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Oyster Reef Habitat Restoration:
A Synopsis and Synthesis of Approaches

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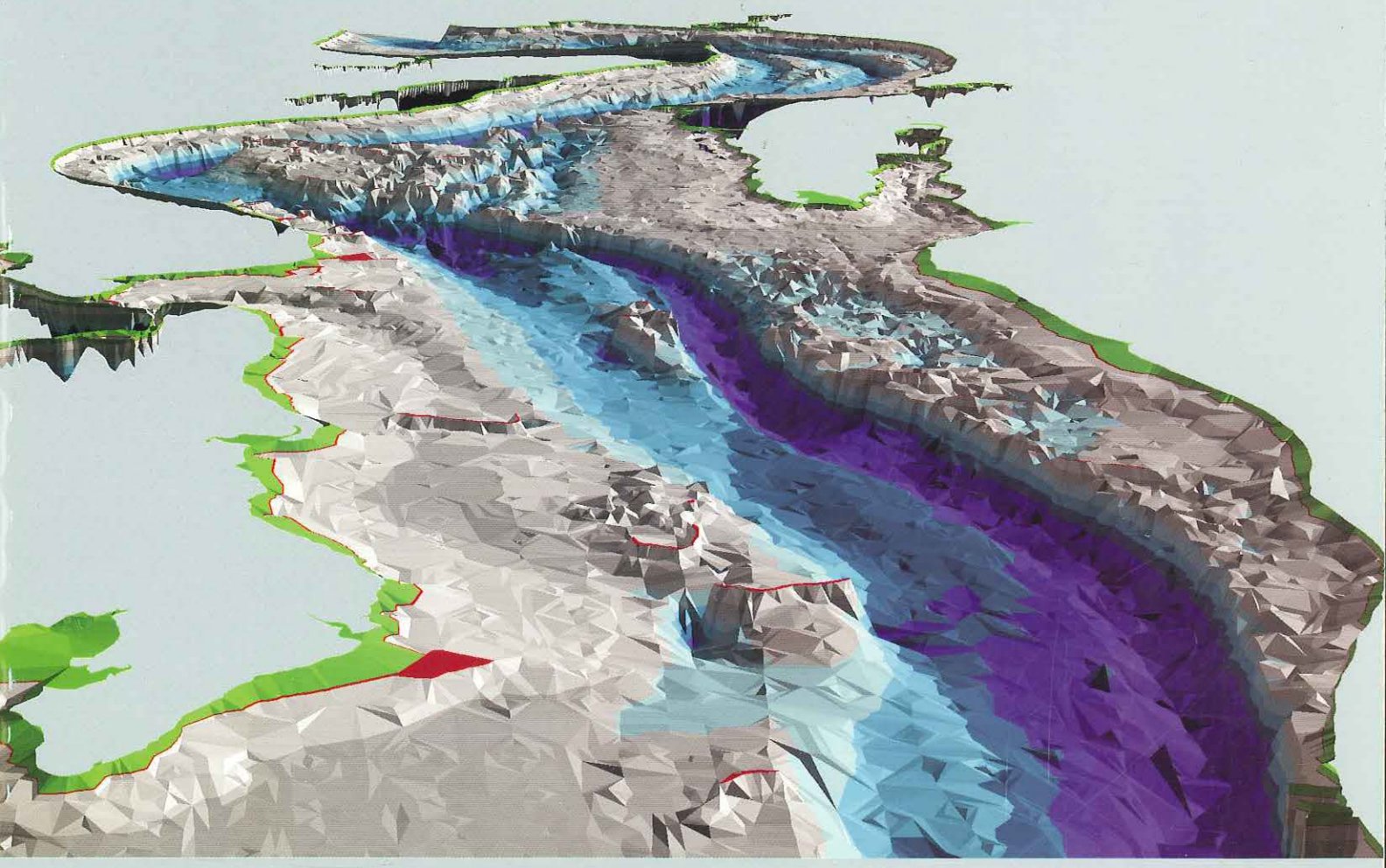

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Chapter 17

Materials Processing by Oysters in Patches: Interactive Roles of Current Speed and Seston Composition

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Abstract

Filtration rates for oysters have typically been measure in still water laboratory experiments and ecosystem-level effects estimated by extrapolation. With the exception of *in situ* measures of oyster filtration by Dame (1999, Chapter 18, this volume and references cited therein) these estimates have failed to account for the effects of hydrodynamic effects on oyster filtration rates and on physical redistribution of particles. In this chapter we report on a series of experiments conducted in a recirculating seawater flume designed to address the effects of flow speed and seston composition on filtration rates in a bed of oysters. In six separate experiments ninety oysters were arranged in the bed of the flume, flow speed adjusted to one of eight levels (0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7 or 22.0 cm s^{-1}), seston added to the flume and particle concentrations upstream and downstream of the oyster bed determined from vertically-arrayed samples. Four experiments investigated the effects of each flow speed on the filtration of a unialgal diet, while two experiments utilized the algal diet in combination with inorganic particles. Control experiments sought to estimate the effects hydrodynamic effects on particle distribution by measuring "filtration" rates over beds of ninety pairs of empty oyster valves. Our findings reveal effects of flow speed and, less evidently, seston composition on particle filtration by oysters. More importantly, our results point to the importance of hydrodynamically-mediated particle redistribution of particles over patches of oysters, and portend sampling difficulties associated with quantifying oyster filtration rates in the field.

Introduction

There is increasing evidence that benthic, filter feeding bivalves may control water quality in shallow water systems. Benthic filter feeding bivalves have been shown to be the primary control of phytoplankton biomass in regions of the Potomac River, the Saint Lawrence River, and the south San Francisco Bay (Cloern, 1982; Cohen et al., 1984; Frechette et al., 1989). Phytoplankton concentrations were reduced 40 to 60% by the filtration activity of a dense bed of Asiatic clams, *Corbicula fluminea,* in the Potomac River (Cohen et al., 1984). Bio-deposition of fine (<3μm) particles by the Eastern Oyster, *Crassostrea virginica*, has been shown to be seven times faster than by gravity alone (Haven and Morales,1966). Estimates of the material processed by a bed of bivalves have been used to extrapolate the potential ecological effects of the filtering activity on estuarine water quality (Dame 1999, Chapter 18, this volume).

