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LARVAL SETTLEMENT OF SOFT-SEDIMENT INVERTEBRATES: SOME PREDICTIONS BASED ON AN ANALYSIS OF NEAR-BOTTOM VELOCITY PROFILES*

CHERYL ANN BUTMAN**

Ocean Engineering Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 (USA)

ABSTRACT

During settlement, planktonic larvae may actively select habitats, they may be passively deposited onto the seabed, or both processes may apply, but for different spatial or temporal scales or for different flow regimes. Proposing realistic settlement scenarios involving both passive deposition and active habitat selection can profit from a priori analyses of near-bed flow characteristics relative to known aspects of larval biology (i.e., swim speeds and fall velocities). Toward this end, smooth-turbulent velocity profiles were calculated for everyday tidal flows at a shallow subtidal study site, where continuous near-bed flow measurements were available. Velocity profiles were constructed for a realistic range of flow conditions. Rough-turbulent flow profiles also were calculated, assuming storm waves periodically are sufficient to resuspend sediments and make a rippled seabed. Under most flow conditions analyzed, mean flow speeds exceed maximum larval swim speeds, even to within tenths of millimeters from the bed. In the smooth-turbulent flows, larvae generally would encounter no opposed velocity if they swam vertically in the viscous sublayer, to heights of about 0.25-cm above the bed. In rough-turbulent flows, eddies regularly penetrate to within tenths of millimeters of the bed, so larvae would experience eddy velocities with components in all directions very close to the bed. It is concluded that, at least at this study site, larvae probably do not search for preferred habitats by horizontal swimming. Larvae may swim vertically down to test the substrate and then swim vertically up to be advected downstream. However, it also is noted that measured larval swim speeds and fall velocities are about the same order-of-magnitude, so at best, larvae may only be able to maintain position when swimming vertically.

INTRODUCTION

In temperate latitudes, most infaunal organisms have planktonic larvae that eventually settle onto the seabed and become benthic adults. Larval settlement sites may be actively selected by larvae, larvae may be passively deposited onto the seabed, or both processes may operate but on different temporal or spatial scales. There is support in the literature for both active selection and passive deposition; however, hydrodynamical conditions in the field that may permit either process have not been determined. In the present study, some realistic bottom boundary-layer flow profiles are constructed, based on physical measurements from a specific field study site. Characteristics of the flow

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very close to (i.e., \leq millimeters of) the seabed are analyzed relative to pertinent aspects of larval biology (e.g., measured swim speeds and fall velocities). Based on these results, insight can be gained regarding flow profiles that would permit active selection and flow profiles where larvae would be advected and deposited like passive particles. In addition, results of the near-bed flow analysis indicate how the larvae may actually move between habitats in the field, thereby suggesting reasonable selection mechanisms for future study.

Active habitat selection by a variety of soft-sediment invertebrate larvae and meiofauna has been demonstrated at very small spatial scales (millimeters to centimeters) in still-water laboratory experiments (e.g., see reviews by Meadows and Campbell, 1972; Scheltema, 1974; Strathmann, 1978). Active selection also is strongly suggested from results of field experiments (e.g., Oliver, 1979; Williams, 1980; Gallagher et al., 1983) conducted at larger spatial scales (tens of centimeters to 20 meters). Experiments performed in controlled laboratory flow regimes that mimic specific field environments are required, however, to determine hydrodynamic conditions that would permit active selection in the field and to specify the spatial scales involved.

Specific mechanisms whereby larvae perceive information about available habitats and then select a particular location for settlement are poorly understood and are primarily speculative for soft-substrate invertebrates (but see Crisp's [1974] and Burke's [1983] reviews of the hard-substrate literature on this topic). Observations of some larval species during settlement in still water indicate that the organisms must contact a surface to perceive a specific cue (e.g., Wilson, 1968; Caldwell, 1972; Cameron and Hinegardner, 1974; Eckelbarger, 1977) and, more recently, Suer and Phillips (1983) demonstrated that the chemical factor promoting metamorphosis of their soft-substrate study organism was effective only if it was absorbed onto a solid surface. Thus, the "tactile chemical sense," coined by Crisp and Meadows (1963) to describe the process of chemoreception in barnacle cyprids, also may apply to the settlement of soft-substrate larvae. Information on the way larvae may move between potential habitats (i.e., by swimming, hopping, crawling, or by being passively distributed) during selection in moving fluid is scant, being limited to some early observations of settling polychaete larvae (Whitlegge, 1890, cited in Gray, 1974; Wilson, 1948, 1958; but see the quantitative work on barnacle cyprids by Crisp, 1955; Crisp and Meadows, 1962).

