

Hydrodynamics of larval settlement: The influence of turbulent stress events at potential recruitment sites

John P. Crimaldi

Department of Civil, Environmental, and Architectural Engineering, 428 UCB, University of Colorado, Boulder, Colorado 80309-0428

Janet K. Thompson,¹ Johanna H. Rosman, Ryan J. Lowe, and Jeffrey R. Koseff

Department of Civil and Environmental Engineering, Stanford University, Stanford, California 94305-4020

Abstract

We describe a laboratory investigation into the effect of turbulent hydrodynamic stresses on clam larvae in the settlement phase of the recruitment process. A two-component laser-Doppler anemometer (LDA) was used to measure time histories of the instantaneous turbulence structure at potential recruitment sites within reconstructed beds of the adult Asian clam, *Potamocorbula amurensis*. Measurements were made for two flow speeds over beds with three different clam densities and two different clam heights. We analyze the statistical effect of the turbulence on the larval flux to the bed and on the probability of successful anchoring to the substrate. It is shown that the anchoring probability depends on the nature of the instantaneous stress events rather than on mean stresses. The instantaneous turbulence structure near the bed is altered by the flow rate and the spacing and height of adult clams living in the substrate. The ability to anchor quickly is therefore extremely important, since the time sequence of episodic turbulent stress events influences larval settlement success. The probability of successful larval settlement is predicted to decrease as the spacing between adults decreases, implying that the hydrodynamics impose negative feedback on clam bed aggregation dynamics.

Species success, population density, and community structure are all dependent on larval recruitment. Therefore, the processes of settlement and recruitment of benthic and epibenthic communities have been the subject of substantial research (see Olafsson et al. 1994; Wildish and Kristmanson 1997 for recent reviews). A major portion of the work has involved the transport of larvae to the bed and settling of the larvae by passive or active selection processes (see reviews by Butman 1987; Abelson and Denny 1997). Several researchers have found that it is the combination of larval behavior (e.g., swimming, crawling, burrowing) and physical processes that deliver the larvae to the bed that is responsible for the recruitment success (Mullineaux and Butman 1990; Butman and Grassle 1992; Grassle et al. 1992; Snelgrove et al. 1993). As summarized by Underwood and Keough (2001), it is no longer a question of whether hydrodynamics or behavior are important in recruitment, rather it is a question of “under which conditions is larval behavior important?” We will expand this question and say that it is also important to determine the periods, during the relevant physical processes, when larval behavior is important.

Related to the interest in larval recruitment is an ecological interest in what regulates temporal, spatial, and age-segregated distributions of species. Thus, the processes important in determining how aggregations of benthic

populations are formed and how existing populations limit or facilitate successful recruitment continue to be examined (Olafsson et al. 1994). Although there is significant literature on the interspecific and intraspecific effect of adults on larval settlement and recruitment, many of these studies have produced conclusions that appear contradictory (Olafsson et al. 1994; Thrush et al. 1996). Some studies have shown that chemical cues originating from adults encourage the settlement of larvae of the same species (Pawlik 1992), which results in gregarious aggregations. However, other researchers have shown that larval recruitment is inversely related to adult bivalve density (Moller 1986; Andre and Rosenberg 1991). It has been suggested that adult predation on larvae (Williams 1980; Andre et al. 1993) and postsettlement processes, including adult behavior and food limitation (Olafsson et al. 1994), are the controlling factors in the inhibition of larval recruitment (Woodin 1976; Osman et al. 1989; Olafsson et al. 1994; Snelgrove et al. 1999). It is likely that the conflicting conclusions in the various studies may be at least partially related to the hydrodynamic constraints on larval settlement in a population of adults with varying densities and shapes, and thus this question is likely to be related to a more general question of what fluid mechanics control and influence settlement. This study will consider two sequential aspects of larval settling: transport of the larvae to the bed and settlement or attachment of the larvae to the bed. Our intent is to demonstrate that near-bed hydrodynamics dominate larval transport to the bed and are the primary control on the first stage of larval settlement. Settlement is defined here as the successful and semipermanent attachment of the larvae to the substratum (Keough and Downes 1982). In as much as “early settlement” refers to the successful attachment of the larvae to the substrate, we discuss only

¹ Present address: U.S. Geological Survey, 345 Middlefield Road, MS-496, Menlo Park, California 94025-3561.

Acknowledgments

The authors gratefully acknowledge support from the National Science Foundation (OCE950408). We would also like to thank Cynthia Brown from the U.S. Geological Survey for supplying the clam shells used in the study.

this phase of the process. The two objectives of this paper are

1. to define the relevant near-bed hydrodynamics that affect the early settlement (hereafter referred to as settlement) of larvae onto the bottom, and
2. to determine how the presence of adults, and the resulting hydrodynamics, affects the successful settlement of larvae.

Our conceptual model about the processes important in the first objective and the scope of our study can be summarized as follows. Successful recruitment of a species with planktonic larvae requires that the suspended larvae first settle to suitable locations on the substratum, usually through some combination of passive sinking, turbulent advection, and possibly through active swimming. Most species have some means of anchoring themselves to the substratum once they arrive at a suitable site in order to resist hydrodynamic resuspension. In this paper, we investigate the role of hydrodynamics in larval settlement, including its effect on larval flux to the bed and on the anchoring process. In particular, we investigate how the near-bed turbulence structure controls the probability of hydrodynamic resuspension during the critical period between larval touchdown and successful attachment to the substratum. We do not discuss the processes that are important in determining successful recruitment (as defined by Keough and Downes 1982, recruitment is the survival of larvae in the substrate until counted by an observer). For example, because we only discuss the physical processes important in the early settlement phase, we will not discuss subsequent movement of the larvae following early settlement to other locations, which may be due to behavioral responses (Butman and Grassle 1992; Grassle et al. 1992) or to a combination of chemical (Pawlik 1992; Woodin et al. 1998) and physical (Woodin et al. 1995; Miron et al. 1996) cues.

Theoretical background

Turbulent boundary layer structure—Larval settlement often takes place within a turbulent benthic boundary layer. Turbulent boundary layers transport momentum from the overlaying flow to the bed through viscous interactions and spatially coherent structures in the flow that, on average, move high-momentum fluid toward the bed and low-momentum fluid away from the bed. This momentum transfer results in shear stresses; the portion of these stresses associated with the coherent flow structures are referred to as turbulent Reynolds stresses.

The average total shear stress, $\bar{\tau}$, is given by

$$\bar{\tau} = \mu \frac{\partial U}{\partial z} - \rho(\overline{uw}) \quad (1)$$

where μ is the fluid dynamic viscosity, U is the average velocity, and \overline{uw} is the correlation between the horizontal and vertical fluctuating velocity components. The first term in Eq. 1 represents the viscous stress component. The second term, the Reynolds stress, is the averaged effect of turbulent advection. See Table 1 for a list of all of the symbols used.

Table 1. List of symbols.

Symbol	Meaning
c	larval concentration
h	above-bed height of adult clam
K	turbulent eddy diffusivity
P_A	probability of successful anchoring
S	spacing between adult clams
t_{hit}	mean time before a larva makes contact with the bed (mean hitting time)
t_{hit}^*	nondimensional mean hitting time
t_r	time remaining in the stress lull after touchdown
t_a	time required for the larva to anchor
\tilde{u}	instantaneous horizontal velocity, $\tilde{u} = U + u$
U	time-averaged horizontal velocity
U_∞	time-averaged horizontal freestream velocity
u	fluctuating portion of the horizontal velocity component
u'	root-mean-square horizontal velocity, $u' = \sqrt{\overline{u^2}}$
u_τ	shear velocity
\overline{uw}	velocity correlation in the vertical plane; Reynolds stress $= \rho \overline{uw}$
w	fluctuating portion of the vertical velocity component
w'	root-mean-square vertical velocity, $w' = \sqrt{\overline{w^2}}$
w_s	larval sinking velocity
z	vertical coordinate, measured upward from the bed
z^+	nondimensional vertical coordinate in wall units, $z^+ = zu_\tau/\nu$
δ	boundary layer thickness
ϵ	dissipation rate
Φ	flux of larvae contacting the bed
ρ	fluid density
τ	instantaneous stress
$\bar{\tau}$	time-averaged stress
$\bar{\tau}_w$	time-averaged stress at the bed
τ_{crit}	critical stress
τ_{crit}^*	nondimensional critical stress
μ	dynamic fluid viscosity

Reynolds stresses result from the evolution of coherent structures in a boundary layer (Cantwell 1981). Fluid in the viscously dominated near-wall region (viscous sublayer) accumulates into an alternating array of high- and low-speed streaks that interact with the overlaying flow and produce a fluid ejection process called a burst. The burst structures can account for up to 70% of the time-averaged Reynolds stress. The burst sequence is usually closely followed by a sweep structure, where upstream and overlaying fluid is injected toward the wall and sweeps out the near-bed fluid. The Reynolds stresses are a direct measure of the strength and coherency of the organized motions in the turbulent boundary layer.

