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Sediment resuspension rates, organic matter quality and food utilization by sea scallops (*Placopecten magellanicus*) on Georges Bank

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ABSTRACT

Benthic detritus, bacteria, and settled phytoplankton are transported into the water column by resuspension, potentially providing a high quality food source to suspension feeders. Two aspects of resuspension must be considered in relation to food supplies for suspension feeders: the flux of particles from the sediments to the water column and its food value. Sediment resuspension rates on Georges Bank and the role of resuspended sediment in the diet of sea scallops (*Placopecten magellanicus*) were determined in laboratory flume experiments and shipboard feeding experiments, respectively. Resuspended carbon flux was estimated from flume bedload transport rates and the mass of organic carbon associated with the silt-clay fraction eroded from Georges Bank sediment during transport. A comparison of sand erosion thresholds with the frequency distribution of shear velocity estimated from field current meters indicated that tidal sediment resuspension will occur 62% of the time. Resuspended material had a carbon content of 4–8% and a C:N of 5–8. Rates of resuspension (33–229 mg C $m^{-2}h^{-1}$) and settling rates indicate that resuspended sediment in a size range available to scallops (>5 μm) remains in suspension for periods of hours to days. Clearance rates of resuspended sediment by scallops were similar to those for water column particles, and filtration rates increased with increasing concentrations of resuspended material. Feeding experiments demonstrated that scallops absorbed organic matter from resuspended sediments with an efficiency of up to 40%. Therefore, in terms of particle retention, ingestion, and digestion, sea scallops are able to exploit resuspended organic matter from a continental shelf habitat. Furthermore, resuspension occurs with sufficient frequency, and resuspended sediment has long enough residence time in the water column to provide a consistent nutritional benefit to scallops.

1. Introduction

Resuspension of bottom sediment is ubiquitous in marine environments as a result of tidal currents, wave action, bioturbation, and human activities such as dredging and trawling (Churchill *et al.,* 1988; Palanques and Biscaye, 1992). For benthic suspension feeders, resuspension causes large variations in particle size, quality, and concentration (Roman, 1978; Anderson and Mayer, 1986). In some cases, sediment resuspension has

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been postulated as being beneficial in enhancing seston concentration and providing additional suspended organic matter as a food source to benthic animals (Rhoads *et al.,* 1984; Cranford and Grant, 1990; Grant *et al.,* 1990). A variety of studies have demonstrated that benthic bacteria and microalgae as well as settled phytoplankton are transported into the water column by resuspension (Baillie and Welsh, 1980; Wainwright, 1990; Ritzrau and Graf, 1992), potentially providing a high quality food source to suspension feeders. Detrital organic matter and attached microbes provide a further source of suspended food originating from the bottom. Previous studies indicate that the advective renewal of phytoplankton food material is a limiting factor for dense assemblages of suspension feeders (Wildish, 1979; Frechette *et al.,* 1989). Resuspension may ameliorate this limitation by increasing the particle load of the water column (Frechette and Grant, 1991; Muschenheim and Newell, 1992), but there are few studies which have attempted to link resuspension to secondary production (Rhoads *et al.,* 1984; Thompson and Nichols, 1988; Grant *et al.,* 1990).

The addition of inorganic sediments and poor-quality organic detritus (e.g. marsh grass) to the seston may become detrimental to suspension feeders if it dilutes the concentration of better food sources such as phytoplankton (Cranford and Gordon, 1992; Cranford, 1995). Moreover, high turbidity can be deleterious by clogging the filtration apparatus, inhibiting feeding and respiration (Grant and Thorpe, 1991), and harming gill tissue (Morse *et al.,* 1982). Despite the influence of resuspension on food quality and quantity, there have been few studies of this process in the field in relation to the transport of organic matter and the provision of food resources for suspension feeders. These problems may be particularly relevant to continental shelf benthos where suspension feeders dominate the macrofauna of sand-gravel bottoms (Wildish *et al.,* 1989) and sediment resuspension is a persistent feature of these high-energy environments. Much of the sediment organic matter is of phytoplankton origin (Walsh, 1988), and resuspension conveys settled phytoplankton back to the water column rather than the refractory detritus (macrophytes) typical of nearshore sediments.

Two aspects of resuspension must be considered in relation to food supplies for suspension feeders: the flux of this material from the sediments to the water column and the food value of resuspended particles. The nature of resuspended fluxes of organic matter is poorly known in the field because no suitable approach has been formulated to address the complex issue of the relationship between organic and inorganic resuspension. The relict glacial sediments typical of most of the western Atlantic continental shelf are a sand-gravel mixture with a small proportion of fine sediment and organic matter (Grant *et al.,* 1991). The fine material (<102 μm) is of interest in the present study as it is organic-rich (e.g. phytoplankton), is of a suitable particle size for ingestion by bivalve filter feeders (Shumway *et al.,* 1987; Cranford and Grant, 1990) and remains in the water column for a period of minutes to hours once resuspended (Jago *et al.,* 1993).

An understanding of the transport of the fine fraction of relict glacial sediments is incomplete because it has different density, texture and mobility than the coarse grains of the bed (Jago *et al.,* 1993; Mayer *et al.,* 1993). The case of a small amount of silt-clay against a dominant background of coarse sediment has rarely been considered in sedimentological studies. Those studies that have dealt with the erosion threshold and transport rate of mixed sediment types have usually considered sand-gravel (Komar, 1987; Wilcock, 1988) or less commonly silt-gravel mixtures (Schalchli, 1992). The silt-clay fraction is found in the interstices of the sand-gravel mixture and a portion of the organic matter is firmly attached to the coarse grains (e.g. bacteria, adsorbed material). The degree to which fine particles are attached to each other and to the larger grains is dependent on floccule size, grain surface area, microbial activity, abrasion, and a variety of other factors (Mayer, 1994; Keil *et al.,* 1994; Grant and Emerson, 1995). Regardless, the maximum amount of fine material available for resuspension is constrained by the silt-clay content of a given quantity of sediment.

As grains are moved at the initiation of bedload sediment transport for sand or gravel, the silt-clay fraction is exposed and released into the water column. Therefore, suspended transport occurs as a consequence of bedload transport of coarse sediment, and is a function of the silt-clay content associated with a given mass of bulk sediment moved. If the carbon or nitrogen content of the fine fraction is known, then a maximum estimate of the resuspended flux of organic matter can be determined. Churchill *et al.* (1994) suggested from field measurements of near-bottom shelf particle fields that a two-component concept of erosion (fines and background coarse sediment) described their observations. This conceptual framework is applied in the present paper to study the advective transfer of organic carbon from coarse sediments to the water column where it is available for ingestion by benthic filter feeders.

A number of studies have approached the nutritional aspects of resuspension by conducting feeding studies with combinations of silt and phytoplankton (Bayne *et al.,* 1987; see references in Grant and Thorpe, 1991). Because the silt is often not representative of natural sediment in terms of organic quality or particle size distribution, these results have limited applicability to natural processes (Grant *et al.,* 1990). Feeding experiments with natural resuspended sediment suggest that it may be a food supplement for sea scallops (*Placopecten magellanicus*) (Cranford and Grant, 1990; Grant and Cranford, 1991), but the importance of this material is difficult to estimate without an indication of (a) the functional responses by suspension feeders to changes in concentration, (b) the retention of resuspended particles compared to phytoplankton and other pelagic particles, and (c) the food value and absorption of resuspended organic matter.

In the present study we focused on sediment resuspension on Georges Bank in terms of tidal movement of sediment and the utilization of these particles by sea scallops. As is typical of many offshore banks, there is a well-mixed frontal region at this site characterized by high primary production and dense populations of suspension feeders, especially large bivalves (Horne *et al.,* 1989). Georges Bank contains the largest offshore scallop fishery in the world. In both shipboard and laboratory experiments, we have examined (a) the distribution of organic matter and particle size in coarse sediments and the silt-clay fraction, (b) the rate of resuspension and its contribution to the seston based on flume erosion experiments, near-bottom water samples, particle fall velocity, organic quality, and field current meter records, and (c) the utilization and value of resuspended sediments as a food source for sea scallops (*Placopecten magellanicus*).

To assess the utilization of resuspended material as a food source for sea scallops, we conducted shipboard feeding experiments on Georges Bank and produced functional feeding relationships for scallops feeding on resuspended sediments. Simultaneous feeding experiments were conducted with water column samples obtained from surface and near-bottom depths. Subsequent shore-based experiments were undertaken to measure the absorption efficiency of scallops consuming resuspended sediments. Taken together these approaches allow us to assess the delivery rate of resuspended organic material to sea scallops and assess its importance relative to "fresh" phytoplankton as a food source for *P. magellanicus.*

2. Materials and methods

a. Study site. Sediment samples were obtained from the northeast peak of Georges Bank (Fig. 1) using ships of opportunity in April 1988 and 1989, and during a two week cruise in August 1988 in which scallop feeding experiments were conducted. Further laboratory feeding experiments were conducted in subsequent years through 1992. The sample sites in August 1988 (42° 5.60′ N, 66° 48.3′ W) and April 1989 (42° 0.03′ N, 67° 1.03′ W) have abundant scallop populations (65–69 m depth), and are in an extensively studied region (Sites 2 and 3 of Loder *et al.,* 1992, respectively). April 1988 sediment samples were taken slightly south of this area (Site 4). These locations are in the commercially fished scallop grounds corresponding to the 'gravelly pavement' described in Valentine and Lough (1991). Bouldery areas of relict moraine are interspersed in this region of the bank.

The study area is in the region of a tidal front between thermally stratified Gulf of Maine waters and well-mixed but warmer Georges Bank waters, and there is a strong topographic effect on flow at the edge of the bank along the Northeast Channel (Loder *et al.,* 1993). Flow rectification along this flank results in a residual current contributing to the frontal mixing along the Northeast Peak. The frontal region is 20–40 km wide and is generally associated with the 60 m isobath, but is both spatially and temporally variable. Scallop populations are in what is generally considered a well-mixed region, but at the time of the study, there was thermal stratification with surface temperatures of 18°C and temperatures as low a 11°C below 35 m. Details of seasonal cycles of stratification are described in (Loder *et al.,* 1992).

b. Sampling and analyses. Sediment was sampled with a 0.25 m^2 Van Veen grab. Subsamples of sediment were set aside for grain size and chemical analyses, and other sediment was transferred to buckets for extraction of "resuspendable" sediment. This fine material was separated from bulk sediment by vigorously swirling approximately 500 g sediment samples with 5 l of 5 μm filtered seawater and immediately pouring the