Until recently, only a handful of researchers (including Pratt, 1953; Baygerman, 1953; Fager, 1964; Moore, 1975; Tyler and Banner, 1977) considered passive deposition of larvae as a realistic alternative hypothesis to active selection. In recent experiments on the role of physical processes in sinking, settlement and recruitment of larval infauna or meiofauna, hydrodynamic null

hypotheses generally could not be rejected. These studies showed that, from fluid-dynamical considerations, it is possible to account for patterns of certain organism distributions by passive accumulation (Eckman, 1979, 1983; Hogue and Miller, 1981), passive sinking (Hannan, 1984a, b) and passive resuspension and transport (Palmer and Gust, 1985; but see also Grant, 1981). The results stipulate that near-bed flow processes must be added to the list of potential factors controlling the population dynamics of soft-sediment organisms.

Active habitat selection and passive deposition need not be mutually exclusive alternative hypotheses to account for patterns of larval settlement. For example, hydrodynamical processes may sort and distribute larvae over relatively large areas (meters to tens of kilometers) of the seabed, just as sediments are sorted and distributed. Then, once larvae have been initially deposited in a particular sedimentary environment, they may redistribute at smaller spatial scales (millimeters to centimeters) by actively choosing a preferred microhabitat. A variety of other scenarios are possible where passive deposition and active selection operate at different spatial or temporal scales. Considerable insight into the plausibility of each scenario can be obtained through an analysis of velocity profiles that are likely to occur close to the seabed in habitats where larvae settle. The mean flow speed at a given height above the bed sets, for example, the required swim speed for a larva to effectively maneuver in a plane parallel to the mean flow and also sets the horizontal distance a larva would be advected if only passive sinking occurred.

In the present study, near-bed velocity profiles are calculated for a specific soft-sediment environment, where experiments with settling larvae have been conducted since 1980 (see Hannan, 1984a, b). Sufficient data on near-bed flows at this site are available to permit profile calculations for a realistic range of flow conditions. The resulting profiles are constrained by the assumptions underlying the calculations (see PROFILE CALCULATIONS AND RESULTS), and thus, they may or may not commonly occur at the study site. However, the profiles shown here are meant only to be illustrative. They represent a first attempt at gaining quantitative insight regarding the order-of-magnitude of flow speeds potentially encountered by a larva as it gets closer and closer to the seabed. In addition, these profiles can be modeled in a laboratory flume, allowing experimental tests of the hypotheses generated from this study.

STUDY SITE AND FLOW MEASUREMENTS

Study site description and surface circulation

The field study site (Fig. 1), Station 35 (from Sanders et al., 1980), is located in Buzzards Bay, Massachusetts (USA) in 15 m of water. Bottom sediments primarily are medium sand (250-500 μ m), periodically overlain with a mud veneer.

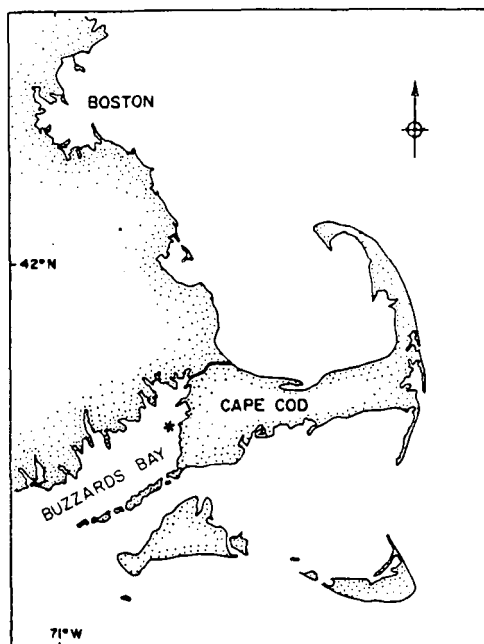


Fig. 1. Map of Southeastern Massachusetts (from Sanders et al., 1980) showing location of Buzzards Bay, on the western border of Cape Cod. The location of Station 35 is indicated by an asterisk.