Hydrodynamic forces on settled larvae—A settling larva in a turbulent flow experiences numerous hydrodynamic forces associated with the fluid motion. These forces fluctuate in time, and the character of the fluctuation is governed by the structure of the turbulence. The hydrodynamic forces include lift, form drag, skin friction, fluid acceleration reaction forces, and forces due to viscous and turbulent shear stresses (Allen 1985; Denny 1988). The relative strength of the various forces depends on the larval morphology, the character of the bed, and the flow state. Predicting all of the

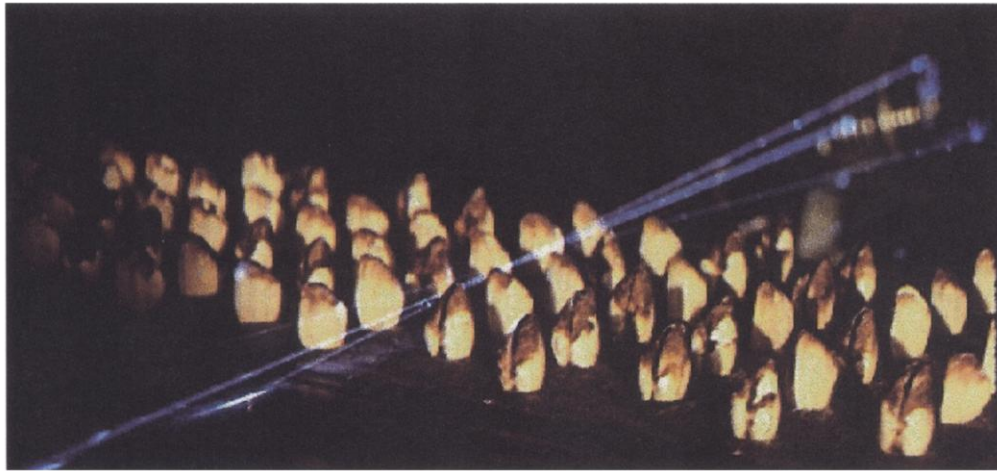


Fig. 1. Photograph of the adult clam model in the flume test section, showing the LDA laser beams. The configuration shown is the clam spacing $S = 30.5$ mm and height $h = 18$ mm.

instantaneous constituent forces acting on a larva is complex. However, at the scale of a larva, the temporal variation of all of the hydrodynamic forces depends *only* on the temporal variation of the local velocity field, i.e., the turbulence structure. A study of the turbulence structure yields information about the temporal fluctuations in the forces acting on the larva. Thus, the temporal character of the Reynolds stress should indicate the temporal character of all of the hydrodynamic forces that potentially influence larval settling. Although other hydrodynamic forces may also be important, we chose to study the Reynolds stresses because (1) they are typically large in turbulent boundary layer flows, (2) we would expect them to be the dominant influence on the vertical transport of larvae, and (3) they are easily measured in the laboratory using nonintrusive measurement techniques.

Methods

The experiments were performed in an open-channel, recirculating water flume with a 3-m long test section; *see* O'Riordan et al. (1993) for a detailed description of the facility. Two flow conditions were used for these experiments: $U_\infty = 8$ cm s⁻¹ and $U_\infty = 40$ cm s⁻¹, where U_∞ is the free-stream velocity. The depth in the test section for the two flow conditions was 28 and 24 cm, respectively.

Models of adult clam populations were placed in a tray in the center of the test section bed. The models were constructed with complete adult *Potamocorbula amurensis* shells embedded into a substrate of clay, as shown in Fig.

1. The models measured 180 cm in length and 20 cm in width. A total of six models were tested, where each model used one of three different clam spacings ($S = 30.5$, 43.6, and 61.0 mm) and one of two different clam heights ($h = 9$ mm and $h = 18$ mm). A top view of the model clam layout for one spacing is shown in Fig. 2. The location where the measurements were taken is marked by the plus symbol in the figure. Because of the geometric similarity of the model clam beds, the hydrodynamics at the chosen location are representative of the hydrodynamics at other possible locations. A side view of a typical model clam (looking upstream) showing the two heights tested is given in Fig. 3. The spacings, heights, and orientations used in the adult clam models were based on laboratory and field observations of live clams in San Francisco Bay made by Thompson (unpubl. data) and Cole et al. (1992). The size of the clam shells varied from 22 to 30 mm in length, but the shells in the vicinity of the measurement location were all approximately 27 mm in length.

A Dantec two-component laser-Doppler anemometer (LDA) was used to make the velocity measurements from which the Reynolds stresses were calculated (*see* Fig. 1). The LDA uses three laser beams that are focused through a 310-mm focal length lens to form a measuring volume inside the test section of the flume. The measuring volume is elliptical in shape, approximately 0.1 mm in the vertical and streamwise directions, and 1 mm in the cross-channel direction. Thus, the LDA captures the scales of motion responsible for the majority of the transport of momentum and the production of turbulent shear stresses.

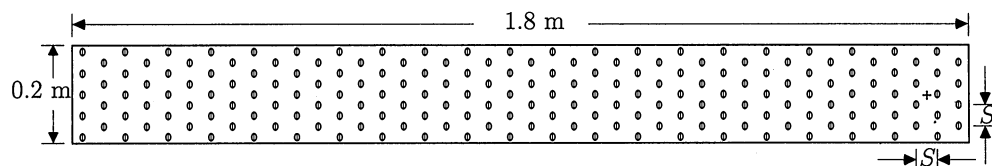


Fig. 2. Top view schematic of adult clam model for intermediate clam spacing $S = 43.6$ mm. Measurements were taken at the location denoted by the plus symbol. Flow is from left to right.

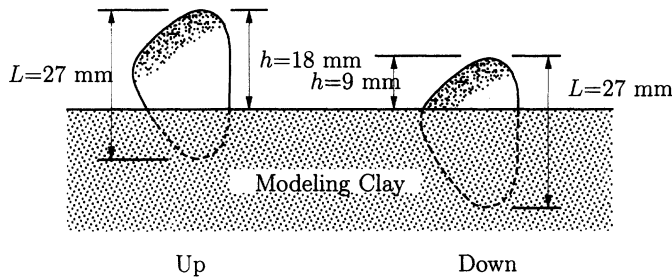


Fig. 3. Vertical placement of clam shells in the model: $h = 18$ mm (left) and $h = 9$ mm (right). Substrate is a smooth modeling clay. View looking upstream.

The LDA laser and optics were mounted on a motorized, computer-controlled traverse that permitted the LDA measuring volume to be positioned anywhere in the test section. The traverse system is accurate to within approximately 200 μ . Time series of velocity were measured at a series of vertical positions, ranging from very close to the bed ($z = 0.7$ mm) to the top of the boundary layer ($z = 140$ to 150 mm), where the local mean velocity was equal to the free stream velocity and velocity correlations were essentially zero. At each vertical position, velocities were sampled at either 63 Hz (for the $U_\infty = 8$ cm s $^{-1}$ flow) or 135 Hz (for the $U_\infty = 40$ cm s $^{-1}$ flow) for a period of approximately 15 min. Analysis of turbulent spectra indicates that this sampling rate is adequate to resolve the turbulent fluctuations relevant to this study.

Analysis

This study separately considers larval transport to the bed and larval anchoring. The transport analysis investigates the effect of measured turbulence on larval flux to the near-bed region. The anchoring analysis computes the probability of anchoring success based on measured stress histories. The “net larval settlement flux” is then defined as the product of the larval flux to the bed and the probability of anchoring success. The analysis predicts the hydrodynamic effect of different flow rates and bed geometries on each of these two constituent processes.

Larval flux calculation—Transport to the bed is the first stage of the settling process, beginning with a larva suspended somewhere in the water column and ending when the larva makes contact with the bed. The transport of larvae to the near-bed region is governed by a combination of active swimming, passive sinking, and turbulent advection. In our analysis, larvae are modeled as passive particles, with a constant sinking velocity that represents the passive sinking and swimming behavior.

The goal of this part of the analysis is to compare the flux of larvae hitting the bed for the three different adult clam spacings and two flow rates. Using a similar reasoning to Eckman and Duggins (1998) for larval settlement onto pipe walls, the flux Φ of larvae contacting the bed (larvae per unit area per unit time) can be estimated by

$$\Phi = \int_0^H \frac{c(z)}{t_{\text{hit}}(z)} dz \quad (2)$$

where $c(z)$ is the number of larvae per unit volume as a function of height above the bed and $t_{\text{hit}}(z)$ is the mean time before a larva starting at height z makes contact with the bed (mean hitting time). The time $t_{\text{hit}}(z)$ is determined by the turbulent flow field and sinking plus swimming behavior of the larvae, and can be estimated from turbulent statistics and sinking velocities. However, a wide variety of concentration profiles $c(z)$ have been observed in nature. For example, some species and some larval stages increase their concentrations near the bed, others favor the near-surface, while still others may respond to pressure and density changes by concentrating part way down the water column (Young 1995). Thus, concentration distributions are determined by many factors including upstream conditions, flow history, and larval behavior. For these reasons, it is not possible to quantify the flux of larvae to the bed without direct and simultaneous measurements of the concentration profile. Because we did not make these measurements, our analysis is limited to estimating how different clam spacings and flow speeds affect mean hitting time profiles.

McNair et al. (1997) estimated the mean hitting time using what they term their local exchange model. The mean hitting time distribution $t_{\text{hit}}(z)$ is calculated by solving the differential equation

$$K(z) \frac{\partial^2 t_{\text{hit}}}{\partial z^2} + \left(\frac{\partial K}{\partial z} - w_s \right) \frac{\partial t_{\text{hit}}}{\partial z} = -1 \quad (3)$$

where $K(z)$ is the turbulent eddy diffusivity distribution and w_s is the larval sinking velocity. The same approach is used in the current analysis.

For each combination of adult clam spacing and flow speed, time series of velocity were recorded at a number of vertical positions above the bed, as described previously. Though the measurements do not cover the whole water column depth, they encompass the full boundary layer, and the top measurement corresponds to a location where the mean velocity is equal to the free stream velocity. Mean velocities U and Reynolds stress correlations \overline{uw} were calculated by averaging over the length of the time records. A sixth-order polynomial was fitted to the velocity and Reynolds stress data versus the logarithm of z , and a continuous eddy diffusivity distribution was estimated from the interpolation functions as $K(z) = \overline{uw}/(\partial U/\partial z)$. The mean hitting time $t_{\text{hit}}(z)$ was then calculated by solving Eq. 3.

