

## EFFECTS OF CAGING ON RETENTION OF POSTLARVAL SOFT-SHELLED CLAMS (*MYA ARENARIA*)

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**ABSTRACT** Postlarval transport is an important process affecting the population dynamics of many coastal benthic species. The first growth season after settlement represents one of the most influential life-history stages of many benthic species, including the commercially important soft-shelled clam *Mya arenaria*. In the present study, the effect of a mesh cage on the retention of postlarval soft-shelled clams was investigated using a laboratory flume. Three size categories of clams were exposed to a range of velocities both with and without the cage. The presence of the cage did not significantly increase the number of clams retained for most clam sizes and velocities tested. Only at the fastest velocity tested did the cage significantly increase the proportion of clams retained. Characterization of flow patterns indicated that flow velocities were reduced inside the cage at the fastest velocity but not at the lower velocity. We propose that the cage effects on retention are negligible in flows up to a critical velocity, above which they protect clams from resuspension. These results can be applied to field applications of mesh cages to optimize the beneficial caging effect.

**KEY WORDS:** *Mya arenaria*, postlarvae, cage, transport, resuspension, shear velocity, flume

### INTRODUCTION

Harvesting of the soft-shelled clam, *Mya arenaria* L., is an important commercial industry along the coast of New England. Adult *M. arenaria* are collected from hundreds of coastal embayments from Canada to Cape Hatteras, producing a total annual revenue in excess of \$12 million (U.S. Fisheries Report 1998). Yet the productivity of soft-shelled clam fisheries is erratic because *M. arenaria* recruitment is subject to extreme temporal and spatial variability (Beukema et al. 1978, Möller and Rosenberg 1983). Because adult population density is linked to recruitment, this variability results in dramatic population changes from season to season and among locations within the local habitat.

The observed variability in recruitment could result from changes in any one or more of the numerous processes operating on larval and postlarval stages. Local recruitment is a result of the following: initial larval supply, proportion of larvae that settle, post-settlement mortality due to predation and/or inadequate resources, and post-settlement transport processes. Although numerous studies have investigated the factors controlling initial larval settlement and mortality (Pfitzenmeyer 1962, Günther 1992, Rodriguez et al. 1993), few have examined the effects of hydrodynamic transport of postlarvae (Emerson and Grant 1991). Both physical processes and behavioral responses, such as depth of burrowing and byssal drifting, contribute to postlarval transport of recruits (Sigurdsson et al. 1976, Newell and Hidu 1986). In addition, over the first growth season, changes in size and burial depth could affect the proportion of clams retained in particular flow regimes. The physical parameter most relevant to hydrodynamic transport of recruits is bottom shear stress, because it controls the suspension and deposition of particles. Shear stress is defined as shearing strain caused by water moving over the bottom and is proportional to the rate of deformation of the fluid (Gerhart and Gross 1985).

In response to the high variability in *M. arenaria* recruitment, some fisheries have implemented programs to increase settlement and decrease resuspension of either "wild" postlarvae or cultivated spat by manipulating benthic conditions. One of the most success-

ful techniques involves placing mesh netting (cages) over the sand flats to alter the hydrodynamics and exclude predators (Beal 1993, Marcotti and Leavitt 1997). Although the beneficial role of predator and disturber exclusion has been demonstrated (Beal 1993, 1994, Dunn et al. 1999), little is known about the mechanisms by which cages may alter the hydrodynamic regime and allow for enhanced population densities.

The goal of the present study is to quantify the effect of caging on the following: near-bottom flow characteristics and postlarval clam retention over a range of clam sizes and benthic shear stresses (as quantified with shear velocity  $u_*$ ). We use a recirculating flume to simulate tidal flows common in the field and to quantify the effect of the cage on clam retention in a test bed of sediment. We define retention as the proportion of clams not eroded from the sediment in the presence of flow and resuspension as the quantity of clams eroded from the sediment and transported downstream. We focus on resuspension because of its relevance to natural situations where clam larvae or postlarvae dropped from suspension and settled in quiescent periods of a tidal cycle, but are subjected to resuspension during vigorous periods of flood and ebb. The flume studies also are relevant to aquaculture situations where clam spat are seeded at low tide and exposed to suspension during subsequent tidal excursions. Our research addresses the following questions:

- How does the cage affect near-bottom velocities and turbulence in the flume?
- How does the cage affect postlarval transport and retention of *Mya arenaria*?
- How do these caging effects vary with clam size (i.e., for recruits during their first growth season) and with flow velocity (i.e., over a range of realistic shear stresses) from a tidal environment?

We expect the cage to alter near-bottom flows by reducing the benthic shear stress under the structure. For a specific clam size, this reduction in shear stress should result in a reduction in numbers of clams resuspended, at flows that typically would erode uncaged buried clams. Because higher shear stresses typically are

required to resuspend larger clams (Emerson and Grant 1991, Dunn et al. 1999), it is important to conduct our flume studies over a range of clam sizes and flow speeds, in order to provide results that can be generalized to the field.