The decline of the primary filter feeder in the Chesapeake Bay may have lead to system wide ecological changes. At one time the Eastern Oyster, *Crassostrea virginica*, was the dominant suspension feeder in the Chesapeake Bay ecosystem. Based on historical densities of *C. virginica*, Newell (1988) calculated that, prior to 1870, the oyster population could filter the entire volume of the Chesapeake Bay in 3.3 days, the estimate for the same activity in 1988 was 325 days. In a model of carbon flux in the mesohaline reaches of the Chesapeake Bay, Ulanowicz and Tuttle (1992) estimated that a decrease in the annual exploitation rate of the oyster by 23% would lead to a 150% increase in oyster standing stocks, a 29% increase in benthic diatom primary productivity, and a 12% decrease in planktonic primary productivity. They suggested that the combined effect of the decrease in planktonic primary productivity and the increase in benthic primary productivity may have the potential to reduce eutrophication in the Chesapeake Bay.

Fundamental to assessing the system level effects of bivalve filtration are reliable estimates of filtration rates in the field. Most filtration rate measurements have been based upon solitary bivalves in small scale experiments with minimal water flow, usually just stirring to keep algae in suspension, and minimal turbidity (e.g. Palmer 1980, Gerdes 1983, Riisguard 1988). The efficacy of extrapolating directly from rates measured on a few oysters in the laboratory to filtration rates of an oyster reef in the field has not been generally established. Dame (1999, Chapter 18, this volume and earlier work cited therein) has made *in situ* measures of materials processing by oysters in tidal creeks which indicate that they may have a controlling influence on benthic-pelagic coupling.

Two factors likely to affect oyster filtration capacity are seston composition and flow speed. In laboratory studies low concentrations of suspended sediments (20 mg kaolinite L^{-1}) apparently do no affect filtration rate on algae (Urban and Kirchman, 1992), but high clay and silt concentrations (100 and 700 mg L^{-1}, respectively) have been shown to affect pumping activity of *C. virginica* (Neilson et al., 1976).

Growth of non-siphonate bivalves has been negatively correlated with increasing flow speeds, presumably as a result of an associated decrease in filtration efficiency (Wildish and Kristmanson 1985; Wildish et al. 1987; Eckman et al. 1989; Grizzle1992). Since growth rates were inhibited at flow speeds > 1 cm s^{-1} for *Crassostrea virginica* (Grizzle 1992), it is expected that there is a negative relationship between increasing flow speed and filtration rate (Wildish and Saulnier 1993).

The filtration capacity of a bed of bivalves depends not only on the filtration capabilities of each animal, but also on current velocity, turbulent mixing, and the density and spacing of organisms. Monismith and co-workers (1990) have shown that refiltration can have a negative effect on the filtration capacity of an infaunal bivalve bed. Metabolic wastes and decreased food concentration in the waters overlying downstream portions of the bed may reduce filtration activity and total food availability. Vertical mixing may redistribute particles in the water column, ameliorating near bed depletion (Officer et al. 1982; Frechette et. al. 1989).

However, for dense assemblages of epifaunal suspension feeders "skimming flow" (Nowell and Church 1979) may reduce particle flux through the patch. The hydrodynamic effects of such patches will depend upon organism density, spacing, and flow velocity.

Time variances in filtration activity among each individual oysters in a group may figure prominently in the overall filtration capacity of the group. Riisguard (1988) and Loosanoff (1958) reported that any oyster that was not open or actively filtering was not included in their results. Palmer (1980) reported filtration rates that ranged from 0 to 5.47 L g^{-1} hr^{-1} and that the percent time each oyster spent filtering water ranged from 49 to 91%. However, Newell (1988) estimated that oysters filter for 23 hours each day at the continuous rate of 5 L g^{-1} hr^{-1}. Filtration rates that do not reflect time variances in oyster filtration will not only overestimate the filtration rates of individual oysters, but will lead to an overestimation of the filtration capacity of an oyster bed.

Small-scale filtration experiments do not account for the complex interactions of flow, suspended particulate matter, seston depletion, resuspension, and refiltration on the filtration rates and feeding behavior of *Crassostrea virginica*. Turbulent mixing and seston depletion across the bed are apt to have antithetical effects. Extrapolation of system-level effects may be improved by evaluation of the effects of environmental factors such as flow speed and seston composition on filtration rates. In addition, estimating the proportion of the population feeding at any one time has important ecological consequences.

Here we report on a series of flume experiments designed to incorporate variation in flow speed and seston composition over a bed of oysters into the measurement of oyster filtration. Evaluating oyster filtration capacity under conditions of turbulent mixing and seston depletion allows for the interplay of both hydrodynamic and biotic factors. Our findings revealed some expected relations between flow speed and feeding activity, and considerable variation in the relationship between flow speed and filtration rates. Unexpectedly, our results reveal considerable variation associated with physical redistribution of particles and underscore the difficulties with making meaningful estimates of seston depletion due to oyster filtration in the field.

Materials and Methods

Flume Description

All experiments were conducted in a recirculating seawater flume, located at the Virginia Institute of Marine Science's (VIMS) Eastern Shore Laboratory. The main flume channel, constructed of Plexiglas®, is 5 m long and 0.60 m wide (Fig. 1). For these experiments, a smaller channel, 18.7 cm wide and 220 cm long, with an attached seston sampler was inserted in the flume channel (Fig. 2). Prior to each experiment, the flume was filled with seawater filtered through four filters in series: two sand-charcoal pool filters and two 20 μm pore diameter cartridge filters wrapped with 1 μm cloth filter. Flow across the flume bed was pressure driven from a constant level in the head tank and velocity controlled through a combination of an inflow gate valve and a vertical louvered exit weir. At the head of the flume, two collimators in series reduced the scale of turbulent eddies in the flume. The flume has been calibrated such that freestream velocities can be selected using dial adjustments on the inflow valve and regulating the depth with the exit weir. (See Orth et al., 1994 for a fuller description of the flume.)

Water depth was maintained at a constant 10 cm and freestream velocities ranged from 0.65 – 22.0 cm/s (see below). Throughout the experiments flow Reynolds numbers (Re= ud/ν; where u=freestream velocity, d=water depth, ν=kinematic viscosity) ranged from 528 to 17,886 and thus spanned a range from laminar to fully rough turbulent. Froude numbers (Fr = $u/[gd]^{1/2}$; where g=gravitational acceleration), which relate the relative strengths of gravitational and viscous forces and are typically less than unity in estuarine boundary flows (Nowell and Jumars, 1984), ranged from 7 10^{-3} to 2.2 10^{-1}

