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Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms

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ABSTRACT: Gross sedimentation of ^{14}C labelled carbon was 58 % greater in mesocosms (13 m^3) containing the bivalve *Mercenaria mercenaria* (16 ind m^{-2}) relative to controls without this filter feeder. This difference was attributable to the activities of *M. mercenaria* and presumably due to filtration of particles from the water column. Of this increase, 32 % and 47 % were attributable to assimilation into clam tissue and respiration by the benthic community respectively. Permanent biodeposition by the clams contributed the least (21 %). The ability of 8 filtration rate models to predict the increase in gross sedimentation was examined. Those models (4) which were based on data for bivalves filtering natural suspensions of particulate matter gave estimates which agreed well with observed differences. Those models (4) which yielded poor predictions used dyes or algal monocultures to generate data and overestimated gross sedimentation due to bivalves by up to an order of magnitude. Such overestimation may exaggerate the role of bivalves in enhancing sedimentation and controlling phytoplankton biomass in shallow waters.

INTRODUCTION

Bivalve filter feeders may comprise a significant conduit of energy and nutrients from the water column to the benthos and control material cycling between these compartments in shallow areas (Dame et al. 1980). In addition, bivalves may limit phytoplankton biomass in overlying waters (Cloern 1982, Officer et al. 1982, Nichols 1984). Depletion of phytoplankton over dense beds of filter feeding bivalves has been observed (Carlson et al. 1984, Cohen et al. 1984, Wright et al. 1982).

Such direct field observations supply circumstantial evidence that bivalves exert significant filtering pressure upon the water column. It is desirable to quantify the ability of bivalves to effect significant removal of water column particulates and compare this with observation. Quantification of removal rates is especially pertinent to models of phytoplankton population dynamics (e.g. Kremer & Nixon 1978, Cloern 1982, Officer et al. 1982) and construction of nutrient budgets (e.g. Jordon & Valiela 1982).

A common approach has been to calculate the amount of material removed by bivalves through application of a laboratory-derived filtration rate model to a field population (e.g. Bernard 1974, Hibbert 1977, Dame et al. 1980, Cohen et al. 1984). Because it is difficult to independently measure the removal due to bivalves, the validity of such an approach is hard to assess.

Use of a radioactive tracer in large contained experimental ecosystems allows measurement of processes such as sedimentation which are not easily quantified in shallow, turbulent coastal areas (Oviatt & Nixon 1975). By manipulation of such systems with respect to the presence or absence of bivalve filter feeders, estimates of bivalve-induced sedimentation or removal of suspended particles can be obtained from observed differences between treatments. These differences can be compared to estimates based on filtration rate models.

We present results of an experiment designed to examine the effects of the filter-feeding bivalve *Mercenaria mercenaria* on carbon cycling in shallow estuarine environments. The investigation was conducted at the Marine Ecosystems Research Laboratory using this facility's outdoor mesocosm tanks (13 m^3). We compare mesocosms with *M. mercenaria* added to

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the benthos, to those with no *M. mercenaria*. Radiocarbon ($NaH^{14}CO_3$) was added to the tank water columns in order to quantify the fate of pelagically produced organic matter. In this report, we compare observed differences in gross sedimentation to those predicted by 8 filtration rate models in order to assess the validity of applying such models to the field situation. Three of the models are derived from our own measurements of filtration rate. Five of the models are from the literature and have been chosen because they have been used to predict consumption of suspended particles by *M. mercenaria* in particular, or the effect of bivalves in general on phytoplankton in the overlying water.

METHODS

Mesocosms

Four mesocosm tanks (Fig. 1) were employed during this study. Each mesocosm contains both seawater and sediments and is designed to simulate a shallow, unstratified coastal ecosystem such as Narragansett Bay, Rhode Island. The mesocosms closely resemble the Bay with respect to temperature, mixing (Nixon et al. 1980), primary production (Oviatt et al. 1981), nutrient concentration and dynamics (Pilson et al. 1980), phytoplankton (Vargo et al. 1982) and benthic community structure (Grassle et al. 1981, Frithsen 1984).

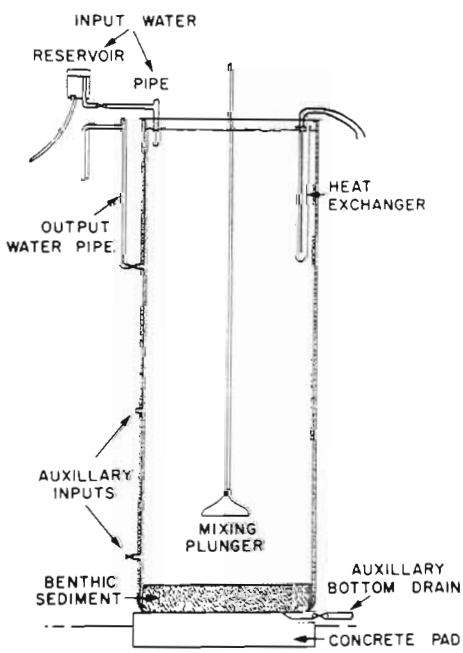

Fig. 1. Cut-away view of MERL mesocosm. Tank diameter 1.83 m; water depth 5 m, volume 13 m^3; sediment depth 37 cm, area 2.52 m^2. The mesocosms are located outdoors and receive natural light