Very close to the bed the flow is affected by strong vortical secondary flows due to individual clam shells. Because of the strong recirculation in this region, gradient diffusion concepts are not valid and the eddy diffusivity model no longer makes sense. For this reason, hitting times were only calculated to the level of the top of the shells. The bottom boundary condition was therefore $t_{\text{hit}}(h) = 0$ where h is the height of the top of the clam shells. The uppermost measurement corresponds to a location where the mean velocity is approximately equal to the free stream velocity. This means that $K(z) = 0$ at this point and therefore the top boundary condition was $\partial t_{\text{hit}}/\partial z = 1/w_s$ (pure sinking). Equa-

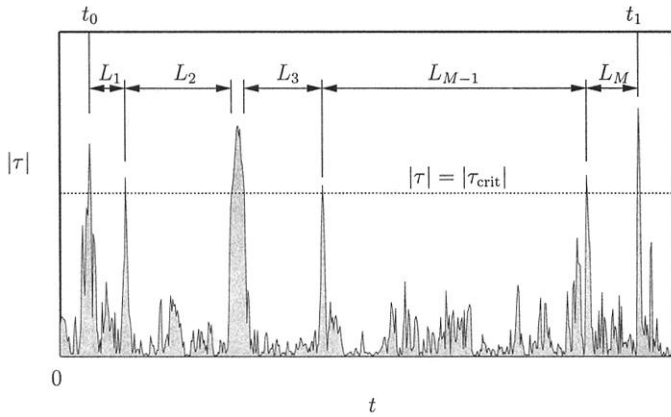


Fig. 4. Representative history of hydrodynamic stress magnitude showing the division of the record into stress lulls, L_1, L_2 , etc., for a given value of the critical stress, τ_{crit} .

tion 3 was solved for two different sinking velocities, $w_s = 0.1 \text{ cm s}^{-1}$ and $w_s = 0.3 \text{ cm s}^{-1}$, representing a range of typical sinking velocities for clam larvae (Wildish and Kristmanson 1997).

Anchoring probabilities—The analysis in this section quantifies the effect of the turbulent hydrodynamics on the ability of larvae to successfully anchor to the substratum upon arrival at the bed. It is assumed that sufficiently large hydrodynamic stress events will tend to dislodge or resuspend the larva until the instant that the larva is completely anchored. A successful anchoring requires that the local hydrodynamic stresses τ be less than a critical (unknown) stress threshold τ_{crit} for the larvae at touchdown and during the time required for anchoring. The analysis presented here is a statistical description of the duration of local stress lulls (defined as contiguous periods where $\tau < \tau_{crit}$) in the highly episodic instantaneous stress record. These statistics are used to calculate the probability of a successful anchoring event as a function of τ_{crit} and the hydrodynamic state resulting from different flow rates and bed geometries. As discussed earlier, the analysis uses measured records of turbulent Reynolds stress magnitude as a measure of the temporal characteristics of *all* of the hydrodynamic forces acting on the larva.

Several simplifying assumptions are made in the anchoring analysis. Although the turbulence is certainly at least partially responsible for the arrival of the larva at the bed, the time at which bed contact occurs is assumed to be independent of the stress history prior to that time. Thus, the analysis starts at the instant of contact with the bed. Also, only the stress magnitude is considered with regard to larval resuspension, meaning that sufficiently large positive and negative stresses are assumed equally likely to terminate the anchoring process.

Figure 4 contains a short, representative history of the hydrodynamic stress magnitude near the bed. The episodic nature of the stress record is a signature of the near-bed turbulence structure. For any chosen value of the critical stress τ_{crit} , the instantaneous stress record can be parsed into a set of periods where $\tau < \tau_{crit}$; the lulls are labeled as L_i ,

where i runs from 1 to M . The variable M is the total number of stress lulls in a stress record for a given value of τ_{crit} . As shown in Fig. 4, the first complete lull begins at time t_0 and the last complete lull ends at t_1 . The total amount of time during the period $t_1 - t_0$ that the instantaneous stress is below the threshold is equal to the sum over M of the individual lull lengths, L_i .

For successful anchoring to be possible, a larva must make contact with the bed during a given stress lull L_i , and the lull must be at least as long as the required anchoring time, t_a . Furthermore, a larva must land early enough in a given lull such that the remaining time in the lull equals or exceeds t_a . This shortens the useful portion of a lull from L_i to $(L_i - t_a)$. Thus, the probability P_A of a successful anchoring event can be expressed as

$$P_A(\tau_{crit}, t_a) = \frac{\sum_{i=1}^M \psi_i}{t_1 - t_0} \quad (4)$$

where

$$\psi_i = \begin{cases} L_i - t_a & \text{if } L_i \geq t_a \\ 0 & \text{if } L_i < t_a \end{cases} \quad (5)$$

For stress data sampled discretely at time intervals Δt , Eq. 5 can be evaluated as

$$\psi_i = \sum_{j=j_a}^{N_{max}} H_i(j) \Delta t \quad (6)$$

where j_a is an integer approximation of the number of sample time steps in t_a and N_{max} is the number of samples in the longest measured stress lull. The variable H_i is defined as

$$H_i(j) = \begin{cases} 1 & \text{if } 1 \leq j < N_i \\ 0 & \text{if } j \geq N_i \end{cases} \quad (7)$$

where N_i is the number of samples in the i^{th} stress lull. Substituting Eq. 6 into Eq. 4 results in

$$P_A(\tau_{crit}, t_a) = \frac{\Delta t}{t_1 - t_0} \sum_{j=j_0}^{N_{max}} \sum_{i=1}^M H_i(j) \quad (8)$$

Equation 8, when combined with an appropriate stress criteria, τ_{crit} , and anchoring time, t_a , allows the probabilities of successful anchoring events to be directly calculated from stress time histories.

Results

Mean turbulence statistics—Figures 5 and 6 contain vertical profiles of mean velocity, turbulence intensities, and Reynolds stresses for all three clam spacings, with clam height $h = 18 \text{ mm}$ and flow speed $U_\infty = 40 \text{ cm s}^{-1}$. For all measurements, $z = 0$ corresponds to the substrate location, and data were taken between adult clams at the horizontal location indicated in Fig. 2. The clam spacing has a significant effect on the mean turbulence statistics. Decreasing the clam spacing reduces the mean near-bed velocity and the mean near-bed shear (Fig. 5a). Decreasing the clam spacing increases the mean Reynolds stress correlation away from

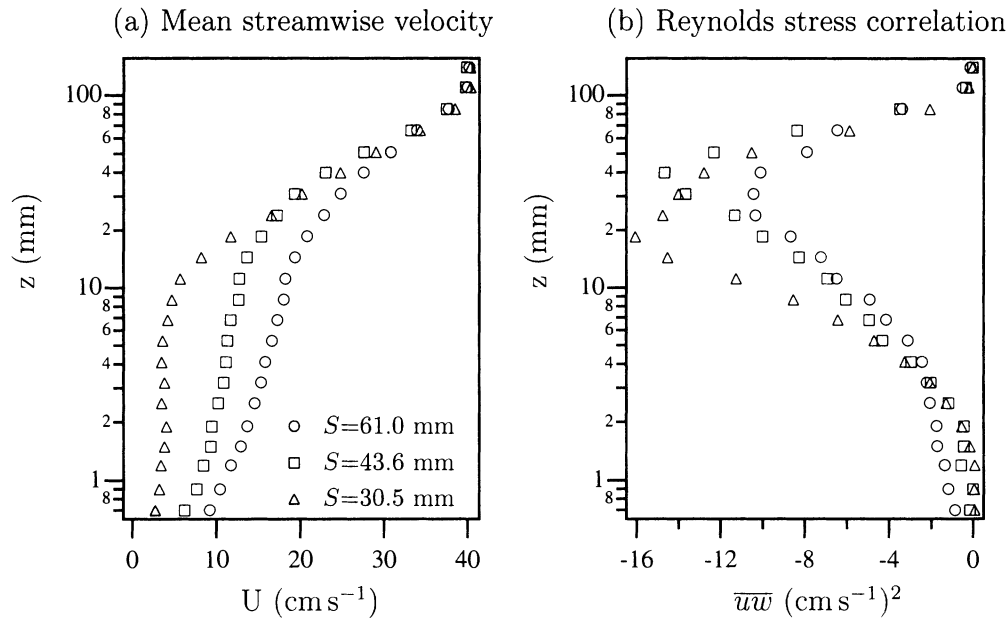


Fig. 5. Effect of adult clam spacing on (a) streamwise velocity and (b) Reynolds stress correlation profiles for $U_x = 40$ cm s⁻¹ and $h = 18$ mm. Values of the adult clam spacing S are shown above.

the bed, but decreases it close the bed ($z < 3$ mm, Fig. 5b). Finally, decreasing the clam spacing increases the streamwise and vertical turbulence intensities (Fig. 6a,b). The effect of clam spacing on the turbulence statistics shown in Figs. 5 and 6 is typical of that measured for the other flow speeds and clam heights. Of particular note to the present study is that very close to the bed the mean velocity, mean shear, and mean turbulent stress decrease as the clam spacing decreases, which suggests that anchoring might be more eas-

ily accomplished at the smaller spacing. However, the statistical stress results presented in a later section (which considers the structure of *instantaneous* rather than mean stresses) shows the opposite result. These seemingly conflicting results highlight the need to consider instantaneous structure rather than mean quantities.