This study is intended to provide a mechanistic understanding of how mesh caging influences resuspension of *M. arenaria*, which represents a potentially important loss to a local population. By focusing on this mechanism, we leave unexplored other potential cage effects such as those on larval settlement and deposition; mortality due to predation; and enhancement or depletion of food supply. However, a characterization of the flow alterations caused by caging provides a reference point for predictions of other hydrodynamically-controlled processes such as deposition and food flux.

## MATERIALS AND METHODS

### Test Organism and Sediment

Flume experiments were conducted in 1997 and 1998 to test the effects of caging on retention of three size-categories of clam recruits (corresponding to a progression of first season sizes of clams resulting from a late spring settlement in Barnstable Harbor, Massachusetts; data not shown) over a range of shear velocities. The shell length (SL) of the small, medium, and large size recruits was measured as  $1.3 \pm 0.17$  mm (mean  $\pm$  st. dev.;  $n = 100$ ),  $1.8 \pm 0.15$  mm, and  $2.3 \pm 0.3$  mm, respectively. Flume studies were conducted in the summer of 1998 and spring 1999 to characterize flow along the flume and around the cage. Postlarval *M. arenaria* were acquired from Beals Island Regional Shellfish Hatchery, Beals, Maine in 1997 and from Mook Sea Farm, Inc., Walpole, Maine in 1998.

All clams were held in plastic containers with  $64 \mu\text{m}$  mesh tops and supplied with  $10 \mu\text{m}$  filtered, running seawater ( $\sim 21^\circ\text{C}$ ) from Vineyard Sound. In 1997, clams were fed Tahitian *Isochrysis galbana* at least once a day, but cultures experienced higher mortality than expected. Thus, in 1998, the clams were fed twice a day with *I. Isochrysis galbana* and *Tetraselmis* sp. (both species from Instant Algae, Reed Mariculture Inc.) and aerated the holding containers to improve survival rates.

Sediment used for the experiments was collected from Barnstable Harbor. Only the surficial, oxic layer of sediment was used to avoid hydrogen sulfide toxicity and provide suitable substrate for the clams. For consistency among experiments, all sediment was passed through a 2 mm sieve and retained on a  $180 \mu\text{m}$  sieve. Based on extensive sampling, over 65% of Barnstable Harbor sediment was within the  $180 \mu\text{m}$  to 2 mm size range (dry wt. basis); therefore, this test sediment was a reasonable approximation of field conditions (authors' unpublished data).

Sediment was kept frozen at  $-4^\circ\text{C}$  until use. After thorough mixing, defrosted sediment was placed in the sediment box and the

surface was leveled. Prepared sediment had a median grain size of 150 to  $180 \mu\text{m}$ .

### Flow Characterization and Cage Setup

Experiments were performed in a recirculating flume at the Woods Hole Oceanographic Institution's Rinehart Coastal Research Center. The flume consisted of a 30 cm deep, 60 cm wide, and 17 m long channel through which water was circulated by an impeller pump (Butman and Chapman 1989). Flow was rectified at the headbox of the flume by a Plexiglas grid of 1.2 cm squares 7.5 cm long. At the very downstream end of the flume, an accordion weir set the area available for water outlet. Simultaneous along-stream and vertical velocities were measured by a two-axis Laser Doppler Velocimeter (LDV) (Trowbridge et al. 1989). Velocity profiles were measured 1.7 m upstream of the test section (Fig. 1). Shear velocities ( $u_*$ ) were estimated from the flow profiles using an iterative method to calculate  $u_*$  in a steady, one-dimensional open-channel flow (Trowbridge et al. 1989). To ensure that the desired velocity was produced, water velocities were measured at 25 hertz and averaged over 4 minutes of measurements at each of 10 heights above the flume bottom (0.9, 1.2, 1.6, 2.1, 2.7, 3.4, 4.2, 5.0, 6.0, and 8.0 cm). These velocity profiles were conducted for all trials to estimate variation in flow among replicates for specific target velocities (target velocities ranged from  $u_* = 0.7$ – $2.0 \text{ cm s}^{-1}$ ).

The working section of the flume was 12.5 m downstream from the water entrance. At this distance the turbulent boundary layer was fully developed. For these experiments, a section of the flume's bottom was replaced with a removable acrylic tray ( $55 \times 55$  cm) containing a central recessed sediment box ( $20 \times 20 \times 2$  cm deep) (Fig. 1). The cage (described below) surrounded the sediment box and was secured to the acrylic tray. For each experiment, fresh sediment was placed in the box and the surface leveled before fitting the tray into the flume. The edges of the tray were flush with the flume bottom. The water depth in the flume was approximately 12 cm and water temperature was  $20^\circ\text{C}$  to  $22^\circ\text{C}$ . We selected a target water depth of 12 cm to maintain a water column width-to-depth ratio of at least 5, thereby maximizing the accuracy of the shear velocity measurements (Nowell and Jumars 1987, Butman and Chapman 1989).