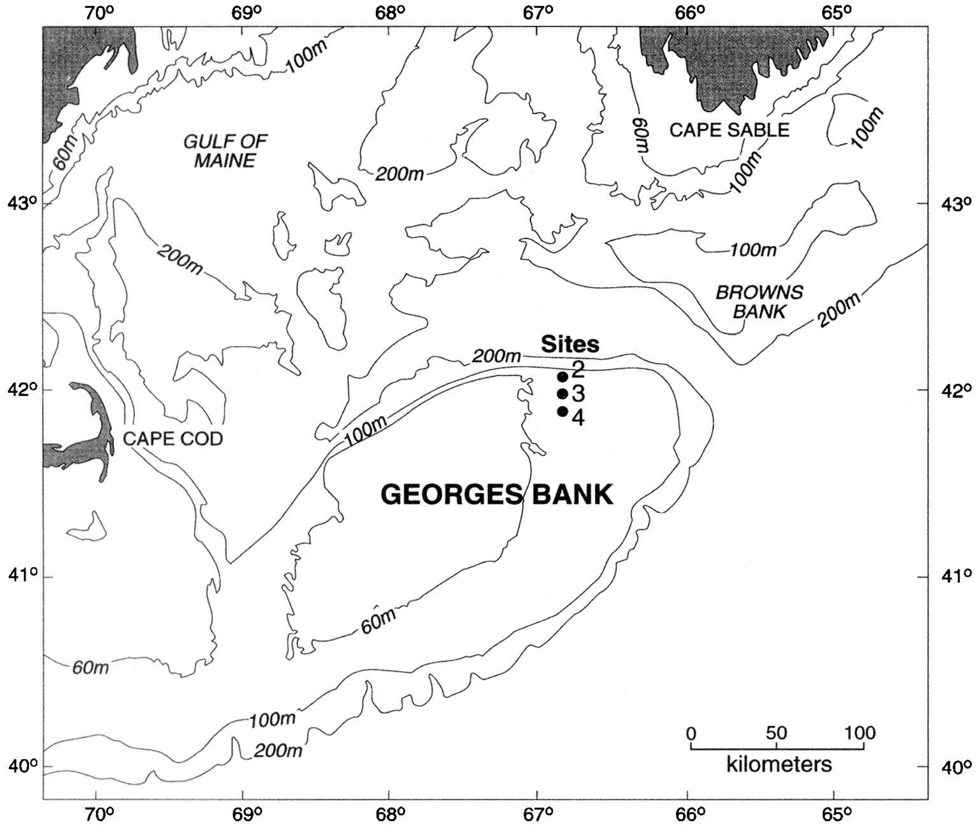

Figure 1. Sampling locations on Georges Bank. The site designations match those in Loder and Petitpas (1991). Site 2 (42° 5.60′ N, 66° 48.3′ W) was sampled in August 1988 and Site 3 (42° 0.03′ N, 67° 1.03′ W) in April 1989. The April 1988 sample location was near Site 4 but the exact location was not recorded. Water depths were 65–69 m.

supernatant through a 102 μm sieve. Two extractions were performed in this manner for each sediment sample. Extra grab samples were stored in a dark cold room for extraction as needed (maximum of 10 days). Additional water samples were collected during the August 1988 cruise at 6 and 65 m depths by pump and 30 l Niskin bottle, respectively.

Particle size distributions of water and resuspended sediment samples were determined immediately aboard ship with a Model Ta II Coulter Counter fitted with 50, 140 and/or 280 μm apertures that were each calibrated for particle diameter and volume with mono-sized microsphere standards. Size-fractionation of water and suspended sediments for organic analyses was performed with 10, 20 and 30 μm Nytex sieves. In the first sediment fractionation (August 1988), sieves were not nested so that particles collected below sieves were cumulative for smaller particle sizes (see Table 2). Samples containing resuspended sediment or seston particles and procedure blanks (blank filters treated as samples) were analyzed as follows for particulate organic matter (POM), organic carbon (POC), nitrogen (PN) and chlorophyll *a* content. Particles collected on prewashed and combusted Whatman GF/F filters for POM analysis were rinsed with isotonic ammonium formate to remove salt. POM content was determined as the percentage of dry weight lost during combustion at 450°C for 6 h. Suspended particles collected on precombusted Hytrex silver filters (0.45 μm pore size) were fumed over concentrated HCl for 1 h to remove inorganic carbon. POC and PN content was determined with a Perkin-Elmer 240B Elemental Analyzer. POM, POC and PN data were blank-corrected. Sediment and particles collected on Millipore HA filters (0.45 μm pore size) were extracted for 24 h with 90% acetone at 0°C in the dark for chlorophyll determination by the fluorometric technique of Holm-Hansen *et al.* (1965).

Bulk sediment grain size distribution was analyzed by wet sieving and filtration of the <63 μm fraction on glass fiber filters. Grain size parameters were calculated as in Leeder (1982). POM content of sediment fractions was determined by combustion as above. Carbon and nitrogen analysis was performed on bulk sediment following acid treatment, but with some difficulty (see below) because of the large inorganic carbon content. The silt-clay component of sediment had less carbonate contamination, which was easily corrected for by acid fuming. The carbon content of this sediment fraction is of greater interest due to its relevance to scallop food resources and forms the basis for much of our discussion of POC.

c. Scallop feeding experiments. Because resuspended sediment was collected as a concentrate, it was possible to present this food to scallops at different concentrations by diluting with 5 μm filtered seawater (8.4–131 mg l^{-1}, 10 concentrations). Natural seston from surface and bottom waters was presented at ambient concentration (4.5 and 4.7 mg l^{-1}, respectively). All diets were passed through a 102 μm mesh prior to analysis and use in feeding experiments. Diets were held in large covered Fiberglass tanks on the deck and kept mixed with submersible pumps.

Sea scallops were collected from Georges Bank by commercial dragger (mean shell height = 91.7 mm ± 4.4 SD; mean dry tissue weight = 3.12 g ± 1.23 SD), and held in the laboratory onshore with cultured phytoplankton as food. On the ship they were held in a Fiberglass tank supplied with flowing natural seawater pumped through the ship's system at ambient surface temperatures (~20°C). There was no mortality during the cruise. Replicate feeding experiments were conducted aboard ship by pumping diet suspensions from a mixing tank with a multichannel peristaltic pump to six identical flow-through feeding chambers (described in Cranford and Gordon, 1992) at between 8 and 10 l h^{-1}. Scallops placed in four of the chambers were allowed a 20 min acclimation period to resume a normal feeding posture. The other two chambers were left empty and served as controls. Water samples were collected at the outlet of each chamber and particles immediately analyzed with the Coulter Counter (50 and 140 μm tubes). Additional samples of water exiting the control chambers were collected in triplicate on Whatman GF/F filters for determination of total suspended particulate matter (SPM) and POM. Comparison of Coulter particle-size spectra of particles added to the mixing tank and exiting the control chambers indicated that the mixing and delivery pumps did not alter the diets.

The presence or absence of pseudofeces in the feeding chambers was noted for all experiments. Retention efficiency (RE), the proportion of particles retained by the scallop, was determined for each animal and particle-size class from Coulter Counter data as: $1\text{-}C_t/C_c$, where C_t and C_c are concentrations in the outlet of the test (scallop) and control chambers, respectively (Cranford and Gordon, 1992). For the purpose of comparing RE values between the different rations, RE data for each particle size-class were normalized by setting the highest RE value to one and adjusting values for the other size-classes proportionately (Cranford and Grant, 1990). Clearance rate ($1\ h^{-1}$), the volume of water cleared of particles per hour by the scallop, was calculated as the product of RE (averaged for all particle-size classes greater than 5 μm) and flow rate ($1\ h^{-1}$) through the feeding chamber. Filtration rate ($mg\ h^{-1}$) was calculated as clearance rate times SPM concentration and is equivalent to ingestion rate if pseudofeces are not produced.

Fecal samples were collected from shipboard feeding experiments for determination of absorption efficiency (AE), the proportion of ingested POM, POC and PN absorbed by the animal, but the feeding chambers were not suitable for the longer term delivery of food required for AE determination. We therefore repeated these experiments onshore using freshly collected material. Surface sediment samples were collected by Van Veen grab from Georges Bank at Site 2 in August 1992 and immediately refrigerated at 10°C for a total period of six days. Upon return to the laboratory, the silt/clay fraction <102 μm was immediately extracted as before with 5 μm filtered seawater and Nytex screens. The concentrated supernatant was diluted with 5 μm filtered seawater and fed to scallops held in recirculating raceway tanks designed to maintain a constant particulate ration in suspension for extended periods. A full description of the raceway tanks and exposure facilities used in this experiment are given in Cranford (1995). Concentrated stocks were also size-fractionated using 10, 20 and 30 μm Nytex screens. The usual analysis was performed on bulk and fractionated samples (POM, POC, PN, CHL *a*).

Three groups of sea scallops were used in the latter feeding experiments: (1) Eight scallops collected by commercial dragger from Georges Bank in May 1992 and ranging in size from 90 to 119 mm shell height (mean = 102.5 mm ± 14.0 SD); (2) Seven scallops collected on Georges Bank with a small dredge from the C.S.S. Parizeau in August 1992. Shell heights ranged from 88 to 125 mm (mean = 97.4 ± 14.9 SD); and (3) 27 animals obtained from commercial suspended culture in August 1992. Mean shell height was 55.3 mm ± 1.9 SD. All groups were maintained in Fiberglass tanks supplied with unfiltered Bedford Basin seawater prior to use.

Scallops maintained in the darkened, recirculating raceway tanks at 11.5 C were initially starved to clear gut contents by exposure to 5 μm filtered seawater for 20 hours prior to addition of the resuspended sediment diet. A continuous supply of diet was then provided for 2.5 days. The concentrated stock solutions of resuspended sediment were pumped from mixing tanks to the raceway tanks at 21 ml min^{-1} and diluted with filtered seawater (5 μm) at 4 l min^{-1}. At 24 h intervals during the course of this experiment, raceway water samples were collected via siphon tubes and composite samples of feces from each group of scallops were collected by pipette. The tanks were siphoned to remove fecal debris after the starvation period and after feces collections.

Methods for the preparation and analysis of diet and feces samples for POM, POC, and PN analysis are the same as reported in Cranford (1995). The percentage of ingested material that was absorbed by the digestive system (AE) was determined using a method that compares absorbed (ash-free dry weight, organic carbon or nitrogen) and nonabsorbed (ash) components of food and feces (Cranford and Grant, 1990). The latter study confirmed that ash is a suitable inert tracer for digestive studies with scallops.

d. Flume experiments. Because flume experiments could not be carried out immediately aboard ship, sediment samples from grabs were frozen for later use. Freezing was deemed to be less harmful to sediment organic matter than prolonged storage in a cold room which would allow microbial blooms to occur. Due to the coarse nature of these sediments, it was difficult to obtain subcores from the grab with plastic core liners for use in the flume. Instead, core liners (7 cm diam.) were filled with sediment placed in with a hand trowel. No reduced sediments occurred in these grab samples so it is unlikely that anaerobic sediments were included in the constructed cores.

Flume experiments were carried out on the 3 m long flow-through flume described in Muschenheim *et al.* (1986), using sediments collected from Site 2 in August 1988. Sediment cores were placed into the flume through an o-ringed opening in the working section. The bed level was adjusted from the core bottom with a plunger so that the sediment was level with the flume bed. Projecting gravel and pebbles were thus above this level. The flume was slowly filled with sand-filtered seawater (10°C), so that no resuspension occurred. Velocity was gradually increased until a general movement of sand grains occurred at the sediment surface. No attempt was made to transport the coarse sand and gravel fractions of the sediment which occurred in the cores. Bedload studies focused on the sand grains <2 mm in diameter. Water depth during erosion was ~ 5 cm.