Major events in the experiment are summarized in Table 1. Sediments (18 % sand, 60 % silt, 22 % clay: Oviatt et al. 1984) were collected using a 0.5 m^2 box corer from a site north of Conanicut Island in Narragansett Bay (Hunt & Smith 1983). Forty clams (16 ind m^{-2}) *Mercenaria mercenaria* (marked with nail polish and measured: anterior-posterior length) were planted in the sediments of 2 mesocosms. The ordinary deposit-feeding community typically found at this site and dominated by the annelid worm *Mediomastis ambesita* and the bivalve mollusc *Nucula annulata* (Grassle et al. 1981, Frithsen 1984) was left intact. *M. mercenaria* lengths ranged from 3.2 to 10.7 cm and averaged (± SD) 6.71 ± 1.89 cm and 6.73 ± 1.87 cm respectively in the 2 mesocosms. The size distribution approximated that given by Stringer (1959) for Narragansett Bay, Rhode Island. Clams were measured again upon recovery on 21 August 1984.

Radiocarbon (^{14}C) was introduced into each tank as sodium bicarbonate (New England Nuclear: 50 mCi $mmole^{-1}$), at mid-depth through a 2.5 m long tygon tube. The spike solution was comprised of 2 mCi of ^{14}C in 2.5 l of filtered (1 µm pore size) sea water adjusted to pH 9.45 to avoid loss of $^{14}CO_2$ gas.

Table 1. Treatment of tanks before the experiment and types of samples and their frequency of collection during the 119 d experiment

Dates	Activity
24–28 Oct 1983	Sediments collected; tanks on flow-through
20 Mar–2 Apr 1984	Tanks drained: predators, epibenthic filter feeders removed. Clams planted, tanks on batch
18 Apr	Addition of radiocarbon (2 mCi $tank^{-1}$)
18 Apr–14 Aug	Sampling

Sample type	Frequency
Water Column	
Temperature	Weekly
ph, alkalinity	Weekly
Salinity	Weekly
Dissolved inorganic ^{14}C (DI ^{14}C)	Weekly
Chlorophyll *a* (Chl *a*)	Weekly
Particulate ^{14}C	Weekly
Sediment	
Core (^{14}C)	Final
Flux (DI ^{14}C)	Fortnightly
Clam tissue (^{14}C)	Final
Clam shell (^{14}C)	Final
Other	
Clam filtering rates	Fortnightly

Tank walls were brushed weekly to eliminate fouling organisms and turbulence was supplied by plungers located 1 m above the sediment, operating on a 2 h on 4 h off schedule. Temperature followed the Bay to within 2 C°, and ranged from 9 to 21 °C over the course of the experiment. Salinity varied between 26 and 29 ‰. Tanks were run in batch mode, receiving no input from Narragansett Bay. Tanks configured in this manner for up to 7 mo do not diverge either from the Bay or tanks receiving input from Narragansett Bay (Pilson et al. 1980).

Samples

The types of samples collected during the study which are pertinent to the present report are summarized in Table 1. All water column samples were withdrawn by siphon from mid-depth (2.5 m) while the mixers were operating and after homogeneity of the water column had been achieved (Nixon et al. 1980). Phytoplankton biomass was assessed by Chlorophyll *a* analysis after Yentsch & Menzel (1963) and Lorenzen (1966).

Total CO_2 concentration was derived from measurements of pH, alkalinity, salinity and temperature using the methods of Strickland & Parsons (1972). Salinity was determined following Grasshoff et al. (1983) using the Mohr-Knudsen ti' -ation of chlorinity. Total alkalinity was calculated by the method of Culberson et al. (1970). pH was determined using a meter after standardization at pH 7 and pH 4. Precision was ± 0.002 pH units. For alkalinity measurements 100 ml of sample were pipetted into a clean vessel with 25.0 ml of 0.010 N HCl. pH was determined within 2 d at 25 °C after buffering the electrode in pH 4. Precision was ± 0.006 pH units.

Radioactive dissolved inorganic carbon ($DI^{14}C$) was determined by purging duplicate acidified (5 ml 6 N H_2SO_4) 250 ml water samples with N_2. CO_2 was removed from the gas stream by extraction in a phenethylamine filled (5 ml) Vigreux column. The column was rinsed (5 ml) twice with scintillation cocktail (Beckman MP). The extraction procedure was 99.2 ± 0.07 % (n = 2) efficient.

The phenethylamine-scintillation cocktail mixture was collected in a 20 ml vial and ^{14}C disintegrations per minute (dpm) determined on a liquid scintillation counter (external standard, channels ratio method with a Beckman LS-3105T counter). Samples were counted 3 times for 10 min yielding counting errors of 1 % or less with an efficiency of about 80 %. The precision of the duplicate samples was ± 5 % of the mean.

The activity of ^{14}C on suspended particles was determined by passing duplicate 1 l water samples through 47 mm Gelman AE glass fiber filters (nominal pore size 0.4 µm). These were rinsed with 100 ml of filtered seawater to remove any soluble ^{14}C. The filters were transferred to 20 ml vials with 15 ml of scintillation cocktail and dpm were determined as above. Counting efficiences averaged about 85 % and the precision of the duplicate samples 2.5 % of the mean.

