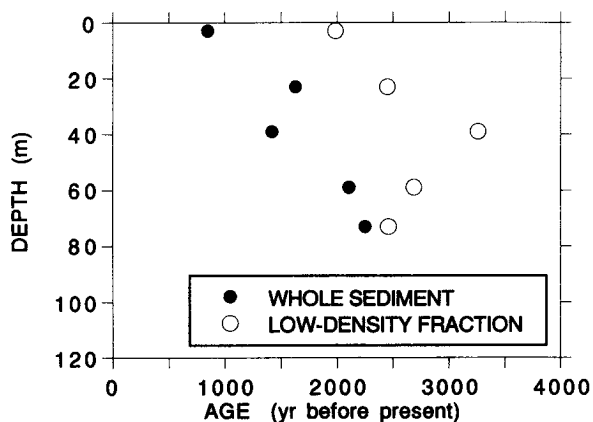


Figure 7. Radiocarbon ages of whole sediment and low-density separates of various depth horizons from shelf core, Gulf of Maine (same core as Fig. 3a).

#### 4. Discussion

The relevance of our density fractionation relies on the degree to which the CsCl separation mimics hydrodynamic sorting or the selection process of deposit feeders encountered in nature. We do not know the extent of this similarity. In working with high-density liquids of four different compositions (CsCl, sodium metatungstate, sodium iodide, and zinc chloride), however, we found that consistently minor fractions of organic matter were separable. We found somewhat higher yields of low-density organic matter with the sodium metatungstate solutions, but these yields came at the cost of dissolution of some of the sedimentary organic matter. This dissolution apparently allowed “ungluing” of low-density particles from mineral

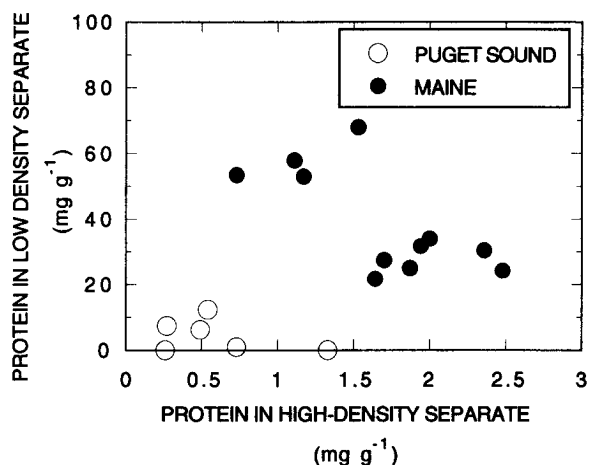


Figure 8. Protein concentrations of low- vs. high-density separates (per g of separate) of samples from Puget Sound and Gulf of Maine.

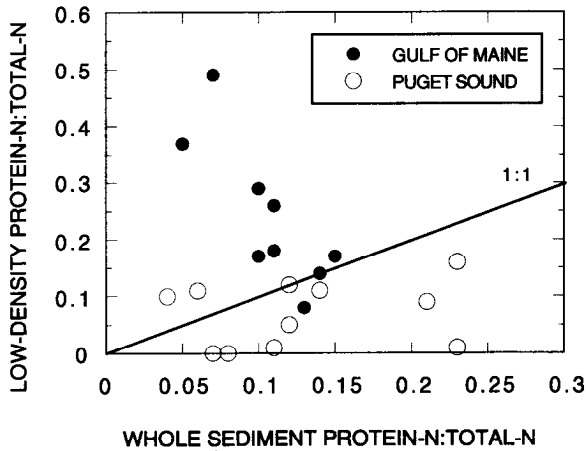


Figure 9. Ratio of protein-nitrogen (calculated as protein/6) to total-nitrogen in the low-density separate vs. that of the whole sediment, for Puget Sound and Gulf of Maine samples. This ratio serves as an indicator of the “quality” of the nitrogen, with higher ratios indicating greater digestibility. Points above the 1:1 line indicate higher protein-N:total-N ratio in low-density separate vs. whole sediment, and vice-versa.

grains. Because we are more interested in simulating the density-based particle separations that might be due to animals or fluid motion, we prefer the CsCl method for the purposes of this study. The small fractions of total or nutritionally available organic matter thus do not necessarily represent the actual amounts of low-density particles in sediments. Our inference of a minor contribution of low-density particles to the overall organic matter pool is likely correct, however, given the similarity of results among different methods employed in this study as well as others (Zaslavskiy, 1981; Prahl and Carpenter, 1983; Ertel and Hedges, 1985; Gershonovich and Zaslavskiy, 1985; Murdoch *et al.*, 1986). Further, many of the trends reported here, such as dependence of abundance or quality of low-density material on water depth or grain size, are unlikely to be significantly affected by artifacts of the separation method.