Eroding sediments were collected in a bedload trap consisting of an opening in the base of the flume (2 cm long streamwise × 8 cm wide crosstream), 5 cm downstream of the core (Grant and Daborn, 1994). To avoid starving the core of sediment or creating a depression in the core, erosion was allowed to proceed only as a thin sheet of sediment which rolled or saltated from the core surface to the trap. The quantity of sediment collected in the trap was small; some samples had insufficient material to analyze grain size composition. Critical shear velocity ($u*_{\text{crit}}$) was measured directly with a flush-mounted hot film probe (Grant and Gust, 1987), calibrated in pipe flow with manometry measurements (Grant and Daborn, 1994). Because trap samples consisted exclusively of sand grains, trap samples were poured through a 63 μm sieve and rinsed with freshwater into weighing tins prior to oven drying.

Several assumptions were required to calculate suspended carbon flux from these flume data. The first is that the bed is transported in proportion to its grain size distribution (i.e. equal mobility *sensu* Wilcock and Southard, 1989) such that all of the interstices in a defined bedload layer are exposed. This assumption is tested by comparing the grain size distribution of bedload samples to the intact sediment. Secondly, the silt-clay component is transported in suspension as it is uncovered and has significant residence time in the water column. Tests of this assumption are more difficult, as discussed below. Thirdly, the silt-clay fraction is uniform in mass for a given quantity of sediment, and has a consistent organic carbon content, tested by comparing POC values from multiple extractions of resuspended sediment.

e. Settling rate. Settling experiments were conducted in a temperature controlled room at 7°C. Frozen samples of Georges Bank sediment were thawed and placed into a bucket with 1.5 l of 0.45 µm filtered seawater and vigorously swirled. A second bucket was painted black on the inside and had an optical backscatter sensor (OBS) placed 6 cm from the bottom which was zeroed in filtered seawater prior to the addition of the sediment slurry. The well-mixed sediment supernatant was poured into the black bucket and stirred gently with a glass rod while a 500 ml water sample was taken. Voltage output from the OBS was then logged on computer for several minutes as a measure of initial suspended sediment concentration. Logging intervals were every second during the first part of the experiment and were gradually increased to 20 min as the deposition rate slowed. OBS voltage is a linear function of suspended sediment concentration (Sternberg *et al.*, 1991). Although a specific calibration curve for Georges Bank has not been derived, our previous work with shelf muds (Emerald Basin) yielded the following calibration which may be used to approximate suspended sediment concentration from OBS voltage:

$$\text{Suspended sediment (mg l}^{-1}) = 155.2\ \text{Volts} - 2.40\ (r = 0.92, n = 24). \qquad (1)$$

In the present experiment, no attempt was made to incorporate particle size changes during settling into this relationship. Water samples were also taken from the bucket at approximately 4 and 18 h, poured through a 102 µm sieve, and analyzed for particle size distribution using a Coulter Multisizer fitted with 30 and 200 µm aperture tubes. The settling rate experiment was repeated a second time on the next day using a fresh supernatant from the same sediment source.

f. Current meter deployments. Aanderaa directional recording current meters were deployed in vertical series at 6 locations on Georges Bank from June–October 1988 (Loder and Petitpas, 1991). Current speed and direction and temperature were recorded every 30 min. Due to current meter malfunctions in this deployment, additional current records from the same site collected in 1991 were also included. Our focus is on data from the two lowest current meters moored 3 and 10 m above bottom at the 67 m site used for August 1988 scallop feeding experiments (Site 2; Fig. 1). To apply flume thresholds for sediment erosion to field data on current speed, we used a quadratic stress law (Sternberg, 1972):

$$u* = C_D^{0.5} U_{100} \tag{2}$$

where $u*$ is shear velocity, and C_D and U_{100} are the drag coefficient and current speed at 100 cm above the bed, respectively. U_{100} was estimated based on the velocity gradient between the 3 and 10 m current meter records. Due to a malfunction in the upper current meter we used the longest continuous data set of 19 days in June–July ($n = 950$) for this comparison (Fig. 9). This data record is too short to characterize temporal variation in tidal speeds because it is biased toward a spring tide period, but provides an adequate record for the height comparison. The velocity gradient was calculated as (Open University, 1989):

$$dU/d\log z = (U_{1000\text{cm}} - U_{300\text{cm}})/(\log 1000 - \log 300), \tag{3}$$

using mean values for $U_{1000\text{cm}}$ and $U_{300\text{cm}}$ from the current meter records. $U_{100\text{cm}}$ was then calculated from the mean $U_{300\text{cm}}$ value by applying the calculated $dU/d\log z$ to the 300 and 100 cm depths. This velocity profile was extrapolated to the seabed to derive a roughness length (z_o) which was used to calculate the critical erosion velocity at $z = 100$ cm ($U_{100\text{crit}}$) corresponding to $u*_{\text{crit}} = 2.14$ cm sec^{-1} (see flume results) according to another expression of the velocity gradient ("law of the wall")

$$U_{100\text{crit}} = u*/\kappa \ln (z/z_o) \tag{4}$$

where κ = von Karman's constant. The $U_{100\text{crit}}$ value was then used in Eq. 2 to solve for C_D. The drag coefficient was applied to the calculated $U_{100\text{cm}}$ time series and used to derive a frequency distribution of $u*$ (Eq. 2) and the percentage of time that $u*_{\text{crit}}$ was exceeded.

3. Results

a. Bulk sediment properties. Sediment collected from two areas of northeastern Georges Bank in spring and summer respectively had somewhat different grain characteristics, although both tended to be poorly sorted gravelly sands (Table 1). Sediment from Site 4 (April 1988) had gravel content (>2 mm) in the range of 40% (Table 1) and had a finer median diameter than Site 2 (August 1988). At Site 2, sediments were more bimodally distributed with dominant peaks in the gravel (>50%) and sand in the 125–500 μm fraction, but with a small component of very coarse sand (3%). Variability in median diameter occurred even within a single grab, probably due to subsampling in which varying amounts of gravel were included. At Site 4 the silt-clay fraction was 0.3–0.6% of total weight, and at Site 2 this fraction was on the order of 0.1% of the total (Table 1).

Bivalve shell debris was very common in the sediment. As a crude assessment of shell content, visible shell pieces in a single sediment sample (Site 2) were removed by hand and the sediment fraction reweighed. The bulk of shell material was contained in three sediment fractions. Sediment retained on 250 and 500 μm sieves, the dominant sand classes at this site, had 0.01 and 0.14% of sediment weight respectively due to shell debris. Most of the shell was in the gravel fraction (>2 mm) which contained 1.04–1.70% by

Table 1. Grain size characteristics of Georges Bank sediments sampled on the Northeast Peak in 1988. Md = median grain diameter. Sorting = standard deviation of grain size in phi units, where 0 is very well sorted and values >1 are poorly sorted. April samples are from two separate grabs; August samples 1 and 2 are from a single grab as are samples 3 and 4. Site locations are given in Figure 1.

	Sample					
Grain characteristic	April (Site 4)		August (Site 2)			
	1	2	1	2	3	4
Md (μm)	1602	1141	2378	5776	1972	3555
Sorting (ϕ)	1.31	1.72	1.42	1.23	1.32	1.28
% silt-clay (<63 μm)	0.29	0.6	0.16	0.09	0.12	0.08
% gravel (>2000 μm)	41.59	36.33	55.19	73.13	50.75	63.68

weight of shell debris. Shell carbonates present in sand and gravel fractions, while comprising a small fraction of total sediment mass, dominated total carbon content. Organic carbon and nitrogen analysis of bulk sediments gave inconsistent results, owing to problems with removal of the large amount of inorganic carbon (shell material) and the low PN content, near the detection limit. The organic matter content of bulk samples (Site 2, August) was only 0.5–0.7% by weight, typical for coarse sediment on the continental shelf (Grant *et al.,* 1991). The silt-clay component (<63 μm) was richest in organic matter compared to other size fractions (Fig. 2A) and ranged in organic content from 12–17%. In grab 2 the 63 μm sieve fraction also had a high organic content. In both grabs the 1000 μm fraction had organic content >1%, but gravel was consistently <1% in organic content (Fig. 2A). When the contribution of each fraction to total organic content was calculated, the gravel sediments dominate due to their large weight (Fig. 2B).

b. Analysis of water and resuspended sediment. Seston concentration was similar in surface (6 m) and bottom waters (65 m) with mean values of 4.5 ($SD = 1.4$, $n = 18$) and 4.7 mg l^{-1} ($SD = 0.4$, $n = 9$). Bulk samples of surface and bottom water seston were generally similar in POM content, but bottom water seston had a slightly higher POC and lower PN content, resulting in a higher C:N ratio (Table 2).

In order to provide more detailed vertical resolution of particle fields, concentrations of POC, PN and CHL in surface and bottom water samples collected at Site 2 (August) were combined with average water column sampling data collected on the same cruise at the identical site (Irwin *et al.* 1990, Stations 23, 34, 55, 65 and 92). Uniform POC, PN and CHL concentration occurred in the water column (Fig. 3), but concentrations 3 m off the seabed appeared markedly different from the water above. *t*-tests comparing data from bottom water and water collected at 50 m depth show significantly higher C:N and C:CHL and significantly lower CHL (6 df; $p < 0.01$). POC and PN values were more variable in bottom water than farther up in the water column (Fig. 3) and no significant differences could be detected through the profile (6 df, $p > 0.1$).

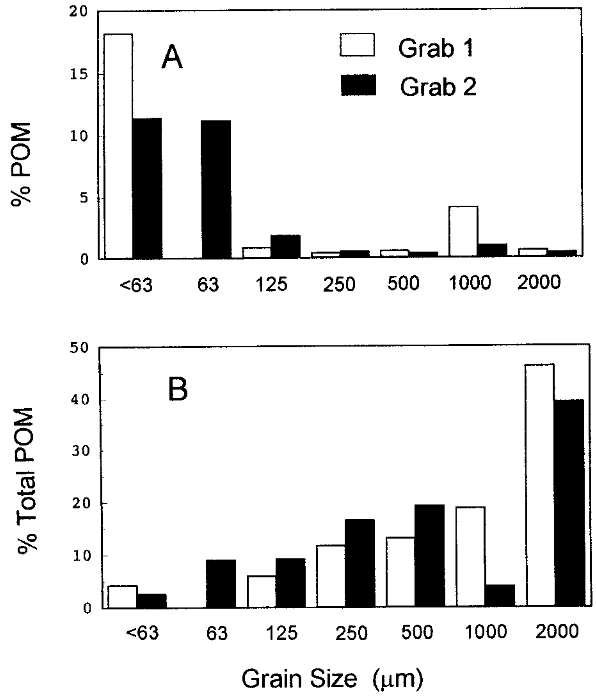

Figure 2. Distribution of organic matter with respect to grain size of sand and gravel in Georges Bank sediments, Site 2, August 1988. (A) The percentage particulate organic matter (%POM) for each sediment grain size fraction in each of two grabs. (B) The percentage that each grain size fraction comprises of total sediment POM from each of the same grabs.

Seston from 6 m (surface) and 65 m (bottom) depths displayed similar size spectra, save for the pronounced peak at 10 μm in surface water (Fig. 4A). Size-fractionation of surface water indicated that despite similarities in total organic content, there were substantial differences in organic carbon and nitrogen content of the size fractions (Table 2). The 30–102 μm fraction was highest in POC and PN, and the <10 μm fraction was carbon and nitrogen-poor compared to the rest of the seston. All had a similar C:N ratio.