Two depth profiles of dpm on suspended particles in the tanks were made on 15 and 21 June. Single samples (100 ml) were taken at 0.0, 2.5, 4.0 and 4.75 m during a mixing cycle and again about 4 h later just prior to the next mixing cycle. Samples were counted for dpm on particles as described above. Data were analysed using a 4-way ANOVA with the following factors: Tank, Depth, Date and Time (initial *vs* final samples). Because only 1 sample/depth was taken, only main effects and 1 interaction term (depth × time) were evaluated. Separate analyses were performed for control and treatment tanks.

Sediment cores (5.067 cm^2, n = 8) were taken from each tank on 14 August 1984, using a remote coring device (Frithsen et al. 1983). A triangulation system employed at the water surface protected against coring the same location twice. In the laboratory cores were sliced to obtain the following vertical intervals: 0 to 0.5 cm, 0.5 to 1.0 cm, 1 to 2 cm, 2 to 6 cm, 6 to 10 cm. All but the surface 0 to 0.5 cm were subcored (1.54 cm^2) to avoid smearing between layers. Two slices from each depth (1 from each of 2 cores) were placed in clean, preweighed vials and wet and dry weight (110 °C) determined.

Radioactivity in the sediments was determined after Rudnick (1984). Sediment was ground and homogenized with mortar and pestle. Subsamples (ca 50 mg) were transferred to preweighed, precombusted crucibles. Dry weight was determined after oven drying (60 °C) for 24 h. Subsequent acidification with 300 µl of 6N H_3PO_4 volatilized any $DI^{14}C$. Samples were burned at 950 °C in a precombusted stream of oxygen (1 l min^{-1}) and the resultant radioactive CO_2 caught in a phenethylamine filled (5 ml) Vigreux column (Burnison & Perez 1974). Treatment and counting of the samples were the same as those for $DI^{14}C$. Counting efficiencies averaged about 80 %. Estimates of dpm m^{-2} of bottom at each depth from the 4 pools of slices varied from 11 to 100 % of the mean (average ± 45 %). These estimates were summed to yield estimates of the total sediment inventory (µCi m^{-2}) from 0 to 10 cm.

Benthic fluxes of $DI^{14}C$ were measured by capping off the entire benthos with a 1.76 m diameter, 13 cm high clear plastic chamber designed to fit over the sediment tray. Initial, midpoint and final samples were withdrawn by siphon after mixing with a hand-operated stirring bar. A control bottle (4 l) was incubated on top of the chamber to correct for changes induced by

the water within the chamber. Samples were analysed in triplicate (precision ± 1.2 % of the mean). Incubation time varied inversely with temperature and ranged from 9 to 4 h over the course of the experiment. The decline in oxygen concentration, although not reported here, was always linear over the incubation period (average $r = -0.990 \pm 0.019$ $n = 28$), implying that oxygen was not limiting.

Benthic fluxes were calculated from slopes of linear regressions of $DI^{14}C$ concentration on time. This slope was corrected for changes over time between the initial sample from the chamber and the control bottle, sampled concurrently with the final chamber sample.

Clams were retrieved from the tanks on 21 August 1984 and frozen until analysis for ^{14}C activity. Seven clams from each of the 2 treatment tanks, spanning the range of sizes, were chosen for analysis. Clams were shucked and tissue treated in the same manner as sediments. Precision of duplicate estimates of μCi $clam^{-1}$ in tissue averaged 19 % of the mean. From these data power functions of length (x cm) and μCi $clam^{-1}$ (y) were calculated. The exponent for each tank was about 2.3 (Tank 13: $r = 0.980$, $p < 0.05$; Tank 14: $r = 0.892$, $p < 0.05$; $n = 14$ in both cases). These regressions were used to calculate the amount of label in the clams in each tank.

Shells from these same clams were pulverized and 50 mg subsamples evaluated for inorganic ^{14}C activity. Subsamples were mixed into 225 ml of deionized water, dissolved by acidification with 10 ml of concentrated HCl (resulting $pH < 2$) and analysed for $DI^{14}C$ as previously described. Precision of duplicate estimates of μCi $(clam\ shell)^{-1}$ averaged 22 % of the mean. To estimate ^{14}C activity in shells of all clams in the tanks linear regressions relating μCi $(clam\ shell)^{-1}$ to a composite variable, clam growth in cm during the experiment multiplied by shell weight, were calculated for the clams from each tank (Tank 13: $r = 0.903$, $p < 0.05$; Tank 14: $r = 0.898$, $p < 0.05$; $n = 14$ in both cases). Shell weight of each clam in the tanks was calculated from power functions of weight on final length determined at the end of the experiment (Tank 13: $r = 0.997$, $p < 0.05$; Tank 14: $r = 0.998$, $p < 0.05$; $n = 7$ in both cases). Growth of extraneous unmarked clams was assumed to be the average for their size class. These relations allowed estimation of the ^{14}C activity in the shell of each clam in the 2 treatment tanks. Clams which died over the course of the experiment were not included in these calculations.