Larval fluxes—The effect of turbulence on the flux of larvae to the bed can be quantified in terms of the mean hitting

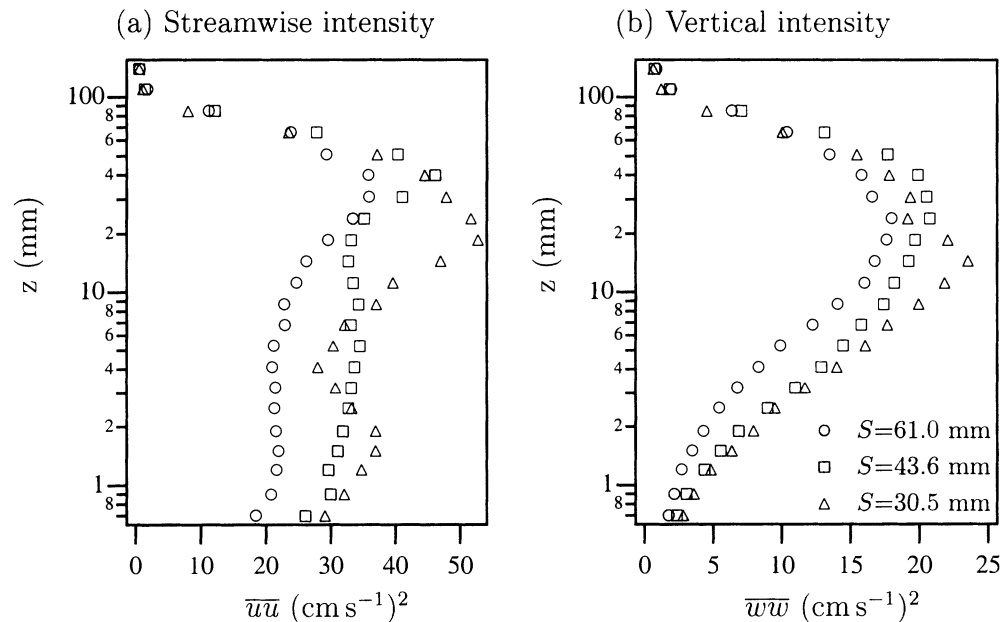


Fig. 6. Effect of adult clam spacing on (a) streamwise and (b) vertical turbulence intensity profiles for $U_x = 40$ cm s⁻¹ and $h = 18$ mm. Values of the adult clam spacing S are shown above.

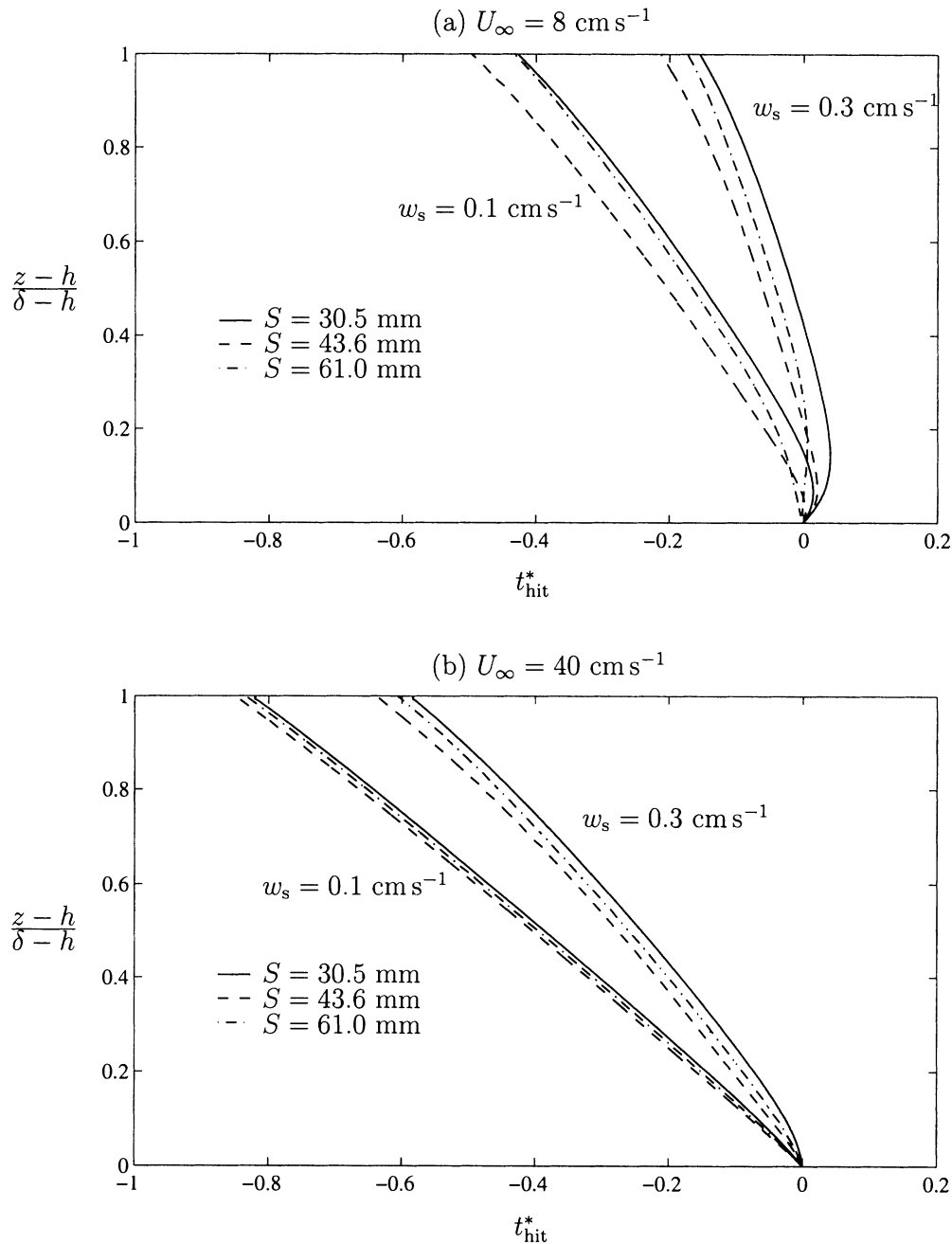


Fig. 7. Mean hitting times as a function of vertical position in the boundary layer (relative to the top of the adults). Hitting times are normalized by the time taken to fall the full depth of the boundary layer in the absence of turbulence and plotted as the difference between the local exchange model estimates and the no-turbulence values. (a) shows the results for the $U_\infty = 8 \text{ cm s}^{-1}$ experiments and (b) shows the results for the $U_\infty = 40 \text{ cm s}^{-1}$ experiments for all three spacings S of adult clams and two sinking velocities w_s .

time profile $t_{\text{hit}}(z)$. Figure 7 shows the local exchange model estimates of mean hitting times for the three clam spacings, two flow velocities, and two sinking rates. Hitting times are plotted as the change in hitting time relative to the pure sinking (no turbulence) case, nondimensionalized by the time taken to fall over the depth of the boundary layer if there were no turbulence. The nondimensional hitting time is denoted t_{hit}^* . Positive values of t_{hit}^* indicate that hitting times

are increased by turbulence, relative to the pure sinking case. That is, it takes a larva longer to reach the bed when released from a given point in the water column. Conversely, negative values of t_{hit}^* indicate that hitting times are decreased by the turbulence relative to the pure sinking case.

There are four notable results:

1. For the high flow speed (40 cm s^{-1}), hitting times are

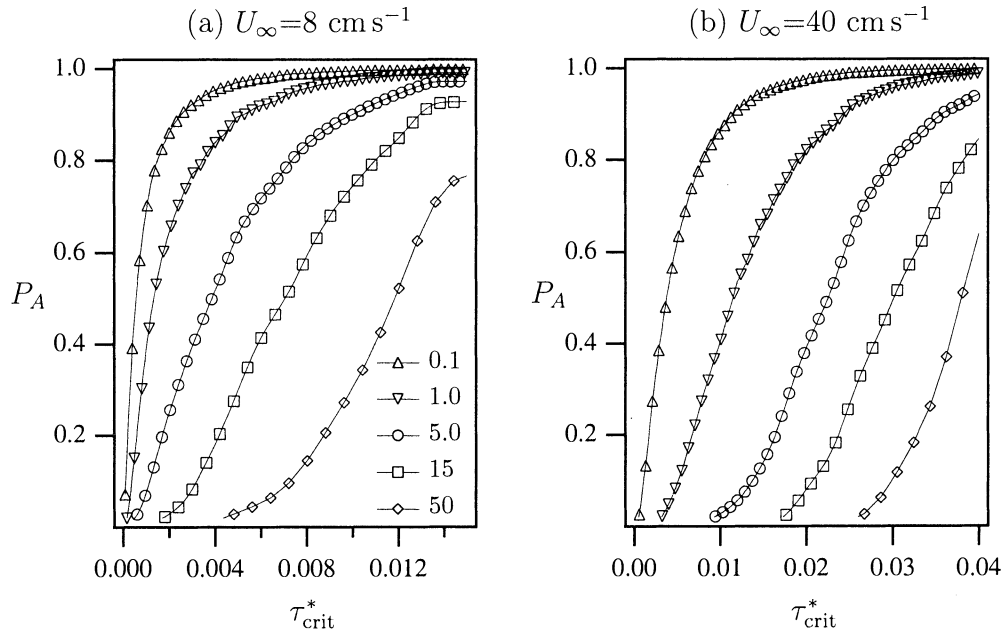


Fig. 8. Probability of successful anchoring versus threshold stress for adult clam spacing $S = 30.5$ mm and height $h = 18$ mm. Results are shown for (a) $U_\infty = 8$ cm s $^{-1}$ and (b) $U_\infty = 40$ cm s $^{-1}$. Values of the anchoring time t_a (in seconds) are given above.

much reduced from the pure sinking case, which indicates that turbulence dominates the vertical movement of larvae in a large part of the water column. Turbulence generated by the mean flow acts to decrease the mean hitting time, thus increasing the flux of larvae to the bed compared with the pure sinking case.

2. For the low flow speed (8 cm s $^{-1}$), turbulence acts to decrease the mean hitting time over most of the water column, though not to the same extent as for the faster flow speed. Close to the bed, turbulence appears to increase the mean hitting time for sufficiently high sinking velocities.
3. Turbulence causes a greater relative reduction in the mean hitting times for the low sinking velocity than for the high sinking velocity. Thus the flux of small, slow-sinking larvae to the bed is likely to be more sensitive to the turbulent flow field than the flux of large, rapidly sinking larvae.
4. Although in all cases considered, the densest assemblage results in slightly longer hitting times (t_{hit}^* is greater than that for the sparsest assemblages), the effect of clam spacing appears to be very weak. When one considers the uncertainties in the hitting time estimates, the difference between the hitting time profiles for the three spacings is probably not significant.