The majority of particles extracted by resuspending sediment were between 2 and 20 μm with a peak at 8 μm, and few particles >40 μm (Fig. 4B). The size spectra for resuspended sediment were similar for samples collected in April and August, but with a slightly smaller dominant mode in August. The organic matter content of resuspended sediment was generally similar for all dates, although the lower C:N ratios in both April periods indicate the nutritional quality of the resuspensate was higher in April than in August (Table 2). Results of size-fractionation from April 1989 indicate that particles <10 μm contained the highest organic matter content (Table 2), but the POC and PN content of all size fractions were similar. The sieving method used in August 1988 (sieves not stacked) makes a comparison with April fractionation (sieves stacked) difficult, but the <10 μm fractions

Table 2. Composition [% of dry weight, (SD, *n*)] and chemical ratios of experimental diets and size fractions used in shipboard scallop feeding experiments. C = Carbon, N = Nitrogen.

Diet	Organic matter (POM)	Organic carbon (POC)	Nitrogen (PN)	C/N	C/Chl
Surface Water (6 m)					
August 1988					
<102 μm	44.7 (10.3, 18)	4.60 (1.18, 5)	0.64 (0.38, 5)	7.2 (1.0, 10)	115.0
30–102 μm	39.7	11.61	1.45	8	
20–30 μm	40	7.63	0.79	9.7	
10–20 μm	36.7	7.45	0.99	7.6	
<10 μm	38.1	1.20	0.13	9	
Bottom Water (65 m)					
August 1988					
<102 μm	34.9 (4.7, 9)	5.68 (2.21, 3)	0.36 (0.23, 3)	19.3 (5.9, 3)	304.7
Resuspended sediment					
April 1988					
<30 μm	28.7 (2.2, 12)	3.59 (0.11, 2)	0.68 (0.04, 2)	5.3 (0.2, 2)	812
August 1988					
<102 μm	30.2 (2.8, 33)	3.81 (0.83, 6)	0.48 (0.21, 6)	8.5 (3.4, 6)	1240
<30 μm	26.8 (3.8, 33)	5.93 (0.84, 2)	0.38 (0.03, 2)	15.6 (0.8, 2)	916
<20 μm	35.1 (3.2, 3)	6.23 (0.48, 2)	0.39 (0.01, 2)	16.2 (0.8, 2)	909
<10 μm	34.7 (1.0, 3)	6.72	0.52	13	558
April 1989					
<102 μm	25.9 (2.1, 3)	7.87	2.02	3.9	844
30–102 μm	16.7	5.69	1.42	4	
20–30 μm	16.3	4.6	1.13	4.1	
10–20 μm	18.4	3.99	0.99	4	
<10 μm	42.2	5.40	1.13	4.8	882

were similar in POM. The <10 μm fraction in August and April sediments were rich in POC and PN compared to a similar size fraction in surface water seston. In general, POM, POC and PN content of resuspended sediment were comparable with values obtained for surface and bottom water seston (Table 2).

c. *Scallop feeding experiments.* The normalized retention efficiency spectra of particles by sea scallops was similar for all rations (surface and bottom water and resuspended sediment), concentrations and particle size-classes greater than 5 μm diameter, but decreased rapidly below 5 μm (Fig. 5). Scallops presented surface and bottom water at comparable concentrations (~4.5 mg l^{-1}) and resuspended sediment at levels below 12 mg l^{-1} displayed similar clearance rates (Fig. 6A). A one-way analysis of variance comparing mean clearance rates between all rations presented at concentrations below 12 mg l^{-1} detected no significant differences ($p = 0.43$). Higher concentrations of the resuspensate were cleared more slowly (Fig. 6A), but filtration rate increased with

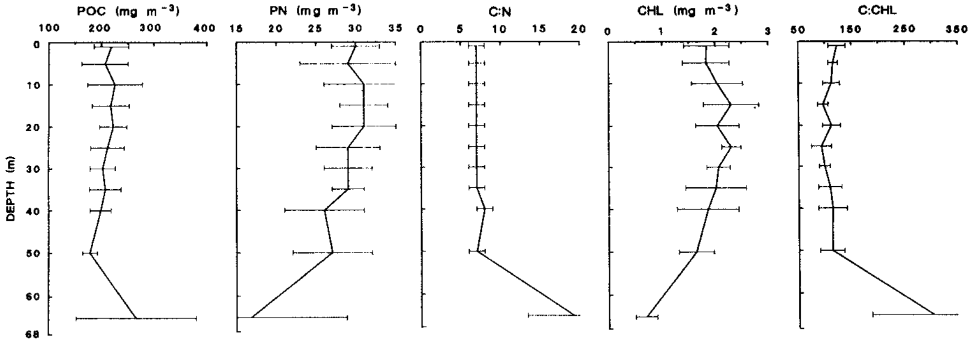

Figure 3. Vertical profiles of particulate organic matter in the water column at the Georges Bank study Site 2, August 1988. Vertical distributions are shown for organic carbon (POC), particulate nitrogen (PN), particulate organic carbon to particulate nitrogen ratio (C:N), chlorophyll *a* (CHL), and particulate organic carbon to chlorophyll ratios (C:CHL) at the study site. Mean values ($\pm$1 SD) are calculated from Irwin *et al.* (1990) (same site, water column samples, $n = 5$) and samples collected concurrently in this study (near-bottom samples, $n = 3$). See text for sampling details.

increasing diet concentration (Fig. 6B). Pseudofeces were observed in feeding chambers only for the resuspended sediment diet at concentrations exceeding 12 mg l^{-1}.

Measurements of absorption efficiency of resuspended sediment confirm the nutritional value of this material to sea scallops, with mean AE values up to 82% for nitrogen absorption (Table 3). There were no differences between the 3 groups of scallops, which included adults and juveniles and wild and cultured animals, as shown by the low standard deviation in the grand mean (Table 3). The organic content of the food source in these laboratory experiments was substantially higher than in the shipboard filtration rate experiments. However, adjusted AE values may be obtained using the data in Cranford (1995) who demonstrated that for a variety of food sources ranging from 25–95% POM,

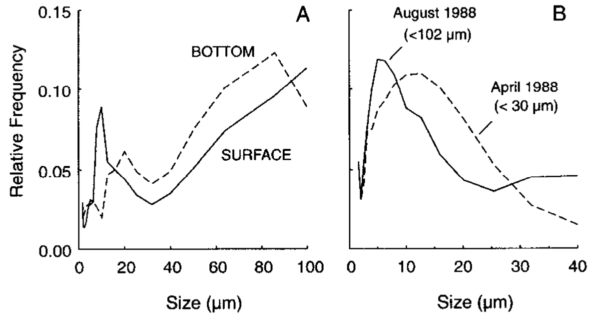

Figure 4. Particle size distribution of: (A) surface (6 m; solid line) and bottom water (65 m; broken line) collected in August 1988 at Site 2; and (B) resuspended sediments collected in August 1988 at Site 2 (solid line) and in April 1988 at Site 3 (broken line) and pre-sieved as specified. Both water column samples and the August 1988 resuspended sediment sample were supplied to sea scallops in feeding experiments. Concentration is expressed as relative frequency for comparability.

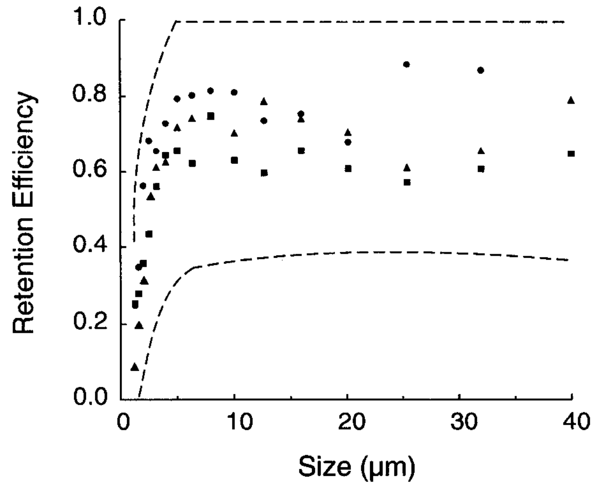

Figure 5. Average normalized particle retention efficiency (RE) by scallops fed resuspended sediment (circles, $n = 24$), surface (squares, $n = 14$) and bottom (triangles, $n = 21$) water. The dashed lines indicate the maximum and minimum calculated RE value for each particle size range measured by the Coulter counter (i.e. the maximum range of error).

absorption efficiency in *P. magellanicus* was a function of the POM, POC and PN content of the ration, with reported regression models explaining 74, 82 and 84% of the variance in AE, respectively. The AE data reported in Table 3 fall within the range of these relationships, such that if we normalize the AE values to the diet organic content of the shipboard feeding experiments (~30%; Table 2), scallops are still able to utilize resuspended sediment organic matter with an efficiency of up to 40%. Therefore, in terms of ingestion, retention, and digestion, sea scallops are able to exploit resuspended organic matter from a continental shelf habitat.

d. Flume experiments. Neither cobbles nor large shell hash were transported at the flows used in these experiments, but act as isolated roughness elements that induce local turbulence and scouring around them. The transport of the smaller sand fractions in the flume was thus affected by the presence of cobbles and shell in the cores as in the field. Results of the erosion experiments focus on the sand sediments (63–2000 μm) of the core and the silt-clay they expose during erosion. Observation of sediment erosion in the flume indicated that sediments of Site 2 (dominant sand fraction of 250–500 μm) had a consistent erosion threshold with mean $u*_{\mathrm{crit}} = 2.14\ \mathrm{cm\ sec^{-1}} \pm 0.08$ SD ($n = 5$).

To calculate the suspended transport of sediment from the core based on the trapped material, it is necessary that the trapped sediment be a representative sample of the source sediment in terms of grain size. A comparison of sand grain size in trap sediments versus core sediments (Table 4) indicated that the bedload sediment was similar in median diameter and sorting to the source material. Because the grain size distribution of bedload

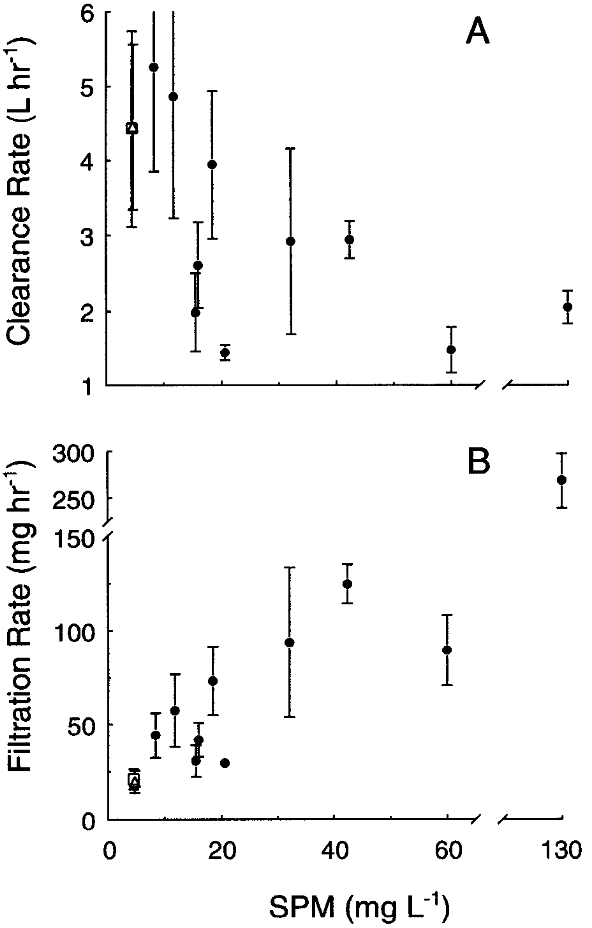

Figure 6. Mean clearance (A) and filtration (B) rates of *Placopecten magellanicus* fed surface (squares, $n = 11$) and bottom (triangles, $n = 16$) water seston and different concentrations of resuspended sediment (circles, $n = 4$) from Georges Bank. Error bars are ±1 SD.