Clam filtering rates defined as volume of water cleared of particles $(unit\ time)^{-1}$ by Winter (1978) were measured by a flow-through technique 6 times during the experiment between 25 May and 7 August (13.5 to 21.0 °C). Individual clams, representing the size range of those in the tanks, were placed in 4 sealed plastic chambers (500 ml). A fifth, empty chamber, served as a control. Water, from either of the clam treatment tanks, was pumped through the chambers and 100 ml samples were collected from the inflow and outflow. These were analysed for ^{14}C activity on particles (dpm l^{-1}) as described earlier. Flow rates were measured at the outflow of each chamber using a graduated cylinder and stopwatch. Filtration rates were calculated as:

$$\frac{[IN] - [OUT]}{[OUT]} \times \text{flow rate} \quad (1)$$

and were corrected for the control. This formulation best approximates the true filtration rate when the concentration inside the chamber is not measured, as with the closed system here (Hildreth & Crisp 1976). At least 3 measurements were made on each clam while siphons were extended, generally over a period of 3 to 4 h. The average decline in dpm l^{-1} between inflow and outflow was 18 ± 7.8 %. Measurements with differences of less than 10 % were considered invalid. Flow rate through the chambers averaged 112 ± 33 ml min^{-1} and ranged from 59 ml min^{-1} at 13.5 °C to 181 ml min^{-1} at 21.0 °C. A total of 41 measurements were used to construct a filtration rate model.

Calculations

Conversion to carbon. In general dpm have been converted to total labelled carbon using the specific activity (dpm μgC^{-1}) of the dissolved inorganic carbon in the water column. Specific activity was determined from the $DI^{14}C$ measurements and estimates of total CO_2 based on pH and alkalinity. The following average specific activities (dpm μgC^{-1}) were employed for each tank (controls: Tank 12 = 12.58 ± 1.86, Tank 15 = 11.89 ± 2.26; treatments: Tank 13 = 11.39 ± 2.47, Tank 14 = 11.59 ± 2.27).

Gross sedimentation. Gross sedimentation is the total amount of labelled carbon which reached the bottom during the experiment. The sediment inventory of labelled carbon at the end of the experiment plus the amount remineralized over the course of the experiment represents an estimate of gross sedimentation. In treatment tanks, the amount of labelled carbon in the clams themselves must be included. Core samples included labelled carbon in the sediment and in small animals but not that in clam tissue. Remineralization, or flux of $DI^{14}C$ out of the sediments was measured by concentration changes within a chamber. Deposition of $DI^{14}C$ in clam shell either directly from the water or from organic matter respired by the clams (Dillaman & Ford 1982) causes an underestimation of $DI^{14}C$ flux out of the sediment. Thus, labelled carbon in clam shell was also included in estimates of gross sedimentation.

Integration. In most instances data are summarized in the 'Results' section using integrated values derived from trapezoidal integration over time. The total time period employed is from Julian Day 109 (18 April 1984) to Julian Day 227 (14 August 1984) inclusive or 119 d beginning on the day ^{14}C was added to the tanks and ending when the final coring for sedimentary carbon occurred.

Filtering rate models

Eight models (Table 2) were used to estimate consumption of suspended particles by clams: 5 from the literature and 3 based on our own data. Models from the literature are all functions of size, temperature or both. For comparative purposes, we derived filtration rate equations from our data based both on each single parameter and their combination. Clam length alone explained 31 % of the variation in filtering rate ($r = 0.560$, $F = 17.80$, $df = 1,39$, $p < 0.05$) while temperature as a sole predictor explained 10 % ($r = 0.307$, $F = 4.13$, $df = 1,39$, $p < 0.05$). The multiple regression including both these variables thus explained about 40 % of the total variation ($r = 0.634$, $F = 12.83$, $df = 2,38$, $p < 0.05$).

Hibbert's (1977) model was specific to *Mercenaria mercenaria* and included clam length (mm) and the parameter *a* which is a function of temperature (range 12 to 25 °C). In an ecosystem model of Narragansett Bay, Kremer & Nixon (1978) estimated *M. mercenaria*'s filtering rate as a function of temperature based on Loosanoffs (1939) activity data and other information from the literature. Below 10 °C they assumed filtering rate to be an exponential function of temperature. The exponent 0.16 T was derived by fitting an exponential curve through the points (0 °C, 1.0 l h^{-1}) and (10 °C, 5.0 l h^{-1}) (Kremer & Nixon 1978). Above 10 °C they assumed a constant filtering rate of 5 l h^{-1} $clam^{-1}$ (Table 2). The Coughlan & Ansell (1964) power function, as given by Winter (1978), actually describes the pumping rate of *M. mercenaria* as a function of dry tissue weight (temperature range 18 to 20 °C). Nevertheless, this has been considered a filtration rate equation (Winter 1978, Officer et al. 1982). Pumping rate, the amount of water circulated through the mantle cavity, and filtration rate, the volume of water cleared of particles per unit time, are equivalent only when retention of particles is 100 % (Winter 1978).

Cloern (1982) used an equation, similar in form to Coughlan & Ansell (1964), to estimate the filtration rate of several species of bivalves in South San Francisco Bay. The equation was derived from the data of Mohlenberg & Riisgard (1979) for 5 species of bivalves (temperature range 10 to 13 °C).

Officer et al. (1982) fit data from Winter (1978) to a power function of total weight. Winter's (1978) data were in dry tissue weight and these were converted to total weight through division by 0.06. Officer et al. (1982) also presented a version of the Mohlenberg & Riisgard (1979) equation used by Cloern (1982). As a compromise they used an equation midway between Winter's and Mohlenberg & Riisgard's equations. Their exact equation is not given and was derived empirically by the present authors.

