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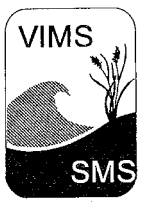

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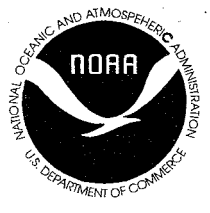

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ABSTRACT

Filtration by suspension-feeding bivalves affects water quality and the postulated impacts include increased light penetration and enhanced benthic primary production. Such system-level predictions are extrapolated from still water experiments which neglect the effects of flow, seston composition, turbulent mixing and refiltration by oysters within groups. Flume experiments were used to investigate the effects of varying flow speed and seston composition on filtration capacity of oysters. Six groups of 90 oysters were used in treatments which varied concentrations of the algae *Thalassiosira weisflogii* separately and in combination with inorganics; four sets of shell only controls were used to evaluate hydrodynamic effects. The results indicate the importance of morphological differences in bed structure on turbulence and particle redistribution which may obscure biological effects and of the importance of the physiological condition of oysters on filtration capacity. Field transplants of eelgrass, *Zostera marina*, and American oysters, *Crassostrea virginica*, were used to evaluate interactions between oyster filtration, water quality and plant survival in the field. Abnormally poor water quality forced the early termination of these experiments, but in conjunction with the flume results they indicate a strong effect of physical forces on seston distribution against which impacts of suspension feeders must judged.

keywords: oysters, suspension-feeding, hydrodynamics, water clarity, submerged aquatic vegetation, Catlett Islands, flume experiments

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). Since water quality in terms of water clarity is a function of the amount of suspended material, organic and inorganic, both must be reduced to increase water clarity. Estimates of fine (< 3μm) particle deposited up to seven times faster by biodeposition by the Eastern Oyster, *Crassostrea virginica*, than by gravity alone have been made by Haven and Morales (1966). They estimated that 250,000 oysters, 5-8 cm in size, could deposit 405 kg dry weight of biodeposits per week. Filter-feeding activity can limit the concentration of suspended particulate material and provides a critical link for carbon and energy transfer from the water column to the benthos. 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.

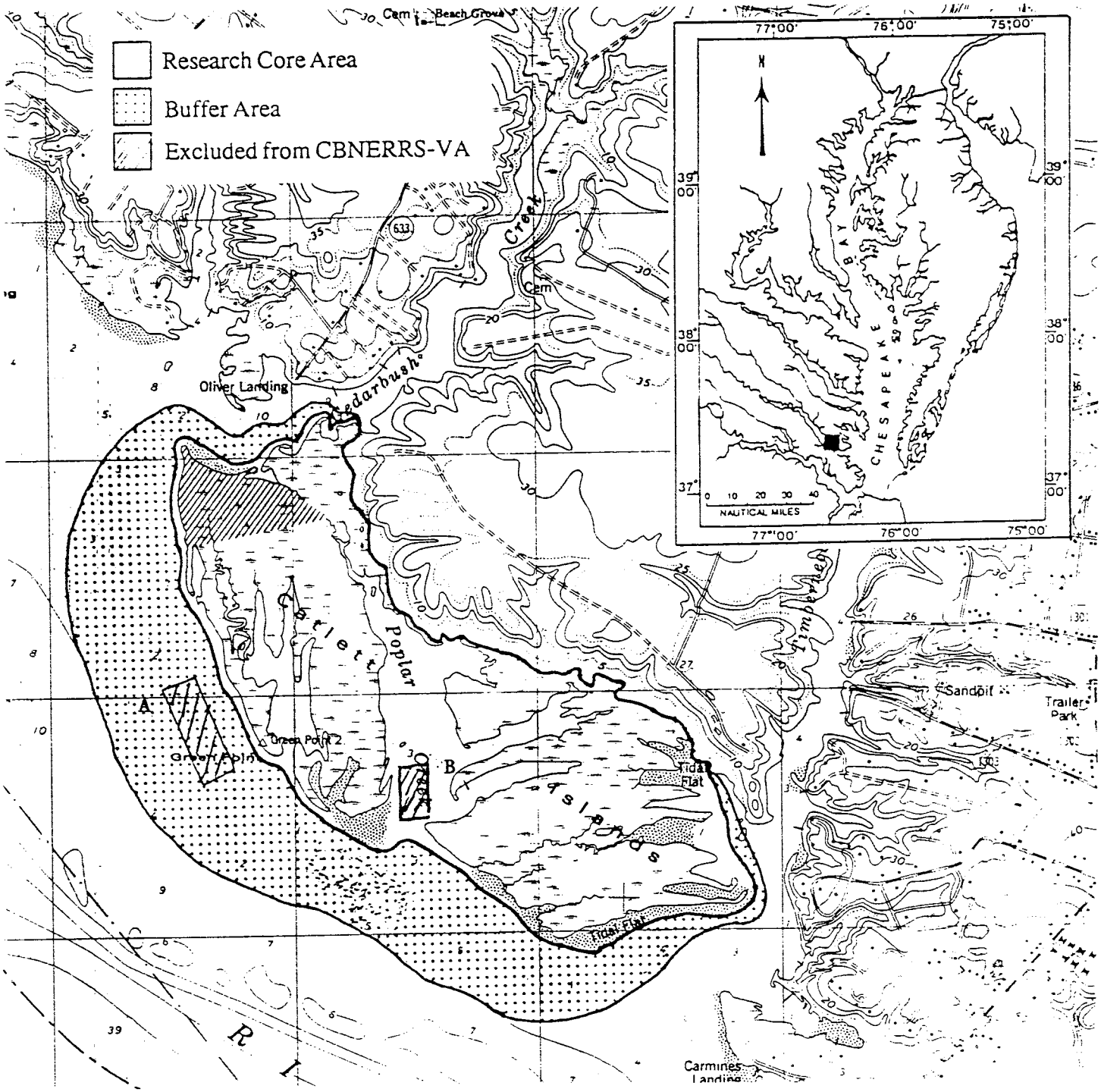
At one time the Eastern Oyster, *Crassostrea virginica*, was considered the dominant suspension feeder in the Chesapeake Bay ecosystem. Since the late 1880's, there has been a general decline in the standing stocks of oysters in the Chesapeake Bay. Based on historical densities of *C. virginica*, Newell (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.

The decline of the primary filter feeder in the Chesapeake Bay may have lead to system-wide ecological changes. Decreased oyster standing stocks may have diminished the capacity of the ecosystem for filtering suspended particulate material resulting in decreased light penetration and increased eutrophication (Ulanowicz and Tuttle, 1992). Declines in submerged aquatic vegetation in the Chesapeake Bay during the 1960's and 1970's have been associated with increased turbidity and nutrients (Orth and Moore, 1983). Distribution of submerged aquatic vegetation is primarily dependent on light penetration which decreases with increasing turbidity (Wetzel and Penhale, 1983).

While transplant efforts with eelgrass, *Zostera marina*, have been successful in many areas in re-establishing seagrass beds (Moore 1991), in some locations where turbidity is too great light remains a limiting factor. One such location is the NERRS Catlett Islands site in the York River, Chesapeake Bay, VA (Fig. 1). Previous efforts to transplant *Z. marina* into the shallow subtidal region of the site have met with only limited success. Establishment of transplant plots in the fall have been successful and plants overwinter well, but high turbidity during May and June result in mortality of the plants. This is

Figure 1. National Estuarine Research Reserve Catlett Islands site in the York River, VA. Locations of the 1992-1993 (A) and 1993-1994 (B) experiments are shown as hatched boxes. Insert shows Chesapeake Bay with Catlett Islands site indicated by black box.



(USGS 7.5 minute series, topographic)

characteristic of a number of environments within Chesapeake Bay which would otherwise be suitable for SAV.

Thus, the expectation arises that the restoration of significant oyster densities to some tributaries of the Chesapeake Bay may reduce turbidity and enhance efforts to restore SAV. We initiated this research program from the point of view that the growing practice of off-bottom oyster aquaculture in Cheaspeake Bay might be expected to affect local water quality and SAV survival. Subsequently, improvements to water quality have been proffered as partial justification for oyster restoration efforts (e.g., numerous papers presented at a symposium on Oyster Reef Habitat Restoration, Williamsburg, VA, April 22-26, 1995). Previous estimates of oyster filtration rates have been made in the laboratory under still water conditions and it was apparent to us that if extrapolations to system level effects were going to be used in resource management decision, refined estimates were needed.

Fundamental to assessing the system level effects of bivalve filtration are reliable estimates of filtration rates in the field. Filtration rates, expressed as the volume of water cleared of all particles per unit time, have been measured for oysters and many other bivalves in the laboratory under conditions of varying water temperatures, algal concentrations, algal species, tidal cycle, and turbidity (Winter, 1978). Filtration rates for *Crassostrea virginica* are summarized on Table 1, expressed in the units reported by the authors. Most filtration rate measurements have been on 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, Riisgard, 1988). Laboratory-

generated oyster filtration rates of oysters may not accurately reflect filtration rates in the field where external factors affect oyster filtration rates and the filtration capacity of the bed. Thus, extrapolating directly from laboratory rates to filtration rates in the field is somewhat suspect.

Turbidity, particle size, particle composition, and flow speed affect the filtration rates of non-siphonate bivalves. Oysters are able to tolerate turbid environments, but increasing concentrations of inorganics may lead to incremental decreases in filtration rates. Clay and silt concentration above 100 mg l^{-1} and 700 mg l^{-1}, respectively, inhibited the pumping activity of *C. virginica* (Neilson et al., 1976). Alternatively, kaolinite concentrations of 20 mg l^{-1} did not significantly inhibit oyster filtration rates of the algae, *Isochrysis galbana* (Urban and Kirchman, 1992). Since algae was not provided in the experiments by Neilson and associates, the inhibition of filter feeding by inorganic components may be related to the ratio of organic to inorganic components. The ability of an oyster to remove particles from suspension is limited by the lower size limit of the particles and *C. virginica* is able to filter particles greater than 1μ in size. Filtration efficiency, the percent of suspended particles removed, for 1-2 μm particles is less than 50% while it is approximately 100% for particles > 3 μm (Jorgensen and Goldberg, 1953; Haven and Morales, 1970; Walne, 1972). The differential filtration efficiency of bivalves and the differential passive deposition of particles with different characteristics will alter seston concentration and seston composition.

Table 1. Summary of published oyster filtration rates.

Author (s)	Rate	Algal Species	Temperature (C)	Salinity (ppt)
Jorgensen, 1966	0.5-0.8 *l* (hr - gm wt weight)$^{-}$	n/a	n/a	n/a
Langefoss and Maurer, 1975	1.85 *l* h^{-1} for 0.211 g dry wt. oyster	n/a	20	n/a
Newell, 1988	5 *l* $(g\text{-}hr)^{-1}$	n/a	n/a	n/a
Palmer, 1980	1.90 *l* $(hr\text{-}g)^{-1}$ 1.43 *l* $(hr\text{-}g)^{-1}$	*Thalassiosira pseudonana* *Isochrysis galbana*		
Riisgard, 1988	2.18 *l* g^{-1} for 0.211 g dry wt oyster	n/a	27-29	n/a
Powell et al., 1992	1.5 to 7.03 *l* hr^{-1} - for oysters 65 mm in length			
Sellner et al., 1995	3.73 *l* $(oyster\text{-}hr)^{-1}$ 2.83 *l* $(oyster\text{-}hr)^{-1}$ 1.95 *l* $(oyster\text{-}hr)^{-1}$ 0.07 *l* $(oyster\text{-}hr)^{-1}$	*Thalassiosira weisflogii* *Isochrysis galbana* *Prorocentrum minimum* *Gyrodininium ucatenun*	21-25 21-25 21-25 9-12	14-18 14-18 14-18 12-14
Luckenbach et al., 1994	0.224 - 0.388 *l* $(oyster\text{-}hr)^{-1}$ 0.117 *l* $(oyster\text{-}hr)^{-1}$	*Thalassiosira weisflogii* *Prorocentrum minimum*	19.8-30.5 19.8-30.5	15-18 15-18

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; Grizzle, 1992). The flow speed at which growth is inhibited varies with the bivalve species. Growth rates were inhibited at flow speeds > 3 cm s^{-1} for *Argopecten irradians concentricus* (Kirby-Smith, 1972), flow speeds > 10 - 20 cm s^{-1} for *Placopecten magellanicus* (Wildish et al., 1987; Wildish and Kristmanson, 1985), and flow speeds > 1 cm s^{-1} for *Crassostrea virginica* (Grizzle, 1992). Decreased filtering activity of non-siphonate bivalves is a result of the pressure of external flowing water on the inhalant opening being greater than the pressure differential established between the inhalant and exhalent regions (Grizzle, 1992). Decreased growth rates are an expected result of decreased filtration rates (Wildish and Saulnier, 1993) and will result in a negative relationship between increasing flow speeds and growth rates.

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. The rate and the extent of the depletion of suspended particles by filtration is dependent upon the filtration rate of the bivalves, the density of the organisms, and current speed (Officer et al., 1982). As the ratios of the water resident time to bivalve density and to filtration rate increase, the rate

of seston depletion should increase. 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 bivalve in a group may figure prominently in the overall filtration capacity of the group. Laboratory estimates of oyster filtration rates have treated this variation differently. Riisgard (1988) and Loosanoff (1958) reported that any bivalve that was not open or actively filtering was not included in their results. Each hour for 24 to 33 hours, Palmer (1980) measured the filtration rate of individual oysters, *C. virginica*. 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%. Whereas, Newell (1988) estimated that oysters filter for 23 hours each day at the continuous rate of 5 l g^{-1} hr^{-1}. Jorgensen (1966) estimated that oysters are open, for at least 10 hours each day, but did not estimate the amount of time spent filtering seawater. Filtration activity varies neither on a tidal nor a diurnal cycle, but may be attributed to alternating periods of filtering and ingestion (Loosanoff and Engle, 1947; Palmer, 1980). 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, turbidity, and seston composition on filtration rates. In addition, estimating the proportion of the population feeding at any one time has important ecological consequences.

The originally stated objective of this work is to investigate the relationship between high density, off-bottom oyster culture, alterations in water clarity, and the growth and survival of submerged aquatic vegetation (SAV). Specifically, we proposed to: (1) determine biomass-specific particle clearance rates as a partial function of seston concentration, flow rate, oyster density and temperature; (2) test this relationship in the field at the NERRS Catlett Islands, VA, site; and, (3) make specific predictions relating oyster culture, light penetration and SAV growth and survival.

A series of flume experiments were designed to incorporate variation in flow speed and seston composition over a bed of oysters into the measurement of oyster filtration under conditions of turbulent mixing and seston depletion. Field deployments of oysters were made in the Catlett Islands; however, excessively high run-off lead to both elevated turbidity and reduced salinity levels which compromised the field experiment. The refined estimates of filtration activity provided by this work need to be coupled with regional hydrographic data to yield an improved understanding of the materials processing capabilities of oysters in off-bottom culture and on restored reefs.

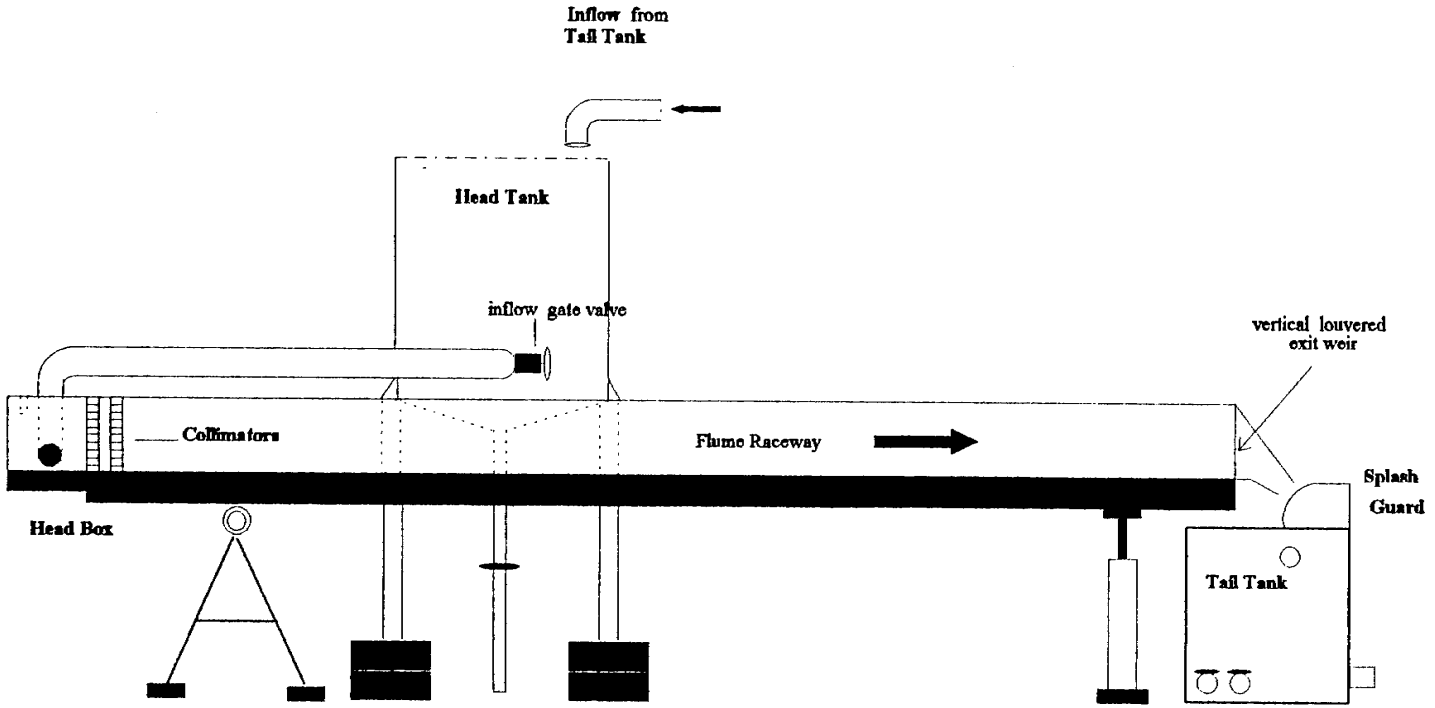
MATERIALS AND METHODS

Flume Experiments

Flume description

All experiments were conducted in the flume, located at the Virginia Institute of Marine Science's (VIMS) Eastern Shore Lab, with a 5 meters long and 60 centimeters wide main flume channel (Fig. 2). For these experiments, the flow was channelized and a smaller channel, 18.7 cm wide and 220 cm long, was created (Fig. 3). Prior to each experiment, the flume was filled with filtered seawater from Wachapreague channel. The seawater was filtered through four filters in series, two sand-charcoal pool filters and two 20μ cartridge filters wrapped by a 1 μ cloth filter. The water temperature can be regulated by a refrigerator or heater depending upon the ambient water temperature. The flume is a recirculating system in which the water flows from the head tank, across the flume bed, into the tail tank, through the two sand-charcoal pool filters, and is pumped back to the head tank. Since the flow across the flume bed is pressure driven, a constant level in the head tank is maintained to insure constant pressure. An inflow gate valve controls the water flow from the head tank into the flume. Settings on the inflow gate valve were calibrated to generate specific free stream velocities in the flume at a water depth of 10 cm. The adjustment of the vertical louvered exit weir and the inflow gate valve control the current speed and water height. At the head of the flume, two collimators in series reduce the scale of the turbulent eddies.