In all experiments, flow was established by adjusting the pump speed and outlet weir setting to attain the target water depth ( $h = 12$  cm at a distance of 21 cm upstream of the test section; Fig. 1) and target free-stream velocity ( $u_b =$  free-stream flow at 8 cm above bottom measured 1.7 m upstream of the test section). Once the target velocity and depth were achieved (within 5–10 minutes of introducing the tray), velocity profile measurements were initiated. Velocity profiles were reproduced with only slight variation ( $<5\%$ ) among replicates for a single target velocity. Afterwards,

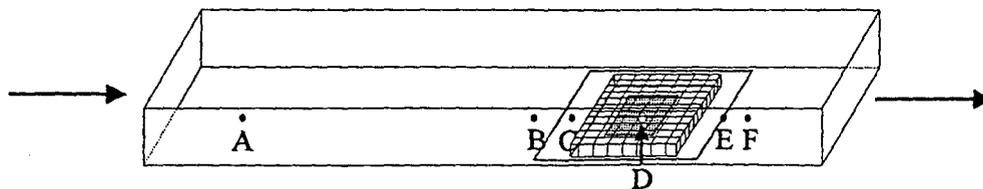


Figure 1. Oblique view of the test section of the flume showing the location of the cage and positions of velocity profile measurements. Respectively, A, B, and C are 170, 21, and 6 cm upstream of the cage front. D is 27 cm downstream from the leading edge of the cage. E and F are 10 and 20 cm downstream of the cage. Gray box within the cage represents the sediment box.

the flow speed was gradually reduced from the target velocity to  $u_g = 3 \text{ cm s}^{-1}$  and the tray was removed from the flume.

The cage used in these experiments was a 46 cm long  $\times$  54 cm wide  $\times$  5 cm high metal frame covered on the top and sides with plastic mesh netting of a size commonly used by aquaculturists and fishery managers (InterNet Inc. Minneapolis, MN; oriented flexible square; mesh size = 0.32 cm). In an ideal setup, the water depth should be at least 3 times the cage height in order to avoid generating free-surface interactions (Nowell and Jumars 1984). For our experiments, we were limited to a water depth of 12 cm and to a cage height of  $>4$  cm to create adequate separation between the bottom of the flume and the roof of the cage. Although the flows above the cage were likely influenced by the structure's proximity to the free surface, the magnitude of this interaction, and its potential effect on bottom shear stress, were expected to be minor. This expectation was evaluated during the experiments using water height and velocity measurements. The cage support rods were positioned  $>5$  diameters from the sediment box and had no detectable influence on water flow or sediment transport (Nowell and Jumars 1987).

At least one representative upstream shear velocity ( $u_*$ ) was measured for each flow regime tested (Table 1). For most flow regimes,  $u_*$  was calculated during each experimental trial, and averaged across the 3 or 4 replicate trials to characterize the flow treatment (note values for  $u_*$  were not recorded in some trials due to technical problems). Shear velocities were selected to fall within the range of typical estuarine and bay flows, as derived from current meter data from Barnstable Harbor. At three sites in Barnstable Harbor, the range of velocities measured during a spring tide in 1998 corresponded to shear velocities of 0–3.8  $\text{cm s}^{-1}$  and, over half of the time, flows were within the range used in these trials (0.7–2.0  $\text{cm s}^{-1}$ ) (authors' unpublished data).

Flow patterns around the cage were quantified by taking centered velocity profiles 6 cm upstream of the cage, mid-cage, and both 10 and 20 cm downstream of the cage (Fig. 1). Velocity profiles were also taken at these locations without the cage present. This array of profiles was conducted at shear velocities of  $u_* = 1.8$  and 2.0  $\text{cm s}^{-1}$ . These velocities were selected after conducting the clam retention trials, to investigate flow patterns at and below a shear velocity that yielded significantly greater clam retention in the caged treatment (See Results, Retention section). Flow deviations caused by the cage were quantified in the two flow regimes by calculating the time-averaged velocity at each measurement point and comparing the difference between the cage and no-cage profiles at both velocities. Fluorescein dye visualizations were

performed to describe qualitatively the turbulence and flow separation generated by the mesh cage.

#### Retention Trials

The main objective of the retention trials was to determine the effect of caging over a realistic range of field flows and first season clam sizes. Three or four replicate trials were conducted with and without the cage for each clam size over a range of selected velocities ( $n = 3$  for all trials except when  $u_* = 0.7$  and 1.3  $\text{cm s}^{-1}$ ). The small clams were exposed to shear velocities of 0.7  $\text{cm s}^{-1}$  and 1.3  $\text{cm s}^{-1}$ ; medium size clams to 1.4–1.8  $\text{cm s}^{-1}$ ; and large clams to 2.0  $\text{cm s}^{-1}$ . This experimental setup did not follow an ideal 3-factor design with caged and uncaged treatments in all combinations of flow speed and clam size for two reasons: the number of first season clams was limited and some data were incorporated from experiments conducted as a component of another study. The large clam data and part of the medium sized clam data ( $u_* = 1.4$  and 1.6  $\text{cm s}^{-1}$  trials) were gathered as part of a caging study we conducted in association with flume trials in Dunn et al. (1999).