General application of models

Clams in the tanks were divided into 4 size classes. For a mean sized clam in each size class a daily filtering rate was determined for each week of the experiment. The amount of particulate matter removed from the water, in dpm, was calculated by multiplying the filtering rate (l d^{-1}) by the dpm l^{-1} on suspended

Table 2. Model formulations used to predict filtering rates for clams in each of 2 mesocosms

Model	Filtering rate (FR)	Units	Remarks
This study	$\frac{(L^{0.96})(T^{0.95})}{2.95}$	ml ind^{-1} min^{-1}	L = length (cm) T = °C
This study	$5.12L^{0.967}$	ml ind^{-1} min^{-1}	L = length (cm)
This study	$1.55T^{0.982}$	ml ind^{-1} min^{-1}	T = °C
Hibbert 1977	$(L^{0.892})/10^{a}$	l ind^{-1} h^{-1}	T = °C L = length (mm) log a = −0.005T + 0.241
Kremer & Nixon 1978	$e^{0.16T}$	l ind^{-1} h^{-1}	T = °C if T > 10 °C, FR = 5 l h^{-1}
Coughlan & Ansell 1964	$2.59W^{0.73}$	l ind^{-1} h^{-1}	W = dry tissue wt (g)
Officer et al. 1982	$0.76W^{-0.40}$	l (g total wt)$^{-1}$ h^{-1}	W = total wt (g)
Cloern 1982	$168W^{0.67}$	l ind^{-1} d^{-1}	W = dry tissue wt (g)

particles (Fig. 2). This method of calculating consumption follows that of Winter (1978) and was used by Hibbert (1977).

Daily consumption for each week of the experiment was integrated for Julian Day 109 to 227 inclusive or 119 d. All models were integrated over the same time intervals within this 119 d period. This procedure gave estimates of total consumption (in dpm) of a mean sized clam in each of 4 size classes. This value was converted to total labelled carbon, multiplied by the total number of clams in each size class, summed over size classes and expressed on an areal basis.

The mean length of clams in each size class was calculated by first determining a mean length for each of the marked clams during the experiment from initial and final lengths. Together with the lengths of any extraneous unmarked clams, these were used to calculate means for size classes. A dry tissue weight for each clam was estimated from regressions of length on dry tissue weight determined at the end of the experiment for each tank (Tank 13: $r = 0.900$, $p<0.05$; Tank 14: $r = 0.997$, $p<0.05$; $n = 7$ in both cases). Average lengths during the experiment were employed. A mean dry weight for each size class was calculated from these data. When necessary, mean dry weight was converted to total weight after Officer et al. (1982).

RESULTS

Of the 40 marked clams planted in each treatment tank, 35 marked and 3 extraneous clams from Tank 13, and 38 marked and 1 extraneous clam from Tank 14 were recovered alive. Although a few *Mercenaria mercenaria* may have been present in control tanks, a thorough search revealed none.

Fluctuation in dpm l^{-1} on water column particulates

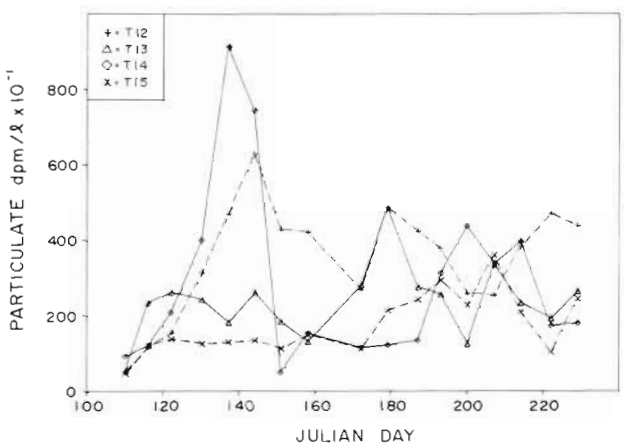

Fig. 2. Activity of ^{14}C on suspended particles in disintegrations per minute (dpm) per l tank water. Control tanks (dashed lines): T12, T15. Treatment tanks (solid lines): T13, T14

(Fig. 2), used in the calculation of clam consumption, were generally correlated with total Chlorophyll *a* (Spearman's rank correlation coefficient Tank 12: 0.513, $p = 0.03$; Tank 15: 0.585, $p = 0.009$; Tank 13: 0.343, $p = 0.08$; Tank 14: 0.821, $p = 0.005$).

Analysis of the depth profiles for control tanks by ANOVA revealed differences in dpm on suspended particles between tanks ($F = 67.20$, $df = 1,22$, $p<0.05$) and between dates upon which profiles were made ($F = 43.53$, $df = 1,22$, $p<0.05$). There were no differences between depths ($F = 1.58$, $df = 3,22$), initial and final samples ($F = 0.38$, $df = 1,22$) or significant interaction between these 2 factors ($F = 1.40$, $df = 3,22$). For treatment tanks the only significant difference detected was between tanks ($F = 40.31$, $df = 1,22$, $p<0.05$). Effects of date, depth, initial *vs* final samples and the interaction between the latter 2 factors were statistically non-significant.

The parameters which are necessary for the calculation of gross sedimentation appear in Table 3. A benthic flux of $DI^{14}C$ (Fig. 3) was not always detectable despite a linear decline in oxygen within the chamber. These fluxes were assumed to be zero. Estimates of gross sedimentation varied by an average of 6.7 % within replicates but were 58 % greater in treatments relative to controls differing on average by 14.2 g C m^{-2}.