Figure 2. Seawater flume used in all laboratory experiments.



The flow across the bed is a one way steady, two-dimensional flow. The flow character across the flume bed is further defined by the Reynolds number and the Froude number, and the development of a boundary layer was calculated using Schlichting's Four-fifths Law (Schlichting, 1967). The Reynolds number is a dimensionless value which measures the relative strength of inertial forces in relation to frictional forces. As the Reynolds number approaches 2000, there is a transition in the flow character from laminar to turbulent. Across all flows, the value for the Reynolds number calculated as:

$$R_e = \frac{\delta U}{\nu} \tag{1}$$

υ= free stream velocity, δ=water depth, ν=kinematic viscosity, ranged from 528 to 17886. In these experiments, the water height was maintained at a constant 10 cm. The Froude number measures the relative strength of gravitational forces to viscous forces. For Froude numbers less than unity, typical of estuarine tidal flats, boundary layer effects are transmitted upstream from downstream by surface waves (Nowell and Jumars, 1984). The Froude number, calculated as:

$$FR = \frac{U}{g\delta^{1/2}} \tag{2}$$

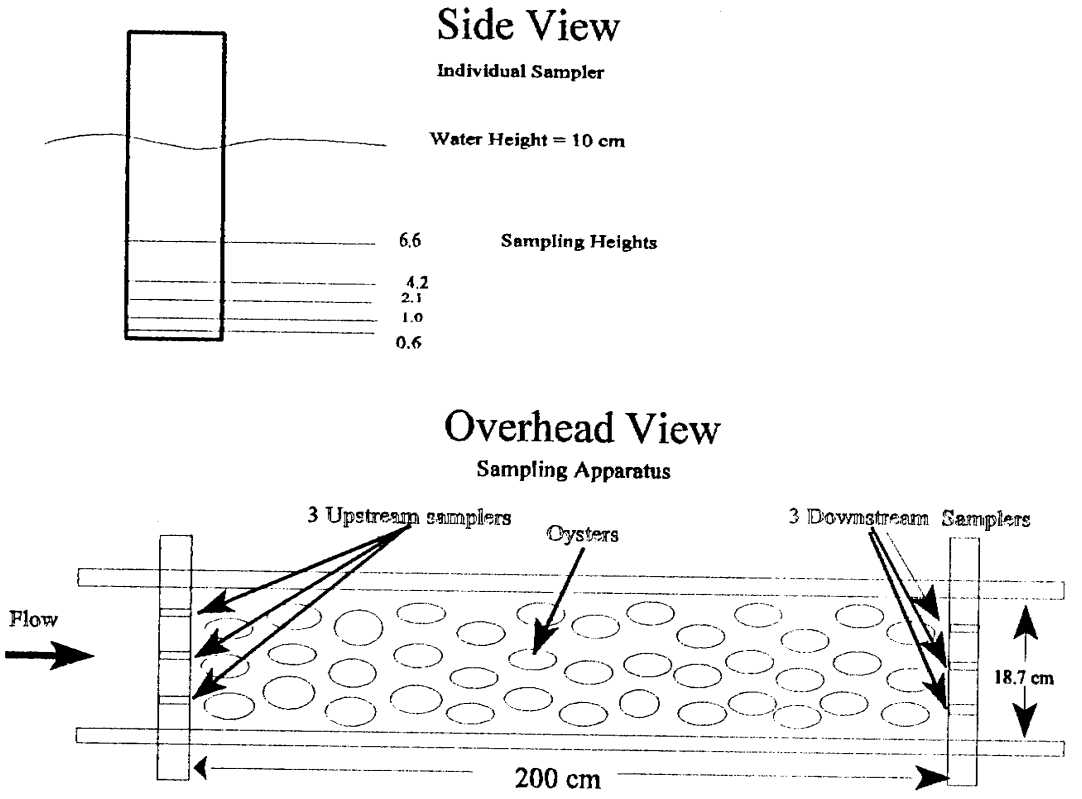
δ=water depth, g=gravity, ranged from 7 e-3 to 2.2 e-1 across all flows.
Schlichting's Four-fifths Law was used to calculate the distance required for the full development of the boundary layer:

$$\left[\frac{U\delta}{\nu}\right] = 0.37\left(\frac{Ux}{\nu}\right)^{4/5} \tag{3}$$

δ=the potential boundary layer thickness, χ=distance downstream, υ= free stream velocity, ν=kinematic viscosity. The boundary layer over the smooth plexiglass bed was fully developed 0.4 meters downstream of the collimators at the maximum flow of 22 cm s^{-1} before the leading edge of the water reached the oyster bed.

Water samples were collected upstream and downstream of the oyster bed by the seston sampling apparatus. Three upstream samplers, laterally arranged across the channel, were approximately 2 meters downstream of the collimators and the three downstream samplers were located 2 meters downstream of the upstream samplers. 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. 3). A logarithmic scale was chosen for the placement of the sampling ports to reflect the theoretical particle distribution above the bed in shearing flow. The water samples collected at each port flowed through fine tubing into individual sampling vials. To allow for unbiased sampling, the flow speed through the tubing was calibrated to be within the range of the water flow speeds.

Figure 3. Seston sampler seen in side and overhead views. Samples were drawn from ports at the designated heights through 1-mm i.d. tubing into individually labelled vials.



Algae cultures and Kaolinite

Monocultures of *Thalassiosira weisflogii* were added in known quantities to the flume and the change in the concentration of these particles across the bed was measured. The unicellular diatom, *T. weisflogii*, was chosen as the organic particle in these experiments because *T. weisflogii* is a premium oyster food and is readily consumed by oysters in still water experiments (Luckenbach et al., 1993). Kaolinite was chosen as the inorganic particle due to its inert nature and for its similarity to the fine suspended matter naturally occurring in estuarine systems.

T. weisflogii suspensions alone and in combination with kaolinite were added to the flume by a gravity feed system. Live *T. weisflogii* cultures were centrifuged into a paste and, at the time of the filtration experiments, the paste was reconstituted with seawater in a blender. Preweighed amounts of kaolinite were stirred into the preblended algae suspensions for the experiments where kaolinite was added. By premixing the kaolinite and algae, the relative concentrations of *T. weisflogii* and kaolinite would remain constant throughout the experiments. The algae suspensions were added to the flume by a gravity feed system where the algae was kept in suspension. The addition of algae was relative to the flow speed so that the algae concentration (million cells ml^{-1}) would remain constant across the flows. In the head box of the flume, the algae suspension and flume water were fully mixed.

Oysters

All oysters used in these experiments were spawned at the VIMS hatchery and were maintained in off-bottom cultures at field sites in Gloucester, VA and near Wachapreague, VA. Prior to the initiation of the experiments, the oysters were brought in from the field

and were maintained on flow through seawater tables. All fouling organisms were removed from the oysters.

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, kaolinite, on the filtration rates. The filtration rates were calculated from the change in particle concentration across the bed of oysters. The first four experiments, E1, E2, E3, and E4, were designed to measure the effect of flow speed on oyster filtration rates (Table 2). Experiments E5 and E6 were designed to measure the effects of flow speed and suspended inorganic particles on oyster filtration rates. The treatments are defined by the composition of the seston added to the system, *T. weisflogii* cells verses *T. weisflogii* cells and kaolinite particles. During E1, E2, E3, and E4, only *T. weisflogii* cells were added while during E5 and E6 *T. weisflogii* cells and kaolinite particles were added. Each individual experiment consisted of a separate oyster batch subjected to eight flow speeds; 0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, and 22.0 cm/sec. Each experiment was a replicate since each individual experiment consisted of a separate batch of oysters. The unique oyster batch associated with each experiment was designated by the same number as the experiment. For the two different seston treatments, control (dead oyster) experiments were conducted to measure the change in particle concentrations due to deposition and resuspension of particles. In these controls, oysters shells were filled with lead shot, glued shut, and substituted for live oysters. For each seston treatment, one to three controls and two to four live experiments were completed.

Ninety oysters were placed within the constrained flume channel in 30 staggered rows of three oysters each and were acclimated to the flume for a minimum of twenty four hours. All oysters remained in the flume for the duration of the experiment with minimal disturbance. The oysters were placed with their beaks facing into the flow and each oyster was numbered to allow for monitoring of individual feeding behavior throughout the experiment.

Each flow began with the addition of the *T. weisflogii* suspension to the head of the flume. At each flow speed within an experiment, particle concentrations were measured upstream and downstream of the bed. The first sampling period began after the oysters had been exposed to the algae for 10 minutes and samples were collected for 20 minutes. Five minutes after termination of the first sampling period, a second sampling was begun. At the end of this sampling period, the addition of algae was terminated.

During each sampling period and for a one hour period after the cessation of algae, the type of feeding behavior exhibited by each individual oyster was monitored. Two types of feeding behavior were monitored 1) the production of feces and pseudofeces and 2) the gape or opening of the oyster's shell. Prior to the initiation of each flow speed, the feces and pseudofeces were removed by siphon, so that the production of feces during each flow speed could be distinguished from the previous flow speed.

Two to three flow speeds were completed each day and each oyster batch was subjected to all flow speeds within a three to four day period. One to two hours after the first flow was completed, the second flow speed of the day was begun. Each experiment

Table 2. Experimental design. Designations for each experiment are used throughout the text. No. of live or dead oysters, seston composition, flow speeds, temperature and salinity in each experiment are given.

Experiment	Treatment	Seston	Flow Speeds (cm/s)	Water Temp (C)	Salinity (ppt)
E1	90 live oysters	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	19.5 - 20.9	30
E2	87 live oysters and 3 shells *	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	20.2 - 21.5	29
E3	90 live oysters	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	20.0 - 21.5	30
E4	90 live oysters	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	19.8 - 21.9	27
E5	90 live oysters	*T. weisflogii* and kaolinite	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	18.4 - 21.9	33
E6	90 live oysters	*T. weisflogii* and kaolinite	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	20.4 -21.8	31
C1	90 oyster shells	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	18.2 - 21.4	32
C2	90 oyster shells	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	20.0 - 21.3	31
C3	90 oyster shells	*T. weisflogii*	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	19.0 - 21.2	31
C4	90 oyster shells	*T. weisflogii* and kaolinite	0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, 22.0	18.1 - 22.0	30

*While removing the oyster meats from the shells, it was discovered that three of the shells were filled with mud rather than an oyster.

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. At the end of each experiment, the height, width, and ash-free dry weight of each oyster in the batch was recorded.

The same procedures were followed in E5 and E6 with the exception of the timing of the sampling periods and the seston added. For Experiments E5 and E6, each flow speed began with the addition of the *T. weisflogii* and kaolinite suspension to the head of the flume. The flow speed of the water samples through the sampling tubes was increased to prevent the settling of fine kaolinite particles in the tubes. To compensate for the increased sampling rate, the sampling period was reduced to 10 minutes. In the event that there was a significant difference in the filtration rates over time, the time between the two sampling periods was increased to ten minutes to maintain consistency in the time between the initiation of algae addition and sampling period 2 for all experiments.

The procedures for sample collection and particle addition were repeated in each control experiment, respective of the seston treatment. The spatial location of each shell was changed prior to each control experiment so that each control experiment, C1, C2, and C3, was a replicate experiment. For C4, a unique set of shells was used by replacing some of the shells used in C1, C2, and C3 with others. At the end of C3 and C4, the height and width of each shell was measured.

Three control experiments, C1, C2, and C3, and four live oyster experiments, E1, E2, E3, and E4, were conducted in which *T. weisflogii* was added and one control, C4, and two live oyster experiments, E4 and E5, in which *T. weisflogii* and kaolinite were added were completed. Since there were more flow speeds than experiments, this was not a full Latin Square design. E1, E2, E3, and E4 were conducted on November 16 to

18, 1993, December 13 to 15, 1994, January 18 to 20, 1994, and March 23 to 25, 1994, respectively. E5 and E6 were conducted on May 5 to 6, 1994 and May 17 to May 19, 1994, respectively. For all experiments, the salinity ranged from 27 to 33 parts per thousand and the water temperature ranged from 18.4 to 21.7 C (Table 2). Three cohorts spawned in 1991, 1992, and 1993 were used in these experiments with ninety oysters of the same cohort randomly assigned to each experiment. In all cases, oysters were of approximately the same size. Oysters spawned in 1991 were randomly assigned to E1, E2, and E3 and are designated as B1, B2, and B3, respectively. The oysters for E4 and E5 were spawned in 1992 and are designated as B4 and B5, respectively. The oysters for E6 were spawned in 1993 and are designated as B6.

Sample Collection and Processing

The upstream and downstream particle concentrations were determined from the water samples collected during each sampling period. For each sampler location, three samples were collected at each height for a total of fifteen upstream and fifteen downstream samples per sampling period. The three samples collected at each height were pooled into one sample for analysis. After pooling samples laterally, there were 5 upstream and 5 downstream samples for each sampling period.

Each pooled sample was analyzed for particle concentration and in vivo chlorophyll levels. Collected samples were kept on ice and in the dark until processed. Five ml of the pooled sample was filtered onto a 0.45 μ-pore diameter Millipore filter. The filters were rinsed with borax to reduce acidity, wrapped in prelabeled aluminum foil, and frozen for later chlorophyll analysis. Following the procedures for the chlorophyll analysis using a

fluorometer described in Strickland and Parsons (1968), the chlorophyll was extracted in acetone for 24 hours and the concentration of chlorophyll a was measured in a fluorometer. The remainder of the pooled sample was preserved with Lugol's solution and refrigerated for particle concentration analysis. All particle concentration analyses were performed on a Coulter Counter and were completed within a 36 hour period due to the agglutination of *T. weisflogii* particles with time. All samples were allowed to come to room temperature and were repeatedly inverted to resuspend the particles. The time between mixing and counting was minimized to prevent the settling of particles which would lead to an underestimation of the particle concentration.

A Coulter Counter was calibrated to measure the concentration of the *Thalassiosira weisflogii* cells and kaolinite particles using the procedures described by Strickland and Parsons (1968). The Coulter Counter was calibrated by determining the optimum threshold settings for two types of particle samples, algae alone and in addition to kaolinite. The calibrated threshold setting was confirmed by comparing the particle concentrations of *T. weisflogii* suspensions determined using the Coulter Counter with concentrations determined using a hemocytometer. The particle samples from the *T. weisflogii* and kaolinite experiments were analyzed at two different threshold settings to separate the *T. weisflogii* concentration from the kaolinite concentration. Individual suspensions of *T. weisflogii,* kaolinite, and known combinations of *T. weisflogii* and kaolinite were counted at the two threshold settings. From the particle concentrations at the two threshold settings, two equations were generated to separate the *T. weisflogii* particle concentrations from the kaolinite particle concentrations. The filtration rates were not calculated from the calculated *T. weisflogii* particle concentrations because of the

error associated with calculating the *T. weisflogii* particle concentrations would have then become incorporated into the filtration rates. The particle concentrations read at the higher threshold setting, which were essentially the concentration of *T. weisflogii*, were used to calculate filtration rates.

The Coulter Counter, fitted with a 100 μ tube, counted particles with a diameter of 2 to 40 μ. Each *T. weisflogii* cell was approximately 16 μ in length, well within the 2 and 40 μ range, but 77.3 percent of the kaolinite particles were less than 2 μ in diameter, so the counts used in estimating filtration rates were corrected for counter efficiency.

Computation of Filtration Rates

Each particle sample was counted three times at the appropriate threshold setting and a mean ($\bar{x}$) and a standard deviation (SD) for the three counts were calculated. A composite standard deviation (SD') value was derived from the individual standard deviations (SD'=$\sum$SD/N) for each threshold setting. All values greater than three composite standard deviations (3SD') from the individual count mean were eliminated. Once all outlying particle concentrations were eliminated, the particle concentrations upstream and downstream of the oyster bed were calculated. For each sampling period, there were 5 upstream and 5 downstream samples. 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:

$$m = \frac{M \dfrac{\ln C_1}{\ln C_2}}{nt} - a \qquad (4a)$$

m - laboratory filtration rate
M - total volume of suspension
$\mathbf{C_1}$- concentration upstream
$\mathbf{C_2}$- concentration downstream

n - biomass of oysters
t - time
a -control particle change rate- determined in a control experiment with no live organisms

$$a = \frac{M \dfrac{\ln C_1'}{\ln C_2'}}{nt}$$

M - 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 (4b)

Each term in the above equation was adapted to calculate filtration rates for these flume experiments. Time was a function of flow and was the resident time of the water parcel over the oyster bed computed as the length of the test section, 200 cm, divided by the free stream 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 water column was partitioned into two regions, the lower and upper region, to isolate the region where oyster filtration would have been most influential. The samples from the lowest two samplers (0.6 and 1.0 cm) were used to calculate the lower region filtration rates. The lower region filtration rates measured the change in particle concentration for the area essentially within the oyster bed, the lower 1.5 cm of the water column. The dimensions of the lower region were 1.5 cm by 18.7 cm by 200 cm, (height, width, and length, respectively), for a total volume 5.61 liters. The upper region filtration rates, the upper 8.5 cm of the water column, measured the change in particle concentration in the region at the top of and above the bed. The samples from the upper three samplers (2.1, 4.2, and 6.6 cm) measured the particle change from the upper 8.5 cm of the water column. The dimensions of the upper region were 8.5 cm by 18.7 cm by 200 cm, (height, width, and

length, respectively), for a total volume 31.79 liters.

In these experiments, the change in particle concentration was measured over a bed of ninety oysters. The three filtration rates calculated were based on the following criteria: 1) the number of oysters in the flume, 2) the number of oysters that were open, a liberal estimate of the number of oysters feeding, and 3) the number of oysters that produced feces, a conservative estimate of the number of oysters feeding. The notation for each of these rates are m-all, m-open, and m-feces, respectively. In B2, there were 87 live oysters and 3 empty shells. While removing the oyster meats from the shells, it was discovered that three of the shells were filled with mud rather than an oyster. All calculations were adjusted for the reduced number of live oysters. All live filtration rates are reported on a per biomass basis by substituting the number of oysters with an ash-free dry weight value. The biomass value used was calculated by multiplying the number of oysters by the average weight of the oysters for the respective batch.

The change in particle concentration with no live organisms was measured in control experiments where live oysters were replaced with sealed oyster shells as previously described. The rates derived from these experiments are referred to as the control rates. A mean control rate (a) from each experiment and flow speed was derived from the control rates for sampling periods one and two. A singular value is reported since only one value is necessary for "a" in the computation of filtration rates (Equation 4a). Rather than reporting the control rates as liters per hour per oyster shell, these rates are reported as a liters per hour per biomass oyster so that comparisons with live filtration rates could be facilitated. The dry weight chosen for this calculation was 0.60 g, the average ash-free dry weight of the oysters used in the live experiments.

Statistical Analyses

Observed differences between upstream and downstream particle concentrations in control (dead oyster) experiments must represent deposition, resuspension, or simply error in the estimation technique. Observed differences between estimates of upstream and downstream particle concentration were computed as given in Equation 4b. The significance of control rate differences were evaluated using a two-way, fixed factor analysis of variance for C1, C2, and C3 and a one-way, fixed factor analysis of variance for C4. For each seston treatment, the relationship between control rates and flow speed was evaluated using linear regression analysis.