Sanders et al. (1980) characterized the sediments as "moderately well to poorly sorted," based on monthly samples of the top 4-cm of sediment for one year; sediment composition was 0.5-6.7 percent gravel (> 2 mm), 59-90 percent sand ($63 \mu\text{m} - 2$ mm), and 10-37 percent mud (silt + clay, $< 63 \mu\text{m}$) during this time.

Previous descriptions of the surface circulation of Buzzards Bay have presumed that currents were primarily tidal (e.g., Redfield, 1953), but until recently (see below), few flow measurements were made. Because the main axis of the bay is oriented northeast/southwest (see Fig. 1), tidal currents generally are oriented along this axis. In some areas of the bay, however, there is a slight tendency for a counterclockwise gyre in the surface circulation of Buzzards Bay. Surface tidal currents generally are weak, rarely exceeding 50 cm/sec, and are slightly stronger and of longer duration during the flood than during the ebb tide.

During the summer, when larvae are settling, the prevailing winds are from the southwest as a result of the Bermuda high-pressure system lying to the southeast of Cape Cod. Winds are strongest in the afternoon, when local

seabreezes augment the prevailing southwesterly winds. At Station 35, winds from the southwest experience the longest fetch, so local seas at the study site can reach heights of 1-1.2 m in 2-3 hrs. However, under these non-storm conditions, locally generated wind waves in the bay are fetch-limited to ~ 4 sec and rarely penetrate to the bottom at the study site. The entire bay generally

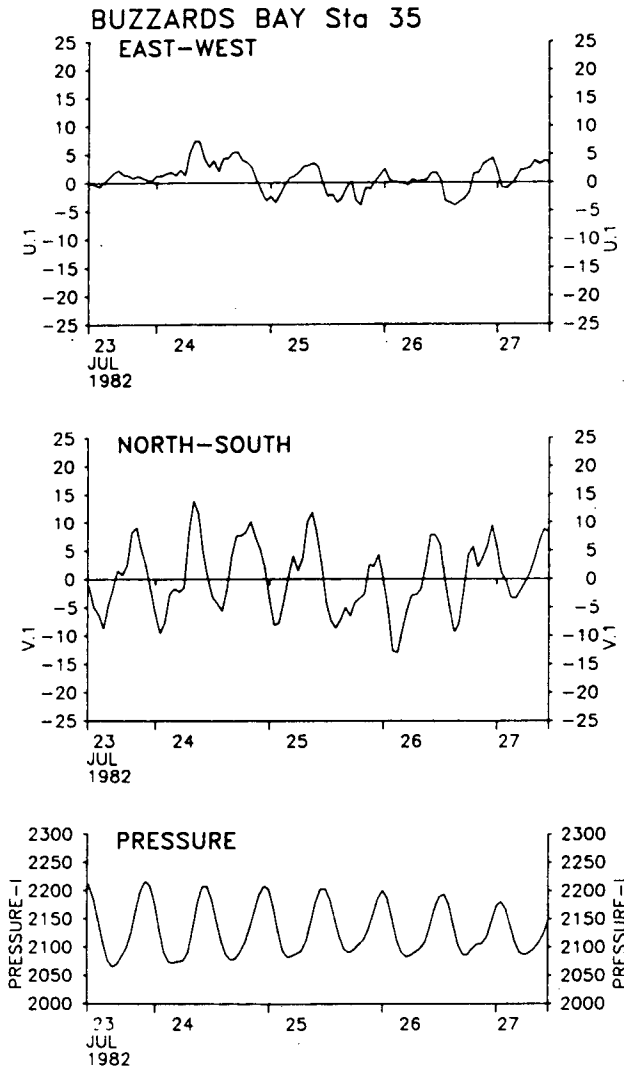


Fig. 2. Plots of the east-west and north-south components to the near-bottom currents (0.5-m above the bed) and near-bottom pressure at Station 35 during a larvae experiment (see Hannan, 1984a, b) from 7/23/82 through 7/27/82. The values plotted are edited one-hour averages during the interval.