The estimates, derived from the models, of labelled carbon filtered from the water by the clams in the 2 treatment tanks (Table 4) varied by an order of magnitude, ranging from 12.2 g C m^{-2} (our temperature model for Tank 13) to 190.7 g C m^{-2} (Cloern's [1982] model for Tank 14). The mean of the 8 estimates for each tank varied by 90 % (Tank 13) and 100 % (Tank 14). The means of the estimates from the 3 models based on our own data varied by 12 % (Tank 13) and 19 % (Tank 14).

The percentages of the difference in gross sedimentation between each of the treatment tanks and the controls that is explained by each model appears in Table 5. The values in Table 4 were calculated assuming that *Mercenaria mercenaria* filters 100 % of the time it is submerged, which in our case was 24 h d^{-1}. *M. mercenaria* exhibits rhythmic patterns of shell opening and closing (Bennett 1954, Brown et al. 1956) and probably does not filter constantly. Both Loosanoff (1939) and van Winkle et al. (1976) have examined activity in *Mercenaria*, the former in relation to temperature and the latter in relation to temperature and salinity. We have used the data in Loosanoff (1939) and the response surfaces depicted in van Winkle et al. (1976) to estimate the time spent filtering under our experimental conditions of temperature and salinity. Loosanoff's data yielded an estimate of 81 %, van Winkle et al.'s 65 %, and personal observations by one

Table 3. Sediment inventory (0 to 10 cm), clam tissue and shell inventory estimated from regressions, integrated benthic respiration and gross sedimentation of labelled carbon during the 119 d experiment. Values are given both in microcuries (μCi) m^{-2} and in g C m^{-2}

	Controls		Treatments	
	Tank 12	Tank 15	Tank 13	Tank 14
Sediment inventory				
μCi m^{-2}	75.5	64.7	90.5	72.0
g C m^{-2}	13.3	12.1	17.6	13.8
Benthic $DI^{14}C$ respiration				
μCi m^{-2}	71.2	57.8	56.8	79.7
g C m^{-2}	12.6	10.8	11.1	15.3
Clam tissue				
μCi m^{-2}	–	–	16.7	30.4
g C m^{-2}	–	–	3.3	5.8
Clam shell				
μCi m^{-2}	–	–	27.5	25.6
g C m^{-2}	–	–	5.4	4.9
Gross sedimentation				
μCi m^{-2}	146.7	122.5	191.5	207.7
g C m^{-2}	25.9	22.9	37.3	39.8
$\bar{x} \pm$ SD	24.4 ± 2.14		38.6 ± 1.77	

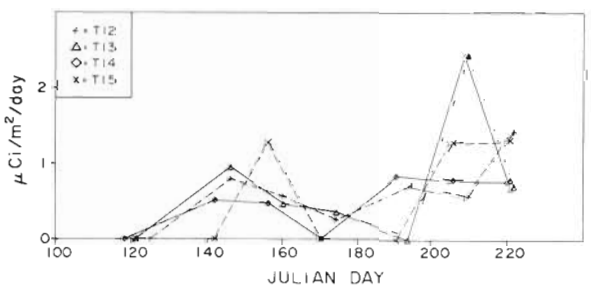

Fig. 3. Benthic flux of dissolved inorganic ^{14}carbon ($DI\ ^{14}C$) in μCi m^{-2} d^{-1} Positive values indicate flux out of the sediment. Control tanks (dashed line): T12, T15. Treatment tanks (solid line): T13, T14

of us (P.D.) 63 %. Thus, the percentage of the difference in gross sedimentation explained by each model (the 100 % value in Table 4) has been adjusted for time spent filtering (81 and 65 %) in Table 5. The models fall into 2 groups: the 3 from this study and Hibbert's (1977), whose estimates explain between 60 and 140 % of the difference in gross sedimentation, and the remaining 4 which overestimate this difference by 200 to 1200 %.

DISCUSSION

In this report we compare gross sedimentation of labelled carbon in mesocosms with and without the filter feeding clam *Mercenaria mercenaria*. Further we attempt to predict the observed differences in sedimentation between clam tanks and controls using several filtration rate models.

Calculation of gross sedimentation

The calculation of gross sedimentation involves summation of the amount of ^{14}C labelled carbon in the sediments, as measured by core samples, and the respiration of $DI^{14}C$, as measured with the benthic flux chamber. Since these were accomplished with the mixer out of the tank, resuspendable material is treated as permanently deposited. The multiple depositional events induced by resuspension are not included. Benthic fluxes include the respiration of some material which would occur in the water column during resuspension. Similarly, core samples contain material which could escape permanent deposition and likewise be respired during resuspension. The sampling procedure thus causes an overestimation of gross sedimentation. The following considerations demonstrate that this overestimation is not large.

Assuming that all the dpm on suspended particles, measured during mixing at the end of the experiment (Fig. 2), were resuspended, and that all dpm would eventually be respired in the water column, it can be calculated that estimates of labelled carbon in the sediment would be overestimated by 7.0 ± 3.8 % for all 4 tanks. Assuming the same respiration rate as ^{14}C already in the sediments, the dpm on suspended particles would result in a 6.9 ± 3.6 % overestimation of the last benthic flux measurements (Fig. 3).