Variation in filtration rates was evaluated in relation to experiment, flow, and sampling period using a three-way, fixed factor, full factorial analysis of variance. Results from E1, E2, E3 and E4 were analyzed separately from those of E5 and E6. The results from the upper and the lower regions were analyzed separately and an analysis of variance conducted for each of the m-all, m-open and m-feces filtration rates. When significant interactions were observed, data sets were partitioned and lower level analysis of variances were performed. Where significant main effects were observed, differences between individual levels were evaluated using Tukey's a posteriori multiple comparison test.

Comparisons of the upstream and downstream particle concentration profiles were completed by using particle counts that were normalized to remove the variance in particle concentrations between experiments. The concentrations were standardized separately for each flow speed. Once particle counts were normalized, visual comparisons of the change in particle concentrations between all experiments, control experiments and live experiments, were completed.

The filtration rates were compared with mean control rates for each respective flow speed to measure the significance of the filtration rates. For each region (lower and upper), mean filtration rates for sampling period 1 and for sampling period 2 were calculated for each flow speed. Assuming a time variance in oyster filtration, the filtration rate for sampling period 1 and sampling period 2 was analyzed separately. A two sample t-test, assuming unequal variances, was used to compare the filtration rate for each sampling period against the control rate.

The effect of the sequence of flows within the experiment and the effect of the daily sequence of flows on oyster feeding behavior were evaluated using linear regression analysis. An entire experiment of eight flow speeds was completed in three to four days with two to four flows completed each day. Each flow speed was assigned a value between one and four based on the chronological order of flows each day and a value between one and eight based on the sequence of flows within each experiment. A linear regression analysis of the number of oysters open and the number of oysters producing feces with the daily flow sequence and the experiment flow sequence were used to measure each effect.

In each experiment, an analysis of variance was used to test for differences in the mean height of oysters between each batch of oysters including the oyster shells used in the controls. A fixed factor, one-way analysis of variance was used to test for differences in the condition index between each oyster batch. A fixed factor, two-way analysis of variance was used to test for differences in the feeding activity of the oysters within each batch and flow speed. For all statistical tests, the alpha level was 0.05.

Field Experiment

Our research plan proposed a field experiment at the Catlett Islands to test the predictions for our laboratory measure of oyster clearance rates in flowing water. The originally proposed location (about 100 m channelward of the marsh islands) was exposed to high water currents. Excessive deposition of sediments and macroalgae at this location lead to the smothering of the eelgrass. As indicated below, in the second year of the field study we moved the experimental site inshore to a more protected site within the Catlett Islands (see Fig. 1) in an attempt to avoid some of these problems.

Zostera marina transplants.

Experimental plots of *Z. marina* were established at the Catlett Island site in October 1992 using bundles of grass collected from further downstream in the York River at the Guinea Marshes. Individual shoots were washed free of sediment and bundled together into groups of 10 to 15 with a metal twist tie. Generally, these bundles were transplanted within 24 hrs. [See Batuik et al. (1992) for a full description of eelgrass transplant techniques]. Six 4-m^2 plots were established and they survived well through the winter of '92-'93. The results section describes the water quality conditions which lead to the early termination of the field experiment in 1993.

A second attempt to conduct the field experiment was initiated with transplants in October 1993 at the more inland site indicated in Fig. 1. Again, six 4-m^2 plots were constructed using the same techniques as the previous year.

Deployment of oysters

All oysters used in the experiment were spawned in the Virginia Institute of Marine Science Oyster Hatchery at Gloucester Point, VA, about 5 km downstream from the Catlett Islands and held in off-bottom culture in Pungoteague Creek, Virginia. The oysters used in this experiment were spawned in 1990 and represented sub-market sized animals (50-56 mm shell height) remaining from an aquaculture demonstration project. Metal racks made of welded reinforcing bar were used to hold plastic mesh bags of oysters. Each bag held approximately 600 oysters and each rack held 10 bags. In May 1993 we deployed 25 such racks, with a total of approximately 150,000 oysters around test plots of *Z. marina* at the Catlett Islands.

In May 1994 we initiated the deployment of a smaller number of oysters (approx. 40,000) in a modified array around the eelgrass transplants. This deployment was just underway when water quality conditions again forced a termination of the field experiment.

Water Quality Measures

As part of a long-term water quality monitoring project which complimented this program, triplicate subsurface water column samples have been taken at the Catlett Islands from October 1985 to the present. This monitoring program includes 6 other stations in the York River and is detailed more fully in Batuik et al. (1992). Triplicate water samples were collected sequentially and stored on ice in the dark for up to 4 hours before processing. Nitrite, nitrate, and ammonium were determined spectrophometrically using methods described by Parsons et al. (1984) and inorganic phosphorus was determined

following EPA (1979) methods. Total suspended solids were determined by collection on a precombusted glass fiber filter, dried at 55° C and combusted for 5 hrs at 550° C. Chlorophyll *a* was determined fluorometrically after collection on a glass fiber filter and extraction and in a solution of actone, dimethylsulfoxide and 1% diethylamine (45:45:10) following the methods of Shoaf and Lium (1976) as modified by Hayward and Webb (unpublished). Attenuation of photosynthetically active radiation (PAR) was determined from water column profiles made with a LI-COR, LI-92 underwater sensor.

RESULTS

Flume Experiments

All outlying particle counts were deleted by the method previously described. Each individual count that was greater than three composite standard deviations from the respective sample mean was deleted. The composite standard deviation for the data from E1, E2, E3, E4, C1, C2, and C3 was 139. The total number of particle counts was 2880 and 196 counts, or 6.8%, of those counts were deleted. In the E5, E6, and C4, the composite standard deviation was 38.9. A total of 1440 particle counts were completed and 33 counts, or 2.3%, of those counts deleted.

The filtration rates were calculated from the change in particle concentration across the oyster bed. Chlorophyll concentrations were not used to compute filtration rates, but the upstream chlorophyll concentrations are reported. A positive relationship existed between particle concentrations and chlorophyll concentrations in all experiments and was used to evaluate the calculation of *T. weisflogii* particle concentrations in E5 and E6. For E5 and E6, the kaolinite concentrations were not used to calculate filtration rates, but the upstream kaolinite concentrations are reported. The three filtration rates computed for each flow speed were the filtration rates for the entire bed of oysters, m-all, the filtration rate for only those oysters open, m-open, and the filtration rate for those oysters producing feces, m-feces. Since the focus of this experiment is to better understand the filtration capacity of an oyster bed, only the plots of the m-all filtration rates were given.

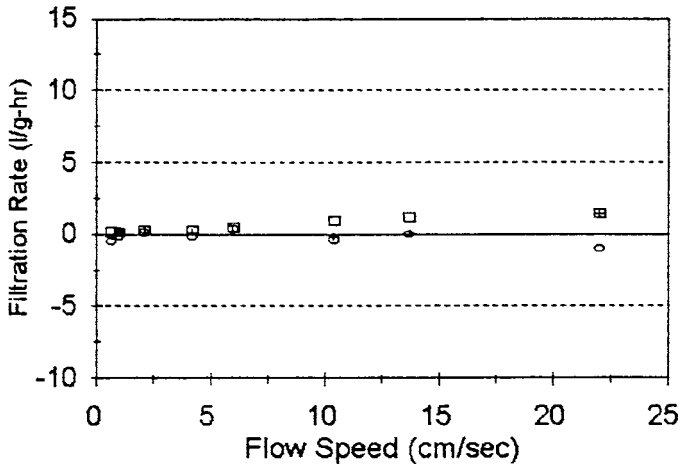
Results of Experiments with *Thalassiosira weisflogii*

There was an incomplete mixing of particles within the water column for the first sampling period of C1 and C2 at the flow speed of 0.65 cm s^{-1}. These samples were not used, but reliable data was available for sampling period 2 at this speed in these experiments. For C3, the data for sampling period 1 of the flow speed of 2.1 cm s^{-1} was incomplete and thus was not used. The lower region control rates were approximately zero (Fig. 4a, Appendix I). Two-way analysis of variance indicated that the lower region control rates were significantly different between controls (Table 3). There was no significant relationship between the lower region control rates and flow speed (Table 4). The relationship between the upper region control rates and flow speed was highly variable (Fig. 4b, Appendix II) and was not statistically significant (Table 3). Upper region control rates did not vary significantly between experiments and flow speed (Table 4). 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 filtration rates.

The upper region filtration rates and flow speed showed no clear relationship for the four live experiments (Fig. 5b) (Appendix III). Experiment, flow speed, and their interaction had significant effects on each filtration rate, m-all, m-open, and m-feces (Table 5). Since sampling period was not a significant factor, the analysis was repeated as a two-way analysis of variance. Using the two sequential sampling periods within each flow speed as replicate samples, significant effects of experiment, flow speed, and their interaction persisted (Table 6). Thus, each experiment was analyzed separately.

Figure 4. Control Rates for C1, C2, and C3, noted by ○, □, and +, respectively, in (A) the lower region and (B) the upper region

A.



B.

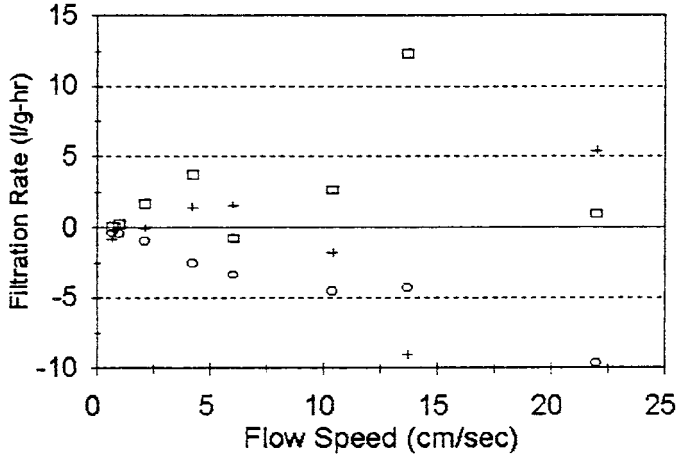


Table 3. Two-way analysis of variance for effect of experiment and flow speed on filtration rates C1, C2, and C3 in the Lower Region (A) and Upper Region (B)

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	2	2.99	1.50	6.00	0.01
FLOW SPEED (B)	7	1.23	0.18	0.71	0.67
ERROR	14	3.49	0.25		
TOTAL	23	7.71	7.71		

B.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	2	51.12	25.56	3.29	0.07
FLOW SPEED (B)	7	3.77	0.54	0.07	1.00
ERROR	14	108.8	7.77		
TOTAL	23	163.7			

Table 4. Regression of control filtration rates on flow speed for C1, C2, and C3 in the lower region (A) and upper region (B)

A.

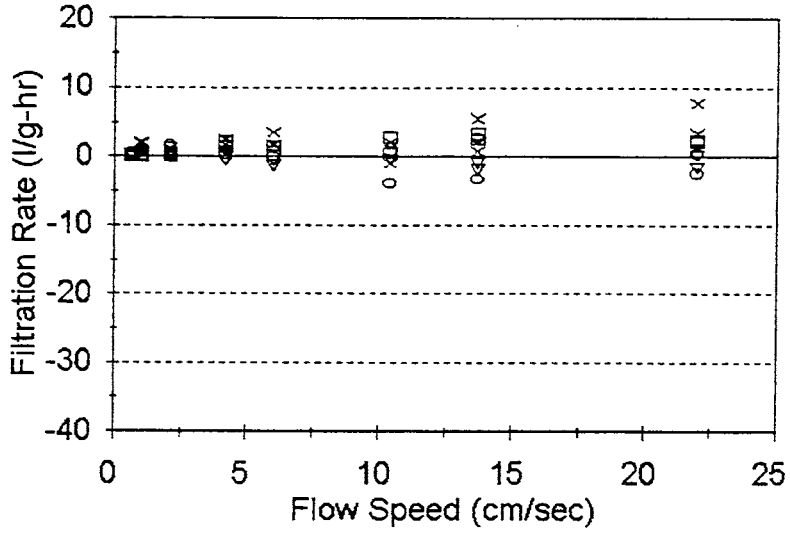
Analysis	r^2 (%)	N	P
Control Rate and Flow Speed	0.11	24	0.11

B.

Analysis	r^2 (%)	N	P
Control Rate and Flow Speed	0.01	24	0.68

Figure 5. Filtration rates for E1, E2, E3 and E4, noted by □, ○, ▽, and ×, respectively, in the a) lower region and b) upper region

A.



B.

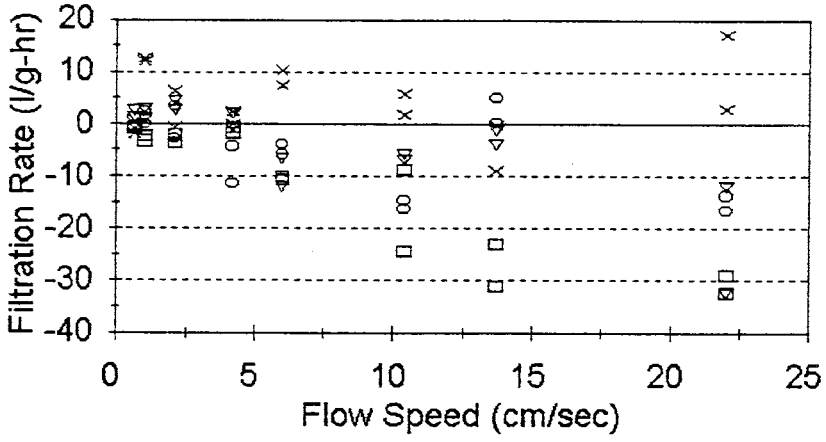


Table 5. Three-Way Analysis of Variance of lower region filtration rates by experiment, flow speed and sampling period for E1, E2, E3, and E4 using rates calculated for (A) all oysters, (B) only open oysters and (C) oysters producing feces.

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	1953	651	31.7	0.000
FLOW SPEED (B)	7	1953	279	13.6	0.000
PERIOD (C)	1	10	10	0.5	0.483
A*B	21	2322	111	5.4	0.000
A*C	3	85	28	1.4	0.277
B*C	7	112	16	0.8	0.610
A*B*C	21	432	21		
TOTAL	63	6868			

B.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	9890	3297	24.2	0.000
FLOW SPEED (B)	7	7665	1095	8.0	0.001
PERIOD (C)	1	28	28	0.2	0.653
A*B	21	14173	675	5.0	0.000
A*C	3	398	133	1.0	0.424
B*C	7	648	93	0.7	0.688
A*B*C	21	2862	136		
TOTAL	63	35664			

C.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	16475	5492	23.3	0.000
FLOW SPEED (B)	7	12555	1794	7.6	0.001
PERIOD (C)	1	23	23	0.1	0.756
A*B	21	25339	1207	5.1	0.000
A*C	3	607	202	0.9	0.477
B*C	7	1004	143	0.6	0.742
A*B*C	21	4946	236		
TOTAL	63	60950			

Table 6. Three-Way Analysis of Variance of upper region filtration rates by experiment, flow speed and sampling period for E1, E2, E3, and E4 using rates calculated for (A) all oysters, (B) only open oysters and (C) oysters producing feces.

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	1953	651	32.6	0.000
FLOW SPEED (B)	7	1953	279	14.0	0.000
A*B	21	2322	111	5.5	0.000
Error	32	639	20		
TOTAL	63	6868			

B.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	9890	3297	26.8	0.000
FLOW SPEED (B)	7	7665	1095	8.9	0.000
A*B	21	14173	675	5.5	0.000
Error	32	3937	123		
TOTAL	63	35664			

C.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	16475	5492	26.7	0.000
FLOW SPEED (B)	7	12555	1794	8.7	0.000
A*B	21	25339	1207	5.9	0.000
Error	32	6581	206		
TOTAL	63	60950			

For each experiment, a one-way analysis of variance was used to evaluate the effect of flow speed on filtration rates in the upper region (Table 7). For E1, E2, and E3, there were significant differences in the filtration rates, for each m-all, m-open, and m-feces, measured at the different flow speeds. For E4, flow speed did not have a significant effect on the filtration rates, m-all, m-open, and m-feces. The variations of filtration rates with flow speed were monotonic for the experiments, E1, E2, and E3 (Table 8). For E1, E2, and E3, the upper region filtration rates for flow speeds ≤ 6 cm sec^{-1} were generally similar, while the filtration rates for flow speeds ≥ 6 cm sec^{-1} were similar (Table 8).

The relationship between the lower region filtration rates and flow speed showed no consistent pattern between the four experiments (Fig. 5a) (Appendix IV). A three-way analysis of variance indicated that there was a significant difference in the filtration rate of each experiment for all filtration rates, m-all, m-open, and m-feces (Table 9). Although there was not a strong interactive term of experiment and flow speed in the lower region analysis, each experiment was analyzed separately as in the upper region analysis. For each experiment, a one-way analysis of variance was completed to evaluate the effect of flow speed on the filtration rates (Table 10). Only in E1 were there significant differences in the filtration rates, m-all, m-open, and m-feces, for the eight flow speeds (Table 10). Tukey's a posteriori multiple comparison test revealed that the variations in filtration rates with flow speeds were non-monotonic (Table 11). In E2, E3, and E4, flow speed did not have a significant effect on the filtration rates, m-all, m-open, and m-feces (Table 10).

Table 7. One-Way Analysis of Variance of Upper Region Filtration Rates for E1, E2, E3, and E4 using rates calculated for all oysters (m-all), only open oysters (m-open) and oysters producing feces (m-feces).

E1 - m-all

Source	DF	SS	MS	F	P
Flow speed	7	2020	289	14.17	0.001
Error	8	163	20		
TOTAL	15	2183			

E1 - m-open

Source	DF	SS	MS	F	P
Flow speed	7	9538	1363	19.77	0.000
Error	8	551	69		
TOTAL	15	10089			

E1 - m-feces

Source	DF	SS	MS	F	P
Flow speed	7	16463	2352	18.08	0.000
Error	8	1041	130		
TOTAL	15	17504			

E2 - m-all

Source	DF	SS	MS	F	P
Flow speed	7	743	106	12.86	0.001
Error	8	66	8		
TOTAL	15	809			

E2 - m-open

Source	DF	SS	MS	F	P
Flow speed	7	4335	619	5.30	0.016
Error	8	935	117		
TOTAL	15	5270			

E2 - m-feces

Source	DF	SS	MS	F	P
Flow speed	7	8048	1150	4.84	0.021
Error	8	1901	238		
TOTAL	15	9948			

Table 7 (cont.)

E3- m-all

Source	DF	SS	MS	F	P
Flow speed	7	1022	146	5.02	0.019
Error	8	232	29		
TOTAL	15	1254			

E3- m-open

Source	DF	SS	MS	F	P
Flow speed	7	5611	802	6.17	0.010
Error	8	1039	130		
TOTAL	15	6649			

E3- m-feces

Source	DF	SS	MS	F	P
Flow speed	7	10471	1496	6.74	0.008
Error	8	1775	222		
TOTAL	15	12247			

E4- m-all

Source	DF	SS	MS	F	P
Flow speed	7	490	70	3.15	0.065
Error	8	178	22		
TOTAL	15	668			

E4- m-open

Source	DF	SS	MS	F	P
Flow speed	7	2354	336	1.91	0.193
Error	8	1411	176		
TOTAL	15	3765			

E4 - m-feces

Source	DF	SS	MS	F	P
Flow speed	7	2912	416	1.79	0.217
Error	8	1864	233		
TOTAL	15	4776			

Table 8. Tukey's a posteriori multiple comparison tests for the upper region filtration rates for E1, E2, and E3. Each group of filtration rates for each flow speed which are not significantly different from one another are grouped in a single column and noted with *.