Table 3. Mean and standard deviation (SD) of absorption efficiency (AE) of sea scallops fed diets of resuspended sediment from Georges Bank. $n = 18$ for the diet samples and $n = 18$ for the AE determinations.

	Diet composition				AE (%)		
Measure	% POM	% POC	% PN	C:N	POM	POC	PN
Mean	64	18.5	3.6	5.3	55.3	70.7	82.2
SD	7	6.8	1.1	2.2	7.6	8.9	5.4

Table 4. Median diameter (μm) of Georges Bank sediments comparing intact sediments (pre-erosion) to material collected from bedload traps. Sorting = standard deviation of grain size in phi units, where 0 is very well sorted and values >1 are poorly sorted. Bulk sediment properties of pre-erosion samples (Table 1) are recalculated below to exclude the silt-clay (s-c <63 μm) and gravel (>2000 μm) fractions to facilitate comparisons to bedload samples. In bedload samples, no gravel was transported, and it was assumed that silt-clay was lost to suspended transport (see text for details). Sample designations identify replicates rather than a match between pre-erosion and bedload samples.

Median diameter (μm)	Sample					
	Pre-erosion				Bedload	
	1	2	3	4	1	2
August −(sc + 2000 μm)	449	423	727	603	467	717
Sorting (ϕ)	0.79	0.76	0.7	0.71	0.77	0.82

transport was proportional to its occurrence in the intact bed, the exposure and transport of the silt-clay fraction as suspended load may be estimated. In these calculations, we assess silt-clay content as a proportion of bulk sediment weight excluding gravel (>2000 μm; for entire size distribution, see Table 1), since only the sand fraction was transported. In Table 5, the mean silt-clay content of sediment <2000 μm and the carbon content of resuspended sediment <30 μm (Table 2) were applied to the bedload mass transport to calculate a resuspended carbon flux (Table 5). All flume experiments were characterized by a similar u_* and degree of transport (i.e. just beyond erosion threshold), but the carbon transport rate varied by an order of magnitude due to variation in bedload mass and the resultant calculation of suspended carbon flux.

Table 5. Calculation of resuspended carbon fluxes based on flume erosion experiments with sediments from Site 2. Mean % silt-clay (s-c, <63 μm) based on sediment grain size analysis is calculated as a proportion of the intact sediment <2000 μm. Standard deviation (SD) of this mean was 0.06 (n = 4). Mean % POC refers to the particulate organic carbon content of the silt-clay fraction (for POC analysis defined as <30 μm particle size); SD is given in Table 2. Core area in all erosion experiments was 4.56×10^{-3} m^2. Mean shear velocity was 2.14 cm s^{-1}, with coefficient of variation = 3.7%.

Date	Bedload wt. (mg)	Time (h)	Mean % s-c	Mean % POC	Resuspended carbon flux (mg C m^{-2} h^{-1})
August—Site 2					
Core 1	1245	0.19	0.27	5.93	229
Core 2	559	0.43	0.27	5.93	51
Core 3	443	0.47	0.27	5.93	33
Core 4	1155	0.33	0.27	5.93	122

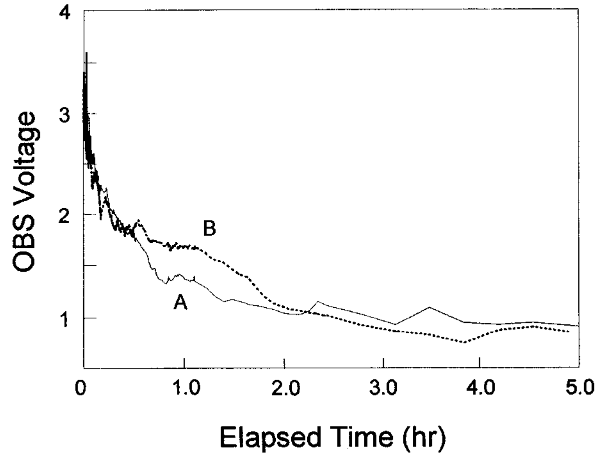

Figure 7. Changes in resuspended sediment concentration over the time-course of particle settling experiments for Georges Bank samples, trials A and B. OBS Voltage refers to the recorded signal of the optical backscatter sensor which has a linear relationship with the mass of suspended particulate matter. Initial concentration, which includes suspended sand, corresponds to ~540 mg l^{-1} based on Eq. 1 (See text).

e. Settling rate. A time series of backscatter voltage in settlement containers indicated a typical exponential decline in suspended sediment (Fig. 7). Some of the rapidly settling heavier material was sand which was included in the supernatant during extraction. Both trials indicate that most settlement of sediment occurred within 3 hours. On the order of 30% of the remaining sediment stayed in suspension for several hours (Fig. 7), and even into the next day. Particle size distribution during these experiments (Fig. 8) indicates that the size spectrum of the initial slurry was dominated by particles 10 μm or more as in freshly extracted sediments (Fig. 4), but that much of the material remaining in suspension after 5 hours was 5 μm or less. However, even after 3.5 hours, particles up to 10 μm were still in suspension indicating that potential food for scallops (>5 μm; Fig. 5) has a long residence time in the water column.

Current meter records from Georges Bank combined with laboratory flume experiments allow us to compare settlement to the frequency of resuspension.

f. Current meter records. Near bottom currents (U_{300cm}; total depth = 64 m) clearly showed a tidal signal with a mean speed of 38.9 ± 16.8 SD cm sec^{-1} (n = 1440 records) and peak speeds of 99.9 cm sec^{-1} (Fig. 9). Because drag coefficients used in calculating shear velocity are referenced to a mean velocity at 100 cm (Eq. 2), we estimated currents at 100 cm based on the velocity gradient between the 3 and 10 m current meter records (Eq. 3) during the 19 day period for which we have a continuous data set (Fig. 9). Using mean values of 55.7 (SD = 19.0) and 47.1 cm sec^{-1} (SD = 14.9) for U_{1000cm} and U_{300cm}, respectively, results in $dU/d \log z = 16.5$ (Eq. 3). Applying this ratio to the 300 and 100 cm

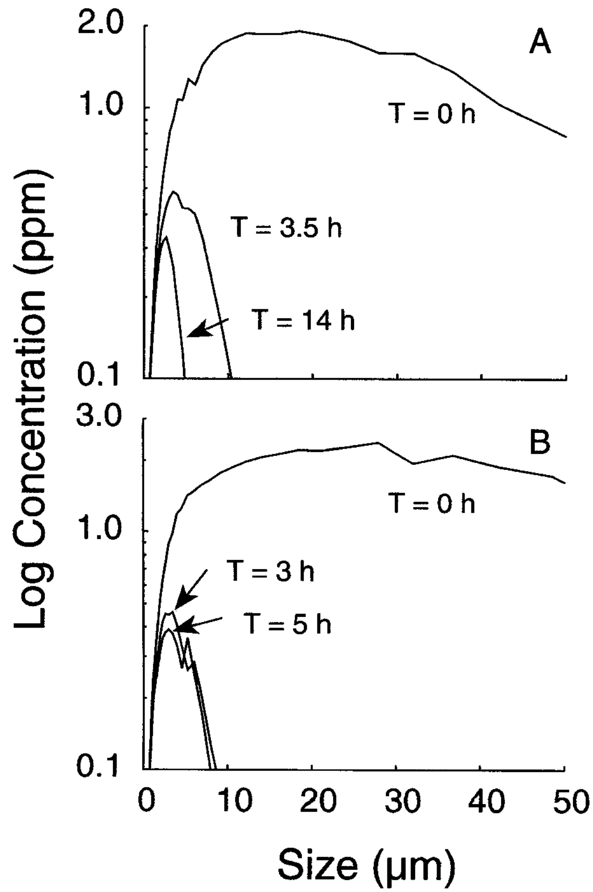

Figure 8. Particle size distribution during three periods following settling of resuspended sediment (see Fig. 7). Samples correspond to hours after the start of the experiment as specified for trials A and B. PPM units refer to total particle volume/water volume.

depths, a mean U_{100cm} was calculated as 39.2 cm s^{-1} ($U_{300cm}/U_{100cm} = 1.2$). Extrapolation of velocity to the bed gives a roughness length (z_o) = 0.4 cm. To assess the incidence of resuspension in the field, we calculated a critical sediment erosion velocity at 100 cm above bottom at Site 2 based on the flume observation of an erosion threshold at a mean $u*_{crit}$ of 2.14 cm sec^{-1} and Eq. 4. These calculations indicate that erosion of sand would occur when $U_{100cm} > 29.5$ cm sec^{-1}, an erosion threshold less than the calculated mean U_{100cm} value of 39.2 cm s^{-1} ($u* = 2.85$ cm s^{-1}). The relationship between $U_{100crit}$ and $u*_{crit}$ (Eq. 2) results in a drag coefficient $C_D = 5.3 \times 10^{-3}$. Using the calculated U_{100} time series and Eq. 2 to calculate a frequency distribution for $u*$ (Fig. 10) indicates that the critical value for erosion was exceeded 62% of the time during which current records were obtained (Fig. 9). Therefore, tidal sediment resuspension of sand and smaller grain sizes would be a consistent feature of Site 2 on Georges Bank.

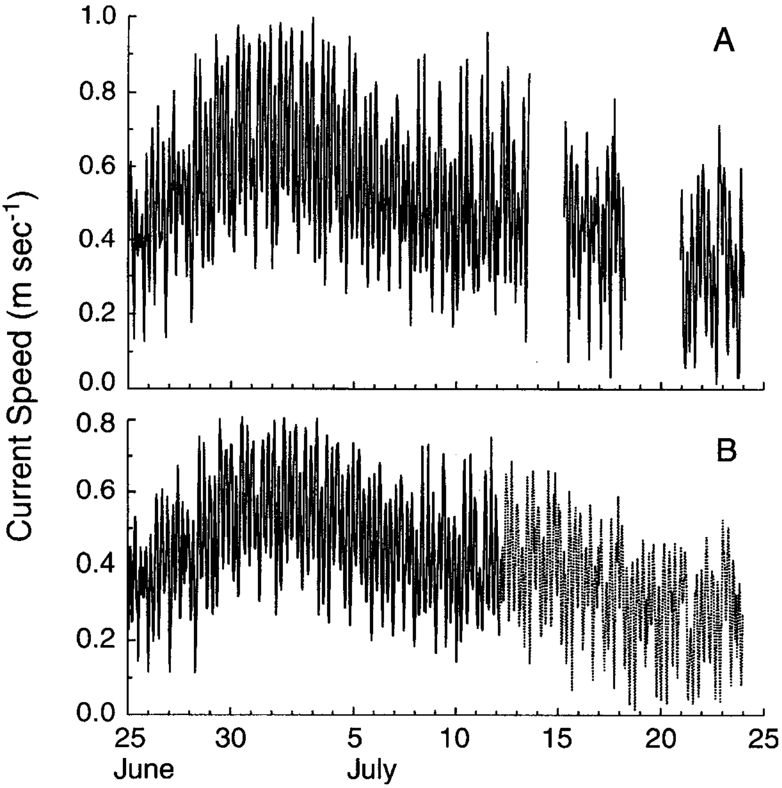

Figure 9. Current meter records at 10 (A) and 3 m (B) above bottom above on Georges Bank, Site 2, starting June 1988. Total water depth = 67 m. After July 12 (day 18), the near-bottom (3 m) current meter record is from a July 1991 deployment at this site (dotted lines).