In order to use the available clams most efficiently, we selected what we anticipated to be the most relevant flow speeds for each clam size. Lower speeds were used for smaller sizes because lower shear velocities were anticipated to erode smaller clams. The velocity ranges selected for each clam size were chosen based on preliminary flume experiments that determined the critical velocities needed for initial movement of sediment and clams, both buried and unburied. The lower velocities were selected to erode non-burrowing clams, but not significantly erode the sediment, while the higher shear velocities were intended to erode a portion of the sediment and thereby allow assessment of the burrowing clam's response to elevated flow.

For each retention trial, we selected 200 active clams. This number corresponds to a density of 5,000 clams per  $\text{m}^2$  (within the 20 cm  $\times$  20 cm sediment box) and approximates actual Barnstable Harbor field densities (authors' unpublished data). The clams were suspended in seawater and then rinsed through a plastic cylinder (10 cm diameter  $\times$  20 cm high) held 1 to 2 cm above the sediment surface. Suspending the clams ensured that they were distributed evenly on the sediment. Use of the cylinder ensured that the clams settled onto the sediment box surface, not the acrylic perimeter. The clams were given 20 minutes to burrow (sufficient time for burial based on previous observations). After the burial time, the sediment tray was removed from the seawater table, the number of non-burrowing clams was recorded and those remaining on the sediment surface were removed. The tray was inserted into the flume under conditions of very low flow ( $u_g = 3 \text{ cm s}^{-1}$ ) and made flush with the adjoining flume bottom. For the cage treatments, the cage and its supports were secured to the tray at this time. All trials were conducted for 40 minutes except for  $u_* = 1.7$  and 1.8  $\text{cm s}^{-1}$  which ran for 10 minutes because these were part of another study.

For all runs, the sediment remaining in the sediment box after the experiment was sieved on a 500  $\mu\text{m}$  sieve and the fraction retained was either sorted for clams immediately or preserved in 80% ethanol, stained with Rose Bengal, and sorted later. In order to ensure that we were not losing clams during sediment transfers, we conducted procedural controls using the medium size clams. Procedural controls followed the same procedure as the retention runs except that the tray was placed in the water table instead of the flume. These controls showed that an average of 99% of seeded

TABLE 1.

Mean alongstream velocities at 8 cm above flume bottom ( $u_g$ ) and mean shear velocities ( $u_*$ ) for all three clam sizes and flow treatments. Standard deviations are in parentheses.

Clam category	$u_g$ ( $\text{cm s}^{-1}$ )	$u_*$ ( $\text{cm s}^{-1}$ )	n
Small	14.3 (0.3)	0.66 (0.01)	8
	30.1 (0.3)	1.30 (0.02)	8
Medium	32.6 (0.8)	1.41 (0.02)	4
	38.1 (0.5)	1.61 (0.02)	6
	40.1 (0.7)	1.73 (0.01)	6
	43.8 (0.4)	1.83 (0.01)	6
Large	47.2 (1.2)	1.97 (0.09)	6

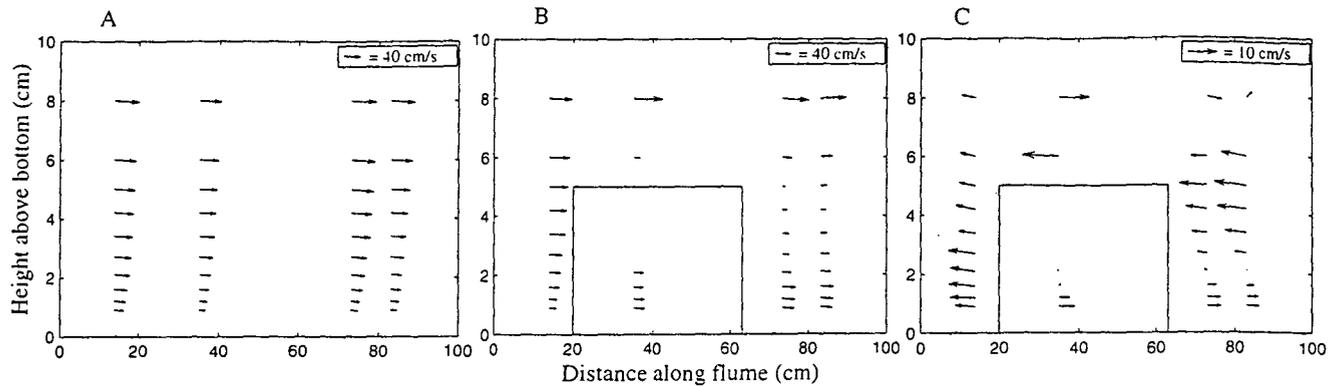


Figure 2. Vertical profiles of flow velocity ( $u$ ) along flume with upstream shear velocity of  $u_* = 1.8 \text{ cm s}^{-1}$ . A) Profiles without the cage ( $u$ ); B) profiles with the cage ( $u_{\text{cage}}$ ); C) deviations in velocity caused by the cage [i.e.,  $u_{\text{cage}} - u$ ]. To emphasize the vertical pattern, only the components of the vectors  $> 27 \text{ cm s}^{-1}$  are graphed for profiles A and B. In profile C, deviations are true differences. Distances along the flume are relative and start 20 cm before the leading edge of the cage.

clams were recovered, indicating that we were not losing clams while transferring the tray from the seawater table to the flume.