is vertically stratified during the summer (Rosenfeld et al., 1984) due to surface heating. Because of variations in bottom topography, relatively cold water can persist at depth in the south and southwestern portions of the bay; this cross-bay temperature gradient may result in weak density-driven flows during the summer (W.D. Grant, personal communication).

Near-bottom flow measurements

During larvae experiments by the author in the summer of 1982 (see Hannan, 1984a, b), Dr. Bradford Butman (U.S. Geological Survey, Woods Hole) deployed a bottom-moored tripod instrument system to continuously measure near-bottom flows. The tripod system (described in Butman and Folger, 1979) has instruments for measuring current speed and direction, pressure, light transmission

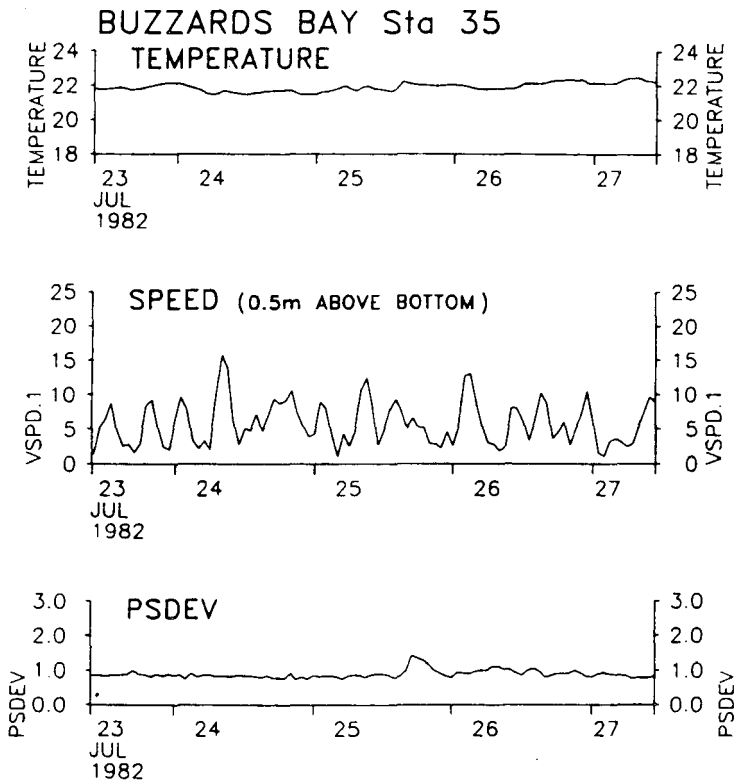


Fig. 3. Plots of near-bottom water temperature ($^{\circ}\text{C}$), current speed (0.5-m above the bed) and pressure standard deviation ("PSDEV") at Station 35 during a larvae experiment (see Hannan, 1984a, b) from 7/23/82 through 7/27/82. The values plotted are edited one-hour averages during the interval.