4. Discussion

Our efforts have been directed toward an estimation of resuspended fluxes of organic matter from gravelly sands and the trophic importance of this material to sea scallops. This requires detection of the transport of a small but organically-rich fraction of the bulk sediment. In the following sections we discuss potential mechanisms of organic matter resuspension, the frequency of resuspension events on Georges Bank, and the organic quality and vertical flux of sediment organic matter. Finally, conclusions on the availability and quality of resuspended sediments are combined with an analysis of sea scallop functional feeding responses to asssess the potential nutritional benefit of resuspended organic matter.

a. Mechanism of sediment organic matter resuspension. In this study, we have adopted a conceptual framework for sediment and organic matter transport that considers the sediment operationally as two distinct fractions: (a) a sand-gravel component (>63 μm)

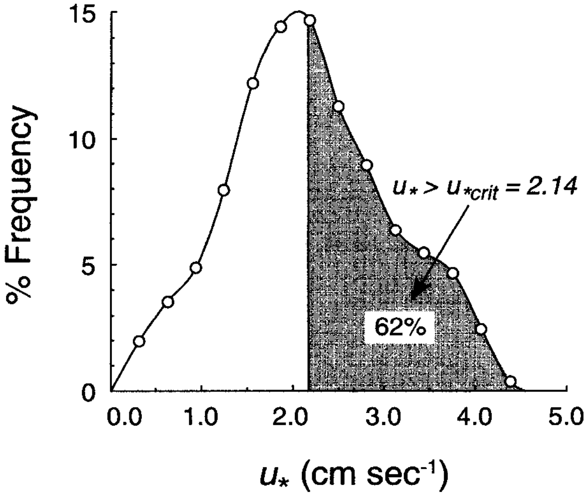

Figure 10. Frequency distribution of calculated shear velocity from Georges Bank current meter records from June to October 1988. The vertical line refers to the critical shear velocity for sediment erosion determined in flume experiments, and the percentage of the distribution for which this value is exceeded. The open circles indicate the endpoint of $u*$ intervals over which frequencies were calculated. A spline curve was fit to the data.

that is organic-poor and has a residence time in the water as brief as seconds and (b) a silt-clay fraction (<63 μm) that has a relatively high organic content of trophic significance to suspension-feeders, and which remains in the water column for minutes to hours once resuspended. The silt-clay fraction lies in the interstices and is armored against erosion by the coarser fraction, but may be released to the water column as a consequence of bedload transport. This conceptual basis for sediment and organic matter transport provides a simple mechanism for the resuspension of organic particles from coarse sediments. We have presented flume results for the mildest degree of bedload transport, i.e. just beyond threshold values. Bedload transport is a power function of excess shear stress (Heathershaw, 1981), and since we have tied our mode of POM transport into bedload transport, there would be a concomitant increase in resuspension with greater boundary stress and subsequent erosion depth. The relationship of our transport mechanism to existing models of sediment transport is considered below.

Depending on flow conditions and the grain composition of the bed, sand fractions may be transported in suspension, as is commonly observed on the shelf including Georges Bank (Parmenter *et al.,* 1983; Muschenheim *et al.,* 1995). Suspended sand concentration (C_a) has been related to bedload concentration and excess shear stress via an empirical resuspension coefficient, γ_0 (Hill *et al.,* 1988; Drake and Caccchione, 1989; Vincent and Green, 1990). It would be desirable to use our rates of resuspension to estimate the resulting concentration of organic matter in near-bottom water. However, the body of literature cited above cannot simply be applied to our work because γ_0 is not intended to relate a mobile layer of sand to a suspended concentration of silt-clay.

Several assumptions are required to link POM transport with bedload transport (see Materials and Methods). One condition is the equal mobility of all grain fractions. It is clear from our flume results (Table 5) that there is variation in bedload transport at similar values of $u*$, as is frequently observed in gravel transport (Kuhnle and Southard 1988). Although heterogeneity in source grain size (Tables 1, 4) would contribute to this variation, observations of erosion in our flume suggest that this is also due to local turbulence around pebbles which caused varying amounts of scour and transport for the different core samples. Equal mobility of all grain fractions is not unconditional during bedload transport, especially at stresses when coarser fractions are immobile and can shelter finer grains (Wilcock and Southard, 1989). Consequently, the supply of sand and finer sediment eroded into the water column will be limited first by supply in the mobile layer (Jago *et al.*, 1993), and secondly by armoring of subsurface layers by immobile and/or interlocking grains (Shi *et al.*, 1985; Lyne *et al.*, 1990; Wiberg *et al.*, 1994). Despite these sources of variance, our condition of equal mobility which allows calculation of suspended carbon flux was supported for the degree of sediment transport in the present experiments.

Our second assumption that all the silt-clay fraction is suspended during bedload transport is more difficult to confirm. If some of the loosely attached silt-clay remains with the grains in bedload transport, or with less mobile gravel, we will overestimate suspended flux. There is clearly POM that is associated with the grains even after sieving (Fig. 2B). Keil *et al.* (1994) found that >90% of POM was adsorbed onto sediment (including the silt-clay fraction) in samples from the Washington continental margin. On the other hand, grain abrasion during transport may scour the grains of even firmly attached POM and bacteria (Miller, 1989) such that the easily dislodged silt-clay fraction is an underestimate of the quantity released during transport. Our third assumption that silt-clay content of bulk sediment is conservative and that the POC content of this fine fraction is constant was supported for August samples by the low variance associated with % silt clay (Table 5) and %POC (Table 2).

b. Critical shear stress and frequency of resuspension. Extrapolation of the mean logarithmic velocity profile for Site 2 to the depth axis (Eq. 4), gives a roughness length (z_o) equal to 0.4 cm. In rough turbulent flow, the ratio d/z_o (where d = grain roughness diameter) should be approximately 30 (Heathershaw and Langhorne, 1988). For our study site with a gravel roughness of ~1 cm, maintaining this ratio would require that $z_o = 0.03$ cm. This value is lower than the z_0 based on the velocity profile, keeping in mind that a two-point semi-log profile is subject to significant error in extrapolating to $z = 0$. Greenberg (1983) used $C_D = 2.5 \times 10^{-3}$ for Georges Bank, similar to other estimates of this parameter (Sternberg 1972; Soulsby 1983), but at Station 2, with $z_0 = 0.4$, solution of Eq. 2 yields a value ($C_D = 5.3 \times 10^{-3}$) more in line with Heathershaw and Langhorne (1988) who estimated $z_o = \sim 0.3$ cm ($C_D = 4.7 \times 10^{-3}$) in the West Solent (England) for coarser gravel than at our site. It was suggested that form drag from gravel bedforms or other unknown roughness elements contributed to this relatively high value, a situation not unlike our region of Georges Bank (Valentine and Lough, 1991). In recent studies over rippled sand, Whitehouse (1995) found $C_D = 6.3 \times 10^{-3}$ and $z_o = 1.2$ cm.

Although Figure 10 suggests that the critical shear velocity for tidal erosion would be exceeded 62% of the time, there are a variety of sources of error in estimating the time series of $u*$ (see also Whitehouse, 1995). Chief among these is a 2 point regression and its extrapolation below the lower current meter to $z = 0$ (Bauer *et al.*, 1992). In addition, our estimated time series for $u*$ does not include wave-current interaction typical of continental shelves (Keen and Glenn, 1995). Previous studies of Georges Bank have also examined frequency distributions of tidal currents causing sediment erosion (Butman, 1987) and found a wide range in % exceedance dependent on Bank location, including values >60%. Although we cannot bracket the error in our estimate of % exceedance, it is likely that sediment transport and thus resuspension of fine POM is not uncommon at this site.

c. *Organic quality of sediment and resuspended material.* The smallest particles that are easily resuspended (silt-clay) are the richest per unit weight (Fig. 2). The presence of resuspended material in the water column can be seen in the C:N ratio and inorganic content of bottom water which has a signature similar to that of material extracted from the sediment (Table 2). Muschenhiem *et al.* (1995) found C:N ratios of 6–7 for August samples of near-bottom water close to our sample site, lower than the values presented in Table 2 for bottom water. Seston quality will be variable given the seasonal nature of primary production on Georges Bank (O'Reilly and Busch, 1984), and the impact of detrital phytoplankton on near-bottom organic matter (Table 2; Fig. 3; see also Jago *et al.*, 1993). Georges Bank bloom periods occur in March–April (O'Reilly and Busch, 1984) and evidence of bloom deposition to the sediment in our study is indicated by the increased organic quality (lower C:N) of resuspended sediment in April compared to August (Table 2). Even in August we observed chloroplast containing cells in microscopic examination of resuspended sediment samples. Falkowski *et al.* (1988) and Palanques and Biscaye (1992) document the presence of near-bottom chlorophyll maxima and increased C:N in bottom compared to surface water, following April phytoplankton bloom periods on the northeast US shelf.

Near-bottom suspended mass concentrations at our study site were not greater than in surface waters. Muschenheim *et al.* (1995) found higher concentrations of suspended material (12 mg l^{-1}) compared to the upper water column in samples taken within 25 cm of the bed near our stations, but concluded that much of this mass was suspended sand grains. In samples taken under calmer conditions, they found near-bottom concentrations of 3–4 mg l^{-1} as well as median particle sizes of 15–20 μm, similar in concentration and in size to the dominant peak in our values (Fig. 4B). Bothner *et al.* (1981) carried out extensive sampling on Georges Bank and found similar suspended matter concentrations in surface and near-bottom waters (<1 mg l^{-1} for non-storm conditions in August). The elevated particulate concentrations characteristic of resuspension events will quickly settle out (Fig. 7), leaving only quality (greater C:N and C:CHL) as a marker of resuspension (Table 2).

d. Vertical flux of sediment organic matter. There are few data for comparison to our POC transport results, but Wainright (1990) conducted annular flume experiments to examine the resuspension of microbes and organic matter from the Georgia continental shelf (4–18 m depth). Rates of resuspension of material from sands ranged from 346–2312 mg C m^{-2} h^{-1}, which are generally larger than measured in our experiments (Table 5). However, Wainright's experiments were conducted at greater excess shear stress than ours which were just beyond $u*_{\mathrm{crit}}$, and he did not discriminate between the resuspension of sand and finer material. Given the carbon content of Wainright's suspended sediments (>5%), there must have been a significant fine fraction relative to sand in suspension. Coupled with the generally finer nature of these sediments relative to Georges Bank, the two studies are not directly comparable. However, taken together they indicate that particulate resuspension from non-cohesive sediments under non-storm conditions will be on the order of 10^1–10^3 mg C m^{-2} h^{-1}.