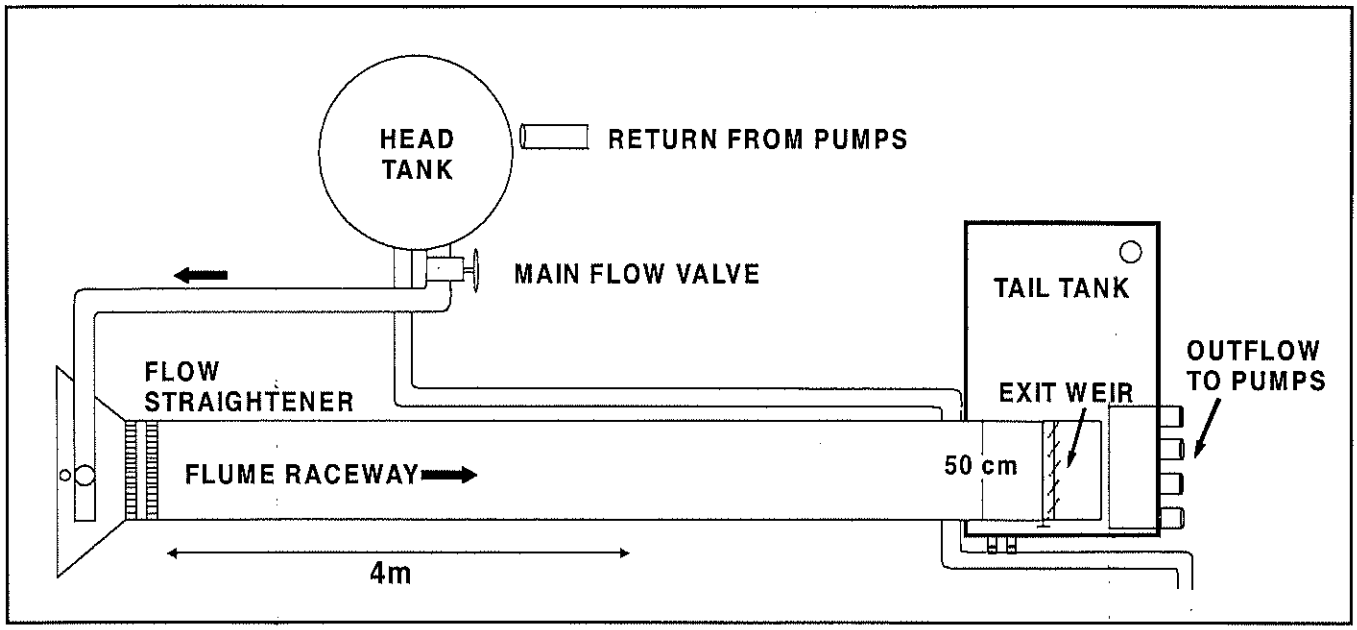

Figure 1. *Recirculating seawater flume located at VIMS' Eastern Shore Laboratory.*

across all experiments. Values computed using Schlichting's Four-fifths Law (Schlichting, 1967) revealed that the boundary layer over the smooth Plexiglas® bed was fully developed within 0.4 m downstream of the collimators at the maximum flow of 22 cm s^{-1}, well before the leading edge of the oyster bed.

Oysters

All oysters used in these experiments were spawned at the VIMS hatchery and maintained in floating rafts at field sites until use. Three cohorts were used in these experiments: oysters used in E1, E2 and E3 were from a cohort spawned in 1991; oysters used in E4 and E5 were from a 1992 cohort; and, E6 oysters were spawned in 1993. Prior to use in the flume experiments all fouling organisms were removed from shell exteriors. At the termination of each experiment all oysters were measured for shell height and ash-free dry weight and condition index was determined as ash-free dry weight of soft tissue (in mg)/shell height (in mm).

Experimental design

Flume experiments were designed to measure the filtration rates of the algae *Thalassiosira weisflogii* by a bed of oysters under different flow speeds and to measure the effect of an inorganic component on the filtration rates. Prior to the initiation of the experiments, the oysters were brought in from the field and maintained on flow-through seawater tables. Each oyster was numbered to allow for monitoring of individual feeding behavior throughout the experiments.

Ninety oysters were placed within the constrained flume channel in 30 staggered rows of three oysters each with their beaks facing into the flow and allowed to acclimate for a minimum of 24 hrs. Freestream velocity in the flume was adjusted to one of eight treatment levels: 0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, and 22.0 cm s^{-1}. Monocultures of the unicellular diatom *Thalassiosira weisflogii* alone and in combination with kaolinite were added to the flume by a gravity-fed system in quantities sufficient to establish a nominal concentration in flume of $1 \cdot 10^5$ particles ml^{-1}, with kaolinite (when used) accounting for 10% of the total particles added to the flume. At each flow speed within an experiment, particle concentrations were measured upstream and downstream of the bed of oysters and the change in the concentration of these particles across the bed was computed as described below.

Four replicate experiments (designated E1, E2, E3, and E4) estimated filtration rates at each of the eight flow speeds on *T. weisflogii* alone and two replicate experiments (E5 and E6) included kaolinite in the seston. Each replicate experiment made use of a separate batch of oysters drawn from the stocks held in the field. Additionally, for each seston type, control (dead oyster) experiments were conducted to measure the change in particle concentrations due to hydrodynamically-mediated deposition and resuspension of particles. In these controls, oysters shells were filled with lead shot, glued shut, and substituted for live oysters. Three replicate control experiments were conducted using *T. weisflogii* alone (C1, C2 and C3) and one (C4) using algae + kaolinite.

Each experimental replicate began with a different flow speed to separate the effect of the sequence of flow speed from the effect of flow speed on the filtration rates. The flume was adjusted to the desired flow and allowed to stabilize for several minutes before the addition of algae (and kaolinte) to the head box. The first sampling period was begun after the oysters had been exposed to the algae for 10 min and samples were collected continuously for 20 min thereafter. Five min after termination of the first sampling period, a second sampling was begun. At the end of the second sampling period the additions of algae and kaolinite were terminated and chlorophyll *a* and particle concentration determined as described below.

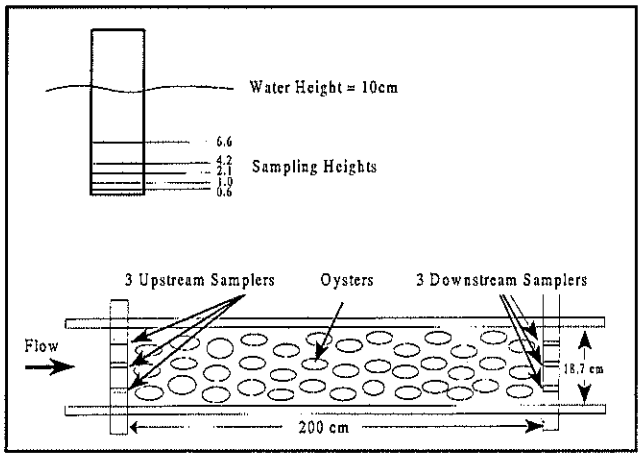

Figure 2. Sampler Diagram.