Anchoring probabilities—The probability of successful anchoring, P_A , was calculated using Eq. 8 for two flow speeds ($U_\infty = 8$ cm s $^{-1}$ and $U_\infty = 40$ cm s $^{-1}$), three clam spacings ($S = 30.5$ mm, $S = 43.6$ mm, and $S = 61.0$ mm), and two clam heights ($h = 9$ mm and $h = 18$ mm). We assumed that the hydrodynamic stresses experienced by a larva settling on the substrate could be represented by those measured at $z = 1.5$ mm above the substrate. The magni-

tudes of the stress events are different at different vertical locations, but the temporal structure of the stresses would likely be very similar to those used for the calculations here. We also assumed that the larva always settled at the location indicated in Fig. 2. For each experimental condition, records of the Reynolds shear stress (calculated from velocity records) were used to calculate P_A . In the analysis, the stress threshold, τ_{crit} , is treated as a variable (since the true critical value is unknown); τ_{crit} is varied over a sufficient range to produce calculated values of P_A over the entire range $0 < P_A < 1$. In the plots that follow, the stress threshold is nondimensionalized as

$$\tau_{crit}^* = \left(\frac{\tau_{crit}}{\rho U_\infty^2} \right) \left(\frac{S}{\delta} \right) \quad (9)$$

where ρU_∞^2 is the free-stream dynamic pressure and S/δ is a length-scale ratio between the clam spacing and the boundary layer thickness. A heuristic argument for this nondimensionalization is given later.

The anchoring probabilities calculated for the adult clam spacing $S = 30.5$ mm and height $h = 18$ mm are plotted for a range of values of the anchoring time t_a in Fig. 8. The results are presented as a function of the nondimensional stress threshold, τ_{crit}^* , for consistency with subsequent plots, although ρU_∞^2 and S/δ are constant within the current plots.

The anchoring probabilities are strongly related to the magnitude of the stress threshold. Larva that are easily resuspended by hydrodynamic stress (small τ_{crit}^*) have markedly lower anchoring probabilities than those that remain on the bed in the presence of larger stress events (larger τ_{crit}^*). In many cases, a small percentage change in τ_{crit}^* can produce a dramatic change in P_A . The time required for a larva to anchor can also have a large impact on the probability of

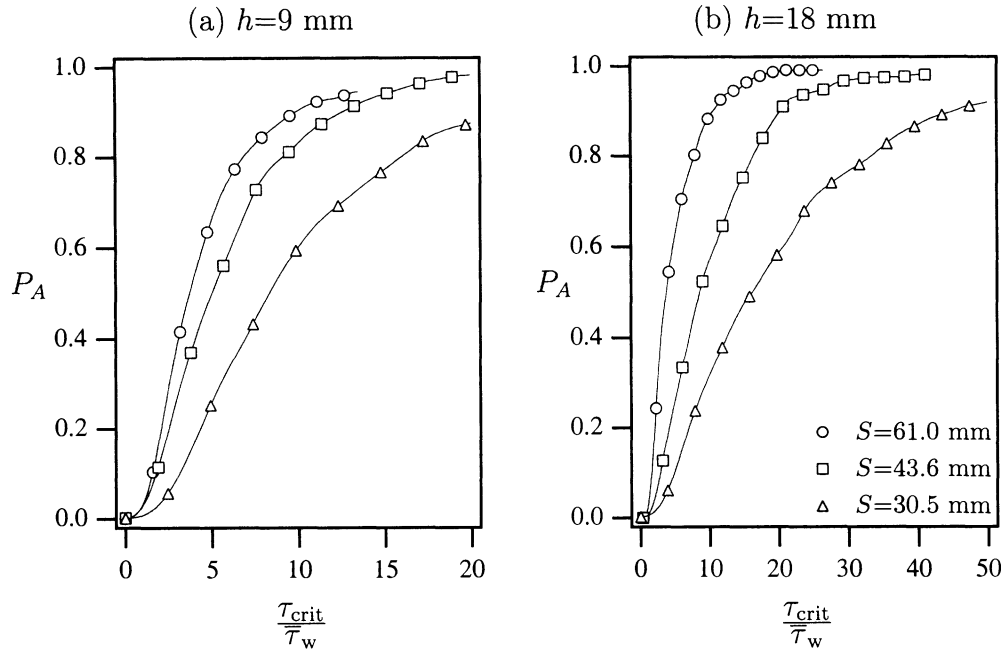


Fig. 9. Effect of adult clam spacing on the probability of successful anchoring as a function of τ_{crit} for $U_\infty = 8 \text{ cm s}^{-1}$ and $t_a = 4 \text{ s}$. The values of τ_{crit} are normalized by the mean wall stress $\bar{\tau}_w$. Results are shown for two adult clam heights: (a) $h = 9 \text{ mm}$, and (b) $h = 18 \text{ mm}$. Values of the adult clam spacing S are shown above.

successful anchoring. For a given value of the stress threshold, a short anchoring time can produce anchoring probabilities near unity, whereas longer anchoring times produce probabilities that approach zero. It can also be seen that, for a given stress threshold, as anchoring time becomes smaller, gains in the success probability diminish (i.e., the curves become more horizontal), since P_A asymptotes to near unity for the shorter anchoring times. The implication of this finding is that, for a given larval type (i.e., one with a set resuspension stress threshold, τ_{crit}), anchoring success is not appreciably improved when the anchoring times are decreased beyond some level.

Of particular note in Fig. 8 is that, although P_A is strongly related to t_a , the general behavior of P_A as a function of τ_{crit}^* is consistent for *all* values of t_a . That is, $P_A = 0$ when $\tau_{crit}^* = 0$, and P_A increases smoothly and monotonically as τ_{crit}^* increases, eventually asymptoting to $P_A = 1$ for sufficiently large values of τ_{crit}^* . This consistent behavior allows us to simplify the subsequent analysis presented in this paper and concentrate on a single value of t_a , *with no loss of generality*. This simplification enables us to easily investigate the effect of other parameters on P_A , using a fixed value of t_a . Different values of t_a produce results with different magnitudes but with nearly identical trends.

The effect of the adult spacing on the probability of successful anchoring is shown in Figs. 9 and 10, where P_A is plotted as a function of the nondimensional critical stress. The results in both of these figures are calculated using a single, illustrative, anchoring time of $t_a = 4 \text{ s}$, as justified above. For a given stress threshold, the probability of a successful settlement event decreases as the clam spacing decreases for all velocities and clam heights. That is, anchoring

success is predicted to be smaller in the dense assemblage of adults compared to the sparse assemblage. Note that this is true despite the fact that the *mean* stresses at the bed are lower for the denser case than for the sparse case (*see*, for example, Fig. 5b). The magnitude and frequency of the large *instantaneous* stresses govern P_A . The stress threshold in Figs. 9 and 10 is normalized by the mean (time-averaged) wall stress $\bar{\tau}_w$ in order to illustrate a related point: large anchoring success probabilities do not arise unless the threshold stress is many times (sometimes several orders of magnitude) larger than the local mean stress. This is especially true for the higher $U_\infty = 40 \text{ cm s}^{-1}$ results in Fig. 10b, where P_A is essentially zero unless the settling larva are able to remain on the bed in the presence of stresses that are 75–100 times greater than the mean stress (for the dense assemblage). Note, however, that the $\tau_{crit}/\bar{\tau}_w$ normalization precludes a determination of the effect of clam height on P_A since $\bar{\tau}_w$ changes when the clam height is changed. This shortcoming motivated the development of the τ_{crit}^* normalization introduced earlier (Eq. 9).

We now present an explanation for the τ_{crit}^* normalization, which will allow us to present data from all of the adult clam configurations on a single reduced plot. The predicted value of P_A will be small when there are very few stress lulls with durations that exceed the value of t_a . Conversely, P_A is large when t_a is short relative to typical stress lull durations. Thus, the value of P_A is directly related to the relative magnitudes of the required anchoring time and the typical stress lull duration (which is itself a function of the stress threshold). The distribution of lull durations can be assumed to be a function of the rapidity of the burst-sweep cycle, since the large near-wall stresses that delineate the

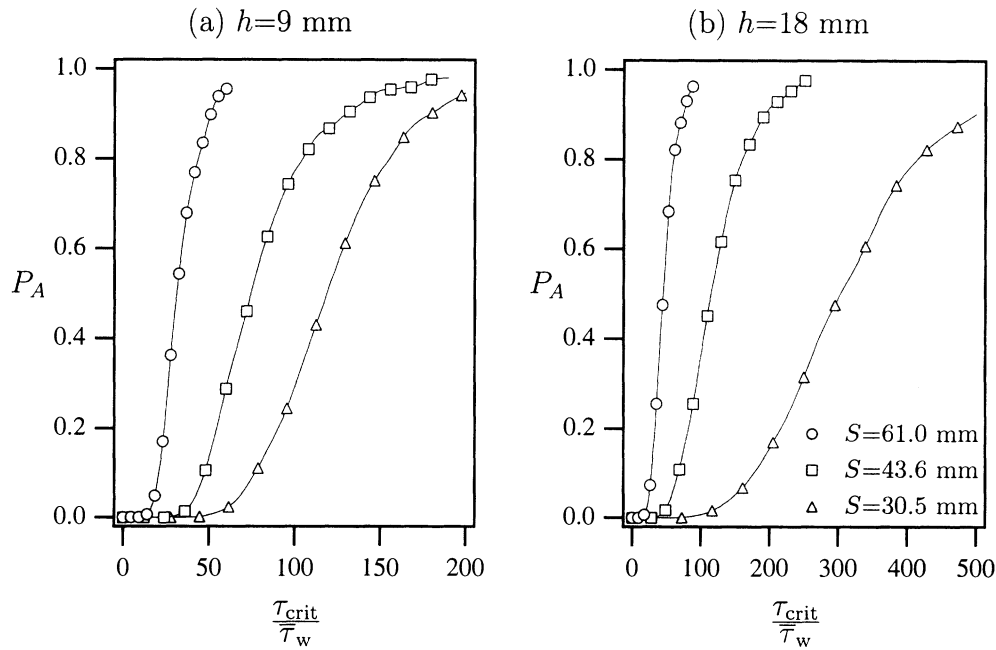


Fig. 10. Effect of adult clam spacing on the probability of successful anchoring as a function of τ_{crit} for $U_{\infty} = 40 \text{ cm s}^{-1}$ and $t_a = 4 \text{ s}$. Results are shown for two adult clam heights: (a) $h = 9 \text{ mm}$, and (b) $h = 18 \text{ mm}$. Values of the adult clam spacing S are shown above.