For retention trials, results were analyzed separately for each clam size, with cage (two levels, present and absent) and velocity as fixed factors in two-way analysis of variance (ANOVA) (Systat version 6.1). The dependent variable was the percentage of clams retained. For the medium size clam results, two separate two-way ANOVAs were performed due to different times of exposure to flow (10 and 40 minutes) and for large-sized clam results a one-way ANOVA for cage effect was performed. Visual inspection did not reveal any pronounced deviations from a normal distribution. Variances were tested and found to be homogeneous (Cochran's test;  $p > 0.05$ ).

## RESULTS

### Cage Effects on Flow

A comparison of velocity profiles conducted with and without the cage indicates that the cage altered near-bed flow at both  $u_* = 1.8 \text{ cm s}^{-1}$  (Fig. 2) and  $u_* = 2.0 \text{ cm s}^{-1}$  (Fig. 3). Without the cage, velocities fit the expected log-linear profile, and changed little ( $< 8\%$ ) with downstream distance (Figs. 2A, 3A). The presence of the cage disrupted this pattern by changing flows inside the cage, just above the upper rim of the cage's frame and just downstream of the trailing edge of the frame (Figs. 2B, 3B). Dye visualizations revealed that the leading face of the cage caused flow separation around the leading cross-sectional portion of the frame. The dye revealed eddies shedding off the upper edges of the cage and contributing to the observed increase in turbulence above and downstream of the cage. The velocity profiles indicated that mean velocities were reduced downstream of the cage at  $u_* = 1.8 \text{ cm s}^{-1}$  and both within and downstream of the cage at  $u_* = 2.0 \text{ cm s}^{-1}$  (Fig. 2C, 3C).

The effect inside the cage was different at  $u_* = 1.8 \text{ cm s}^{-1}$  than at  $u_* = 2.0 \text{ cm s}^{-1}$ . Flow deviations (Fig. 2C, 3C) indicated that velocities at  $u_* = 1.8 \text{ cm s}^{-1}$  were increased inside the cage (at heights of 0.9, 1.2, 1.6 cm), yet at  $u_* = 2.0 \text{ cm s}^{-1}$  these velocities were consistently reduced inside the cage. The vertical patterns of flow alteration were different at the two velocities. At  $u_* = 1.8 \text{ cm s}^{-1}$  the flow deviations became less pronounced with height off of bottom, but at  $u_* = 2.0 \text{ cm s}^{-1}$  the flow deviations became more

pronounced with height off of bottom. These patterns suggest that the cage alters the flow most strongly at the sediment interface at  $u_* = 1.8 \text{ cm s}^{-1}$  and at a height above the sediment interface at  $u_* = 2.0 \text{ cm s}^{-1}$ .

The cage did have a small but measurable effect on water height in the flume. Upstream water heights along the flume increased in the presence of the cage, while downstream water heights decreased in comparison to no-cage heights at comparable target velocities. Water heights were elevated approximately 7% just in front of the cage (position C in Fig. 1) yet at the positions of our water height measurements and velocity profiles the increase was  $< 3\%$ . From the trailing edge of the cage to 3 m downstream, the heights were decreased by about 3% as compared to the no cage water heights. For the flow profiles at  $u_* = 2.0 \text{ cm s}^{-1}$  and  $u_* = 1.8 \text{ cm s}^{-1}$ , water heights over the cage were increased 4% and 2%, respectively. These water height deviations are relatively small and probably do not have a noticeable effect on flows within the cage. The proximity of the free-surface of the water to the upper face of the cage, however, may constrain the flow over the top of the cage.

### Retention Trials

The cage tended to enhance retention of clams at some, but not all, combinations of clam size and shear velocity (Fig. 4). For small clams, slightly more clams were retained in cages, but the result was not statistically significant (Table 2). With medium size clams, there was no clear pattern of cage effect; neither treatment consistently retained more clams (Fig. 4). The only significant increase in clam retention with the cage ( $p = 0.046$ ) occurred with the large clams at the greatest shear velocity used,  $u_* = 2.0 \text{ cm s}^{-1}$  (Table 2). Potentially significant differences for the smallest category of clams could have been obscured by the high variability in results. On average, fewer than 8% of clams placed on the sediment box did not burrow.