During each sampling period and for a one hr period after the cessation of algae additions, the type of feeding behavior exhibited by each individual oyster was monitored and scored as (1) not feeding, (2) open (and presumably feeding) or (3) open and producing feces (certainly feeding).

Determinations of Chlorophyll and Particle concentrations

Water samples for seston characterization in the flume were collected upstream and downstream of test oyster beds using a seston sampling apparatus with ports arrayed laterally across the channel and vertically through the water column (Fig. 2). Three vertically arrayed samplers, constructed of thin Plexiglas® with beveled edges, were evenly spaced across the channel and the upstream and downstream edges of the test section. Each sampler had 5 vertically arrayed ports located at 0.6 cm, 1.0 cm, 2.1 cm, 4.2 cm and 6.6 cm above the flume bed (see Fig. 2). A logarithmic scale was chosen for the placement of the sampling ports to reflect the theoretical particle distribution above the bed in shearing flow. Water samples collected at each port were gravity fed through Tygon® tubing (i.d. = 300 μm) into individual sampling vials, the heights of which were adjusted such that flow speed through the tubing approximated flow speeds in the flume channel, thereby minimizing bias in particle sampling. The entire apparatus, including seston samplers and the 18.7 cm wide channel, comprised the test section in these experiments and was positioned were approximately 2 meters downstream of the collimators.

The three samples collected at a given height were pooled, yielding a total of 5 vertically-arrayed upstream and 5 downstream samples for each collection period. Five ml of each sample was removed, filtered through a 0.45 μm-filter and chlorophyll *a* determined with *in vivo* fluorescence as described by Strickland and Parsons (1968). The remainder of the sample was used to determine particle concentrations of

Thalassiosira weisflogii and kaolinite with a Coulter counter following procedures outlined in Strickland and Parsons (1968). The counter was configured to count particles in the size range of 2 to 40 μm; *T. weisflogii* cells are approximately 16 μm in diameter, while 77.3% of the Kaolinte particles were < 2 μm. Thus, by analyzing at two different threshold settings we were able to distinguish the particle types. Further calibrations were established using direct counts under light microscopy with a hemocytometer. Filtration rates were computed using estimates of algal cell concentrations determined in this manner.

Computation of filtration rates

Coughlan's (1969) equation for filtration rates in still water was adapted and used to calculate filtration rates of the oyster bed in flowing water as follows:

Eq. 1A

$$m = \frac{V\dfrac{\ln C_1}{\ln C_2}}{nt} - a$$

V - total volume of suspension
C_1 - concentration upstream
C_2 - concentration downstream
n - biomass of oysters
t - time
a - control particle change rate determined in a control experiment with no live organisms

Eq. 1B

$$a = \frac{V\dfrac{\ln C_1'}{\ln C_2'}}{n't}$$

V - total volume of suspension
C'_1 - concentration upstream in control experiment
C'_2 - concentration downstream in control experiment
t - time
n - number of oyster shells x mean biomass of live osyters

Each term in the above equation was adapted to calculate filtration rates for these flume experiments. Time (t) represents the residence time of a water parcel over the oyster bed and was computed as the length of the test section, 200 cm, divided by the freestream velocity. The volume of suspension was calculated from the dimensions of the constricted area of the flume in which particle change was being measured. The term *a* in still water experiments represents the settling rate of seston in the absence of grazers. In the flume experiments conducted here this term accounts for the redistribution of particles due to the physical presence of oyster shells. These rates were derived from the control experiments using dead oyster shell. For comparative purposes both *n* and *n'* in Eq. 1a and 1b, respectively, were converted to biomass using the ash-free dry weights measured for the live oysters.

Three filtration rates were calculated using the follow numbers of oysters: (1) m_a, all 90 oysters in the flume (2) m_o, the number of oysters that were open [a liberal estimate of the number of oysters feeding] and (3) m_f, the number of oysters that produced feces [a conservative estimate of the number of oysters feeding].

Finally, to better clarify seston dynamics within and above the bed of oysters, for analytical purposes we partitioned the water column into two regions and calculated filtration rates for each. The samples from the lowest two samplers (0.6 and 1.0 cm) measured the change in particle concentration for the area essentially within the oyster bed, while the upper region samples (2.1, 4.2, and 6.6 cm above the bed) measured the change in particle concentration in the region at the top of and above the bed.

RESULTS

Particle Concentrations

Measured particle concentrations in the flume ranged from 3.056×10^3 to 8.150×10^4 particles ml^{-1} over all experiments and samples.

Table 1. Morphometrics of oysters and oyster shells used in each experiment and control. Values are means (and standard deviations). Tissue weight is expressed as ash-free dry weight. Condition index is as defined in the text.

Experiment	Shell Height (mm)	Shell Width (mm)	Tissue Weight (g)	Condition Index
E1	65.2 (5.8)	20.6 (2.3)	-	-
E2	66.1 (5.7)	21.4 (2.5)	0.271 (0.101)	4.15 (1.00)
E3	65.3 (6.2)	21.0 (2.2)	-	-
E4	64.6 (6.4)	17.9 (2.0)	0.471 (0.192)	7.22 (2.70)
C1, C2, C3	67.7 (7.3)	21.7 (2.8)	-	-
E5	63.9 (6.4)	18.9 (2.4)	0.625 (0.256)	9.73 (3.70)
E6	70.9 (3.9)	19.7 (1.4)	1.055 (0.197)	14.90 (2.80)
C4	66.8 (7.3)	21.2 (2.6)	-	-

Regression analysis of chlorophyll *a* concentrations vs estimates of algal particle concentration varied between the experiments with algae alone (Particle concentration = -0.348+ 0.002 Chl *a*; R^2=0.85; n=417) and algae + Kaolinte (Particle concentration = 8.68 + 0.002 Chl *a*; R^2=0.69; n=192) in the intercept, but not the slope of the relationship. This indicates that our approach in distinguishing between algal and inorganic particles, while a bit conservative (i.e., it discounted a fixed amount of algae), did not bias our determinations of relative concentrations.

Oysters

The mean shell height of oysters used in the various replicate experiments ranged from 63.9 mm to 70.9 mm, with the group used in E6 significantly larger than those used in the other experiments (Table 1). Ash-free dry weight samples for E1 and E3 where lost during processing, so the mean weight for E2 oysters (which did not differ in shell height) was used in the calculation of filtration rate. The condition index of the oysters used in E6 exceeded that of all other groups of oysters.