Due to frequent transport events, Georges Bank sediment is impoverished with respect to the silt-clay fraction. For a given erosion depth, Lyne *et al.* (1990) demonstrated that the bed is rapidly starved of fine sediments available for resuspension. Jago *et al.* (1993) suggested that resuspension at the sediment surface is limited by the supply of fine particles in a veneer fluff layer, a finding supported by Wheatcroft and Butman (1997). Despite the small standing stock of this fraction, it has the richest organic content (Fig. 2) and greatest surface area for microbial attachment (Mayer, 1994). Mayer *et al.* (1993) emphasized the importance of this low density material as food for deposit feeding benthos; when mobilized it may also provide significant nutrition for suspension feeders. Previous studies of Georges Bank in sandier sediments (62 m) than at our site (<2% silt-clay; Parmenter *et al.,* 1983) recorded resuspended material in a sediment trap (3 m above bottom) with up to 68% silt-clay. For resuspension of organic matter to continually occur, there must be a deposition mechanism that restores fines to the sediment. Particles produced in surface waters are easily mixed to bottom waters under the turbulent regime of Georges Bank (Yoshida and Oakey, 1996). Despite the slow settling rate of much of this material under calm conditions (Fig. 7), processes such as particle aggregation enhance the delivery of phytodetritus to the benthos (Auffret *et al.,* 1994). Once in the near-bed region, trapping by of particles in sediment interstices and near biogenic structure increases retention by the bed (Pilditch *et al.,* 1997).

e. Scallop functional responses to resuspended organic matter. Our measurements with sea scallops are the first bivalve feeding experiments to be conducted at sea using natural shelf seston. *P. magellanicus* retained natural particles (Fig. 5) with efficiency similar to laboratory rations (Cranford and Grant, 1990; Cranford and Gordon, 1992), with RE plateauing at >5 μm particle size. The shape of the RE curve for >5 μm particles did not change with increasing concentration as has been reported for seston/clay diets by Cranford and Gordon (1992). This RE spectrum is optimal for the clearance of the majority of resuspended sediment particles (Fig. 4B), and a fraction of those particles even after a settling period of 5 h under calm conditions (Fig. 8). Many laboratory studies with bivalves predict an initial increase in clearance rate with the addition of low concentrations of suspended sediments followed by an asymptotic or declining rate as concentrations increase (Winter, 1978; Bricelj and Malouf, 1984; Cranford and Gordon, 1992). We did not detect a significant increase in clearance rate at the lowest concentration of resuspended sediments (8 mg l^{-1}) compared to feeding on surface and bottom waters (4.5 mg l^{-1}; Fig. 6). However, sediment concentrations used in the present study were above the 1 mg l^{-1} level where Cranford and Gordon (1992) observed enhanced clearance rates in *P. magellanicus* with the addition of sediment.

When presented sediment concentrations above 10 mg l^{-1}, the scallops produced pseudofeces and clearance rates declined (Fig. 6A). Scallops behaved similarly to increasing concentrations of clay particles (Cranford and Gordon, 1992), except that the threshold for pseudofeces production and the reduction in clearance rate occurred at a clay concentration of 2 mg l^{-1}. These data suggest that sea scallop feeding responses to increased sediment loads depend on particle type and that they process resuspended sediments from Georges Bank more effectively than the finer particles (2 μm mean diameter) used in the previous study.

The initiation of pseudofeces production generally indicates the food concentration at which ingestion rate is maximum (Bayne *et al.*, 1989). Sea scallops appear to maintain a constant ingestion rate at elevated food concentrations by simultaneously regulating clearance and pseudofeces production rates (this study; Cranford and Gordon, 1992). MacDonald and Thompson (1986) reported that *P. magellanicus* does not appear to produce pseudofeces when feeding on natural seston, however, seston concentrations in that study were low and below the pseudofeces threshold. Based on previous estimates of nonstorm conditions for Georges Bank (Bothner *et al.*, 1981; Muschenheim *et al.*, 1995), we would expect near-bottom seston concentrations on Georges Bank to also be less than the 10 mg l^{-1} pseudofeces threshold concentration. Moderate resuspension may thus be of benefit, or at least non-detrimental to scallop populations if there is enhanced seston concentration, a likely condition, but one not apparent at the time of our samples. The high turbidity and increased particulate inorganic matter (PIM) content that results from more extreme resuspension events would reduce clearance rate and may actually inhibit food acquisition. Turbidity would persist after a storm as particle residence time in the water column may be long (Fig. 8; see also Jago *et al.*, 1993). However, at suspended particle concentrations above the pseudofeces production threshold, *Placopecten* has the ability to preferentially select organic particles such as microalgae from inorganic particles (Cranford and Gordon, 1992; MacDonald and Ward, 1994) and the benefits of resuspension may be even greater than predicted from the bulk organic quality of the food.

Even without pre-ingestive particle selection, the AE of up to 40% signifies the potential of resuspended sediment as a food source. In comparison, sea scallops feeding on natural seston in a coastal region absorbed between 65 to 90% of POM having an average organic content of 55% (Cranford and Hargrave, 1994). Storm-induced resuspension at the same study site caused a reduction in AE, but the scallops still absorbed 40% of resuspended material having an organic content of 30% (Cranford *et al.*, 1997), which is similar to the AE and average organic content of Georges Bank resuspended sediment (Table 2).

Recent literature on bivalve ecology has focused on the ability of both infaunal and epifaunal bivalves to deplete the water column of seston in shallow coastal regions (Dame, 1993). This phenomenon seems unlikely for deeper offshore regions such as Georges Bank. While we cannot determine whether Georges Bank scallop populations are food limited, it is apparent that resuspended material contributes to the available food supply and is of sufficiently high quality (especially in spring) to provide adequate nutrition (Table 3). Resuspension occurs with sufficient frequency, and resuspended materials have long enough residence time in the water column to provide a consistent nutritional benefit to scallops. Considering the abundance of suspension feeders on Georges Bank (Thouzeau *et al.*, 1991), resuspension is likely important in recycling settled phytoplankton from the sediments back into the seston. This process is known to be important in coastal areas (Tenore, 1977), and should be equally significant on areas of the continental shelf where there is high primary production, a well mixed water column, and little refractory organic matter or silt to dilute the value of resuspended seston.

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REFERENCES

Anderson, F. E. and L. M. Mayer. 1986. The interaction of tidal currents on a disturbed intertidal bottom with a resulting change in particulate matter quantity, texture and food quality. Estuar. Coast. Shelf Sci., *22,* 19–29.

Auffret, G., A. Khirpounoff and A. Vangriesheim. 1994. Rapid post-bloom resuspension in the northeastern Atlantic. Deep-Sea Res., *41,* 925–939.

Baillie, P. W. and B. L. Welsh. 1980. The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. Estuar. Coast. Mar. Sci., *10,* 165–180.

Bauer, B. O., D. J. Sherman and J. F. Wolcott. 1992. Sources of uncertainty in shear stress and roughness length derived from velocity profiles. Prof. Geogr., *44,* 453–464.

Bayne, B. L., A. J. S. Hawkins and E. Navarro. 1987. Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia, Mollusca) in mixtures of silt and algal cells at low concentrations. J. Exp. Mar. Biol. Ecol., *111,* 1–22.

Bayne, B. L., A. J. S. Hawkins, E. Navarro and I. P. Iglesias. 1989. Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis.* Mar. Ecol. Prog. Ser., *55,* 47–54.

Bothner, M. H., C. M. Parmenter and D. Milliman. 1981. Temporal and spatial variations in suspended matter in continental shelf and slope waters off the northeastern United States. Estuar. Coast. Shelf Sci., *13,* 213–234.

Bricelj, V. M. and R. E. Malouf. 1984. Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria.* Mar. Biol., *84,* 155–165.

Butman, B. 1987. Physical processes causing surficial sediment movement, *in* Georges Bank, R. H. Backus, ed., MIT Press, Cambridge, MA, 147–162.

Churchill, J. H., P. E. Biscaye and F. Aikman III. 1988. The character and motion of suspended particulate matter over the shelf edge and upper slope off Cape Cod. Cont. Shelf Res., *8,* 789–809.

Churchill, J. H., C. D. Wirick, C. N. Flagg and L. J. Pietrafesa. 1994. Sediment resuspension over the continental shelf east of the Delmarva Peninsula. Deep-Sea Res. Part II, *41,* 341–363.

Cranford, P. J. 1995. Relationships between food quantity and quality and absorption efficiency in sea scallops *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol., *189,* 123–142.

Cranford, P. J., C. W. Emerson, B. T. Hargrave and T. G. Milligan. 1997. *In situ* feeding and absorption responses of sea scallops *Placopecten magellanicus.* J. Exp. Mar. Biol. Ecol., (in press).

Cranford, P. J. and D. C. Gordon Jr., 1992. The influence of dilute clay suspensions on sea scallop (*Placopecten magellanicus*) feeding activity and tissue growth. Neth. J. Sea Res., *30,* 107–120.

Cranford, P. J. and J. Grant. 1990. Particle clearance and absorption of phytoplankton and detritus by the sea scallop *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol., *137,* 105–121.

Cranford, P. J. and B. T. Hargrave. 1994. *In situ* time-series measurement of ingestion and absorption rates of suspension-feeding bivalves, *Placopecten magellanicus.* Limnol. Oceanogr., *39,* 730–738.

Dame, R. F. 1993. Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. NATO ASI Ser., Vol. 33, Springer-Verlag, Berlin, 579 pp.

Drake, D. E. and D. A. Cacchione. 1989. Estimates of the suspended sediment reference concentration (C_a) and resuspension coefficient (γ_0) from near-bottom observations on the California shelf. Cont. Shelf Res., *9,* 51–64.

Falkowski, P. G., C. N. Flagg, G. T. Rowe, S. L. Smith, T. E. Whitledge and D. Wirick. 1988. The fate of a spring phytoplankton bloom, export or oxidation. Cont. Shelf Res., *8,* 457–484.

Frechette, M., C. A. Butman and W. R. Geyer. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. Limnol. Oceanogr., *34,* 19–36.

Frechette, M. and J. Grant. 1991. An *in situ* estimation of the effect of wind-driven resuspension on the growth of the mussel *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol., *148,* 201–213.

Grant, J. and P. J. Cranford. 1991. Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus.* J. Mar. Biol. Assoc. U.K., *71,* 437–450.

Grant, J. and G. R. Daborn. 1994. The effects of bioturbation on sediment transport on an intertidal flat. Neth. J. Sea Res., *32,* 63–72.

Grant, J. and C. W. Emerson. 1995. Resuspension and stabilization of sediments with microbial biofilms, implications for benthic-pelagic coupling, *in* Biostabilization of Sediments, W. E. Krumbein, D. M. Paterson and L. J. Stal, eds., Verlag Rosemeier, Bad Zwischenahn, 121–134.

Grant, J., C. W. Emerson, B. T. Hargrave and J. L. Shortle. 1991. Benthic oxygen consumption on continental shelves off Eastern Canada. Cont. Shelf Res., *11,* 1083–1097.

Grant, J., C. T. Enright and A. Griswold. 1990. Resuspension and the growth of *Ostrea edulis,* a field experiment. Mar. Biol., *104,* 51–59.

Grant, J. and G. Gust. 1987. Prediction of coastal sediment stability from photopigment content of mats of purple sulfur bacteria. Nature, *330,* 244–246.

Grant, J. and B. Thorpe. 1991. Effects of suspended sediment on growth, respiration, and excretion of the soft-shell clam (*Mya arenaria*). Can. J. Fish. Aquat. Sci., *48,* 1285–1292.