Flow Speed	E1			E2		E3	
	Homogeneous Groups			Homogeneous Groups		Homogeneous Groups	
0.65	*			*		*	
1.0	*			*		*	
2.1	*			*		*	
4.2	*			*	*	*	
6.0	*	*		*	*	*	*
10.4		*	*		*	*	*
13.7		*	*	*		*	*
22			*		*		*

Table 9. Three-Way Analysis of Variance in Filtration Rates in the lower region for E1, E2, E3, and E4 computed using (A) all oysters, (B) open oysters and (C) oysters producing feces.

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	61.1	20.4	8.1	0.001
FLOW SPEED (B)	7	14.7	2.1	0.1	0.566
PERIOD (C)	1	2.7	2.7	1.1	0.309
A*B	21	67.7	3.2	1.3	0.284
A*C	3	4.9	1.6	0.7	0.593
B*C	7	8.6	1.2	0.5	0.832
A*B*C	21	52.6	2.5		
TOTAL	63	212.3			

B.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	274.2	91.4	6.5	0.003
FLOW SPEED (B)	7	97.7	14.0	1.0	0.463
PERIOD (C)	1	29.4	29.4	2.1	0.163
A*B	21	357.8	17.0	1.2	0.332
A*C	3	56.2	18.7	1.3	0.291
B*C	7	31.2	4.5	0.3	0.938
A*B*C	21	295.4	14.1		
TOTAL	63	1142.0			

C.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	3	348.8	116.3	5.3	0.007
FLOW SPEED (B)	7	158.8	22.7	1.0	0.435
PERIOD (C)	1	46.3	46.3	2.1	0.160
A*B	21	614.8	29.3	1.3	0.254
A*C	3	77.9	26.0	1.2	0.338
B*C	7	41.0	5.9	0.3	0.960
A*B*C	21	458.5	21.8		
TOTAL	63	1746.1			

Table 10. One-way Analyses of Variance in filtration rates in the lower region for E1, E2, E3, and E4 computed using (A) all oyster, (B) only open oysters and (C) oysters producing feces.

E1 (A) all oysters

Source	DF	SS	MS	F	P
Flow speed	7	16.38	2.34	5.01	0.019
Error	8	3.74	0.47		
TOTAL	15	20.12			

E1 (B) open oysters

Source	DF	SS	MS	F	P
Flow speed	7	80.89	11.55	6.70	0.008
Error	8	13.81	1.73		
TOTAL	15	94.69			

E1 (C) oyster producing feces

Source	DF	SS	MS	F	P
Flow speed	7	141.29	20.18	5.24	0.016
Error	8	30.82	3.85		
TOTAL	15	172.11			

E2 (A) all oysters

Source	DF	SS	MS	F	P
Flow speed	7	12.43	1.78	0.42	0.862
Error	8	33.51	4.19		
TOTAL	15	45.95			

E2 (B) open oysters

Source	DF	SS	MS	F	P
Flow speed	7	77.63.91	11.09	0.77	0.627
Error	8	115.01	14.38		
TOTAL	15	192.65			

E3 (C) oysters producing feces

Source	DF	SS	MS	F	P
Flow speed	7	125.11	17.87	0.73	0.653
Error	8	195.26	24.41		
TOTAL	15	320.37			

Table 10. (cont.).

E3 (A) all oyysters

Source	DF	SS	MS	F	P
Flow speed	7	6.57	0.94	2.26	0.138
Error	8	3.33	0.42		
TOTAL	15	9.90			

E3 (B) open oysters

Source	DF	SS	MS	F	P
Flow speed	7	77.18	11.03	2.31	0.132
Error	8	38.25	4.78		
TOTAL	15	115.43			

E3 (C) oysters producing feces

Source	DF	SS	MS	F	P
Flow speed	7	197.03	28.15	3.07	0.069
Error	8	73.36	9.17		
TOTAL	15	270..385			

E4 (A) all oysters

Source	DF	SS	MS	F	P
Flow speed	7	47.04	6.72	1.91	0.192
Error	8	28.15	3.52		
TOTAL	15	75.18			

E4 (B) open oysters

Source	DF	SS	MS	F	P
Flow speed	7	219.86	31.41	1.02	0.480
Error	8	245.16	30.64		
TOTAL	15	465.01			

E4 (c) oysters producing feces

Source	DF	SS	MS	F	P
Flow speed	7	310.13	44.30	1.09	0.447
Error	8	324.32	40.54		
TOTAL	15	634.45			

Table 11. Tukey's a posteriori multiple comparison test for the Lower Region Filtration Rates for E1. Each filtration rate that was not significantly different from one another are grouped in a single column and noted by *.

Flow Speed	E1- m-all	
	Homogeneous Groups	
0.65	*	
1	*	
2.1	*	*
4.2	*	*
6	*	
10.4	*	*
13.7		*
22	*	*

Although neither the lower region filtration rates nor the upper region filtration rates were significantly different from the lower region control rates and upper region control rates (except in one case), mean filtration rates were greater than the control rates at low flow speeds (Tables 12 - 15) . For each sampling region and each sampling period, the mean filtration rates for each were compared with the mean control rates. The mean lower region filtration rates were greater than the mean control rates for flow speeds ≤ 6 cm sec^{-1} (Figure 6a). The mean upper region filtration rates were greater than the mean control rates for flow speeds ≤ 1.0 cm sec^{-1} (Fig. 6b).

During each flow speed, the feeding behavior of the oysters in the flume was monitored. The percent of oysters open throughout all flow speeds varied from 16 to 68% and for feces producing oysters from 9 to 54% (Table 16). There were significant positive relationships between flow speed and the number of oysters open (Fig. 7a) and between flow speed and the number of oysters producing feces (Fig. 7b) (Table 17).

The sequence of flow speeds for each experiment and for each day of each experiment is given on Table 18. No relationship between the number of open oysters and the daily flow sequence was observed (Figs. 8a and 8b). There was, however, a weak indication of a relationship between daily flow sequence and the number of oysters producing feces (Table 17). No significant relationship between the experiment flow sequence and neither the number of open oysters (Fig. 8c) nor the number of oysters producing feces (Fig. 8d) was observed (Table 17).

Mean shell height varied between 63.9 and 70.9 mm for all oyster batches used in the various controls and experiments (Table 19), but distinctively different groups were indicated. Due to discrepancies in the dry weights of the oysters in E1 and E3, the dry

Table 12. T-tests between lower region control and filtration rates by flow speed--Sampling period 1

Flow Speed - 0.65 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.151	4.0	1.23	.1435
Live	0.168			

Flow Speed - 1.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.085	3.5	1.95	0.066
Live	0.883			

Flow Speed - 2.1 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.199	3.1	1.05	0.184
Live	0.660			

Flow Speed - 4.2 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.083	3.8	2.57	0.033
Live	1.054			

Flow Speed - 6.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.388	3.1	0.16	0.442
Live	0.467			

Flow Speed - 10.4 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.135	3.4	0.01	0.495
Live	0.156			

Flow Speed - 13.7 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.414	3.4	1.12	0.167
Live	2.184			

Flow Speed - 22.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.623	3.8	0.56	0.304
Live	1.916			

Table 13. T-tests between lower region control and filtration rates by flow speed--Sampling period 2

Flow Speed - 0.65 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.151	2.7	0.35	0.375
Live	-0.071			

Flow Speed - 1.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.085	3.3	1.16	0.161
Live	0.702			

Flow Speed - 2.1 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.199	3.3	1.23	0.150
Live	0.541			

Flow Speed - 4.2 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.083	3.2	1.43	0.121
Live	1.140			

Flow Speed - 6.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.388	3.0	0.34	0.380
Live	0.756			

Flow Speed - 10.4 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.135	4.7	-0.27	0.600
Live	-0.019			

Flow Speed - 13.7 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.414	3.5	-0.29	0.606
Live	-0.012			

Flow Speed - 22.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.623	4.9	0.38	0.360
Live	1.146			

Table 14. T-tests between upper region control and filtration rates by flow speed--Sampling period 1

Flow Speed - 0.65 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.392	3.5	1.05	0.181
Live	0.533			

Flow Speed - 1.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.032	3.0	1.09	0.178
Live	3.450			

Flow Speed - 2.1 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.221	3.8	0.86	0.220
Live	2.118			

Flow Speed - 4.2 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.843	4.7	-0.95	0.806
Live	-2.518			

Flow Speed - 6.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.858	3.6	-0.81	0.767
Live	-4.598			

Flow Speed - 10.4 cm sec^{-1}

Variable	Mean	df	t	P
Control	-1.220	4.6	-1.48	0.898
Live	-7.520			

Flow Speed - 13.7 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.321	4.7	-0.52	0.686
Live	-4.964			

Flow Speed - 22.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-1.080	3.8	-1.20	0.851
Live	-16.070			

Table 15. T-tests between upper region control and filtration rates by flow speed--Sampling period 12

Flow speed - 0.65 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.392	3.8	-0.28	0.603
Live	-0.597			

Flow speed - 1.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.032	3.0	0.88	0.222
Live	2.840			

Flow speed - 2.1 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.221	4.2	-0.23	0.587
Live	-0.199			

Flow speed - 4.2 cm sec^{-1}

Variable	Mean	df	t	P
Control	0.843	4.0	-0.85	0.779
Live	-1.122			

Flow speed - 6.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.858	3.6	-0.50	0.676
Live	-3.250			

Flow speed - 10.4 cm sec^{-1}

Variable	Mean	df	t	P
Control	-1.228	3.6	-1.26	0.858
Live	-9.744			

Flow speed - 13.7 cm sec^{-1}

Variable	Mean	df	t	P
Control	-0.321	4.9	-1.12	0.843
Live	-10.981			

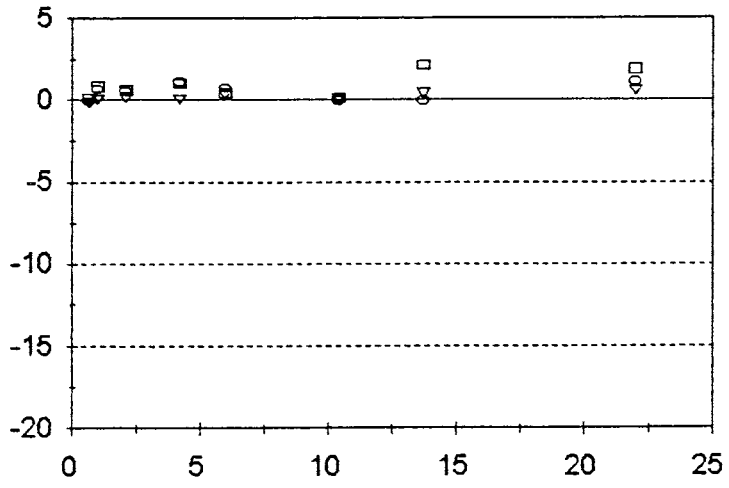
Flow speed - 22.0 cm sec^{-1}

Variable	Mean	df	t	P
Control	-1.088	4.9	-1.51	0.9033
Live	-12.987			

weights for the oysters in E1 and E3 were not used and in the calculation of filtration rates the dry weight for E2 was substituted. Since there was no significant difference in the height between E1, E2, and E3, and the batches were of the same cohort, the mean dry weight from E2 was used for E1, E2, and E3.

Figure 6. Comparison of Control Rates and Filtration Rates, with Controls, Sampling Period 1, and Sampling Period 2 noted as ▽, □, and ○ respectively, in the (A) lower region and (B) upper region

A.



B.

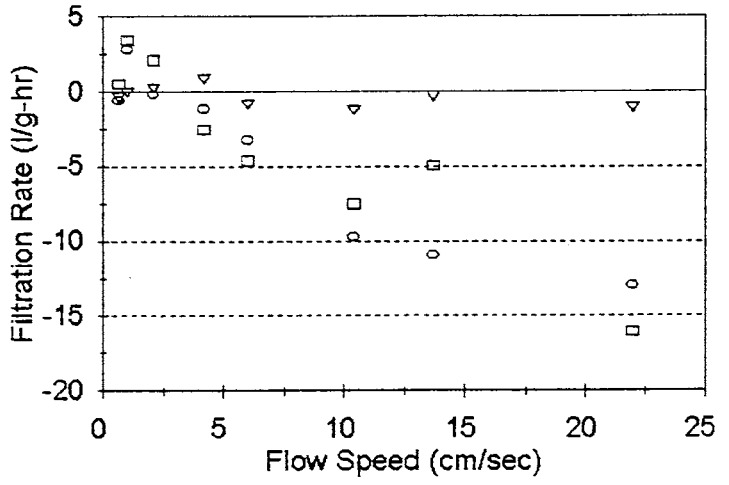
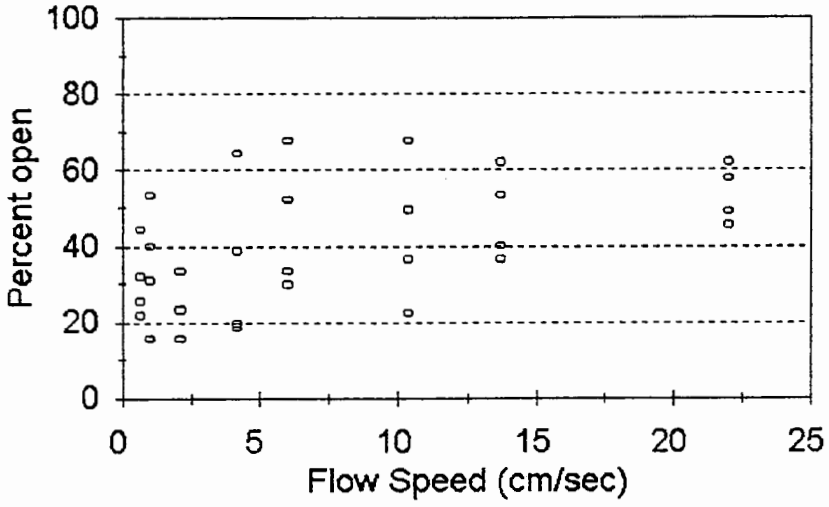


Table 16. Oyster Feeding Behavior in E1, E2, E3, E3 and E4

Batch	Flow Speed (cm/sec)	% of open oysters	% of feces producing oysters
E1	0.65	32	26
E2	0.65	22	9
E3	0.65	26	20
E4	0.65	44	42
E1	1.00	40	33
E2	1.00	31	20
E3	1.00	16	9
E4	1.00	53	51
E1	2.10	16	8
E2	2.10	33	28
E3	2.10	23	18
E4	2.10	23	21
E1	4.20	64	40
E2	4.20	20	14
E3	4.20	19	13
E4	4.20	39	33
E1	6.00	68	57
E2	6.00	33	25
E3	6.00	30	19
E4	6.00	52	50
E1	10.40	68	54
E2	10.40	49	45
E3	10.40	37	30
E4	10.40	22	19
E1	13.70	40	30
E2	13.70	62	49
E3	13.70	53	42
E4	13.70	37	33
E1	22.00	49	38
E2	22.00	62	41
E3	22.00	58	50
E4	22.00	46	38

Figure 7. Oyster Feeding Behavior as a Function of Flow Speed in E1, E2, E3, E4 a) open oysters b) feces producing oysters

a)



b)

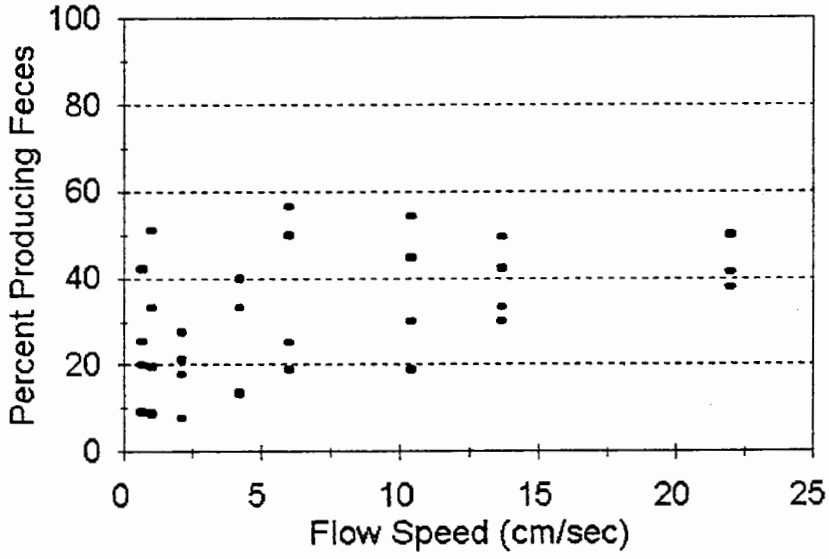


Table 17. Regression analyses of oyster feeding behavior in E1, E2, E3, and E4

Regression Analyses	r^2 (%)	N	P
Flow Speed and Open Oysters	26	32	0.003
Flow Speed and Feces producing Oysters	21	32	0.008
Daily Flow Sequence and Open Oysters	4	32	0.262
Daily Flow Sequence and Feces producing Oysters	12	32	0.058
Experiment Flow Sequence and Open Oysters	0	32	0.961
Experiment Flow Sequence and Feces producing Oysters	1	32	0.586

Table 18. Order of Flows in E1, E2, E3, and E4

Sequential Order of Flows within E1, E2, E3, and E4

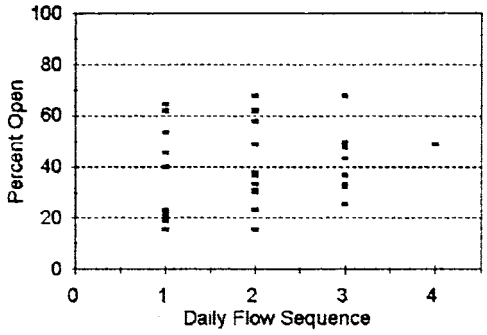
Experiment Flow Sequence	Flow Speed (cm/sec)							
	0.65	1	2.1	4.2	6.0	10.4	13.7	22
E1	8	2	1	3	4	5	6	7
E2	3	4	5	6	7	8	1	2
E3	8	6	7	1	2	3	4	5
E4	6	7	1	2	3	4	5	8

Sequential Order of Flows within Each Day of E1, E2, E3, and E4

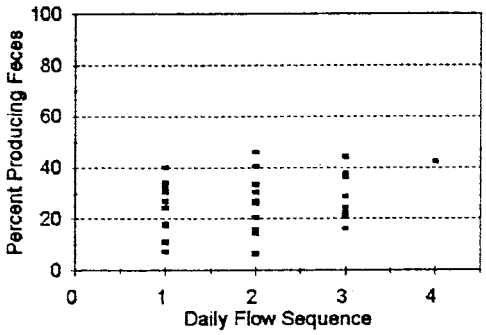
Daily Flow Sequence	Flow Speed (cm/sec)							
	0.65	1	2.1	4.2	6.0	10.4	13.7	22
E1	3	1	2	1	2	3	1	2
E2	1	2	3	1	2	3	1	2
E3	3	1	2	1	2	3	1	2
E4	3	4	1	2	3	1	2	1

Figure 8. Oyster Feeding Behavior as a function of Daily Flow Sequence and Experiment Flow Sequence for E1, E2, E3, and E4

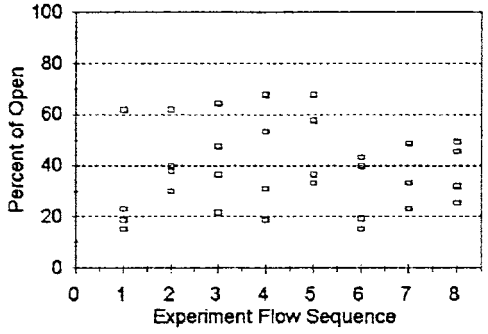
A. E1



B. E2



C. E3



D. E4

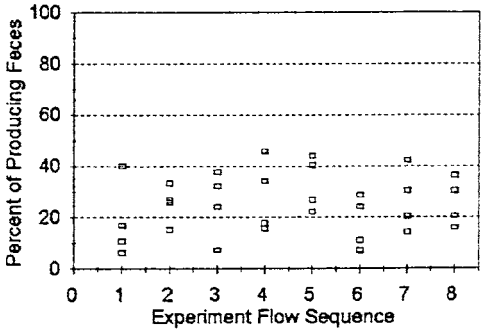


Table 19. Data on batches of oysters used in each experiment

Experiment	Batch	Height (mm)	SD	Width (mm)	SD	AFDW (g)	SD	Condition Index	SD
C1, C2, and C3	CB1	67.7	7	21.7	2.8				
E1	B1	65.2	6	20.6	2.3				
E2	B2	66.1	6	21.4	2.5	0.271	0.101	4.15	1.00
E3	B3	65.3	6	21	2.2				
E4	B4	64.6	6	17.9	2	0.471	0.192	7.22	2.70
C4	CB2	66.8	7	21.2	2.6				
E5	B5	63.9	6	18.9	2.4	0.625	0.256	9.73	3.70
E6	B6	70.9	4	19.7	1.4	1.055	0.197	14.90	2.80

Table 20. Analysis of variance in shell height in E1, E2, E3, E4 and C1.