lulls are dominated by these structures. Thus, a parameterization of the variations in P_A should include a measure of the frequency content of the burst-sweep cycle. In his extensive review on turbulence structure, Cantwell (1981) assembles evidence from several sources that suggests that the mean burst period scales with the free-stream velocity U_{∞} and boundary layer thickness δ . Furthermore, a study by Rao et al. (1971) suggests that the mean period between bursts, t_{burst} , is only a weak function of the distance from the wall and can be estimated as

$$t_{\text{burst}} = 6\delta/U_{\infty} \quad (10)$$

Combining this knowledge with the observed behavior that P_A varies strongly with S (and temporarily ignoring the weak effect of h , a finding that will be used to test our parameterization) allows us to propose the following functional relationship based on dimensional arguments:

$$P_A = f\left(\frac{\tau_{\text{crit}}}{\rho U_{\infty}^2}, \frac{S}{\delta}\right) \quad (11)$$

Dimensional analysis of the relationship given by Eq. 11 provides information about the nondimensional groups of presumed-relevant parameters. The dimensional argument does not specify the form of the functionality. However, we determined by a trial-and-error approach that the product of the two parameter groups is an effective means of parameterizing the probability P_A . This leads to the nondimensional stress threshold, τ_{crit}^* , given previously in Eq. 9.

The anchoring success probabilities, when plotted as a function of τ_{crit}^* , show very similar trajectories for all 12 of the experimental configurations for the $U_{\infty} = 8 \text{ cm s}^{-1}$ and the $U_{\infty} = 40 \text{ cm s}^{-1}$ flow cases (Fig. 11). The parameter τ_{crit}^* is seen to be a reasonably good nondimensional predictor

of P_A for the range of clam spacings and heights tested. The shapes of the data bands in Fig. 11a,b show the effect of adult clam spacing on the anchoring probabilities (since τ_{crit} increases as S increases). Regardless of the dimensional value of the critical stress τ_{crit}^* , the anchoring probabilities decrease as the spacing decreases. This implies that anchoring becomes less successful as the density of the adult clam bed increases. The data support this conclusion regardless of the value of t_a used in the analysis.

The parameter τ_{crit}^* does not predict the value of P_A across different velocities (which is why the data from the two different flow rates are plotted separately). Also, τ_{crit}^* is more successful as a predictor of P_A for the $U_{\infty} = 8 \text{ cm s}^{-1}$ data than for the $U_{\infty} = 40 \text{ cm s}^{-1}$ data. We suspect that this may be due to a larger experimental uncertainty in calculating δ for the higher flow rate case. Finally, the fact that τ_{crit}^* (which is independent of the clam height, h) is reasonably successful at predicting P_A at a given velocity justifies our initial assumption that the clam height is not as strong an influence on the anchoring process as the clam spacing is.

The difference in the shapes (note the different x-axis scales) of the data bands in Fig. 11a,b results from differences in the turbulence structure between the $U_{\infty} = 8 \text{ cm s}^{-1}$ and $U_{\infty} = 40 \text{ cm s}^{-1}$ flow cases; the burst-sweep cycle occurs at a much more rapid frequency for the higher flow rate. However, the P_A distributions for both flow velocities were calculated for the same value of t_a (based on the assumption that a clam larva can anchor no more rapidly in a fast-moving flow than in a slow-moving flow). In order to directly compare P_A distributions associated with two different flow velocities, it would be necessary to calculate each distribution with two corresponding different values of t_a (scaled according to the burst-sweep cycle rate), which is not biologically appropriate.

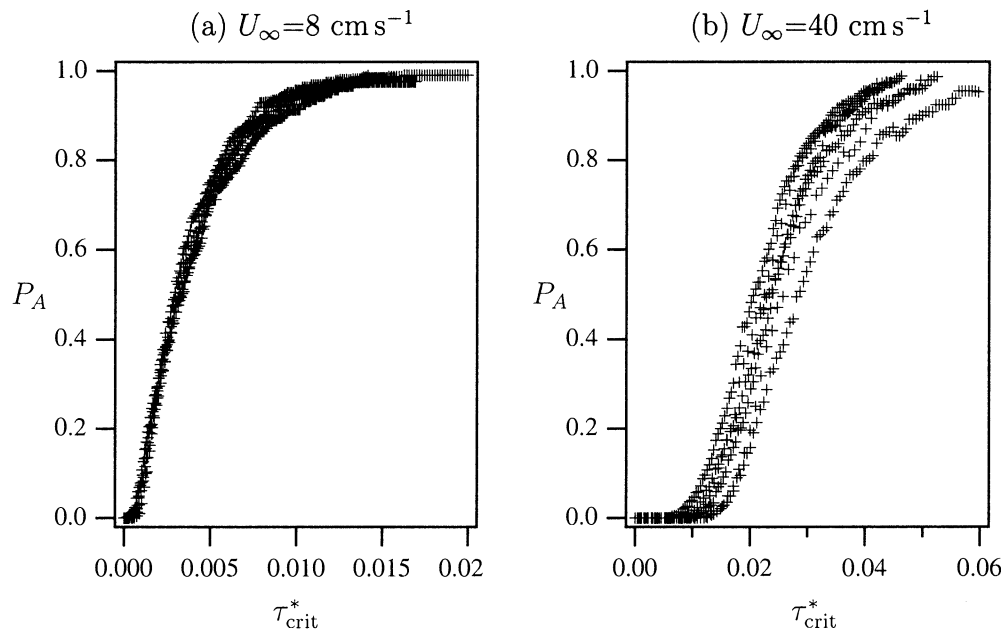


Fig. 11. Anchoring success probability for all experimental conditions versus the nondimensional stress parameter τ_{crit}^* with $t_a = 4$ s. Results are shown for (a) $U_\infty = 8 \text{ cm s}^{-1}$ and (b) $U_\infty = 40 \text{ cm s}^{-1}$.

Discussion

Hydrodynamics—We investigated the effect of hydrodynamics on two aspects of the settlement process: larval flux rate to the bed, and the ensuing probability of successful anchoring. Because the structure of the hydrodynamics varies with flow rate and the nature of the bed roughness, the results were calculated with data from two different flow rates, three adult clam spacings, and two adult clam heights.

Larval fluxes to the bed (as represented by the inverse of mean hitting times) were much larger for the higher Reynolds number ($U_\infty = 40 \text{ cm s}^{-1}$) flow than for the low Reynolds number ($U_\infty = 8 \text{ cm s}^{-1}$) flow, which suggests that, in general, turbulence is important in determining the flux of larvae to the bed. For a given sinking velocity and flow speed there is not a significant difference between the mean hitting time profiles for different clam spacings. This, in turn, suggests that, for the roughness scales tested here, there were no major differences in the fluxes of larvae hitting the bed for different spacings of adult clams. This finding differs from the results of Eckman (1990) who, based on predictions of bed contact from a one-dimensional model, showed that flux of larvae to the bed should increase with the density of roughness elements on the bed. Our results show that (1) the adult clam spacing strongly affects the anchoring success probability (given contact with the bed) and (2) the variations in this anchoring probability have a larger impact on the overall settlement success than the probability of contacting the bed.

It has been suggested that turbulence, and specifically the short time-scale burst and sweep cycles, is important in the process of larval settlement in several conceptual models (see reviews by Denny and Shibata 1989 and Abelson and Denny 1997) and in at least three numerical modeling stud-

ies (Eckman 1990; Gross et al. 1992; Eckman et al. 1994). In addition, in their laboratory study with cyprid larvae, Eckman et al. (1990) found that larval detachment, following successful settlement, was more closely tied to the instantaneous drag forces than to the maximum drag forces exerted on the larvae and that detachment was not strongly related to the mean force exerted. They conclude that this “pattern would have emerged if detachments of cyprids were linked to large amplitude, intermittent bursts of high shear.” It is consistent with these conceptual models, and Eckman et al.’s laboratory study, that the anchoring probability analysis in our study is a reflection of the structure of the instantaneous hydrodynamic stresses that act to disrupt the anchoring process. Although the Reynolds shear stress, as measured here, is just one of many different instantaneous hydrodynamic forces acting on a larva, all of the forces depend on the local turbulence structure. Since the Reynolds stress measurements capture the structure of the episodic burst-sweep cycle that dominates the near-bed hydrodynamics, the Reynolds stress is an excellent predictor for the structure of the sum total of the hydrodynamic forces. Results of the present study also confirmed findings reported by Eckman et al. (1990) that mean stresses did not accurately predict successful larval settlement.

The overall effect of hydrodynamics on the settling process can be determined by combining the larval flux results with the anchoring probability results. The rate at which larvae successfully anchor to the bed can be calculated as the product of the larval flux to the bed and the associated anchoring probability. Eckman (1990) states that if researchers could measure the rate of larval settlement (his variable p) for conditions that incorporate larval behavior and physical transport, his model could be used to predict larval settlement. We suggest here that his larval settlement rate can be

defined as equivalent to our probability P_A and that once τ_{crit} and t_a are known for a larva then the anchoring analysis shown in this study can be used to estimate P_A and ultimately to predict larval settlement with his model. The probability from our anchoring analysis can then be compared to what is measured in the laboratory, and the effect of behavior can then be estimated. Laboratory studies could also examine behavioral issues related to settling, such as rejection of a site due to chemical cues, that can be controlled in the laboratory. From these experiments, the probability of anchoring given a range of physical stresses can be measured and compared to our results independent of at least some effects of behavior.