Feeding Behavior

Oyster feeding activity, as measured by the percentage of oysters open and the percentage producing feces, was highly variable (Fig. 3). Feeding activity varied markedly between

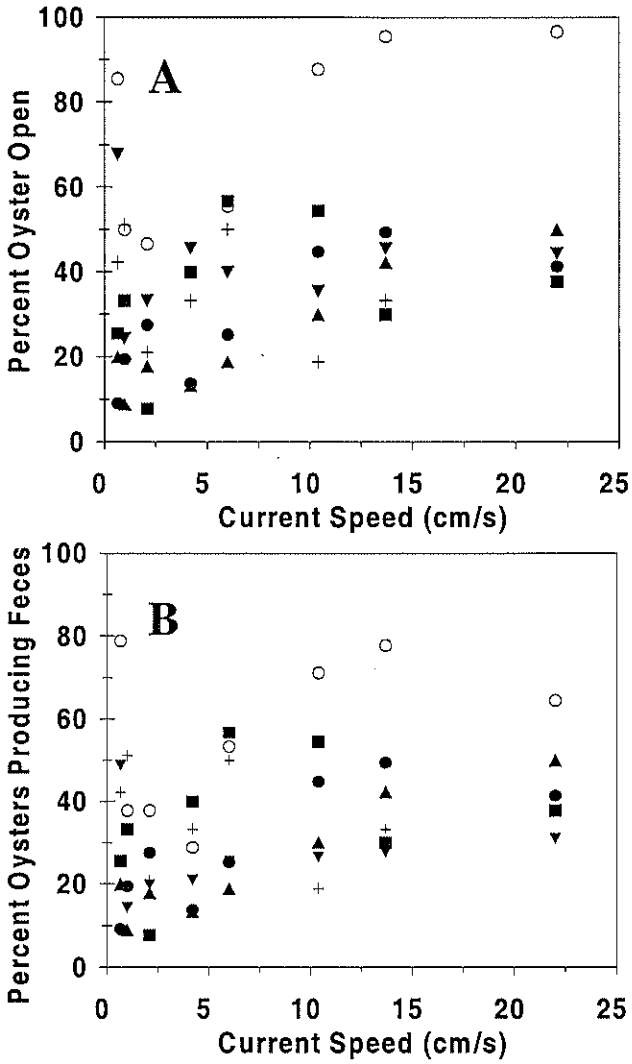

Figure 3. Oyster feeding behavior vs current speed. (A) Percentage of oysters open at each current speed by experiment. (B) Percentage of oysters producing feces at each flow by experiment. (■ = *E1*, ● = *E2*, ▲= *E3*, + = E4, ▼ = E5, ○ = E6.)

Table 2. One-way ANOVA's of the effects of the daily sequence of flow speeds and the sequence throughout the entire experiment on oyster feeding behavior (measured as the numbers of oysters open and the numbers producing feces.

	SS	d.f.	F	P
Effect of Daily Flow Sequence on				
1. Number of oysters open	201 .14	2	0.4753	0.628
2. Number of oysters producing feces	331.33	2	1.1773	0.328
Effect of Experimental Flow Sequence on				
1. Number of oysters open	997.96	7	0.6344	0.727
2. Number of oysters producing feces	893.91	7	0.7467	0.636

groups of oysters used in the various experiments, with a greater number of oysters in E6 feeding (Fig. 3). Two-way fixed factor ANOVA's without replication, using flow speed and experiment as factors, revealed significant effects of experiment on the percentage of oysters open ($F = 9.9690$, d.f. = 5, $p < 0.0001$) and the percentage of oysters producing feces ($F = 6.0490$, d.f. = 5, $p = 0.0004$). However, when E6 was removed from the analysis neither the percentage of oysters open ($F = 1.930$, d.f. = 4, $p = 0.1331$) nor the percentage producing feces ($F = 1.2134$, d.f. = 4, $p = 0.3273$) varied with experiment. Feeding behavior was not affected by the sequence in which flows were offered over the course of the day or throughout the experiment (Table 2).

Physical Redistribution of Particles

Estimates of changes in particle concentration between the upstream and downstream edges of the "dead" oyster bed reflect physical redistribution of particles throughout the water column. "Filtration" rates in the region within the bed for the control experiments (i.e., term *a* in Equations 1A & B, which equates with physically-mediated particle redistribution) were approximately zero (Fig. 4a) and did not vary linearly with flow speed ($r^2 = 0.11$, $n = 24$, $p = 0.11$). In the region above the bed *a* varied considerably, but not consistently, across experiments (Fig. 4b) and again there was not a statistically significant linear relation with flow speed ($r^2=0.01$, $n=24$, $p=0.68$). Since the relationship between the control rates and flow speed was neither significant nor evident, a value of zero was chosen to be used for the control rate in the calculation of the live oyster filtration rates.

Filtration Rates

Filtration rate estimates obviously varied depending upon the numbers of oysters used in the calculations, with the lowest estimates derived from using all 90 oysters in the bed and the highest values using only those oyster producing feces (Table 3). Because our primary focus here is on the filtration capacity of a bed

Table 3. Mean (and standard deviations) of filtration rates for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4) and *T. weisflogii* in combination with Kaolinite (E5 & E6). Filtration rates are computed using all oysters (m_a), only oysters open during the experiment (m_o) and only oysters producing feces (m_f).

	Filtration Rate (L g^{-1} hr^{-1})	
	Within the bed	Above the bed
Algae alone	m_a: 0.73 (1.46)	m_o: 1.88 (3.28)
	m_f: 2.37 (4.08)	m_a - 4.10 (9.87)
	m_o: -8.60 (22.27)	m_f:-11.88 (29.15)
Algae + Kaolinite	m_a: 0.50 (0.87)	m_o: 0.89 (1.92)
	m_f: 1.35 (3.06)	m_a: 2.95 (2.30)
	m_o: 5.57 (4.92)	m_f: 8.329 (8.01)

of oysters, subsequent results are reported for m_a (all 90 oysters), but we will discuss the implications of these different rates below. The negative values in the region above the oyster bed in the experiments using algae only (Table 3) indicate an increase in suspended particles at the downstream end of the bed. Summary plots of mean filtration rates (m_a only) vs current speed reveal differing patterns within and above the bed and between diet types (Fig. 5).