A consistent trend across all of the geographic areas examined in this study is a small contribution of the low-density fraction (as measured by our method) to either total organic matter or its nutritionally useful component. In very few cases does the low-density fraction contain more than 25% of the TOC or enzymatically hydrolyzable protein. These standing stock fractions may not, however, represent their importance in utilization by the benthos. To the extent that sedimentary food supply—as imported food for deposit-feeders (Miller *et al.*, 1984) or resuspended food flux for suspension feeders (Muschenheim, 1987b)—relies on relatively high resuspendability of low-density particles, these particles may have even greater importance. They are trapped efficiently in the feeding pits of a diversity of benthic animals (Yager *et al.*, 1993).

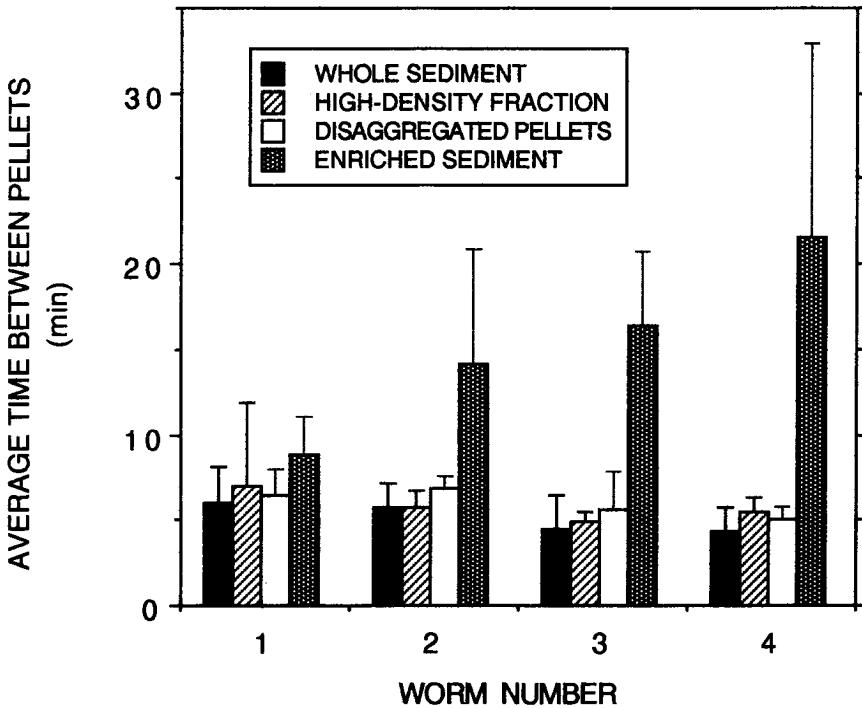


Figure 10. Average time between pellets for *Streblospio benedicti* feeding on four sediment treatments—unfractionated sediment, its high-density fraction, disaggregated *Streblospio benedicti* pellets that were previously fed unfractionated sediment, and high-density fraction amended with unusually high concentration of low-density separate. Vertical bars are standard deviations for  $n$  ranging from 3 to 11.

We found that separations resulted in greater purity of organic matter in coarse- relative to fine-grained sediments (Fig. 4). The net ability of particles to separate in a heavy liquid is a result of the opposing forces of (1) differential buoyancy—which leads to separation, and (2) adhesion—which prevents separation. Buoyancy forces are proportional to the mass of the particle, and hence to the cube of the particle radius. Adhesion forces, on the other hand, are likely proportional to the surface area of the particle, and hence to the square of its radius. With increasing particle size, therefore, differential buoyancy increases to a greater extent than adhesive forces. Hence in finer-grained sediments our separation technique and those of animals or fluids ought to be less effective at separating organic-rich particles on the basis of density than in coarser-grained sediments.

We tested whether low-density organic particles accumulate preferentially in fine-grained sediments—the hydrodynamic equivalence hypothesis—by examining correlations of the amount of low-density TOC with specific surface area (Fig. 11). Over the entire range of samples analyzed there was no correlation, positive or

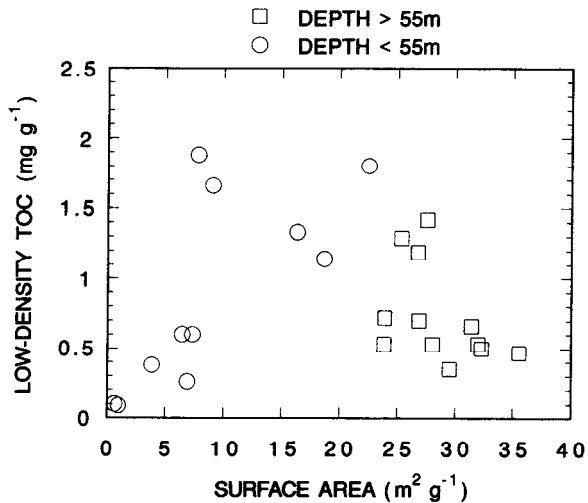


Figure 11. Amount of low-density organic carbon (OC) per g of whole sediment vs. surface area of whole sediment, for samples collected from different water depths of the Gulf of Maine. Correlation coefficient for <55 m depth samples is 0.71 ( $p < 0.05$ ).

otherwise. This lack of correlation, however, is likely due to a combination of two factors. First, water depth seems to be the dominant control on the amount of low-density organic matter (Fig. 1b). Finer-grained sediments, with relatively high surface area, are found preferentially in deeper waters, perhaps cancelling any tendency for low-density materials to correlate with surface area over the entire depth range. This possibility is supported by the fact that samples from a narrower depth range (0–55 m) did show positive correlation of low-density organic content with surface area, indicating the potential for this hydrodynamic concentration to be effective locally. Second, our analytical ability to separate all of the low-density material from the bulk sediment may be inhibited in fine- relative to coarse-grained sediments, for reasons described above, thus preventing us from finding an existing relation between grain size and low-density materials. As noted above, however, this analytical difficulty may have relevance to the ability of either deposit feeders or fluids to perform the same separation.