Biological implications: how this study fits into present paradigms—In his review paper on how to link larval ecology to population dynamics, Eckman (1996) states that if we can model larval dispersal at a large scale, the final step that is required to close the larval loop is the ability to predict the probability of larvae successfully anchoring to the substratum and staying there. We have developed a predictive relationship for the first component needed for this prediction.

We do not solve the question of larval recruitment being a passive or active process in this study, rather we identify the period of time when behavior can affect the settlement process: as long as the larval swimming speed is less than the vertical transport rate, the only period when larval behavior can affect settling is during a lull period. Because larvae are unlikely to be able to swim against either the currents or turbulence in a natural tidal system, except during some slack tides, the process of being transported to the bed is likely to be passive most of the time. If there is insufficient time between the turbulent resuspension events (i.e., during the lull periods), a larva is likely to be resuspended in a manner similar to a passive particle. However, if the lull duration is sufficient for the larva to react, behavior can influence the probability of settlement. Larval behavior in these cases can include either an attachment to the bed or the lack of an effort by the larva to attach to, or burrow into the bed due to an unfavorable chemical, tactile, or hydrodynamic cue in the water column or at the bed. This scenario of larval settlement supports the findings of Abelson et al. (1994) and Butman and Grassle (1992) and the suggestion by Abelson and Denny (1997) that if the larvae are unable to swim against the prevailing hydrodynamic forces, settling in areas other than those predicted from the distribution of initial substrate contacts of the larvae is due to “desertion of unfavorable sites rather than to exploration and active selection of an appropriate site.” Conclusions from this study thus support the suggestions of Abelson and Denny (1997) and others (Butman 1987) that active habitat selection and passive deposition are not competing hypotheses of larval recruitment but are complementary processes.

The two key factors found in this study that determine whether a larva can settle once it contacts the bed are: (1) the time that it takes the larva to either attach or burrow, in comparison to the duration of the lull period and (2) the shear stress required to resuspend a larva that is in contact with the bed compared to the instantaneous shear stresses.

One conclusion from these findings could be that most larvae will settle during relatively calm and low-velocity periods, when instantaneous shear stresses are smallest and lull periods are longest. Two other modeling studies (Gross et al. 1992; Eckman et al. 1994) predicted that the majority of settlement would occur during relatively low velocity periods. As suggested by Gross et al., this hypothesis has some appeal because it could be used to explain some recruitment patchiness that is prevalent in the benthic community. The effect of such low velocity, low turbulence periods on settlement cues needs to be considered before we conclude that settlement periods are limited to times of low velocity and turbulence. Once the larvae are at the bed, settlement cues that may induce behavior resulting in settlement have been hypothesized by Abelson and Denny (1997) to include flow characteristics and other factors that are mediated by flow characteristics (e.g., delivery of chemical attractants and suspended sediment). Most flow characteristics that are relevant to settling larvae, including flow direction, shear stress, pressure gradient, turbulence intensity, boundary-layer or viscous sublayer thickness, and acceleration (Abelson and Denny 1997) would be changed by reduced velocities and calm conditions. Thus, if the larvae are using these flow characteristics as cues, they are responding to a reduced range in values that may not represent the critical characteristics of the locality and as suggested by Eckman et al. (1994), such misrepresentations may reduce a larva's ability to successfully locate a suitable settlement site. It is of course possible that the larvae may attach or burrow and then use these cues at another time to determine the suitability of the location, but such repeated settlement tries would require a competent larva to settle during an unknown number of tidal cycles. However, lower velocity may also aid in the ability of a larva to detect other factors that are mediated by flow, such as the delivery of chemical attractants. With settlement cues that are dependent on transport, reduced turbulence would result in a stronger, less dispersed signal than would be delivered during periods of higher turbulence, which could result in a more successful selection of settlement site.

Data that would be needed to support the hypothesis of larval settlement in low velocity periods are limited. Laboratory studies of settlement in epifaunal organisms have shown that these larvae can settle in high velocities (Abelson et al. 1994) and over a wide range in velocities (Eckman et al. 1990; Mullineaux and Butman 1991; Pawlik and Butman 1993). These organisms all have adhesive appendages or filaments so they may represent a specific group of organisms adapted for settling at high velocities. There have been fewer studies of larval settlement with varying velocities in the infaunal community, but work by Grassle et al. (1992) showed *Capitella* sp. I larvae settled at a higher rate in flume experiments with flows of 15 cm s^{-1} than at 5 cm s^{-1} . Further laboratory studies will be needed to determine whether organisms preferentially settle at low-flow, low-turbulence conditions, or whether short anchoring times and high stress thresholds are adaptations that allow some, if not all, species to settle during hydrodynamic conditions that are representative of the range of conditions found in locales where adult populations are found.

It should be noted that in this study we considered only

the sinking behavior of a larva down to the height of the top of the clamshells. Below this height, larval motion is likely to be dominated by the flow effects of individual clamshells and possibly by the active swimming of the larvae. Larvae have been observed swimming in the near-bed region during laboratory experiments (Jonsson et al. 1991; Butman and Grassle 1992; Grassle et al. 1992; Snelgrove et al. 1993). Based on our experimental results, these periods of swimming could have occurred during the turbulence lulls but not during bursts and sweeps, unless the larva was attached by some tethering structure (Eckman et al. 1990). It is also possible that on a hydraulically smooth bed, the larvae are confined to the viscous sublayer (VSL) very close to the bed and, as reported by Jonsson et al. (1991), are able to swim within this layer; in the VSL, velocity fluctuations are likely to be small enough that active swimming can become more effective. For hydraulically rough flows, it is likely that the process of getting to the bed is largely determined by local hydrodynamic processes until the larva is influenced by flow around a bottom feature (e.g., recirculation zones). The effects of protruding bodies from the sediment and depressions in the sediment have been well described in several papers (see Abelson and Denny 1997 for a recent review) and such a review will not be repeated here. The relevance of flows, within and over bottom features, to the results of this study is that recirculation reduces the impact of turbulence on larvae entrained in a recirculation cell and allows the larvae to settle at reattachment locations (for example, see Mullineaux and Butman 1990 and Snelgrove et al. 1993 among others).

Although previous studies have shown that hydrodynamics can facilitate aggregation of organisms around solitary tubes and solitary individuals due to entrainment of larvae in recirculation cells and horseshoe vortices (Eckman 1979, 1983; Gallagher et al. 1983; Eckman 1985; Ertman and Jumars 1988), the results of the present study might be viewed as contradicting these observations. Our results show (for the range of adult clam spacing, S , tested) that the probability of successful settlement is at a maximum when the fewest adults are present, and that the settlement probability continually decreases as the adult bed density increases. However, it should be noted that we measured stress at a single location within the clam bed (see Fig. 2), and it is certain that the value of P_A varies as the location with respect to the nearest adult clam is varied. In fact, we consistently observed aggregation of small particulates in the wake structure of individual clams. Nonetheless, this study has shown how and why aggregation may be limited when higher organism densities are seen. As a clam bed becomes more heavily populated by adult clams (thus decreasing the mean clam spacing, S), the "net larval settlement flux" (the product of the larval flux to the bed and the probability of anchoring success) decreases due to changes in the structure of the turbulent stress. Thus, the hydrodynamic processes impose a type of negative feedback into the clam bed population dynamics: as the bed density increases, the likelihood of receiving more larvae starts to diminish. Consistent with our findings, Olafsson et al. (1994), in a review of the studies on adult-larval interactions, conclude that in general, adult organisms inhibit larval recruitment. It is not clear, however,

how much of the inhibition occurs at the settlement or post-settlement stage of recruitment. If our proposed negative feedback occurs, it is probable that the near-bed hydrodynamic processes play an important role in population patchiness and the presence of some age structure within patches of benthic bivalves.

We cannot extend our conclusions into very dense beds of adult bivalves because optical access to the settlement site for the LDA measurements limited our ability to reduce the clam spacing in our study below a certain distance. In an extremely dense bed, turbulence might not consistently intrude into the very small settlement sites, thereby reducing the magnitude (Gambi et al. 1990) and frequency of the resuspension stresses. However, this same reduction in turbulent activity may decrease the rate at which larvae are transported to the bed, making the net effect unclear. Studies such as those by Eckman (1987), where bivalve settlement decreased with increasing grass density, and Bologna and Heck (2000), where bivalve recruitment was greater at the edge of seagrass patches than in the middle, may suggest that decreased flux of larvae to the bed is more important than reduced resuspension in very dense aggregations. However, it is unclear how much of the larval settlement at the edge of the patches in the later study was due to bedload transport, which might have resulted in similar distribution patterns.

There are ecological advantages for aggregation in benthic infaunal and epifaunal communities, such as increased reproductive success, reduced predation pressure on the individual, increased sediment stability and thus decreased disturbance, decreased erosion with support from neighboring individuals, and feedback to juveniles indicating successful habitats. Therefore it should not be assumed that species with the capability of delaying metamorphosis (Butman and Grassle 1992; Snelgrove et al. 1993) and being selective of habitat do not eventually succeed in settling into dense beds despite unfavorable hydrodynamic conditions. Certainly postrecruitment migration and bed-load transport can be effective in populating dense beds (Minchinton 1997; Underwood and Keough 2001; Norkko et al. 2001). However, competition for resources (food and space) can become limiting in dense assemblages and the disadvantages inherent in aggregation can outweigh the advantages for some species. These disadvantages can be reduced by individual behavior (e.g., *Potamocorbula*'s vertical movement at the sediment-water interface, J.K. Thompson unpubl. data) and the physical structure of the community, such as epifaunal reefs and hummocks, which can increase turbulence and therefore increase food to aggregated organisms (Frechette et al. 1989; Bertness et al. 1998; Thomason et al. 1998). Therefore, the degree of aggregation for a population may reflect species specific characteristics such as the time period needed to attach to the substrate, the size (centroid location) of the larvae, the ability of a larva to test the substrate and delay metamorphosis, the hardness of the larvae when moved with bedload material, and larval availability.