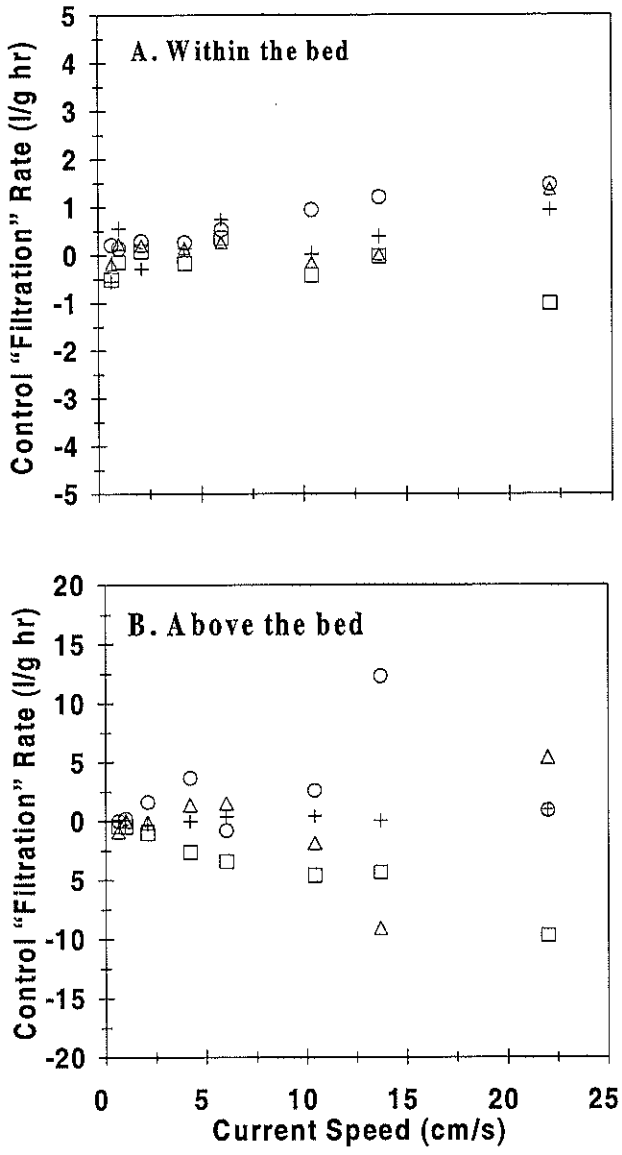

Figure 4. "Filtration" rates vs flow speed for control experiments using dead oysters in the (A) lower region within the oyster bed and (B) upper region above the oyster bed. Control rates are reported as l filtered per g ash-free dry weight of oyster per hr; positive values indicate the removal of particles across the bed of oysters and negative values indicate particle generation. The symbols ❑, ○, △, and + indicate experiments C1, C2, C3 and C4, respectively.

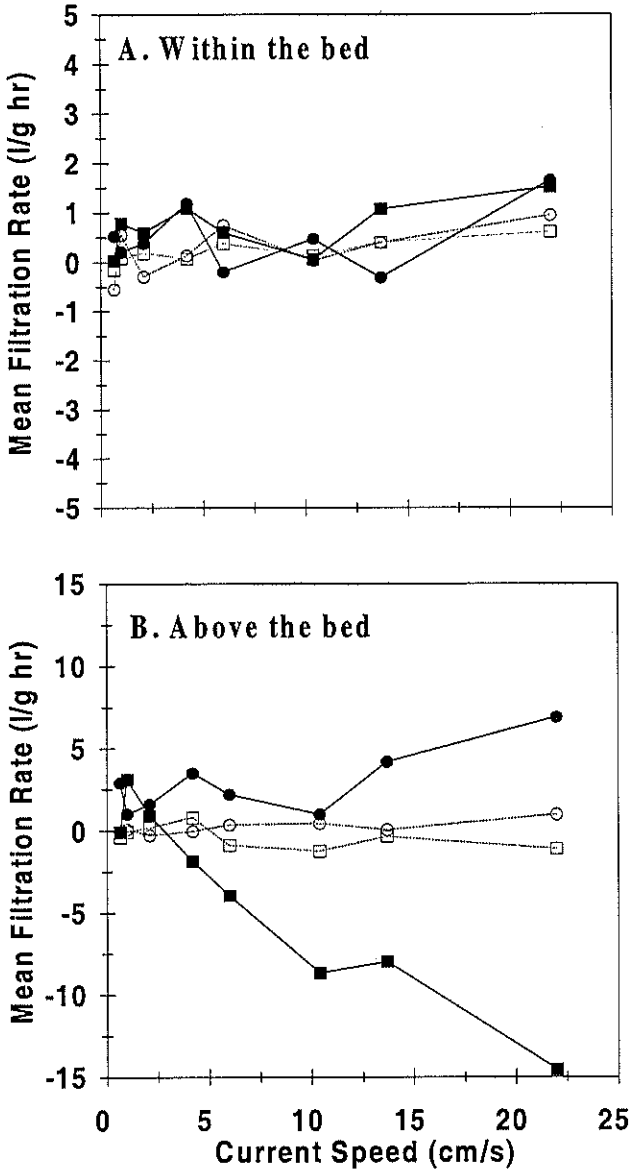

Figure 5. Mean filtration rate vs current speed (A) within the bed and (B) above the bed of oysters. ❑ = dead oyster control, algae only diet; ○ = dead oyster controls, algae + Kaolinite diet; ■ = live oysters, algae only diet; ● = live oysters, algae + Kaolinite diet.

Table 4. ANOVA's of the effect of flow speed on filtration rates (m_a) within the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Experiment	Source	DF	SS	F	P
E1	Flow speed	7	16.38	5.01	0.019
E2	Flow speed	7	12.43	0.42	0.862
E3	Flow speed	7	6.57	2.26	0.138
E4	Flow speed	7	47.04	1.91	0.192

The relationship between filtration rates within the bed and current speed varied between the four experiments (Fig. 6a). Two-way ANOVA indicated that there was asignificant difference in the filtration rate among experiments (d.f.=3, F=8.1, P=0.001), but no significant effect of flow speed (d.f. = 7 F=0.1, P=0.566). Thus, the effect of flow speed on filtration rates within the oyster bed were analyzed separately for each experiment. In E2, E3, and E4, flow speed did not have a significant effect on the filtration rates (Table 4). Only in E1 were there significant differences in the filtration rates for the eight flow speeds (Table 4). While there was a trend towards more negative rates with greater flow speed in E1, Tukey's a posteriori multiple comparison test revealed that this relationship was not monotonic (Table 5).