We previously found that bulk organic matter concentrations in sediments—as TOC, TN, or THAA—were controlled primarily by grain size in the Gulf of Maine (Mayer *et al.*, 1988). The nutritionally valuable component of sedimentary organic matter—as indicated by protein or chlorophyll concentrations—was controlled predominantly by water depth, however, which is in turn inversely correlated with grain size. In this context, the distribution of low-density materials in the Gulf of Maine sediments found in the present study—decreasing strongly with water depth—is much like that of nutritionally valuable materials described in Mayer *et al.* (1988).

The extremely high nutritional quality of the low-density material relative to the

high-density fraction or whole sediment, found in all Maine and several of the Puget Sound sediments, provides ready explanation for the demonstrated proclivity of some deposit feeders to select on the basis of this physical parameter (Jumars *et al.*, 1982; Self and Jumars, 1988). Volume rather than weight of ingested sediments is probably the more relevant parameter to the process of digestion (Penry and Jumars, 1987). The nutritional differences that we find are even greater if we normalize nutritional content to sediment volume rather than to weight. Assuming the low-density fraction to have a mean density of, say, two-thirds that of the high-density fraction, the relative nutritional quality per unit of volume increases by a factor of another 50%.

While this low-density fraction is very high in nutritional value, it nevertheless makes up but a minor fraction of the protein, and presumably total nutritional, content of sediment. Thus it is not surprising that deposit feeders show only partial preference for low-density particles (Self and Jumars, 1988) and therefore pursue a largely bulk-feeding strategy to maximize rate of nutritional gain from sediment. It is of course quite possible that a correlate of density, such as olfactory properties, serve to focus an animal's effort toward selection of low-density phases.

The high protein contents of the low-density materials from the Gulf of Maine are similar to values found for seston in Maine estuaries (Anderson and Mayer, 1986). To the extent that hydrodynamic sorting during resuspension of material from the sediment-water interface selects for low-density materials, these protein contents explain the nutritional advantage of near-bottom suspension feeding as described by Muschenheim (1987a,b).

We also emphasize that at several sites we found no significant nutritional enhancement in the low-relative to the high-density fractions. Most of these sites probably had a low-density fraction dominated by woody debris, which has the nutritional quality of mineral matter for a marine deposit feeder (indigestible core with perhaps a digestible rind). Poor nutritional quality in the two Mediterranean sites analyzed lends further caution to extrapolating our Maine data to all localities.

Our bioassay with *Streblospio benedicti* demonstrates that Maine intertidal sediment enriched with low-density fraction of enhanced nutritional quality is treated differently than the bulk sediment or high-density separate. The protein content of the high-density separate was likely about 10% lower than the bulk sediment (Fig. 2), while we estimate a minimum 50% increase in protein content in the enriched sediment. *Streblospio* fed on the high-density separate and bulk sediment at similar rates, while feeding rate declined 26–77% on the enriched sediment. These trends are generally similar to results from *Abarenicola pacifica*, another deposit-feeding polychaete, in which feeding rate declined by 40% when the protein content of bulk sediment was experimentally increased by 25% (Taghon and Greene, 1990). Thus the lack of an obvious change in feeding rate of *Streblospio* when offered bulk

sediment or high-density separate (Fig. 10) is probably due to the minimal difference in protein content and not to any residual effect of CsCl.

The fact that feeding rate decreases dramatically on the enriched sediment, without further data from a broader range of nutritional quality parameters, allows at least three alternative hypotheses: a non-monotonic relation between feeding rate and food quality (Phillips, 1984; Cammen, 1989; Dade *et al.*, 1990; Taghon and Greene, 1990); the food digested and absorbed by *Streblospio* is kinetically simple, like that of hummingbirds (Martinez and Karasov, 1989), giving them a monotonically decreasing feeding rate with increasing food quality (c.f. Dade *et al.*, 1990); mechanical differences (i.e. low density and its correlates) simply alter the mechanics (and thereby the net rate) of food gathering, ingestion and passage. Thus we suggest that our present data are consistent with an influential role for the low-density fraction in nutrition, but do not allow us to distinguish among alternative models (e.g., Kofoed *et al.*, 1989; Dade *et al.*, 1990; Willows, 1992) of digestion and absorption. They are, further, compatible with the view of deposit feeders as animals constrained to feed at such high particle throughput rates that mechanical correlates of food quality become foci for the action of natural selection on the functional morphology of diet choice.

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