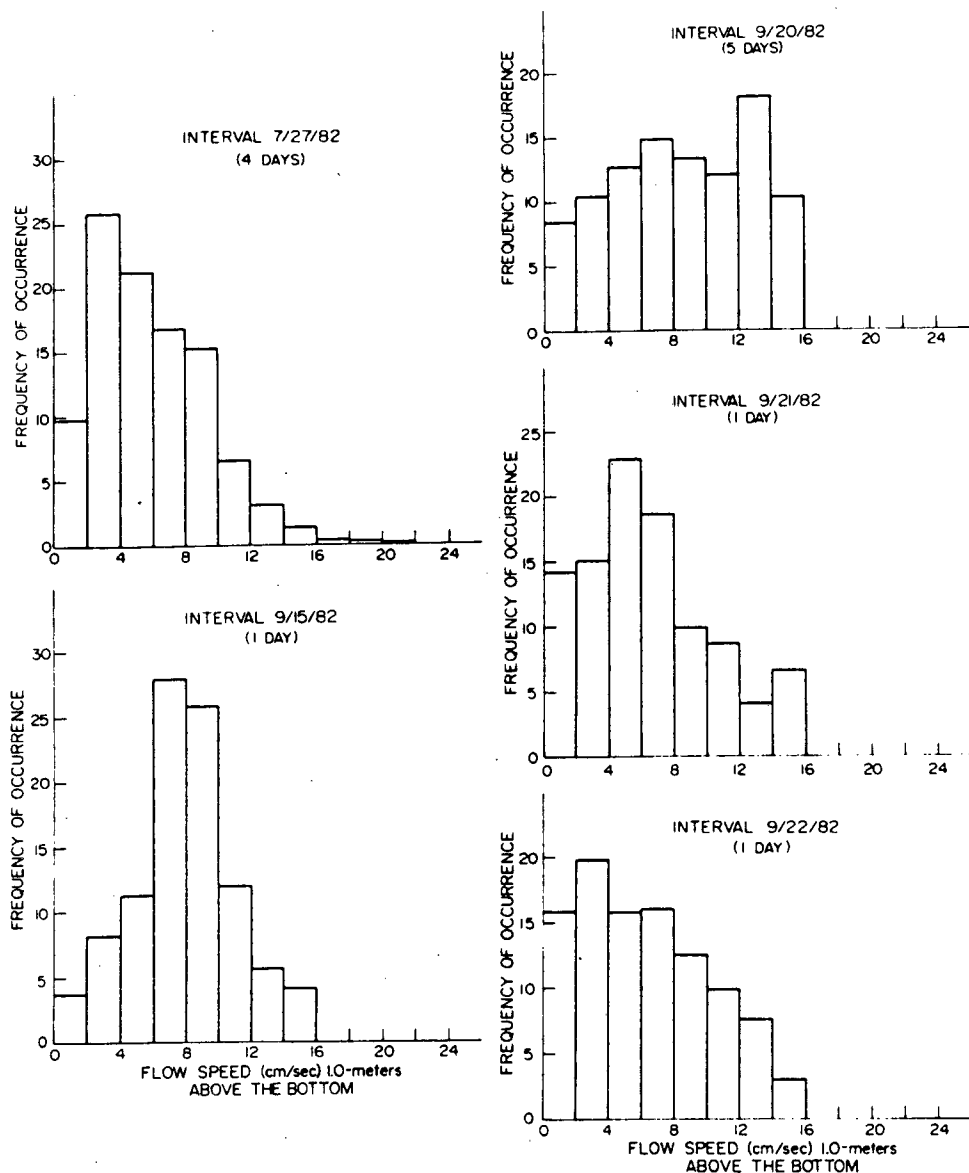


Fig. 4. Flow speed-frequency histograms for currents measured 1.0-m above the bottom at Station 35 during five different intervals when larvae experiments were conducted (see Hannan, 1984a, b). Intervals are identified on the graphs by the date that they ended; interval duration, in days, also is shown. Average values for the edited "burst" measurements are plotted for all intervals except 7/27/82, where measurements taken at the midpoint of the 3.75-min intervals are plotted.

and temperature, and also is equipped with a camera that takes bottom photographs. Savonius rotors for measuring current speed are located 0.5- and 1.-m above the seabed; small vanes are mounted below each rotor for sensing current direction. Currents and pressure were sampled in two ways (see Butman and Folger, 1979); an average measurement was made over a 3.75-min interval and a "burst" of measurements were taken in the middle of this interval (24 burst measurements were taken at 2-sec intervals). The current speed and pressure measurements reported here usually are from the 3.75-min averages and the current directions are from the burst samples. Light transmission and temperature were sampled only at the midpoint of each 3.75-min interval. Bottom photographs were taken every hour.

The near-bed flow measurements indicate that bottom flows at Station 35 are primarily tidally driven (Fig. 2). The semidiurnal periodicity typical of tides at this latitude can be seen in the pressure record. As with the surface currents, the flows are oriented primarily north-south and there is little flow east-west, indicating that the tidal flows traverse approximately the long axis of Buzzards Bay (see Fig. 1), at least near the coast where flows are polarized by the shore.