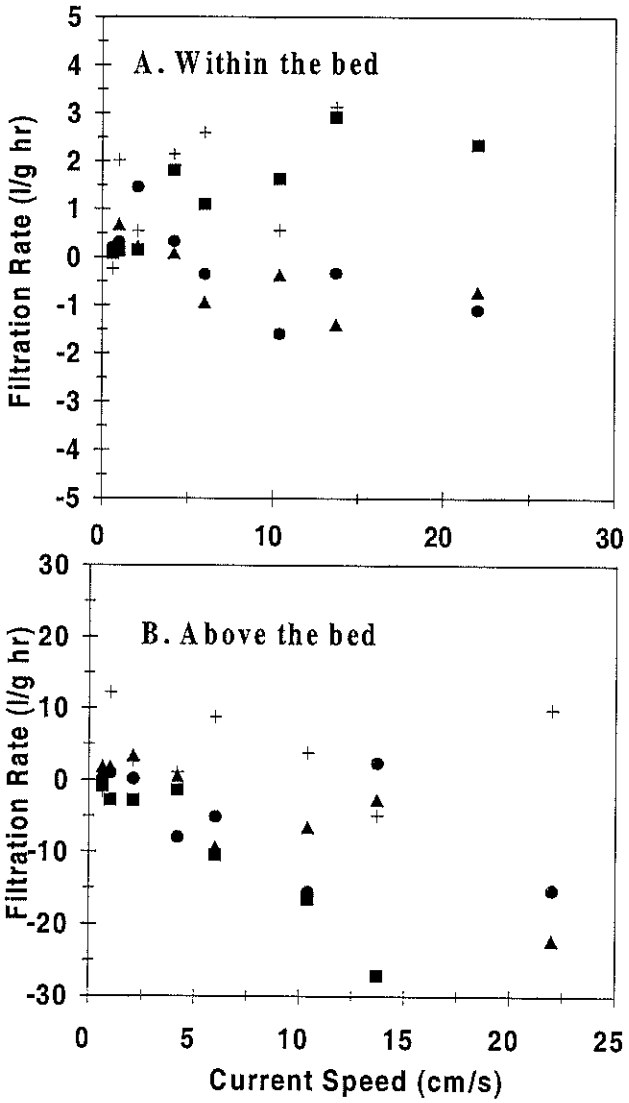

Figure 6. *Filtration rates vs current speed in experiments using algae only diets (A) within the oyster bed and (B) above the oyster bed. (■ = E1, ● = E2, ▲= E3 & + =E4).*

Table 5. Tukey's a posteriori multiple comparison test of filtration rates (m_a) within the oyster bed in experiment E1. (Flow speeds for which filtration rates were not significantly different are grouped in a single column and denoted by *.)

Flow speed (cm/s)	Homogeneous groups	
0.65	*	
1.0	*	
2.1	*	*
4.2	*	*
6.0	*	
10.4	*	*
13.7		*
22.0	*	*

Filtration rates in the region above the oyster bed varied between experiment, flow speed and

Table 6. Two-ANOVA of the effects of experiment and flow speed on filtration rates (m_a) above the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Source	DF	SS	F	P
Experiment (A)	3	1953	32.6	<0.0005
Flow speed (B)	7	1953	14.0	<0.0005
A*B	21	2322	5.5	<0.0005
Error	32	639		
Total	63	6868		

the interaction of the two (Fig. 6b and Table 6), so the data set was partitioned by experiment and the effects of flow speed on filtration in this region analyzed using one-way ANOVA's (Table 7). Flow speed was thus revealed to have an impact on filtration rate estimates in three of the four experiments which used algae only diets. A posteriori multiple comparisons within these three experiments revealed that oysters within an experiment generally had similar filtration rates at flow speeds < 6 cm s^{-1} and similar, but more negative, rates > 6cm s^{-1} (Table 8). Though there were exceptions, measured filtration rates at flows < 6 cm s^{-1} were approximately zero, while rates at flows > 6 cm s^{-1} were negative, indicating particle redistribution into the region above the bed.

Discussion

The filtration capacity of an oyster bed is not solely a function of the cumulative filtration rate of the oysters, but is a composite of biological and physical processes. Particle distribution and concentration within the water column are functions of the vertical mixing, horizontal advection, resuspension, settling, and filtration by the oysters. Dame et al. (1984) suggested that removal of particulate carbon by an oyster reef was greater than expected by biofiltration alone and suggested that physical factors may have been important.

Table 7. ANOVA's of the effect of flow speed on filtration rates (m_a) above the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Experiment	Source	DF	SS	F	P
E1	Flow speed	7	2020	14.17	0.001
E2	Flow speed	7	743	12.86	0.001
E3	Flow speed	7	1022	5.02	0.019
E4	Flow speed	7	490	3.15	0.065

In these experiments, particle reductions were not of the magnitude expected from totaling filtration rates reported for individual oysters in static flow conditions. Using Newell's (1988) estimate for oyster the filtration rate of 5 L hr^{-1} gm^{-1}, the expected filtration capacity of the entire bed of oysters used in these studies would have been 75 ml sec^{-1} and should have reduced particle concentrations from 63% to 2% for the lowest to highest flow speed. Factors which may have contributed to the measured rates being lower than expected were 1) the effect of water flow on changes in particle concentration across the oyster bed, 2) the reduced number of oysters feeding at any one time, and 3) time variance in the filtering activity of each individual oyster.

The significance of flow-mediated effects is evident from the particle concentration profiles upstream and downstream, both within and between experiments in this study. The control

Table 8. Tukey's a posteriori multiple comparison test of filtration rates (m_a) above the oyster bed in experiments E1, E2 & E3. (Flow speeds for which filtration rates were not significantly different are grouped in a single column and denoted by *.)

	E1					E2	E3
Flow speed (cm/s)	Homogeneous groups			Homogeneous groups		Homogeneous groups	
0.65	*			*		*	
1.0	*			*		*	
2.1	*			*		*	
4.2	*			*	*	*	
6.0	*	*		*	*	*	*
10.4		*	*	*	*	*	
22.0			*		*		*

experiments, using oyster shells, provide an estimate of the effect of flow speed on the change in particle concentration across the oyster bed in the absence of filtration. In the water column upstream of the oyster bed a logarithmic particle profile describe by the Rouse equation is expected. Upon encountering the bed, particles in the lower region are uplifted by turbulent eddies, increasing particle concentrations above the bed. We had anticipated that a relation between flow speed and particle redistribution in the control experiments would have been evident. However, the observed pattern varied sufficiently between control experiments (Fig. 4) such that the "average" pattern did not reveal a significant effect of flow speed. We are not certain of the cause of this variation, but suspect that subtle differences in the placement of the 90 oysters within the bed (recall that each control experiment involved the placement of 90 different oyster shell pairs) resulted in differing turbulence patterns. It seems unlikely that our two 20-min sample collection periods were inadequate to average over normal variations in particle concentrations associated with turbulent fluctuations.

Between experiment variance in filtration rates increased with increasing flow speeds and was greatest in the upper region filtration rates. This increase reflected the increased turbulence generation associated with increasing flow speed. The negative filtration rates were not a result of a generation of particles downstream, but were due to turbulent redistribution of particles. The relocation of particles and the non-uniform effects of turbulence on particle concentration contributed to the differences in filtration rates between experiments.