Source	DF	SS	MS	F	P
Heights	4	279	70	1.78	0.130
Error	445	17455	39		
TOTAL	449	17734			

Experiments with *T. weisflogii* and kaolinite

The lower region control rates and the upper region control rates showed oscillatory patterns across all flow speeds (Fig. 9, Appendix V). The relationship of the lower region control rate and flow speed was not significant (Table 21). The relationship between upper region control rates and flow speed was significant (Table 21).

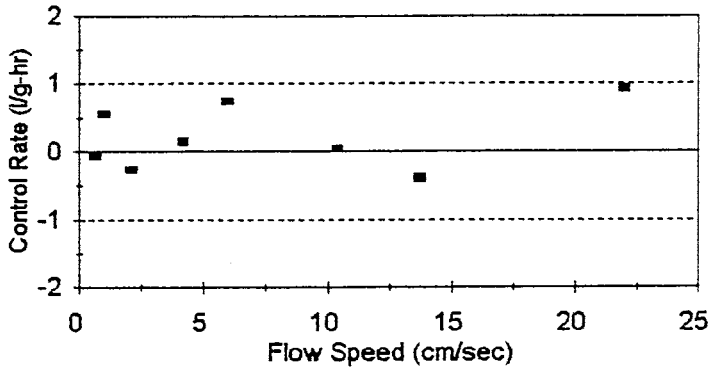
The lower region and the upper region filtration rates tended to increase with flow speeds (Fig. 10) (Appendices VI and VII). Neither the lower region filtration rates nor the upper region filtration rates were significantly different between experiments and flow speeds (Tables 22 and 23). The lower region filtration rates were greater than the control rates for flows $\leq$ 4.2 cm sec^{-1} except at 1.0 cm sec^{-1} (Fig. 11A). Upper region filtration rates were greater than control rates for most flows (Fig. 11B).

During E5 and E6, the percent of oysters open ranged from 24 to 97% and the percent of feces producing oysters ranged from 14 to 79% (Table 24). Although oyster feeding activity varied throughout each experiment, the number of oysters open and the number producing feces were not related to flow speed (Fig. 12) (Table 25). Daily flow sequence and experiment flow sequence were altered for each E5 and E6 (Table 26). Daily flow sequence and experiment flow sequence appeared to have no effect on oyster feeding behavior (Fig. 13 and Table 26).

The E5 and E6 oysters were not cohorts. There were significant differences in the shell heights between the batches (Table 27) with the mean height of each batch being 63.9 mm and 70.9 mm, respectively (Table 19). The shell heights of E5, E6, and C2 were all significantly different (Tables 27 and 28).

Figure 9. Control rates for C4 in the (A) lower region and (B) upper region

A.



B.

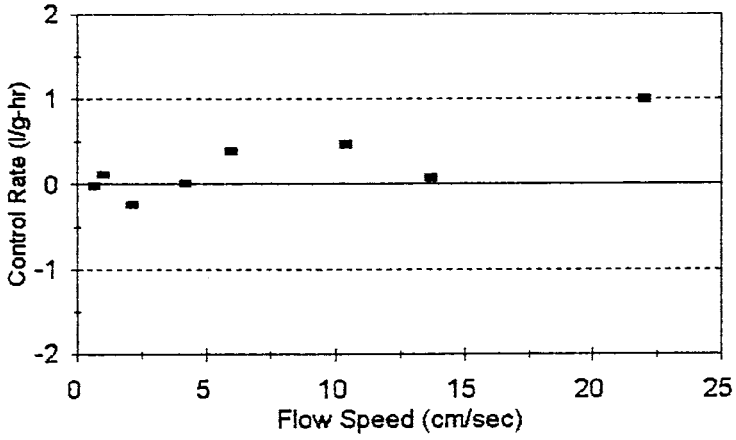


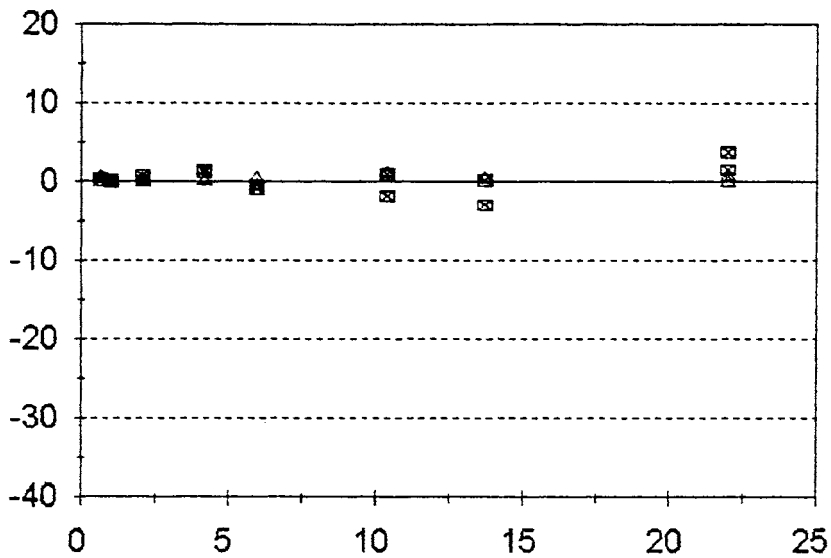
Table 21. Regression Analyses for C4

Analysis - Lower Region	r^2 (%)	N	P
Control Rate and Flow Speed	0.10	8	0.45

Analysis - Upper Region	r^2 (%)	N	P
Control Rate and Flow Speed	0.66	8	0.01*

Figure 10. Oyster filtration rates for E5 and E6, noted as □ and △, respectively, in the (A) lower region and (B) upper region

A.



B.

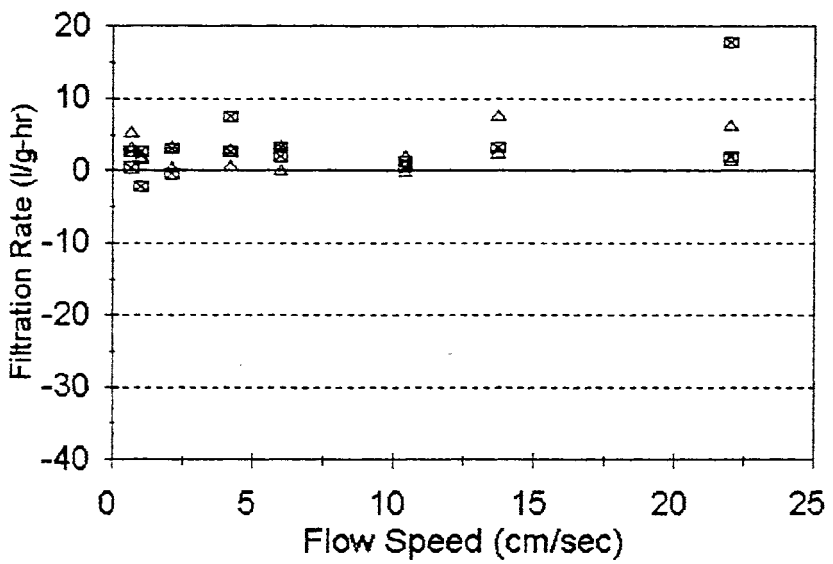


Table 22. Three-Way Analysis of Variance for the lower region filtration rates computed for (A) all oysters, (B) open oysters and (C) oysters producing feces in E5 and E6.

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	0.5	0.5	0.6	0.483
FLOW SPEED (B)	7	12.1	1.7	1.9	0.203
PERIOD (C)	1	0.0	0.0	0.0	0.866
A*B	7	11.8	1.7	1.9	0.214
A*C	1	0.7	0.7	0.8	0.401
B*C	7	5.8	0.8	0.9	0.537
A*B*C	7	6.3	0.9		
TOTAL	31	37.2			

B.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	0.0	0.0	0.0	0.943
FLOW SPEED (B)	7	63.6	9.1	1.8	0.220
PERIOD (C)	1	0.1	0.1	0.0	0.898
A*B	7	54.2	7.7	1.6	0.284
A*C	1	3.8	3.8	0.8	0.411
B*C	7	36.4	5.2	1.1	0.473
A*B*C	7	34.6	4.9		
TOTAL	31	192.7			

C.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	0.9	0.9	0.1	0.780
FLOW SPEED (B)	7	172.6	24.7	2.3	0.152
PERIOD (C)	1	0.4	0.4	0.0	0.851
A*B	7	126.3	18.0	1.7	0.261
A*C	1	6.9	6.9	0.6	0.454
B*C	7	76.7	11.0	1.0	0.498
A*B*C	7	76.3	10.9		
TOTAL	31	460.2			

Table 23. Three-Way Analysis of Variance for the upper region filtration rates computed for (A) all oysters, (B) open oysters and (C) oysters producing feces in E5 and E6.

A.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	1.0	1.0	0.1	0.742
FLOW SPEED (B)	7	109.2	15.6	1.9	0.218
PERIOD (C)	1	4.4	4.4	0.5	0.492
A*B	7	59.2	8.5	1.0	0.499
A*C	1	8.1	8.1	1.0	0.361
B*C	7	128.9	18.4	2.2	0.163
A*B*C	7	59.1	8.4		
TOTAL	31	369.9			

B.

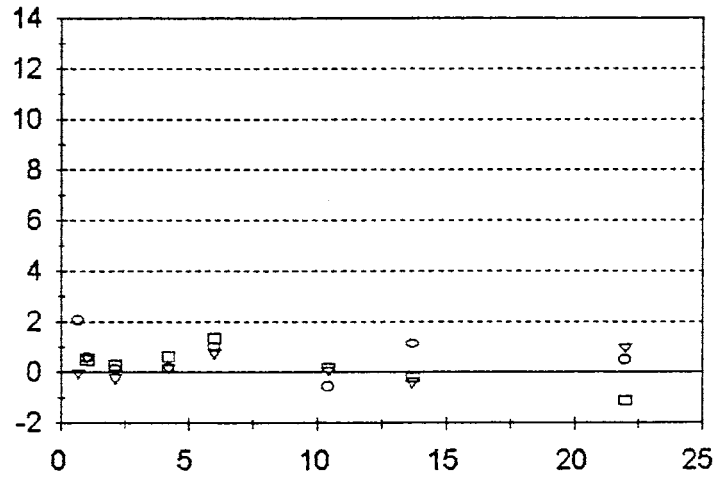
Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	79.8	79.8	1.3	0.290
FLOW SPEED (B)	7	375.0	53.6	0.9	0.566
PERIOD (C)	1	4.6	4.6	0.1	0.792
A*B	7	320.2	45.7	0.8	0.643
A*C	1	18.1	18.1	0.3	0.603
B*C	7	591.3	84.5	1.4	0.339
A*B*C	7	427.1	61.0		
TOTAL	31	1816.2			

C.

Source	DF	SS	MS	F	P
EXPERIMENT (A)	1	352.2	352.2	2.4	0.168
FLOW SPEED (B)	7	990.4	141.5	1.0	0.526
PERIOD (C)	1	9.5	9.5	0.1	0.808
A*B	7	708.6	101.2	0.7	0.688
A*C	1	33.6	33.6	0.2	0.649
B*C	7	1347.1	192.4	1.3	0.372
A*B*C	7	1042.4	148.9		
TOTAL	31	4483.9			

Figure 11. Comparison of control rates and filtration rates, with controls, sampling period 1, and sampling period 2 noted as ▼, □, and ○ respectively, in the (A) lower region and (B) upper region

A.



B.

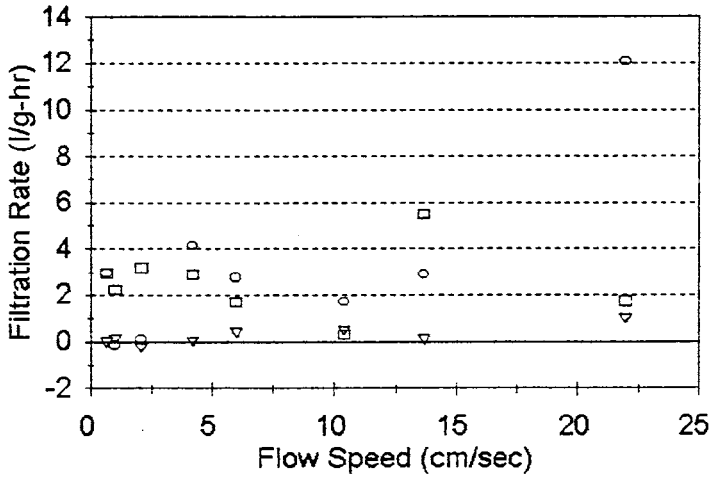
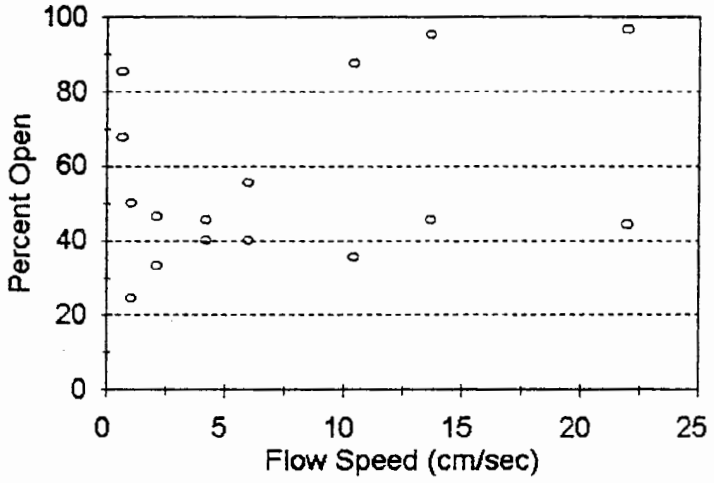


Table 24. Oyster feeding behavior in E5 and E6

Experiment	Flow Speed (cm/sec)	% of open oysters	% of feces producing oysters
E5	0.65	68	49
E5	1.00	24	14
E5	2.10	33	20
E5	4.20	46	21
E5	6.00	40	26
E5	10.40	36	27
E5	13.70	46	28
E5	22.00	44	31
E6	0.65	86	79
E6	1.00	50	38
E6	2.10	47	38
E6	4.20	40	29
E6	6.00	56	53
E6	10.40	88	71
E6	13.70	96	78
E6	22.00	97	64

Figure 12. Oyster feeding behavior as a function of flow speed in E5 and E6 for oysters (A) open and (B) producing feces.

A.



B.

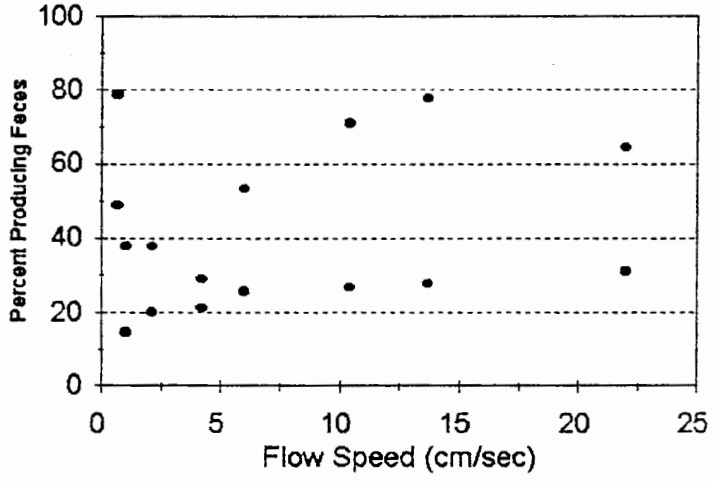


Table 25. Regression analyses of oyster feeding behavior in relation to flow for E5 and E6.

Regression Analyses	r^2 (%)	N	P
Flow and Open Oysters	12	16	0.1848
Flow and Feces producing Oysters	5	16	0.4246
Daily Flow Sequence and Open Oysters	17	16	0.1161
Daily Flow Sequence and Feces producing Oysters	12	16	0.1881
Experiment Flow Sequence and Open Oysters	5	16	0.3910
Experiment Flow Sequence and Feces producing Oysters	2	16	0.6138

Table 26. Sequential order of flows in E5 and E6 (A) over the experiment and (B) within each day.

A. Sequential Order of Flows within E5 and E6

Experiment Flow Sequence	Flow Speed (cm/sec)							
	0.65	1.0	2.1	4.2	6.0	10.4	13.7	22.0
E5	7	1	2	3	4	5	6	8
E6	4	5	6	7	8	1	2	3

B. Sequential Order of Flows within Each Day of E5 and E6

Daily Flow Sequence	Flow Speed (cm/sec)							
	0.65	1.0	2.1	4.2	6.0	10.4	13.7	22.0
E5	4	1	2	3	1	2	3	1
E6	4	1	2	1	2	1	2	3

Figure 13. Oyster feeding behavior as a function of daily flow sequence and experiment flow sequence in (A & B) E5 and (C & D) E6.