In general, depth profiles measured the net change in dpm on suspended particles during intermixing periods. Thus, if production and loss are equivalent no change will be detected. Nevertheless, that no signifi-

Table 4. Clam consumption (g C (size class)$^{-1}$ and g C m^{-2} of bottom) in the 2 treatment mesocosms as estimated by various filtering rate models. Number (n) of clams recovered in each size class at the end of the experiment is also given. Sizes of clams represent average length during the experiment

	n	This study			Hibbert 1977	Coughlan & Ansell 1964	Kremer & Nixon 1978	Officer et al. 1982	Cloern 1982
		Size + Temp.	Size	Temp.					
Tank 13									
Size class (cm ± SD)									
3.58 ± 0.28	3	1.7	1.8	–	1.5	2.4	–	1.3	6.8
4.47 ± 0.28	6	4.2	4.4	–	3.6	7.8	–	12.6	21.2
5.88 ± 0.46	15	13.7	14.3	–	11.7	35.7	–	52.0	92.6
8.27 ± 0.98	14	17.7	18.5	–	14.7	71.4	–	90.6	173.9
Total consumption g C m^{-2}		14.8	15.5	12.2	12.5	46.6	42.0	63.3	116.9
Tank 14									
Size class (cm ± SD)									
3.71 ± 0.39	4	2.6	3.1	–	2.5	5.1	–	8.7	14.2
4.69 ± 0.41	4	3.2	3.9	–	3.0	8.7	–	13.4	23.1
5.99 ± 0.45	14	14.6	17.3	–	13.3	51.8	–	72.5	131.9
8.29 ± 1.04	17	23.9	28.7	–	21.3	129.6	–	159.7	311.4
Total consumption g C m^{-2}		17.6	21.0	14.2	15.9	77.5	53.6	100.9	190.7

Table 5. Percentage of the gross sedimentation difference (treatment $-\overline{X}$ control: Tank 13 = 12.90 g C m^{-2}, Tank 14 = 15.40 g C m^{-2}) explained by clam consumption as estimated by various filtering rate models. The 3 estimates given for each model assume different percentages of time spent filtering by *Mercenaria mercernaria*

	This study			Hibbert 1977	Coughlan & Ansell 1964	Kremer & Nixon 1978	Officer et al. 1982	Cloern 1982
	Size + Temp.	Size	Temp.					
Tank 13								
Filtering time								
100 %	115	120	95	97	361	326	491	906
81 %	93	97	77	78	293	264	397	734
65 %	75	78	61	63	235	212	319	589
Tank 14								
Filtering time								
100 %	114	136	92	103	503	348	655	1238
81 %	93	110	75	84	408	282	531	1003
65 %	74	89	60	67	327	226	426	805

cant variation in dpm l^{-1} was found, either with time or depth, supports the conclusion of the above calculation. Furthermore, these profiles indicate that the concentration of particulate ^{14}C in the water column was not ruled by events of resuspension driven by the mixer. In fact, the correlation of dpm l^{-1} on suspended particles and Chl *a* implies the expected dependence on phytoplankton.

In treatment tanks the amount of ^{14}C in clam tissue and shells also comprises a portion of gross sedimentation. Both compartments have been measured and estimated on an areal basis for each tank. Empty shells of clams which died over the course of the experiment were not included because stability of ^{14}C in the shell after death and some average specific activity up to the time of death, which could not be established, would have to be assumed for conversion to total labelled carbon. If included as live shells, estimates of gross sedimentation would increase by 0.1 % in Tank 14 and 1.0 % in Tank 13. Although core samples include smaller animals in the sediment, other large animals (>2.5 cm) in diameter were not sampled, but these are generally rare in these sediments (Frithsen 1984, Rudnick 1984).

Mercenaria mercenaria and gross sedimentation

Particles labelled with ^{14}C presumably reached the sediment by physical settling in both control and treatment mesocosms. Since the control mesocosms apparently had no *Mercenaria mercenaria,* an additional mode of sedimentation, filtration of suspended particles by clams, was operative in the treatment mesocosms. The difference in gross sedimentation (58 %) between control and treatment is attributable to this filtration of suspended particles by *M. mercenaria.* Once a suspended particle is filtered from the water by *M. mercenaria* it may be biodeposited as faeces or pseudofaeces, assimilated into tissue, or respired to $DI^{14}C$ which may return to the water or be used to create shell (Dillaman & Ford 1982).

The difference in gross sedimentation between controls and treatment averaged 14.2 g C m^{-2} (Table 3). Of this difference, 32 % (4.5 ± 1.8 g C m^{-2}) was due to assimilation of ^{14}C into clam tissue. When converted to g C m^{-2} the ranges of estimates of the sediment inventory for control and treatment do no overlap, yet the difference between the highest control and lowest treatment is slight (Tanks 12 and 14; Table 3). This difference, attributable to biodeposition by *M. mercenaria,* averaged 3.0 g C m^{-2} or 21 % of the difference in gross sedimentation. Measured benthic fluxes of $DI^{14}C$ did not differ between control and treatment (Fig. 3, Table 3). However, when the treatments are corrected for deposition of $DI^{14}C$ in clam shell, the difference in respired label becomes larger (6.6 g C m^{-2}) and accounts for 47 % of the difference in gross sedimentation. As some of the $DI^{14}C$ in shell derives directly from the water and some from respiration by the clam (in unknown proportion: Dillaman & Ford 1982), it is not possible to ascribe this increase in respired carbon to respiration by the clams themselves or to respiration of biodeposits. It can be concluded however, that the increase in gross sedimentation between control and treatment was mainly a result of assimilation into clam tissue (32 %) and respiration (47 %). Permanent deposition of biodeposits made the smallest contribution to this difference.