Within a clam size, more clams tended to be eroded at higher velocities, but this trend was significant only for medium size clams for the comparison of  $u_* = 1.7$  and  $1.8 \text{ cm s}^{-1}$  (Table 2). We had anticipated a direct relationship between shear velocity and clam erosion based on the study of Dunn et al. (1999). For our medium size clams, the relationship between velocity and clam

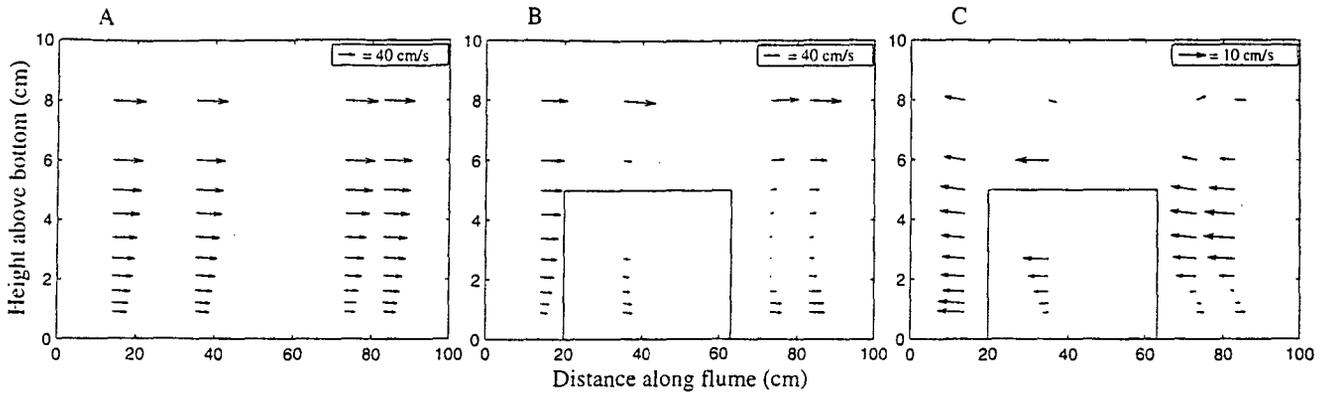


Figure 3. Vertical profiles of flow velocity ( $u$ ) along flume with upstream shear velocity of  $u_* = 2.0 \text{ cm s}^{-1}$ . A) Profiles without the cage ( $u$ ); B) profiles with the cage ( $u_{\text{cage}}$ ); C) deviations in velocity caused by the cage [i.e.,  $u_{\text{cage}} - u$ ]. To emphasize the vertical pattern, only the components of the vectors  $> 27 \text{ cm s}^{-1}$  are graphed for profiles A and B. In profile C, deviations are true differences. Distances along the flume are relative and start 20 cm before the leading edge of the cage.

retention was not linear but appeared to have some critical velocity above which there was a notable reduction in clam retention.

DISCUSSION

Cage Effect on Clam Retention in the Flume

The most consistent result from our flume studies was the lack of a significant cage effect on clam retention in most flow regimes. This result was a surprise because the presence of a mesh structure along a flow path is known to alter flow patterns (Hulberg and Oliver 1980, Nowell and Jumars 1984), and natural mesh-like

obstacles such as marsh grasses have been observed to reduce flow velocities by two to 10-fold (Gambi et al. 1990, Leonard and Luther 1995). A reduction in flow velocity was expected to occur in the cages and result in enhanced clam retention. The lack of significance did not appear to be due solely to low power of the statistical tests, as an increase in the number of replicate trials per treatment (from 3 to 4) did not result in higher significance ( $n = 4$  for target shear velocities of  $u_* = 0.7$  and  $1.3 \text{ cm s}^{-1}$ ).

The one treatment that did show a significant effect of the cage on retention was the combination of the highest flow velocity ( $u_* = 2.0 \text{ cm s}^{-1}$ ) with the large clam size (SL = 2.3 mm). We