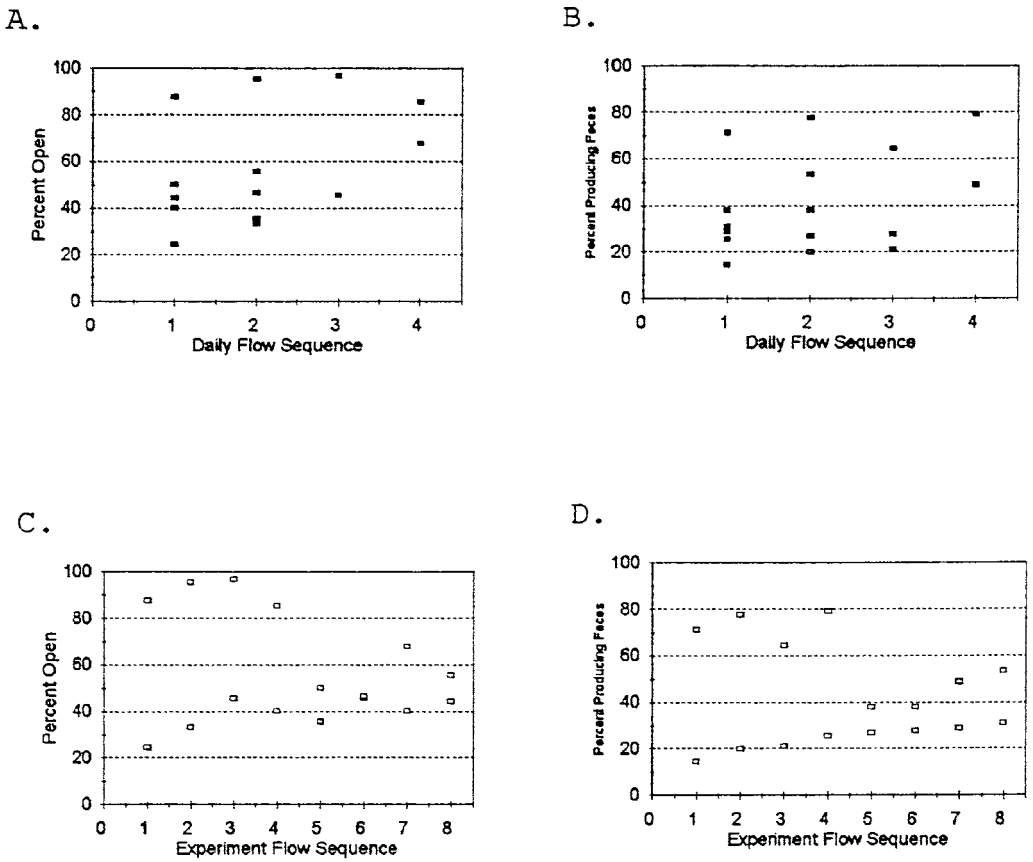


Table 27. Analysis of Variance in shell height for (A) E5, E6, and C2 and (B) E1, E2, E3, E4, E5, and E6.

A.

Source	DF	SS	MS	F	P	
Height	2	2180	1090	29.74	0.000	*
Error	267	9782	37			
TOTAL	269	11962				

B.

Source	DF	SS	MS	F	P	
Height	5	2810	562	16.55	0.000	*
Error	534	18138	34			
TOTAL	539	20947				

Table 28. Analysis of variance in condition index for E2, E4, E5, and E6 oysters.

Source	DF	SS	MS	F	P	
Index	3	5488	1829	238	0.000	*
Error	350	2693	8			
TOTAL	353	8181				

Table 29. Tukey's a posteriori multiple comparison tests for the height of oysters

A. Experiments E5, E6, and C2

Batch	Homogeneous Groups		
C2	*		
E5		*	
E6			*

B. All experiments with live oysters

Batch	Homogeneous Groups	
E1	*	
E2	*	
E3	*	
E4	*	
E5	*	
E6		*

There were significant differences in the condition indices for E2, E4, E5 and E6 (Tables 19 and 28). The condition indices for each batch were significantly different from one another (Table 29). Both flow speed and the condition index had significant effects on the number of oysters producing feces for all experiments (Table 30). The feeding activity in E6 was significantly greater than that for all other batches (Table 30). There were also significant differences between the shell heights of different batches of live oysters used in all experiments (Table 29) and again the E6 oysters were significantly larger than all other batches (Table 30).

Particle Concentrations

The *Thalassiosira weisflogii* concentrations for E5, E6, and C4 were calculated from cell counts at two threshold settings on the Coulter Counter. To measure the error associated in calculating the *T. weisflogii* concentrations from the experiments, E5, E6, and C4, the relationship between chlorophyll *a* concentrations and *T. weisflogii* cell concentrations from E1, E2, E3, E4, C1, C2, and C3 was compared with the relationship from E5, E6, and C4. The relationships were both positive (Table 31 and Fig. 14). Yet, at all *T. weisflogii* particle levels, the associated chlorophyll concentration was greater for each respective *T. weisflogii* cell concentration in the E5, E6, and C4 when compared with the cell concentration of E1, E2, E3, E4, C1, C2, and C3.

Table 30. Analysis of oyster feeding behavior between batches; (A) two-way ANOVA and (B) Tukey's *a posteriori* comparison among batches

A.

Source	DF	SS	MS	F	P
Batch (A)	5	5454	1090	5.98	0.000
Flow (B)	7	3526	504	2.76	0.021
A * B	35	6382	182		
TOTAL	47	15359			

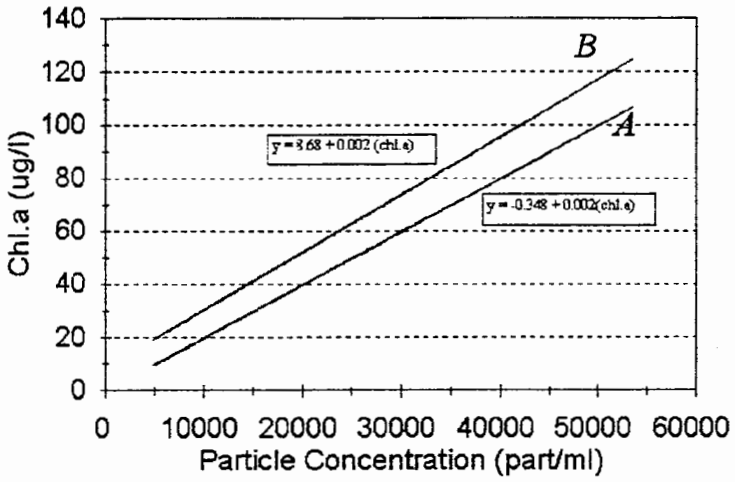
B.

Batch	Homogeneous Groups	
E1	*	
E2	*	
E3	*	
E4	*	
E5	*	
E6		*

Table 31. Regression of chlorophyll *a* concentrations and *T. weisflogii* cell concentrations from all experiments.

Regression Analyses	y intercept	x coefficient	r^2 (%)	N	P
E1, E2, E3, E4, C1, C2, and C3	-0.348	0.002	85.0	417	0.00
E5, E6, and C4	8.68	0.002	69.2	192	0.00

Figure 14. Regression of chlorophyll *a* concentrations and *T. weisflogii* cell concentrations from (A) E1, E2, E3, E4, C1, C2 and C3, and (B) E5, E6 and C4.



Field experiment

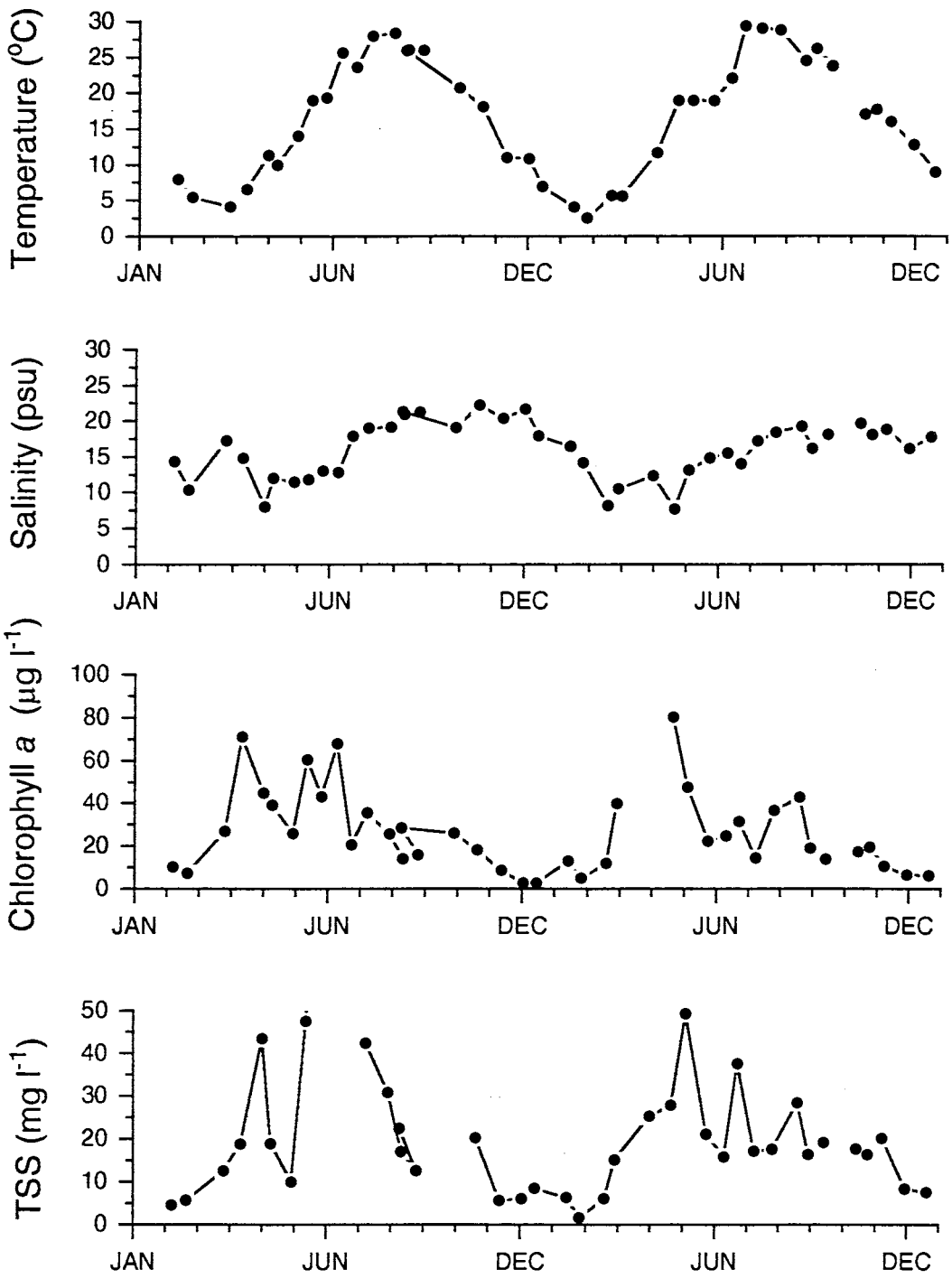
Water quality

The springs of 1993 and 1994 were marked by record high percipitation and run-off in the Chesapeake Bay watershed. At the Catlett Islands salinity dropped to around 6‰ in each of these springs, down about 10‰ from normal salinity in the region (Fig. 15). Turbidity levels at the site were extremely high at the site during the spring of both years as a result of phytoplankton blooms and suspended solids. Chlorophyll *a* levels were between 60 and 80 $mg \cdot l^{-1}$ during the springs of 1993 and 1994. Total suspended solids above 45 $mg \cdot l^{-1}$ were measured in both years and levels above 30 $mg \cdot l^{-1}$ were recorded throughout much of the spring (Fig. 15). These levels exceed those measured at the site in most previous years and the minimum habitat requirements developed by Batuik et al. (1992).

Oysters and SAV

Several aspects of water quality and experimental design lead to a failure of the field experiments with oysters and SAV to produce meaningful results. First, as indicated above both 1993 and 1994 were exceptionally wet years, leading to much lowered salinities at the site. *Z. marina* transplants, which were established in the preceding fall and grew well through the winter, were in poor condition in the spring prior to the addition of oysters. This occurred in 1993 and 1994 and we initially attributed it to the reduced mean salinity at the site. Recent work by Moore (unpublished) indicates the importance of pulsed changes in salinity, turbidity and nutrient levels in the survival of *Z. marina* and it now seems likely that a variety of water quality factors may have affected the health of the plants.

Figure 15. Biweekly water sample data from the Catlett Islands from January 1993 - December 1994. (TSS: Total Suspended Solids)



In 1993 the oysters and the manner in which they were deployed around the transplants also had a negative effect upon the survival of plants. At the time the oysters were deployed to the site the salinity at the site was 11‰, considerably lower than the 22‰ from which they were taken in Pungoteague Creek. This degree of salinity change is likely to have reduced oyster filtration rates and apparently resulted in some mortality of oysters, especially those weakened by *Perkinsus marinus* infections.

Additionally, the rack structures which contained the oysters resulted in a reduction in current velocity leading to deposition of suspended sediments. Together with macroalgae which became entrapped, these sediments covered the plants resulting in near compleate mortality.

During a no-cost extension to the project in 1993 and 1994, we hoped to overcome these problems by moving the experimental plots to a less exposed site and modifying the manner in which the oysters were deployed. Again, however, water quality problems arose. Even as the oysters were being deployed it was clear that the grass was dying and that salinities were once again in the range that the oysters themselves were highly stressed. At this stage we deemed it prudent to redirect the remaining resources to the enhancement of the flume experiments which were yielding meaningful results.

DISCUSSION

Oyster Filtration in the Flume Experiments

The filtration capacity of an oyster bed is not solely a function of the cumulative filtration rate of the oysters, but is a function 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 and associates (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. Physical parameters are inherent to the oyster environment, yet their influence on oyster filtration rate and the community level effects are just now being investigated. Significant differences in filtration rates between experiments, E1, E2, E3, and E4, can be attributed to variation in hydrodynamic and biotic factors.

In these experiments, particle reductions of the expected magnitude were not measured. When an expected filtration capacity of the bed was calculated using 5 l hr^{-1} g^{-1} (from Newell 1988) and the volume flux through the flume, the 90 oysters yielded a predicted rate of 75 ml sec^{-1}, a rate which should have reduced particle concentrations 63% to 2% with increasing flow speed. Factors which may have contributed to the measured rates being lower than expected were 1) the effect of water flowing 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 experiments were expected to be a measure of the effect of flow speed on the change in particle concentration across the oyster bed. In the upstream parcel, the greatest relative concentration should have been adjacent to the bed while a more uniform vertical profile was expected downstream of the bed due to the vertical uplift and turbulent mixing of particles. A logarithmic particle profile was expected upstream of the oyster bed, as proposed by the Rouse equation. Once the parcel reached the bed, particles in the lower region should have been uplifted by turbulent eddies above the bed of oysters, as seen in dye flow studies. The vertical particle concentration profiles across all experiments and controls were evaluated across all flow speeds and experiments (Appendix VIII). Yet, the vertical particle concentration profiles and the change in particle concentrations varied between controls and experiments. For each flow speed, no single function could describe the vertical concentration profiles nor the change in particle concentration across all experiments, control and live experiments.

The vertical particle profiles were not as expected, but instead varied across replicate controls, live experiments, and flow speeds. Turbulence is a function of the flow speed and the roughness of the bed (Frechette et. al., 1989). In this study for all flow speeds greater than 2 cm s^{-1}, the flow conditions were turbulent (as defined by the Reynolds number). At the smooth-rough bed transition, the lower region particles were expected to be uplifted to the upper region as flow was accelerated due to the decrease in the channel's cross-sectional area above the bed. For each flow speed, the redistribution of particles was not consistent across experiments, live and controls. The inability to define the vertical particle profiles in the controls indicates that the turbulent effects can have significant effects on particle concentrations.

Between experiment variance in filtration rates increased with increasing flow speeds and was greatest in the upper region filtration rates. Increased variance reflected the increased turbulent modification of particle distribution with increasing flow speed and distance from the bottom. 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.

The oyster bed configuration 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 inherently different between experiments. Regions of depression between the oyster shells create quiescent regions which could potentially enhance particle deposition and increase the resident time of the parcels within the bed (Nowell and Jumars, 1987). Bed roughness is a function of the height of the components above the bottom. Not only would differences in the width of the oysters create differences in bed roughness, but in the live experiments open oysters would protrude higher than closed shells into the water column. The variation in the bottom topography between each batch was further enhanced by the number of oysters open and their location within the bed. Between experiment variation in filtration rates occur even when the height of the oyster batches were not statistically different. Therefore, some of the hydrodynamic effects can be attributed to the interaction of the spatial arrangement of oysters and their respective shell heights and widths.

The non-uniform particle redistribution due to turbulent mixing may have obscured some of the biological impact on particle concentration. Filtration rates reported at low

flow speeds are within the range of previously reported rates (Table 1). These rates are also approximately the same as the "lower curve" rates which Powell and associates believed best represent the filtration rates in the field. Although there were not significant differences between the filtration rates and the control rates, the lower region filtration rates were greater than the control rates for flow speeds $\leq$ 4.2 cm sec^{-1} and the upper region filtration rates were greater than the control rates for flow speeds $\leq$ 1.0 cm sec^{-1} and lower (Tables 12 and 13, Fig. 6). 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.

Using feces production and shell gape as indicators of feeding activity, flow speeds up to 22 cm/sec did not inhibit oyster feeding activity in these experiments. There was a positive relationship between oyster feeding behavior and increasing flow speeds. Wildish et al. (1993) speculated that although shell gape and filtration rates of *Placopecten magellanicus* decreased with increasing flow speed, ingestion rates can remain high at sufficiently high algal concentrations. It was not until flow speeds exceeded 30 cm s^{-1} that the filtration activity of *Placopecten magellanicus* ceased (Wildish et al., 1993). Grizzle et al. (1992) found that there was a negative relationship between growth rates of *Crassostrea virginica* and flow speeds > 1 cm s^{-1} and these decreased growth rates can apparently be attributed to decreased filtration rates (Wildish and Saulnier, 1984).

The apparent difference between the positive relationship between feeding behavior and flow speed observed in these experiments and the negative relationship between growth rates and flow speed in Grizzle's experiments may be due to differences in

experimental design or reduced filtration efficiencies. The oysters in the experiment by Grizzle et al. (1992) were placed with the hinge facing into the direction of flow, whereas in this study, the oysters were placed with the beak facing into the direction of the flow. The orientation of the *Argopecten irradians concentricus* was shown to have an effect on the pressure exerted by the external water on the inhalant region (Eckman et al., 1989) and the same may be true for *Crassostrea virginica.* At faster flow speeds, an external water pressure greater than the inhalant - exhalent pressure differential may occur and should have a negative effect on the filtration rates. The pressure of the external flow on the inhalant region of an oyster within the bed will be affected by local flow variations and by skimming flow. Yet, the physical structure of the bed may moderate the pressure of the external flow. Thus, in these flume experiments, the pressure of the external water directly adjacent to the inhalant of the oyster may have been much lower for each respective flow speed due to the baffling effect of the bed.

In these experiments, the inhibition of feeding activity was not observed for flow speeds up to 22 cm s^{-1}. Although the relationship between shell gape and flow speed was not evaluated in this study, the oysters may have reduced their shell gape to compensate for increasing external pressure with increasing flow speeds. It is possible that at higher flows, the algae concentration was not of sufficient quantity to promote faster growth rates in the experiments by Grizzle and associates (1992). The differences between this study and theirs may have been the result of differences in orientation, flow speed, and algae concentrations and their effects on oyster feeding behavior.

The feeding behavior of the oysters may also be affected by the health of the oysters within the bed. The mean condition index, the ratio of dry weight to shell height, of each

batch was used as an indicator of the batch's health. The larger the index value the presumed better health of the oysters. In these experiments, the condition index of oysters varied across experiments with Batch 6 having the highest index. This significantly greater condition of Batch 6 may have contributed to the significantly greater percent of oysters producing feces across the batches. The condition index appears to have an influence on the percent of oysters filtering at any one time. The effective filtration capacity of a bed of oysters is dependent on the actual number of oysters filtering at any one time and the individual filtration rate of those feeding oysters.