References

- ABELSON, A., AND M. DENNY. 1997. Settlement of marine organisms in flow. *Annu. Rev. Ecol. Sys.* **28**: 317-339.

- , D. WEIHS, AND Y. LOYA. 1994. Hydrodynamic impediments to settlement of marine propagules, and adhesive filament solutions. *Limnol. Oceanogr.* **39**: 164–169.
- ALLEN, J. 1985. Principles of Physical Sedimentology. Allen and Unwin.
- ANDRE, C., P. R. JONSSON, AND M. LINDEGARTH. 1993. Predation on settling bivalve larvae by benthic suspension in feeders: The role of hydrodynamics and larval behaviour. *Mar. Ecol. Prog. Ser.* **97**: 183–192.
- , AND R. ROSENBERG. 1991. Adult-larval interactions in the suspension feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Mar. Ecol. Prog. Ser.* **71**: 227–234.
- BERTNESS, M. D., S. D. GAINES, AND S. M. YEH. 1998. Making mountains out of barnacles: The dynamics of acorn barnacle hummocking. *Ecology* **79**: 1382–1394.
- BOLOGNA, P. A. X., AND K. L. HECK. 2000. Impacts of seagrass habitat architecture on bivalve settlement. *Estuaries* **23**: 449–457.
- BUTMAN, C. A. 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Annu. Rev.* **25**: 113–165.
- , AND J. P. GRASSLE. 1992. Active habitat selection by *Capitella* sp. 1 larvae. I. Two-choice experiments in still water and flume flows. *J. Mar. Res.* **50**: 669–715.
- CANTWELL, B. 1981. Organized motion in turbulent flow. *Annu. Rev. Fluid Mech.* **13**: 457–515.
- COLE, B., J. THOMPSON, AND J. CLOERN. 1992. Measurement of filtration rates by infaunal bivalves. *Mar. Biol.* **113**: 219–225.
- DENNY, M. 1988. Biology and the Mechanics of the Wave-Swept Environment. Princeton Univ. Press.
- , AND M. F. SHIBATA. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* **134**: 859–889.
- ECKMAN, J. E. 1979. Small-scale patterns and processes in a soft-substratum, intertidal community. *J. Mar. Res.* **37**: 437–457.
- . 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* **28**: 241–257.
- . 1985. Flow disruption by an animal-tube mimic affects sediment bacterial colonization. *J. Mar. Res.* **43**: 419–435.
- . 1987. The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J. Exp. Mar. Biol. Ecol.* **106**: 165–191.
- . 1990. A model of passive settlement by planktonic larvae onto bottoms of differing roughness. *Limnol. Oceanogr.* **35**: 887–901.
- . 1996. Closing the larval loop: Linking larval ecology to the population dynamics of benthic invertebrates. *J. Exp. Mar. Biol. Ecol.* **200**: 207–237.
- , AND D. O. DUGGINS. 1998. Larval settlement in turbulent pipe flows. *J. Mar. Res.* **56**: 1285–1312.
- , W. SAVIDGE, AND T. GROSS. 1990. Relationship between duration of cyprid attachment and drag forces associated with detachment of *Balanus amphrite* cyprids. *Mar. Biol.* **107**: 111–118.
- , F. E. WERNER, AND T. F. GROSS. 1994. Modelling some effects of behavior on larval settlement in a turbulent boundary layer. *Deep-Sea Res. II* **41**: 185–208.
- ERTMAN, S. C., AND P. A. JUMARS. 1988. Effects of bivalve siphon currents on the settlement of inert particles and larvae. *J. Mar. Res.* **46**: 797–813.
- FRECHETTE, M., C. BUTMAN, AND W. GEYER. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnol. Oceanogr.* **34**: 19–36.
- GALLAGHER, E. D., P. A. JUMARS, AND D. D. TRUEBLOOD. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* **64**: 1200–1216.
- GAMBI, M. C., A. NOWELL, AND P. A. JUMARS. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. *Mar. Ecol. Prog. Ser.* **61**: 159–169.
- GRASSLE, J. P., C. A. BUTMAN, AND S. W. MILLS. 1992. Active habitat selection by *Capitella* sp. i. larvae. II. Multiple-choice experiments in still water and flume flows. *J. Mar. Res.* **50**: 717–743.
- GROSS, T., F. WERNER, AND J. ECKMAN. 1992. Numerical modeling of larval settlement in turbulent bottom boundary layers. *J. Mar. Res.* **50**: 611–642.
- JONSSON, P. R., C. ANDRE, AND M. LINDEGARTH. 1991. Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: Evidence for near bottom confinement. *Mar. Ecol. Prog. Ser.* **79**: 67–76.
- KEOUGH, M. J., AND B. J. DOWNES. 1982. Recruitment of marine invertebrates: The role of active larval choices and early mortality. *Oecologia* **54**: 348–352.
- MCNAIR, J. N., J. D. NEWBOLD, AND D. D. HART. 1997. Turbulent transport of suspended particles and dispersing benthic organisms: How long to hit bottom? *J. Theor. Biol.* **188**: 29–52.
- MINCHINTON, T. 1997. Life on the edge: Conspecific attraction and recruitment of populations to disturbed habitats. *Oecologia* **111**: 45–52.
- MIRON, G., B. BOUDREAU, AND P. ARCHAMBAULT. 1996. Scale of observation and distribution of adult conspecifics: Their influence in assessing passive and active settlement mechanisms in the barnacle *Balanus crenatus* (Brugiere). *Mar. Ecol. Prog. Ser.* **201**: 137–158.
- MOLLER, P. 1986. Physical factors and biological interactions regulating infauna in shallow boreal areas. *Mar. Ecol. Prog. Ser.* **30**: 33–47.
- MULLINEAUX, L. S., AND C. BUTMAN. 1990. Recruitment of encrusting benthic invertebrates in boundary layer flows: A deep-water experiment on cross seamount. *Limnol. Oceanogr.* **35**: 409–423.
- , AND ———. 1991. Initial contact, exploration and attachment of barnacle (*Balanus amphitrite*) cyprids settling in flow. *Mar. Biol.* **110**: 93–103.
- NORKKO, A., V. J. CUMMINGS, S. F. THRUSH, J. E. HEWITT, AND T. HUME. 2001. Local dispersal of juvenile bivalves: Implications for sandflat ecology. *Mar. Ecol. Prog. Ser.* **212**: 131–144.
- OLAFSSON, E. B., C. H. PETERSEN, AND W. G. AMBROSE. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* **32**: 65–109.
- O'RIORDAN, C., S. MONISMITH, AND J. KOSEFF. 1993. A study of concentration boundary-layer formation over a bed of model bivalves. *Limnol. Oceanogr.* **38**: 1712–1729.
- OSMAN, R. W., R. B. WHITLATCH, AND R. N. ZAJAC. 1989. Effects of resident species on recruitment into a community: Larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* **54**: 61–73.
- PAWLICK, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* **30**: 273–335.
- , AND C. A. BUTMAN. 1993. Settlement of a marine tube worm as a function of current velocity: Interacting effect of hydrodynamics and behaviour. *Limnol. Oceanogr.* **38**: 1730–1740.
- RAO, K., R. NARASIMHA, AND M. NARAYANAN. 1971. Bursting in a turbulent boundary layer. *J. Fluid Mech.* **48**: 339–352.
- SNELGROVE, P. V. R., C. A. BUTMAN, AND J. P. GRASSLE. 1993.

- Hydrodynamic enhancement of larval settlement in the bivalve *Mulina lateralis* (Say) and the polychaete *Capitella* sp. 1 in microdepositional environments. *J. Exp. Mar. Biol. Ecol.* **168**: 71–109.
- , J. GRANT, AND C. A. PILDITCH. 1999. Habitat selection and adult-larvae interactions in settling larvae of soft-shell clam *Mya arenaria*. *Mar. Ecol. Prog. Ser.* **182**: 149–159.
- THOMASON, J. C., J. M. HILLS, A. S. CLARE, A. NEVILLE, AND M. RICHARDSON. 1998. Hydrodynamic consequences of barnacle colonization. *Hydrobiologia* **375**: 191–204.
- THRUSH, S. F., J. E. HEWITT, R. D. PRIDMORE, AND V. J. CUMMINGS. 1996. Adult/juvenile interactions of infaunal bivalves: Contrasting outcomes in different habitats. *Mar. Ecol. Prog. Ser.* **132**: 83–92.
- UNDERWOOD, A., AND K. KEOUGH. 2001. Supply-side ecology: The nature and consequences of variations in recruitment of intertidal organisms, p. 183–200. *In* M. Bertness, S. Gaines, and M. Hay [Eds.], *Marine Community Ecology*. Sinauer.
- WILDISH, D., AND D. KRISTMANSON. 1997. *Benthic suspension feeders and flow*. Cambridge Univ. Press.
- WILLIAMS, J. G. 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *J. Mar. Res.* **38**: 729–741.
- WOODIN, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. *J. Mar. Res.* **34**: 25–41.
- , S. M. LINDSAY, AND D. S. WETHEY. 1995. Process-specific recruitment cues in marine sedimentary systems. *Biol. Bull.* **189**: 49–58.
- , R. L. MARINELLI, AND S. M. LINDSAY. 1998. Process-specific cues for recruitment in sedimentary environments: Geochemical signals. *J. Mar. Res.* **56**: 535–558.
- YOUNG, C. 1995. Behavior and locomotion during the dispersal phase of larval life, p. 249–277. *In* L. McEdward [Ed.], *Ecology of Marine Invertebrate Larvae*. CRC.

Received: 18 May 2001

Accepted: 25 January 2002

Amended: 2 April 2002