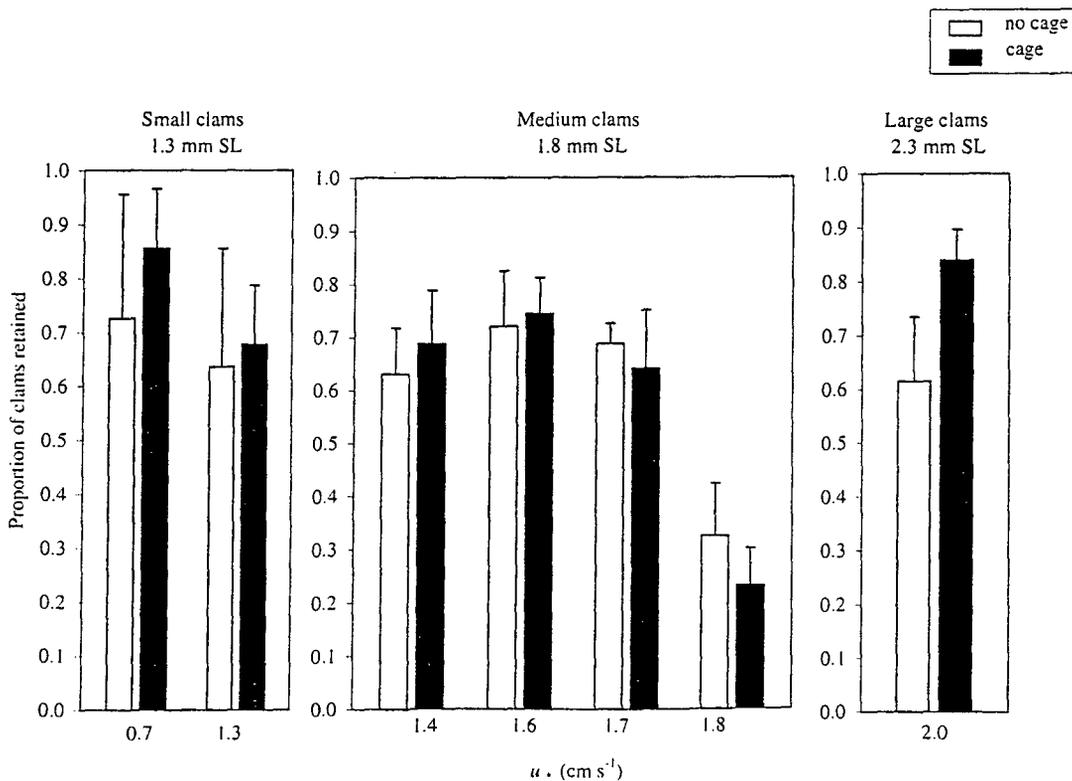


Figure 4. Mean proportion ( $\pm 1$  S.D.) of clams retained over a range of shear velocities with and without cage treatments.  $N = 3$  for all runs except  $u_* = 0.7$  and  $1.3 \text{ cm s}^{-1}$  where  $n = 4$ .

suggest that the mechanism for this cage effect is a substantial reduction in flow velocities within the cage in this particular flow regime. Reduced flow velocities should reduce the shear stress exerted on the sediment surface, thereby decreasing the rate of erosion of sediment and clams. This relationship between shear stress and erosion was observed in the present study for the medium size clam treatment at  $u_* = 1.7$  and  $1.8 \text{ cm s}^{-1}$  (significant effect of velocity in Table 2), and has been reported by Roegner et al. (1995) and Dunn et al. (1999). We suspect that the absence of a significant cage effect on clam retention in flows slower than  $u_* = 2.0 \text{ cm s}^{-1}$  was due to the failure of the cage to reduce boundary shear stress in these conditions.

Flow measurements recorded within the cage in the fastest oncoming flow treatment ( $u_* = 2.0 \text{ cm s}^{-1}$ ) and a slower flow ( $u_* = 1.8 \text{ cm s}^{-1}$ ) support our explanation for the clam retention results. The cage caused a measurable decrease in velocities near the sediment only in the fastest oncoming flow (Fig. 3). One plausible explanation for this effect is that the cage was starting to act more as a bluff body at the higher flows, blocking flow through the mesh and forcing the water up over the upper cage surface. This effect of producing a 'skimming flow' has been predicted and demonstrated for a sufficiently dense array of tubes or cylinders in boundary-layer flows (Morris 1955, Eckman et al. 1981, Nowell and Jumars 1984). We speculate that a comparable process occurs in our cage at oncoming flows of  $u_* = 2.0 \text{ cm s}^{-1}$  and higher: in this flow regime, the velocities are high enough to produce turbulent wakes downstream of the mesh filaments, increasing their effective diameter and decreasing the fluid 'porosity' of the cage (Taylor 1948, Gerrard 1978).

An alternative explanation for the observed significant cage effect in the  $u_* = 2.0 \text{ cm s}^{-1}$  treatment is that suspension of the larger-sized clams was more sensitive than that of the smaller ones to flow alterations caused by the cage. We do not think this is a valid explanation for several reasons. Firstly, there is no evidence for an increasing sensitivity of clam suspension to caging with increased clam size; instead, the small and large clams tended to have increased retention under the cage, whereas the medium size clams showed a mixed response. Secondly, because larger clams are capable of burrowing deeper than small ones, one would expect

them to be less, and not more, sensitive to caging effects. Finally, we have no independent evidence for the "clam size" hypothesis, whereas we do have independent flow measurements in the cage that support the "flow threshold" hypotheses. For these reasons, we constrain our discussion to the latter.

#### Behavioral Effects on Clam Retention

A reduction in near-bottom flow velocity may enhance clam retention through both hydrodynamic and behavioral mechanisms. A critical shear stress is necessary to suspend clams of any particular size; reducing the shear stress below this level will result in more limited transport. Reducing the shear stress will also reduce the rate of sediment erosion, potentially allowing clams more time to burrow below the unstable sediment layer. Either or both of these processes are likely responsible for the relationship between higher shear stresses and enhanced clam transport reported in flume (Roegner et al. 1995, Dunn et al. 1999) and field (Emerson and Grant 1991) studies.