Since water flowing can enhance the vertical flux of particles through turbulent mixing and reduce seston depletion, a minimum velocity of water is required to transport sufficient food to a reef for its continued growth and survival. Seston is replenished in the region directly above the oysters by the vertical flux of particles. The vertical flux is facilitated by turbulent mixing which is a function of flow speed and bed roughness. At low flows, the possibility of particle depletion increases due to the lower turbulence and the greater residence time above the bed. Less vertical repletion of particles would be expected at low levels of turbulence, and at sufficient bivalve densities, seston depletion could occur. For the filtration activity of a bed of bivalves to impact a system, the suspended particles must be circulated into the feeding zone of the oysters, so unless vertical mixing occurs filtration of that material cannot occur.

A balance between the inhibition of feeding activity at increasing flow speeds and sufficiently large algae concentrations to support oyster growth, even at the depressed filtration rates, are required for continued growth. Unsatisfactory food quality and quantity should reduce growth rates. Although kaolinite is not a satisfactory food, it did

not appear to adversely affect feeding activity in this study. Urban and Kirchman (1992) speculated that turbidity may actually increase ingestion of certain organic particles by decreasing particle rejection. The level of turbidity should alter the absolute filtration rates of oysters. At very high kaolinite concentrations, filtration may be inhibited even with organic components present. Particle composition and concentration will affect the filtration rates of non-siphonate bivalves.

In an estuarine system the factors influencing the removal of particles from the water column by a group of oysters (on a reef or in an aquaculture operation) are complex. As shown by these experiments, the filtration capacity of an oyster bed is not simply the cumulative filtration rate of the individual oysters in the bed. Interaction of the bed with the surrounding water column is dependent upon hydrodynamic factors which may be influenced by subtle changes in bed morphology. The ecological function of the bed may be related to the health of the oysters within the bed and the local conditions which will vary within the bed. Neither the flow-mediated effects nor the variance in filtration rate related to oyster condition have been incorporated into the extrapolations of system-level effects. Improved system-level ecological models should take into account flow, particle concentration, particle composition, seston depletion, refiltration, vertical exchange of particles, and the actual number of oysters filtering at any one time.

Estimating the Effects of Oyster Filtration in the Field

Unfortunately, our efforts to establish experimental plots of oysters in the field and measure clearance rates *in situ* were unsuccessful. Record precipitation dropped the salinity at the Catlett Island site. While both eelgrass and oysters can tolerate low salinities

in the observed range, these values are near tolerance limits for *Zostera marina* and sub-optimal for *Crassostrea virginica*. Additionally, the elevated seston levels reduced light penetration, further stressing the eelgrass transplants. Prior to the deployment of oyster in both 1993 and 1994, the *Z. marina* transplants were severelly stressed, presumably from a combination of low salinity and low light availability. At the site of this study the strusctures used for containment in the 1993 deployment contributed to particle deposition and trapping of macroalgae which smothered the plants. Further, seston concentrations in the water column at the site during the period of the oyster deployments were so elevated that calculations based upon even the highest reported rates for oyster filtration indicate that an extraodinary number of oysters would be required to affect water clarity.

The flume studies, however, point to an even more fundamental problem associated with estimating seston depletion in the field. The redistribution of particles associated with the generation of turbulence by the oysters, their natural reef or the aquaculture containment system make not only the estimation of biological filtration effects difficult, but pose real sampling difficulties in estimating net change in seston concentration. The spatial and temporal variability in local seston concentration imparted by turbulent fluctuations limit our ability to clearly identify biological effects. This has implcations for management. Evaluating the water quality effects *in situ* of shellfish culture operations and oyster reefs will require adequate replication across spatial and temporal scales of variation.

CONCLUSIONS

Clarifying the interactions between hydrodynamics, morphology of an oyster bed, seston distribution and filtration rate is required to better define the filtration capacity of an oyster reef or aquaculture operation. As shown by these experiments, the filtration capacity of a group of oysters is not simply a summation of still water rates for individual oysters. The effects of flow velocity, seston depletion, refiltration, flow speed, particle composition, and particle concentration on the individual filtration rates of oysters are needed to quantify material porcessing by a group of oysters.

Additional information about the effect of flow speed on oyster filtration behavior is needed. Decreased growth rates of oysters have been observed above a relatively low (1 cm sec^{-1}) flow speed (Grizzle et. al. 1992). Yet, flow speeds greater than 1 cm sec^{-1} are prevalent in regions surrounding oyster reefs and may be necessary to provide sufficient food flux. The physiological condition of oysters may be affected by numerous factors including disease status, salinity and reproductive cycle; this study clearly indicates that physiological condition (as indicated by a condition index) may have a very significant influence on the net filtration of a group of oysters. As positive environmental impacts of oysters, in part related to water quality, are increasingly being proffered as justification for the restoration of natural reef populations and the support of aquaculture, the importance of refining our understanding of oyster filtration on water quality grows. This work provides a foundation for continued investigations in this area.

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APPENDICES

Appendix I. Control rates in lower region for C1, C2, C3.

Experiment	Upstream Flow Speed (cm/sec)	Upstream Sampling Period	Downstream Chlorophyll a Concentration (ug/l)	Control Rates Particle Concentration (part/ml)	Particle Concentration (part/ml)	Average m-allo-all (l/shell-hr)	Average (l/g-hr)**
Control 1	0.65	1					
Control 1	0.65	2	22.60	7362	11151	-0.3028	-0.5002
Control 1	1	1	12.90	9398	10384		
Control 1	1	2	24.95	9638	10151	-0.0851	-0.1406
Control 1	2.1	1	15.10	6203	6411		
Control 1	2.1	2	29.35	9584	8839	0.0564	0.0931
Control 1	4.2	1	23.70	7557	7989		
Control 1	4.2	2	41.50	11583	11441	-0.1020	-0.1686
Control 1	6	1	34.36	13763	13281		
Control 1	6	2	52.75	22548	21912	0.2164	0.3575
Control 1	10.4	1	41.25	20808	21950		
Control 1	10.4	2	22.75	26985	26683	-0.2462	-0.4068
Control 1	13.7	1	50.00	36793	36113		
Control 1	13.7	2	74.70	45360	46256	-0.0072	-0.0120
Control 1	22	1	32.25	40768	40975		
Control 1	22	2	74.50	57446	60022	-0.6039	-0.9976
Control 2	0.65	1					
Control 2	0.65	2		23102	19197	0.1350	0.2231
Control 2	1	1	39.00	18025	15065		
Control 2	1	2	39.00	18497	18800	0.0915	0.1512
Control 2	2.1	1	51.25	21491	19598		
Control 2	2.1	2	45.75	23055	21712	0.1794	0.2963
Control 2	4.2	1	55.00	26906	25649		
Control 2	4.2	2	68.50	32639	31983	0.1606	0.2654
Control 2	6	1	63.20	27587	26674		
Control 2	6	2	72.50	31824	29900	0.3232	0.5339
Control 2	10.4	1	97.50	49200	46719		
Control 2	10.4	2	103.50	56457	53843	0.5784	0.9556
Control 2	13.7	1	26.00	16739	15764		
Control 2	13.7	2	80.50	41483	39994	0.7425	1.2267
Control 2	22	1	121.35	69711	67840		
Control 2	22	2	176.00	82793	79107	0.8979	1.4833
Control 3	0.65	1		8816	9889		
Control 3	0.65	2		6885	8223	-0.1066	-0.1761
Control 3	1	1	15.75	24008	21392		
Control 3	1	2	50.25	22612	19480	0.1484	0.2451
Control 3	2.1	1	36.75	20104	18708		
Control 3	2.1	2	33.50	16870	16297	0.1255	0.2073
Control 3	4.2	1	16.20	11192	10966		
Control 3	4.2	2	14.70	9032	8865	0.0919	0.1518
Control 3	6	1	19.40	10787	10287		
Control 3	6	2	21.10	11916	11899	0.1646	0.2719
Control 3	10.4	1	24.25	14161	13572		
Control 3	10.4	2	22.70	12962	13727	-0.0868	-0.1435
Control 3	13.7	1	27.50	15656	15867		
Control 3	13.7	2	29.25	17600	17329	0.0164	0.0270
Control 3	22	1	19.00	10577	10370		
Control 3	22	2	21.65	12750	12151	0.8375	1.3836

Appendix II. Control rates in upper region for C1, C2, and C3

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Concentration (ug/l)	Upstream Chlorophyll a Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Control Rates Particle m-all (l/shell-hr)*	m-all (l/g-hr)**
Control 1	0.65	1					
Control 1	0.65	2	19.47	7679	8140	-0.2411	-0.3983
Control 1	1	1	22.70	9274	8702		
Control 1	1	2	26.37	8788	10152	-0.2562	-0.4233
Control 1	2.1	1	14.77	5750	6219		
Control 1	2.1	2	27.67	9067	9148	-0.5822	-0.9618
Control 1	4.2	1	19.51	7057	7689		
Control 1	4.2	2	31.83	10611	10954	-1.5710	-2.5955
Control 1	6	1	29.83	13152	13716		
Control 1	6	2	38.00	21032	22461	-2.0550	-3.3950
Control 1	10.4	1	33.83	19752	20543		
Control 1	10.4	2	39.92	25640	26797	-2.7579	-4.5562
Control 1	13.7	1	52.32	33869	36345		
Control 1	13.7	2	80.00	46201	45694	-2.5921	-4.2823
Control 1	22	1	58.17	39414	41389		
Control 1	22	2	84.47	55349	57302	-5.8442	-9.6551
Control 2	0.65	1					
Control 2	0.65	2		25010	24791	0.0364	0.0601
Control 2	1	1	43.17	20826	20324		
Control 2	1	2	35.83	19071	18579	0.1609	0.2658
Control 2	2.1	1	51.25	21491	19598		
Control 2	2.1	2	45.75	23055	21712	1.0163	1.6791
Control 2	4.2	1	55.50	28751	26239		
Control 2	4.2	2	58.33	32924	30497	2.2429	3.7055
Control 2	6	1	58.00	27849	27786		
Control 2	6	2	54.17	30989	31792	-0.4449	-0.7350
Control 2	10.4	1	95.00	47609	45496		
Control 2	10.4	2	95.33	55380	55185	1.6180	2.6731
Control 2	13.7	1	32.17	17134	15723		
Control 2	13.7	2	69.83			7.4859	12.3673
Control 2	22	1	137.67	69412	69397		
Control 2	22	2	173.67	80177	79532	0.5793	0.9570
Control 3	0.65	1	14.63	9219	9231		
Control 3	0.65	2	10.57	6355	8115	-0.5079	-0.8391
Control 3	1	1	48.50	23848	22236		
Control 3	1	2	43.50	19312	20466	0.0381	0.0630
Control 3	2.1	1					
Control 3	2.1	2	32.33	16753	16795	-0.0333	-0.0549
Control 3	4.2	1	19.17	10419	10213		
Control 3	4.2	2	14.70	9459	9049	0.8583	1.4180
Control 3	6	1	21.10	11054	10518		
Control 3	6	2	20.60	11796	11799	0.9411	1.5548
Control 3	10.4	1	20.33	13586	13374		
Control 3	10.4	2	20.22	12485	13108	-1.0897	-1.8002
Control 3	13.7	1	24.67	14933	15540		
Control 3	13.7	2	28.33	17012	18538	-5.4771	-9.0485
Control 3	22	1	18.50	10588	10636		
Control 3	22	2	24.23	13664	12978	3.2885	5.4328

Appendix III. Filtration rates in the upper region for E1, E2, E3, and E4

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Oyster Filtration Rates m-all (l/g-hr)*	m-open (l/g-hr)*	m-feces (l/g-hr)*
1	0.65	1	52.17	21345	22298	-0.67	-2.07	-2.61
1	0.65	2	36.83	15843	16780	-0.88	-2.72	-3.43
1	1	1	18.63	11132	12204	-2.16	-5.40	-6.48
1	1	2	18.23	10678	12234	-3.20	-7.99	-9.59
1	2.1	1	13.33	8851	9515	-3.57	-22.93	-45.86
1	2.1	2	19.70	10787	11216	-1.92	-12.35	-24.70
1	4.2	1	32.17	16483	16613	-0.78	-1.21	-1.94
1	4.2	2	45.67	22833	23251	-1.79	-2.78	-4.48
1	6	1	48.33	25372	27235	-9.99	-14.74	-17.63
1	6	2	59.83	30955	33386	-10.66	-15.72	-18.80
1	10.4	1	63.12	35156	36417	-8.61	-12.71	-15.82
1	10.4	2	71.67	37052	40922	-24.28	-35.82	-44.60
1	13.7	1	36.33	17310	18595	-23.05	-57.61	-76.82
1	13.7	2	38.83	20586	22668	-31.01	-77.53	-103.4
1	22	1	59.83	26392	28101	-32.43	-66.34	-85.85
1	22	2	109.00	47772	50529	-29.00	-59.32	-76.77
2	0.65	1	16.67	9903	9169	1.18	5.39	12.80
2	0.65	2	9.87	5880	6100	-0.56	-2.58	-6.12
2	1	1	39.67	19912	18042	2.32	7.47	11.86
2	1	2	48.83	19402	19512	-0.13	-0.42	-0.67
2	2.1	1	35.00	17924	16771	3.28	9.84	11.89
2	2.1	2	41.43	16243	17177	-2.76	-8.28	-10.00
2	4.2	1	24.70	11898	13348	-11.35	-58.09	-82.30
2	4.2	2	31.00	14262	14901	-4.33	-22.14	-31.36
2	6	1	31.83	14676	15100	-4.02	-12.05	-15.88
2	6	2	40.17	19306	20138	-5.95	-17.85	-23.53
2	10.4	1	35.33	15745	16828	-16.25	-32.88	-36.25
2	10.4	2	47.83	17600	18694	-14.73	-29.80	-32.85
2	13.7	1	38.33	24441	24071	4.90	7.90	9.92
2	13.7	2	90.00	39702	39688	0.12	0.19	0.24
2	22	1	109.00	48050	49622	-16.64	-26.81	-40.22
2	22	2	189.00	77134	79215	-13.76	-22.17	-33.26
3	0.65	1	24.99	19784	16657	2.63	10.28	13.14
3	0.65	2	24.10	18225	16854	1.19	4.67	5.97
3	1	1	23.37	22451	21501	1.02	6.53	11.43
3	1	2	25.33	23008	20472	2.74	17.64	30.87
3	2.1	1	20.63	16384	15584	2.47	10.58	13.89
3	2.1	2	24.50	18246	16662	4.48	19.20	25.20
3	4.2	1	25.67	15827	15492	2.11	11.16	15.81
3	4.2	2	27.50	19026	19165	-0.72	-3.81	-5.40
3	6	1	39.67	26624	28965	-11.88	-39.61	-62.91
3	6	2	52.50	33244	34841	-6.62	-22.05	-35.02
3	10.4	1	57.67	37571	38653	-6.94	-18.93	-23.13
3	10.4	2	58.83	46935	48080	-5.89	-16.06	-19.63
3	13.7	1	53.33	35307	35438	-1.19	-2.24	-2.83
3	13.7	2	70.33	42020	42542	-3.98	-7.46	-9.42
3	22	1	59.00	44880	47770	-32.26	-55.83	-64.51
3	22	2	81.17	54114	55340	-11.98	-20.04	-23.16
4	0.65	1	7.23	9219	10337	-1.00	-2.26	-2.38
4	0.65	2	1.21	6355	8115	-2.14	-4.82	-5.08
4	1	1		21720	8521	12.63	23.67	24.70
4	1	2		24079	9936	11.94	22.40	23.37
4	2.1	1	41.83	21231	17004	6.29	26.96	29.80
4	2.1	2	27.70	15521	15850	-0.59	-2.55	-2.81
4	4.2	1	38.17	20739	20757	-0.05	-0.13	-0.15
4	4.2	2	26.33	17679	16961	2.35	6.04	7.05
4	6	1	32.50	16579	15113	7.50	14.35	14.99
4	6	2	33.50	17740	15638	10.21	19.55	20.42
4	10.4	1	31.33	16389	16190	1.72	7.73	9.09
4	10.4	2	27.83	14477	13879	5.92	26.64	31.34
4	13.7	1	24.67	12140	12174	-0.52	-1.42	-1.56
4	13.7	2	22.80	9412	9885	-9.05	-24.69	-27.16
4	22	1		16264	15357	17.05	37.42	45.13
4	22	2		15442	15297	2.79	6.13	7.40

Appendix IV. Filtration rates in the lower region for E1, E2, E3, and E4

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Oyster Filtration Rates m-all (l/g-hr)*	m-open (l/g-hr)*	m-feces (l/g-hr)*
1	0.65	1	49.00	24206	21523	0.32	0.98	1.24
1	0.65	2	36.50	16215	16558	-0.06	-0.17	-0.22
1	1	1	19.85	12104	11984	0.04	0.10	0.12
1	1	2	19.50	12034	11350	0.24	0.61	0.73
1	2.1	1	15.01	9055	9098	-0.04	-0.26	-0.53
1	2.1	2	18.75	11287	10831	0.36	2.31	4.62
1	4.2	1	32.25	16626	15304	1.44	2.24	3.61
1	4.2	2	45.00	24852	21906	2.20	3.41	5.49
1	6	1	50.00	26877	26073	0.75	1.11	1.33
1	6	2	52.25	32802	30917	1.47	2.17	2.60
1	10.4	1	72.25	37692	35341	2.78	4.10	5.10
1	10.4	2		39947	39469	0.52	0.77	0.95
1	13.7	1	53.50	18908	18108	2.46	6.14	8.19
1	13.7	2	39.25	23199	21856	3.39	8.47	11.30
1	22	1	118.00	27896	27228	2.21	4.52	5.85
1	22	2	66.50	51083	49698	2.51	5.13	6.64
2	0.65	1	17.55	10170	8404	0.51	2.35	5.59
2	0.65	2	9.75	5445	5636	-0.09	-0.42	-1.01
2	1	1	47.50	21503	17205	0.92	2.98	4.73
2	1	2	50.25	20505	21891	-0.27	-0.87	-1.39
2	2.1	1	46.00	20080	16599	1.66	4.97	6.01
2	2.1	2	42.50	19477	16815	1.28	3.84	4.64
2	4.2	1	29.00	12590	12441	0.21	1.06	1.50
2	4.2	2	32.38	15061	14657	0.47	2.43	3.44
2	6	1	39.25	15081	15086	-0.01	-0.02	-0.03
2	6	2	48.00	19646	20188	-0.68	-2.03	-2.68
2	10.4	1	36.20	15792	17295	-3.92	-7.93	-8.74
2	10.4	2	33.33	16804	16513	0.75	1.52	1.68
2	13.7	1	105.50	25672	24508	2.64	4.25	5.33
2	13.7	2	51.75	40504	42918	-3.29	-5.30	-6.65
2	22	1	190.00	50162	51539	-2.47	-3.98	-5.97
2	22	2	130.00	80207	79949	0.29	0.47	0.71
3	0.65	1	22.18	17359	17242	0.02	0.07	0.09
3	0.65	2	25.57	17233	16368	0.14	0.54	0.69
3	1	1	25.25	23526	20129	0.65	4.16	7.28
3	1	2	28.45	21139	17835	0.70	4.53	7.93
3	2.1	1	23.40	17141	17329	-0.10	-0.41	-0.54
3	2.1	2	23.45	18021	16941	0.54	2.30	3.03
3	4.2	1	26.50	16040	15353	0.76	4.04	5.72
3	4.2	2	28.25	18453	19091	-0.59	-3.13	-4.43
3	6	1	43.75	27051	27704	-0.59	-1.98	-3.14
3	6	2	60.00	33896	35675	-1.27	-4.24	-6.74
3	10.4	1	45.50	38850	39153	-0.33	-0.91	-1.11
3	10.4	2	79.00	47708	48126	-0.38	-1.03	-1.25
3	13.7	1	72.00	35201	36379	-1.87	-3.51	-4.43
3	13.7	2	46.50	43631	44341	-0.92	-1.72	-2.17
3	22	1	73.00	46321	46241	0.16	0.27	0.31
3	22	2	84.75	55622	56596	-1.58	-2.74	-3.17
4	0.65	1	6.05	8816	9889	-0.18	-0.40	-0.42
4	0.65	2	7.78	6885	8223	-0.27	-0.62	-0.65
4	1	1	n/a	20708	9252	1.92	3.60	3.75
4	1	2	n/a	23724	9689	2.13	4.00	4.17
4	2.1	1	44.75	21114	16888	1.12	4.79	5.29
4	2.1	2	29.00	15427	15473	-0.01	-0.06	-0.07
4	4.2	1	39.50	21710	18128	1.80	4.64	5.41
4	4.2	2	34.00	19899	15504	2.50	6.42	7.49
4	6	1	36.25	17702	15699	1.72	3.28	3.43
4	6	2	33.00	19206	15032	3.50	6.70	7.00
4	10.4	1	17.25	16981	15601	2.10	9.45	11.12
4	10.4	2	31.25	13890	14446	-0.97	-4.37	-5.15
4	13.7	1	27.00	12864	10863	5.51	15.04	16.54
4	13.7	2	25.75	10530	10284	0.77	2.10	2.31
4	22	1		16783	14471	7.77	17.05	20.56
4	22	2		16458	15434	3.37	7.39	8.91

Appendix V. Control Rates for C4 in (A) the lower region and (B) the upper region

A.