Filtration rate models and gross sedimentation

The comparison between consumption of particulate matter by clams and the difference in gross sedimentation between control and treatment depends on whether our measure of gross sedimentation accounts for the fate of particles filtered by clams as well as on our estimate of consumption. The discussion just completed demonstrates that our calculation of gross sedimentation includes the necessary parameters to account for the fate of particles filtered by clams: assimilation, respiration, and permanent biodeposition.

We have calculated consumption of suspended particles by multiplying the filtration rate, or volume of water cleared of particles per unit time, by the concentration of labelled carbon on suspended particles. Since it is measured while the mixers are operating, this concentration includes resuspended material. Thus, labelled, resuspended particles are included in estimates of both consumption and gross sedimentation.

An estimate of consumption derived from any of the models is in error to the extent that the average concentration sampled at 2.5 m does not reflect the average concentration in the immediate vicinity of clam siphons. We could not measure the latter concentration. However, analysis of the depth profile data detected no differences between samples taken at various depths either during or just before mixing. Thus, samples taken at 2.5 m were similar to those taken close to the bottom at 4.75 m and are representative of the average conditions in the tanks.

The 8 models yielded widely varying estimates of consumption by the clams and fall into 2 groups: those from this study and Hibbert's (1977) model juxtaposed against the remaining 4 models. There are several explanations for this discrepancy. The former group of models are specific to *Mercenaria mercenaria.* In the latter group the Coughlan & Ansell (1964) and Kremer & Nixon (1978) models are also specific to *M. mercenaria.* Of the more generic models, Officer et al.'s (1982) includes data for *M. mercenaria* and Cloern's (1982) includes data for animals of the same general size, shape and weight (e.g. *Arctica islandica)*: differences amongst animals used to derive these models do not appear to be of major importance.

Although the temperature ranges over which the data for the various models were taken differ, this does not seem sufficient to account for the observed discrepancies either. Only the Coughlan & Ansell (1964) (18 to 20 °C) and the Cloern (1982) (10 to 13 °C) models apply to narrow ranges of temperature. The rest encompass to within a few degrees the range experienced by the clams in the mesocosms. There are still large differences between the broad temperature range models (e.g. Kremer & Nixon 1978, Hibbert 1977).

The number and kinds of variables used in the models may also account for the differences. Most of the models are functions of either temperature or size (length or weight). Only 2 (this study and Hibbert 1977) include both. Although modelling our data with either size or temperature alone gave consumption estimates which diverged from the 2-variable, multiple regression model, the estimates differed by much less

than all models viewed in concert. Clearly, the 2-variable model explained more variation in observed filtration rates than the single variable formulations, and came closer to explaining observed differences in gross sedimentation between control and treatment. Using either temperature or size alone would still have done better than all other models from the literature excepting Hibbert (1977). We do not believe that the discrepancy between groups of models depends on the particular variables included.

We believe that the dissimilarity among model predictions stems from the differences in suspensions used to measure filtration rate. Those models which are based on natural suspension of particles (this study and Hibbert 1977) yielded the lowest estimates of consumption and these agreed reasonably well with observed differences in gross sedimentation.

The remaining 4 models overestimated gross sedimentation by 200 to 1200 %. These models were based on filtration of a variety of suspensions and solutions. Coughlan & Ansell (1964) used dye. Officer et al. (1982) and Cloern's (1982) models are based on data from laboratory studies using algal monocultures. The data of Mohlenberg & Riisgard (1979) figure prominently in the latter formulations. These authors chose cultures of algae which were retained completely by the bivalves they studied (Mohlenberg & Riisgard 1979). None of the data, tabulated in Winter (1978), and used by Officer et al. (1982), are for bivalves feeding on natural suspensions of particulate matter. Kremer & Nixon (1978) based their model on a variety of data most of which was for dye solutions or algal monocultures. We conclude that filtering rate models founded on other than natural suspensions of particulate matter are unlikely to accurately reflect processes in the field.

We emphasize that 3 of these models (Kremer & Nixon 1978, Officer et al. 1982, Cloern 1982) have been used to estimate the effect of *Mercenaria mercenaria* in particular or bivalves in general on phytoplankton populations in the water column. Data from Coughlan & Ansell (1964), the fourth model, was used in constructing the filtration rate model of Officer et al. (1982). All probably overestimate removal of particulate matter by bivalves and therefore exaggerate their role in controlling phytoplankton biomass. We agree with the above authors that bivalves can represent an important control on phytoplankton populations. However, overestimation of filtration rate can result in an underestimation of the density necessary to exert a significant control (e.g. Officer et al. 1982) and may cause investigators to disregard other benthic organisms which may also remove phytoplankton from the water column (e.g. spionid polychaetes, Donaghay et al. 1984).

Two models reasonably predicted the difference in gross sedimentation of labelled carbon between treatment and control mesocosms which was attributable to *Mercenaria mercenaria*. These results suggest that filtering rate models can be used to predict the effect of bivalves on the fate of particulate carbon in the field.

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