Although surficial sediment was eroded under the cage in our trials at  $u_* = 2.0 \text{ cm s}^{-1}$ , the reduction in rate of erosion relative to uncaged flows may have allowed clams to remain buried in the sediment. In order to maintain access to the sediment-water interface, postlarval *M. arenaria* of 1.3 to 2.3 mm SL can only burrow as deep as their siphons are long, usually to depths of 7.5 mm or less (Zwarts and Wanink 1989). We speculate that *M. arenaria* may actively burrow to avoid being exposed and eroded as Sakurai and Seto (1998) demonstrated for the surf clam, *Pseudocardium sachalinensis* at the reduced shear velocities but not at ambient uncaged shear velocities. Thus we suggest that the reduction in shear stress offered by the cage at  $u_* = 2.0 \text{ cm s}^{-1}$  sufficiently reduced the erosion rate so that 2.3 mm clams could maintain their position in the sediment and avoid resuspension.

Based on the siphon length-burial limitation, we expected to find that for any specific shear velocity, retention of larger clams would be greater than retention of the smaller clams. Although our data alone do not strongly support this hypothesis, comparison with another study demonstrates a retention-size relationship. We found that 25–35% of our 1.8 mm clams were retained at  $u_* = 1.8$

TABLE 2.  
Summary of ANOVAs examining the effects of cage and velocity on retention over a range of size categories.

Clam Size	Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Small	Cage	0.030	1	0.030	0.939	0.352
	Velocity	0.072	1	0.072	2.289	0.156
	Cage*Velocity	0.008	1	0.008	0.243	0.631
	Error	0.378	12	0.031		
Medium	Cage	0.005	1	0.005	0.609	0.457
	Velocity	0.016	1	0.016	1.912	0.204
	Cage*Velocity	0.001	1	0.001	0.104	0.755
	Error	0.066	8	0.008		
Medium*	Cage	0.015	1	0.015	2.099	0.185
	Velocity	0.448	1	0.448	64.70	<0.001
	Cage*Velocity	0.002	1	0.002	0.232	0.643
	Error	0.055	8	0.007		
Large	Cage	0.076	1	0.076	8.129	0.046
	Error	0.037	4	0.009		

\* Separate ANOVAs were performed on two sets of mid-season clams because those tested at  $u_* = 1.7$  and  $1.8 \text{ cm s}^{-1}$  were exposed to flow for only 10 min (Systat version 6.1).

cm s<sup>-1</sup>, yet Roegner et al. (1995) reported that 0% of their 0.24–0.29 mm clams were retained at a comparable velocity ( $u_* = 1.75$  cm s<sup>-1</sup>). Thus smaller clams were more readily transported at this particular velocity and retention appeared to correlate with clam size.

#### Relevance to Field Applications

Our flume results suggest that mesh cages used in the field may enhance retention of recently settled bivalves in flow velocities above a critical level. The extent to which our flume experiments are applicable to field environments depends on how well they represent field situations hydrodynamically, biologically, and structurally. The shear stresses used in the flume experiments fall within those measured at Barnstable Harbor (authors' unpublished data), indicating that boundary-layer flows in the flume are a reasonable representation of field flows. The cultured clams burrowed actively, and their sizes covered the range observed in field populations during first season growth. The cage used in the flume had the same mesh size and composition (flexible mesh), but a much smaller overall size, as mesh enclosures used in the field. Thus, we expect our qualitative prediction (mesh enclosures enhance bivalve retention only above a threshold shear stress) to be broadly applicable, but the specific threshold level to depend somewhat on the geometry and mesh size of the cage.

A reduction in resuspension caused by caging will notably influence population density only if loss via resuspension is a significant source of total loss. Other processes influencing loss include mortality through predation, disease, and/or inadequate resources. Manipulative field experiments evaluating the relative influences of hydrodynamic resuspension and predation on *M. arenaria* recruits indicate that resuspension is a significant cause of loss, especially in smaller size-classes (authors' unpublished data). Therefore, we expect that the possible increase in retention caused by caging could have a significant impact on population density by the end of the first season.

Our flow and retention results are consistent with experimental field evidence suggesting that clam recruitment under cages could be enhanced at high flows. Marcotti and Leavitt (1997) tested the hypothesis that cages, in the form of suspended tents of plastic mesh (mesh size = 0.5 cm), would increase clam recruitment in

field manipulations at Barnstable Harbor, Massachusetts. They found that the only site at which the cages significantly enhanced recruitment (Green Point) was one of the two sites with the highest tidal flow rates. Velocity records from the Green Point site indicated that over a 10 h period during a spring tide, 40% of the flow velocities corresponded to  $u_* = 2.0$  cm s<sup>-1</sup> or greater (authors' unpublished data). Thus velocities at Green Point commonly were high enough to produce the caging effect demonstrated in our flume experiments, suggesting that the enhanced recruitment may have been due to cage-induced retention.

Because mesh enclosures are more likely to retain clam juveniles in vigorous rather than quiescent flow environments, the hydrodynamic setting of a site is an important factor to be considered in their use. This consideration should be included with others, such as the potential of the enclosures to enhance initial settlement, enhance or deplete food resources or reduce mortality through predator exclusion, when predicting whether they are likely to increase population densities. Mesh enclosures are currently in use in multiple embayments along the New England coast and the results of these applications will help refine the cost-benefit analysis of their use and identify the habitats where they will substantially increase the numbers of harvestable soft-shell clams.

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