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Kaolinite Concentration (mg/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Control Rates m-all (l/shell-hr)*	m-all (l/g-hr)**
Control 4	0.65	1	78.00	1.52	25392	23785		
Control 4	0.65	2	62.50	1.20	17603	20558	-0.0328	-0.0541
Control 4	1	1	40.00	1.29	11007	6790		
Control 4	1	2	34.25	1.23	9195	8137	0.3396	0.5610
Control 4	2.1	1	41.25	1.35	12165	13437		
Control 4	2.1	2	47.15	2.26	16763	17567	-0.1723	-0.2848
Control 4	4.2	1	65.05	1.90	20348	19862		
Control 4	4.2	2	83.50	2.34	26110	25797	0.0854	0.1411
Control 4	6	1	107.45	2.14	32260	31402		
Control 4	6	2	116.50	2.16	38470	34536	0.4539	0.7499
Control 4	10.4	1	82.50	2.28	23152	22485		
Control 4	10.4	2	76.50	2.04	23562	24162	0.0238	0.0393
Control 4	13.7	1	38.25	1.51	25905	26222		
Control 4	13.7	2	69.00	1.40	26893	27228	-0.2459	-0.4062
Control 4	22	1	97.50	1.40	26555	25508		
Control 4	22	2	102.60	1.82	35482	35250	0.5772	0.9535

B.

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Kaolinite Concentration (mg/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Control Rates m-all (l/shell-hr)*	m-all (l/g-hr)**
Control 4	0.65	1	77.33	1.44	25648	24343		
Control 4	0.65	2	65.33	1.16	16983	18506	-0.0123	-0.0203
Control 4	1	1	27.00	1.21	9977	8827		
Control 4	1	2	33.00	0.99	8500	8494	0.0691	0.1141
Control 4	2.1	1	47.50	1.29	11998	12996		
Control 4	2.1	2	55.83	1.85	15700	16389	-0.1447	-0.2391
Control 4	4.2	1	63.13	1.74	19623	19001		
Control 4	4.2	2	92.00	2.43	26033	26832	0.0047	0.0078
Control 4	6	1	101.33	2.10	31306	31109		
Control 4	6	2	117.33	2.10	35197	33018	0.2363	0.3903
Control 4	10.4	1	75.67	2.24	22970	22788		
Control 4	10.4	2	89.67	1.97	24461	23486	0.2839	0.4691
Control 4	13.7	1	84.43	1.57	26023	26211		
Control 4	13.7	2	90.50	1.88	26454	26107	0.0464	0.0767
Control 4	22	1	92.00	1.34	26929	26441		
Control 4	22	2	105.43	1.86	35446	34381	0.6022	0.9948

* control rates reported as liter / shell - hour - see in text notation

** control rates reported as liter / avg. gram ash free dry weight - hour

control rates reported as an average of sampling period 1 and 2

Appendix VI. Filtration rates in the lower region for E5 and E6

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Kaolinite Concentration (mg/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Oyster Filtration Rates m-all (l/g-hr)*	m-open (l/g-hr)*	m-feces (l/g-hr)*
5	0.65	1	39.75	0.71	18240	16402	0.12	0.18	0.25
5	0.65	2	9.83	2.20	34200	21722	0.53	0.78	1.08
5	1.0	1	34.05	1.24	12828	10232	0.41	1.66	2.81
5	1.0	2	55.00	1.65	19792	18873	0.09	0.35	0.59
5	2.1	1	22.00	0.62	6670	5398	0.80	2.39	3.99
5	2.1	2	35.40	0.76	10633	10125	0.18	0.55	0.92
5	4.2	1	34.75	1.57	15653	13140	1.32	2.90	8.25
5	4.2	2	21.95	0.73	10947	8803	1.64	3.61	7.79
5	6.0	1	64.50	1.09	21873	22532	-0.32	-0.80	-1.25
5	6.0	2	66.00	0.96	20000	21655	-0.86	-2.14	-3.35
5	10.4	1	55.75	0.92	18477	20318	-1.77	-4.99	-8.68
5	10.4	2	59.00	1.04	21877	20723	1.01	2.85	3.79
5	13.7	1	56.65	0.87	22091	24763	-2.81	-8.17	-10.12
5	13.7	2	66.80	1.32	28158	27878	0.25	0.54	0.88
5	22.0	1	48.50	1.47	15829	14373	3.81	8.58	12.25
5	22.0	2	78.25	1.52	25257	24270	1.57	3.54	5.06
6	0.65	1	102.50	3.16	40080	11447	0.87	1.01	1.10
6	0.65	2	71.25	2.52	40607	16667	0.62	0.72	0.78
6	1.0	1	15.50	1.43	7160	5757	0.23	0.46	0.61
6	1.0	2	28.25	2.81	12448	10772	0.15	0.31	0.41
6	2.1	1	33.75	1.73	14737	12018	0.46	0.98	1.21
6	2.1	2	27.55	1.42	11645	11033	0.12	0.26	0.32
6	4.2	1	49.75	1.74	17580	12865	1.40	3.49	4.83
6	4.2	2	48.00	1.10	18145	16575	0.40	1.01	1.40
6	6.0	1	48.00	1.94	24313	21825	0.69	1.24	1.29
6	6.0	2	71.50	1.49	24848	25873	-0.26	-0.46	-0.48
6	10.4	1	64.50	0.78	17758	15635	1.41	1.60	1.98
6	10.4	2	80.25	0.92	24647	21970	1.27	1.45	1.79
6	13.7	1	69.00	1.41	25010	23998	0.60	0.63	0.77
6	13.7	2	64.50	3.11	33937	32242	0.75	0.78	0.96
6	22.0	1	89.50	3.19	34873	34453	0.28	0.29	0.44
6	22.0	2	99.50	2.10	43580	41838	0.95	0.99	1.48

* filtration rates are reported in liters / g. dry wt. oyster - hour

Appendix VII. Filtration rates in the upper region for E5 and E 6

Experiment	Flow Speed (cm/sec)	Sampling Period	Upstream Chlorophyll a Concentration (ug/l)	Upstream Kaolinite Concentration (mg/l)	Upstream Particle Concentration (part/ml)	Downstream Particle Concentration (part/ml)	Oyster Filtration Rates m-all (l/g-hr)*	m-open (l/g-hr)*	m-feces (l/g-hr)*
5	0.65	1	34.30	0.22	18097	16978	0.42	0.62	0.86
5	0.65	2	7.30	0.25	28962	19482	2.62	3.87	5.37
5	1	1	34.27	0.14	13569	10442	2.67	10.91	18.46
5	1	2	44.33	0.25	15651	19397	-2.18	-8.93	-15.12
5	2.1	1	19.60	0.07	6157	5354	2.98	8.95	14.92
5	2.1	2	31.77	0.13	9530	9711	-0.40	-1.21	-2.01
5	4.2	1	32.50	0.19	15147	14206	2.74	6.02	12.99
5	4.2	2	28.83	0.12	10700	8969	7.54	16.56	35.73
5	6	1	58.67	0.26	21160	20037	3.33	8.33	13.03
5	6	2	56.83	0.27	21334	20636	2.03	5.08	7.96
5	10.4	1	44.50	0.26	19803	19684	0.64	1.79	2.39
5	10.4	2	44.67	0.26	20498	20249	1.29	3.64	4.85
5	13.7	1	62.83	0.29	22601	22074	3.29	7.22	11.84
5	13.7	2	64.17	0.36	28663	28000	3.26	7.17	11.75
5	22	1	47.83	0.20	15100	14972	1.90	4.28	6.12
5	22	2	63.67	0.31	25447	23502	17.80	40.05	57.21
6	0.65	1	94.33	0.10	41481	10260	5.47	6.40	6.94
6	0.65	2	63.83	0.16	37371	16294	3.25	3.80	4.12
6	1	1	21.90	0.05	7219	5364	1.79	3.58	4.74
6	1	2	26.33	0.09	12822	9376	1.89	3.77	5.00
6	2.1	1	20.83	0.10	14192	10854	3.39	7.27	8.98
6	2.1	2	23.74	0.09	11348	10827	0.60	1.28	1.58
6	4.2	1	37.50	0.12	15486	13729	3.05	7.82	10.55
6	4.2	2	50.50	0.14	17050	16519	0.80	2.00	2.77
6	6	1	45.15	0.21	22407	22319	0.14	0.26	0.27
6	6	2	50.67	0.23	26190	23752	3.53	6.36	6.63
6	10.4	1	60.17	0.09	16859	16860	-0.00	-0.00	-0.01
6	10.4	2	78.00	0.13	24212	23413	2.10	2.40	2.96
6	13.7	1	63.67	0.20	25677	23376	7.75	8.11	9.97
6	13.7	2	85.33	0.31	34539	33474	2.59	2.71	3.33
6	22	1	93.47	0.35	34817	34399	1.60	1.66	2.48
6	22	2	72.00	0.48	44680	42586	6.37	6.59	9.88

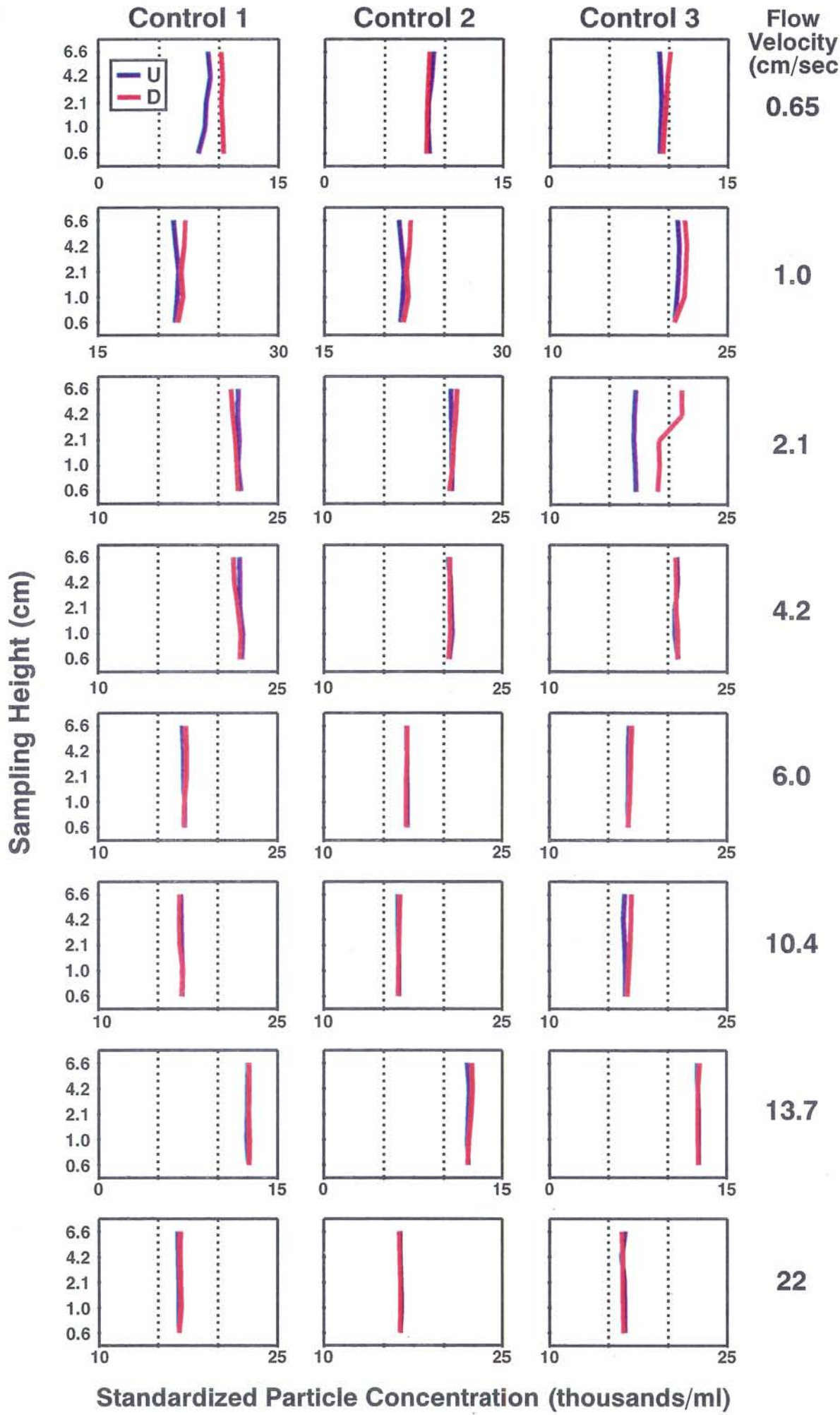
* filtration rates are reported in liters / g. dry wt. oyster - hour

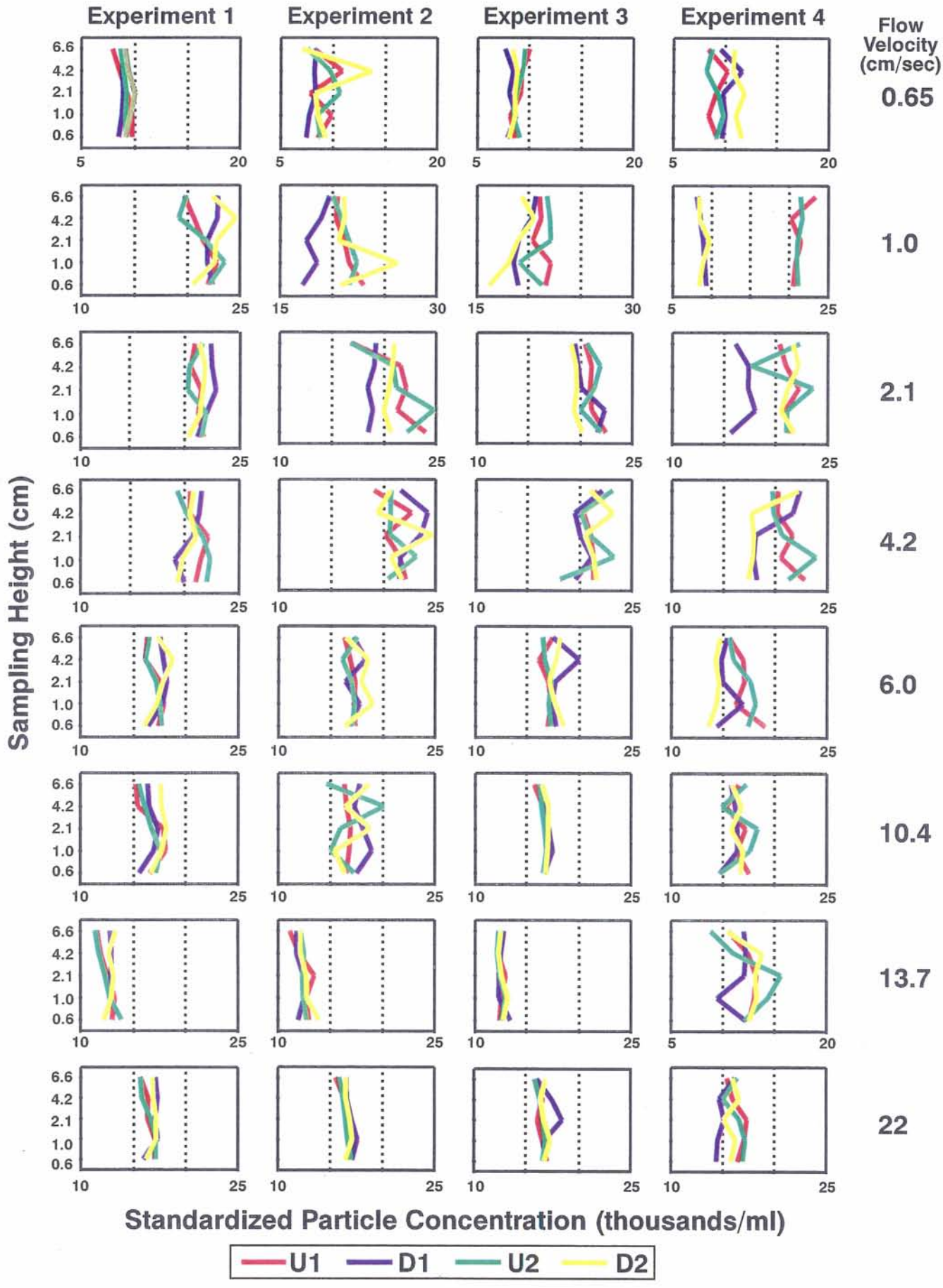
Appendix VIII. Vertical Particle Concentration Profiles for all Controls (A) and Experiments (B). Experiments / Controls are arranged by columns and the flow speeds by row.

Explanation of the notation in the legends.

For the controls:
U= upstream concentration
D= downstream concentration

For the Experiments:
U1= upstream concentration- Sampling Period 1
U2= upstream concentration- Sampling Period 2
D1= downstream concentration- Sampling Period 1
D2= downstream concentration- Sampling Period 2


Control 1
Control 2
Control 3
Flow Velocity (cm/sec
0.65
1.0
2.1
4.2
6.0
10.4
13.7
22
U
D
Sampling Height (cm)
6.6
4.2
2.1
1.0
0.6
0
15
30
10
25
Standardized Particle Concentration (thousands/ml)


Experiment 1
Experiment 2
Experiment 3
Experiment 4
Flow Velocity (cm/sec)
0.65
1.0
2.1
4.2
6.0
10.4
13.7
22
Sampling Height (cm)
6.6
4.2
2.1
1.0
0.6
Standardized Particle Concentration (thousands/ml)
U1
D1
U2
D2