Oyster bed configuration appears to have affected particle dynamics as indicated by the significant differences in the control rates of C1, C2, and C3. Although the oysters were all placed in 30 staggered rows for each experiment, the bed morphology was subtly different between experiments. In experiments with live oysters variation in the bottom topography between each batch was further enhanced by the

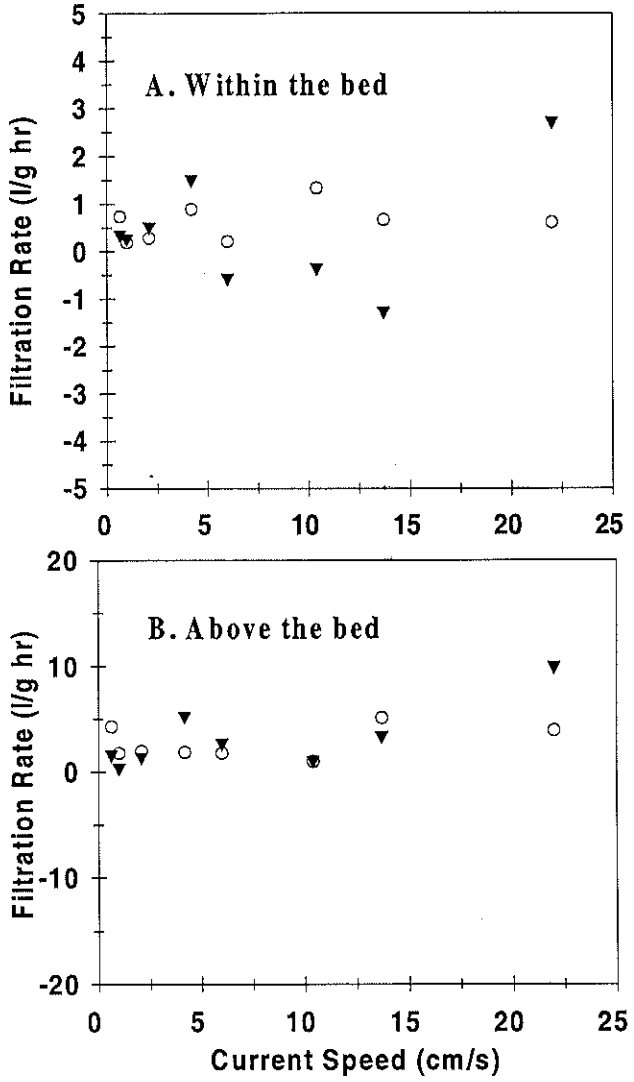

Figure 7. Filtration rates vs current speed in experiments using algae + Kaolinte diets (A) within the oyster bed and (B) above the oyster bed. (▼ =E5, ○ =E6).

number of oysters open and their location within the bed.

The non-uniform particle redistribution due to turbulent mixing may have obscured some of the biological impact on particle concentration. Filtration rates reported here within the oyster beds at low flow speeds are within the range of previously reported rates (Haven and Morales-Alamo, 1970; Powell et al., 1992; Luckenbach et al., 1993; Sellner et al., 1995). These rates are also approximately the same as the "lower curve" rates which Powell et al. (1992) believed best represent the filtration rates in the field. Although there were not significant differences between the filtration rates and the control rates,

abundant fecal production by the oysters indicated that large amounts of particles were being removed from the water column by the filtration activity of the oysters. It appears that the biotic factors were not of sufficient strength to produce filtration rates that would be significantly different from control rates in these experiments.

Using feces production and shell gape as indicators of feeding activity, we observed a positive relationship between oyster feeding activity and flow speed, and flow speeds up to 22 cm sec^{-1} did not inhibit oyster feeding activity in these experiments. This is counter to the findings of Grizzle et al. (1992) who found a negative relationship between growth rates of *C. virginica* and flow speeds greater than 1 cm s^{-1}, suggesting inhibition of feeding activity at higher flow speeds. This apparent difference may be due to differences in experimental design between the two studies. Oysters in the experiment by Grizzle et al. (1992) were placed with the hinge facing into the direction of flow, whereas in this study, oysters were placed with the beak facing into the direction of the flow. The orientation of the *Argopecten irradians concentricus* has been shown to affect the pressure exerted by the external water on the inhalant region (Eckman et al., 1989) and the same may be true for *C. virginica.* At sufficient flow speeds, external water pressure may exceed the inhalant-exhalant pressure differential and have a negative effect on the filtration rates. External flow pressure on the inhalant region of an oyster within the bed will be affected by the mean flow field and by local flow variations. In the context of these flume experiments, we lack sufficient details of the flow environment to estimate these impact on filtration rates.

We expected to observe the greatest depletion in the near-bed environment within the oyster bed at low flow speeds, both because of low advective flux and minimal turbulent mixing of particles from upper layers. That this was not clearly the case suggests either that turbulent mixing rates where sufficient at all flows to resupply oysters with particles or (more likely) that physical mixing processes generally obscured the effects of oyster filtration. Further, if biological processes predominated, we would expect that in the region above the oyster bed, at least up to a point, filtration rate would have increased with flow speed, because turbulent mixing would bring more particles in contact with the oysters. In fact, the reverse pattern was generally observed, at least for the algae alone diet, indicating that physical redistribution of particles was primarily responsible for the observed pattern. Turbulence generation due to the bottom roughness of the oysters tended to redistribute particles upward above the bed.

Food quality has been observed to have variable effects on bivalve feeding rates. Urban and Kirchman (1992) speculated that suspended inorganic matter may actually increase ingestion of certain organic particles by decreasing particle rejection. At high concentrations of inorganic particles ingestion may be reduced as pseudofecal production increases, but the effects on measured filtration rates are unclear. In the current study, there was no evident effect of inorganic particles on the filtration rates measured within the oyster bed. The pattern observed above the bed differs somewhat from that in the algae alone diets in that filtration rates were uniformly positive. This may be the result of reduced resuspension of the heavier inorganic particles or merely a reduced sample size relative to the algae alone diets (two vs four experiments).

These experiments were designed to provide greater dynamic similarity to natural oyster habitats than previous experiments on oyster filtration rates. They nevertheless represent a gross over simplification of the hydrodynamic regime associated with an oyster reef. Moreover, the biotic component of these experiments--a single size-class of oysters in a uniform spatial arrangement--represents a considerable simplification of a natural reef. Yet, it is still apparent that the interaction of a bed of oysters with the surrounding water column is the result of a complex of hydrodynamic and biotic factors. As interest grows in restoring oyster reefs for

the ecosystem services which they provide, including particle filtration, our findings should serve both as a warning about the difficulties of measuring particle depletion in the field and the importance of improving *in situ* filtration estimates. Reconciling these difficulties will be necessary for improving estimates of filtration rates by individual oyster reefs and estimating system-level ecological of oyster restoration.

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