Greenberg, D. A. 1983. Modeling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr., *13,* 886–904.

Heathershaw, A. D. 1981. Comparisons of measured and predicted sediment transport rates in tidal currents. Mar. Geol., *42,* 75–104.

Heathershaw, A. and D. N. Langhorne. 1988. Observations of near-bed velocity profiles and seabed roughness in tidal currents flowing over sandy gravels. Estuar. Coast. Shelf Sci., *26,* 459–482.

Hill, P. S., A. R. M. Nowell and P. A. Jumars. 1988. Flume evaluation of the relationship between suspended sediment concentration and excess boundary shear stress. J. Geophys. Res., *93,* 12499–12509.

Holm-Hansen, O., C. J. Lorenzen, R. N. Holmes and J. D. Strickland. 1965. Fluorometric determination of chlorophyll. J. Cons., *30,* 3–15.

Horne, E. P. W., J. W. Loder, W. G. Harrison, R. Mohn, M. R. Lewis, B. Irwin and T. Platt. 1989. Nitrate supply and demand at the Georges Bank tidal front. Scient. Mar., *53,* 145–158.

Irwin, B. W., J. Anning, C. Caverhill, A. MacDonald and T. Platt. 1990. Primary production on Georges Bank—August 1988. Can. Data Tech. Fish. Aquat. Sci. *785,* 197 pp.

Jago, C. F., A. J. Bale, M. O. Green, M. J. Howarth, S. E. Jones, I. N. McCave, G. E. Millward, A. W. Morris, A. A. Rowden and J. J. Williams. 1993. Resuspension processes and seston dynamics, southern North Sea. Phil. Trans. R. Soc. Lond. A, *343,* 475–491.

Keen, T. R. and S. M. Glenn. 1995. A coupled hydrodynamic-bottom boundary layer model of storm and tidal flow in the middle Atlantic Bight of North America. J. Phys. Oceanogr., *25,* 391–406.

Keil, R. G., Tsamakis, C. B. Fuh, J. C. Giddings and J. I. Hedges. 1994. Mineralogical and textural controls on the organic composition of coastal marine sediments, Hydrodynamic separation using SPLITT-fractionation. Geochim. Cosmochim. Acta, *58,* 879–893.

Komar, P. D. 1987. Selective grain entrainment by a current from a bed of mixed sizes, a reanalysis. J. Sediment Petrol., *57,* 203–211.

Kuhnle, R. A. and J. B. Southard. 1988. Bedload transport fluctuation in a gravel bed laboratory channel. Water Resour. Res., *24,* 247–260.

Leeder, M. R. 1982. Sedimentology, George Allen and Unwin, London, 344 pp.

Loder, J. W., D. Brickman and E. P. W. Horne. 1992. Detailed structure of currents and hydrography on the northern side of Georges Bank. J. Geophys. Res., *97,* 14331–14351.

Loder, J. W., K. F. Drinkwater, N. S. Oakey and E. P. W. Horne. 1993. Circulation, hydrographic structure and mixing at tidal fronts, the view from Georges Bank. Phil. Trans. R. Soc. Lond. A, *343,* 447–460.

Loder, J. W. and R. G. Petitpas. 1991. Moored current and hydrographic measurements from the Georges Bank Frontal Study, 1988–89. Can. Data. Rep. Hydrog. Ocean Sci., *94,* 139 pp.

Lyne, V. D., B. Butman and W. D. Grant. 1990. Sediment movement along the U.S. east coast continental shelf—II. Modelling suspended sediment concentration and transport rate during storms. Cont. Shelf Res., *10,* 429–460.

MacDonald, B. A. and R. J. Thompson. 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus* III. Physiological ecology, the gametogenic cycle and scope for growth. Mar. Biol., *93,* 37–48.

Macdonald, B. A. and J. E. Ward. 1994. Variation in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca, Bivalvia). Mar. Ecol. Prog. Ser., *108,* 251–264.

Mayer, L. M. 1994. Surface area control of organic carbon accumulation in continental shelf sediments. Geochim. Cosmochim. Acta, *58,* 1271–1284.

Mayer, L. M., P. A. Jumars, G. L. Taghon, S. A. Macko and S. Trumbore. 1993. Low-density particles as potential nitrogenous foods for benthos. J. Mar. Res., *51,* 373–389.

Miller, D. C. 1989. Abrasion effects on microbes in sandy sediments. Mar. Ecol. Prog. Ser., *55,* 73–82.

Morse, M. P., W. E. Robinson and W. E. Wehling. 1982. Effects of sublethal concentrations of the drilling mud components attapulgite and Q-Broxin on the structure and function of the gill of the scallop *Placopecten magellanicus* (Gmelin), *in* Physiological Mechanisms of Marine Pollutant Toxicity, W. B. Vernberg, A. Calabrese, F. P. Thurberg and F. J. Vernberg, eds., Academic Press, NY, 235–259.

Muschenheim, D. K., J. Grant and E. L. Mills. 1986. Flumes for benthic ecologists: theory, construction and practice. Mar. Ecol. Prog. Ser., *28,* 185–196.

Muschenheim, D. K., T. G. Milligan and D. C. Gordon, Jr. 1995. New technology and suggested methodologies for monitoring particulate wastes discharged from offshore oil and gas drilling platforms and their effects on the benthic boundary layer environment. Can. Tech. Rep. Fish. Aquat. Sci., *2049,* 55 pp.

Muschenheim, D. K. and C. R. Newell. 1992. Utilization of seston flux over a mussel bed. Mar. Ecol. Prog. Ser., *85,* 131–136.

Open University Course Team. 1989. Waves, Tides, and Shallow-Water Processes, Open University/ Pergamon Press, Oxford, 187 pp.

O'Reilly, J. E. and D. A. Busch. 1984. Phytoplankton primary production on the northwestern Atlantic shelf. Rapp. Cons. Inter. l'Explor. Mer, *183,* 255–268.

Palanques, A. and P. E. Biscaye. 1992. Patterns and controls of the suspended matter distribution over the shelf and upper slope south of New England. Cont. Shelf Res., *12,* 577–600.

Parmenter, C. M., M. H. Bothner and B. Butman. 1983. Characteristics of resuspended sediment from Georges Bank collected with a sediment trap. Estuar. Coast. Shelf Sci., *17,* 521–533.

Pilditch, C. A., C. W. Emerson, and J. Grant. 1997. Effect of scallop shells and sediment grain size on phytoplankton flux to the bed. Cont. Shelf Res., (in press).

Rhoads, D. C., L. F. Boyer, B. L. Welsh and G. R. Hampson. 1984. Seasonal dynamics of detritus in the benthic turbidity zone (BTZ); implications for bottom-rack molluscan mariculture. Bull. Mar. Sci., *35,* 536–549.

Ritzrau, W. and G. Graf. 1992. Increase of microbial biomass in the benthic turbidity zone of Kiel Bight after resuspension by a storm event. Limnol. Oceanogr., *37,* 1081–1086.

Roman, M. R. 1978. Tidal resuspension in Buzzards Bay, Massachusetts II. Seasonal changes in the size distribution of chlorophyll, particle concentration, carbon and nitrogen in resuspended particulate matter. Estuar. Coast. Mar. Sci., *6,* 47–53.

Schalchli, U. 1992. The clogging of coarse gravel river beds by fine sediment. Hydrobiologia, *235,* 189–197.

Shi, N. C., L. H. Larsen and J. P. Downing. 1985. Predicting suspended sediment concentrations on continental shelves. Mar. Geol., *62,* 255–275.

Shumway, S. E., R. Selvin, and D. F. Schick. 1987. Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin 1791), a qualitative study. J. Shellfish Res.; *6,* 89–95.

Soulsby, R. L. 1983. The bottom boundary layer of shelf seas, *in* Physical Oceanography of Coastal and Shelf Seas, B. Johns, ed., Elsevier, Amsterdam, 189–266.

Sternberg, R. W. 1972. Predicting initial motion and bedload transport of sediment particles in the shallow marine environment, *in* Shelf Sediment Transport Process and Pattern, D. J. P. Swift, D. B. Duane, and O. H. Pilkey, eds., Dowden, Hutchinson, and Ross, Stroudsberg, PA, 61–82.

Sternberg, R. W., G. C. Kineke and R. Johnson. 1991. An instrument system for profiling suspended sediment, fluid, and flow conditions in shallow marine environments. Cont. Shelf Res., *11,* 109–122.

Tenore, K. R. 1977. Food chain pathways in detrital feeding benthic communities: a review with new observations on sediment resuspension and detrital recycling, *in* Ecology of Marine Benthos, B. C. Coull, ed., Univ. South Carolina Press, Columbia. SC, 37–54.

Thompson, J. K. and F. H. Nichols. 1988. Food availability controls seasonal cycle of growth in *Macoma balthica* (L.) in San Francisco Bay, California. J. Exp. Mar. Biol. Ecol., *116,* 43–61.

Thouzeau, G., G. Robert and R. Ugarte. 1991. Faunal assemblages of benthic megainvertebrates inhabiting sea scallop grounds from eastern Georges Bank, in relation to environmental factors. Mar. Ecol. Prog. Ser., *74,* 61–82.

Valentine, P. C. and R. G. Lough. 1991. The sea floor environment and the fishery of Eastern Georges Bank. USGS Open File Report 91–439.

Vincent, C. E. and M. O. Green. 1990. Field measurements of the suspended sand concentration profiles and fluxes and of the resuspension coefficient γ_0 over a rippled bed. J. Geophys. Res., *95,* 11,591–11,601.

Wainright, S. C. 1990. Sediment-to-water fluxes of particulate material and microbes by resuspension and their contribution to the planktonic food web. Mar. Ecol. Prog. Ser., *62,* 271–281.

Walsh, J. J. 1988. On the Nature of Continental Shelves. Academic Press, San Diego, 520 pp.

Wheatcroft, R. A. and C. A. Butman. 1997. Spatial and temporal variability in aggregated grain-size distributions, with implications for sediment dynamics. Cont. Shelf Res., *17,* 367–390.

Whitehouse, R. 1995. Observations of the boundary layer characteristics and the suspension of sand at a tidal site. Cont. Shelf Res., *15,* 1549–1567.

Wiberg, P. L., D. E. Drake and D. A. Cacchione. 1994. Sediment resuspension and bed armoring during high bottom stress events on the northern California inner continental shelf—measurements and predictions. Cont. Shelf Res., *14,* 1191–219.

Wilcock, P. R. 1988. Methods for estimating the critical shear stress of individual fractions in mixed-size sediment. Water Resources Res., *24,* 1127–1135.

Wilcock, P. R. and J. B. Southard. 1989. Bed load transport of mixed size sediment, fractional transport rates, bed forms, and the development of a coarse bed surface layer. Water Resources Res., *25,* 1629–1641

Wildish, D. J. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. J. Fish. Res. Bd. Can., *36,* 1197–1206.

Wildish, D. J., A. J. Wilson and B. Frost. 1989. Benthic macrofaunal production on Brown's Bank. Can. J. Fish. Aquat. Sci., *46,* 584–590.

Winter, J. E. 1978. A review of the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture, *13,* 1–33.

Yoshida, J. and N. S. Oakey. 1996. Characterization of vertical mixing at a tidal-front on Georges Bank. Deep-Sea Res. Part II, *43,* 1713–1744.

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