Near-bottom current speed oscillates between approximately a minimum and maximum value twice daily (Fig. 3), as expected for these tidally driven flows. However, because other physical phenomena (e.g., density-driven and wind-driven currents) also contribute to the flows, current speeds do not always go to zero and the curves are not smooth. Periodically, surface storm activity was detected in the near-bottom flows at Station 35 (e.g., see peak in PSDEV on 7/25/82 in Fig. 3); such strong surface winds cause the regularly oscillating tidal flows to deviate substantially. Near-bottom water temperature varied little on the short-term, but gradually cooled about 5°C between 7/27/82 and 9/22/84 (Hannan, 1984b). Flow speed 1.0-m above the bed varied between zero and a maximum of 22 cm/sec during the summer and early fall of 1982 (Fig. 4); however, usually only a maximum of 16 cm/sec was reached.

GENERAL DESCRIPTION OF BOUNDARY-LAYER FLOWS OVER SOFT SEDIMENTS

As water flows over the seabed, a region of shear (the slope of the velocity profile, du/dz , where u = the horizontal velocity component and z = the perpendicular distance from the surface; refer to Fig. 5) develops as a result of the retarding effect of the boundary on the flow. This region of shear near the bed is referred to as a "boundary layer". The mean velocity profile is constrained by conditions at each end of the boundary layer: $u = 0$ at $z = 0$ (the "no-slip" condition at the boundary) and $u = U$ (the free-stream velocity at $z = \delta$) (the boundary-layer thickness) (see Fig. 5). The shape of the velocity

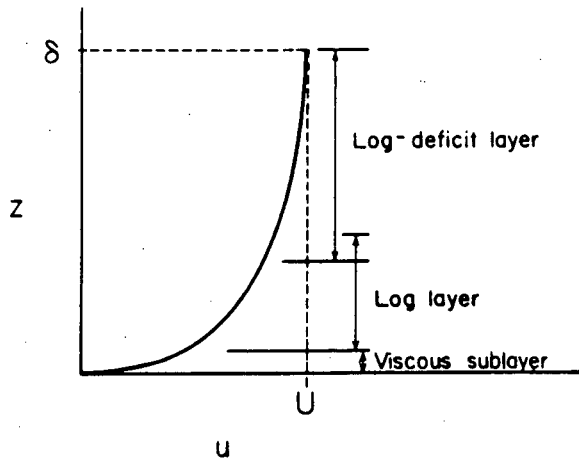


Fig. 5. Diagram of a turbulent bottom boundary layer plotted on a linear scale for both axes, showing the relative positions of the viscous sublayer, the log layer, and the log-deficit layer.

profile varies depending on flow properties (e.g., the flow Reynolds number, the background turbulence, and accelerations), fluid properties (e.g., stratification induced by temperature, salinity, and suspended sediments) and boundary characteristics (e.g., the bed roughness and the cohesiveness of sediments). The boundary-layer thickness depends on the boundary shear stress and inversely on the forcing frequency for the flow, $\kappa u_* / \sigma$, where u_* is the bottom shear velocity ($\sqrt{\tau / \rho}$, where τ is the bottom shear stress and ρ is the fluid density), κ is von Karman's constant of 0.4, and σ is $2\pi/P$ (where P is the period of the flow).

because larval settlement takes place inside the bottom boundary layer, it is instructive to briefly review relevant characteristics of boundary layers that may form over soft sediments under simple, steady-flow conditions (see also the recent discussion by Nowell and Jumars, 1984). Velocity profiles which may occur at the study site then are calculated (see PROFILE CALCULATIONS AND RESULTS), based on both field data and assumptions about profile characteristics. The following discussion is somewhat idealized, for the sake of posing logical predictions concerning the role of hydrodynamical processes in larval settlement; for this modest goal, the idealization does not significantly affect the outcome of this study. For recent reviews of the state-of-the-art in geophysical boundary-layer flows, see Nowell (1983) and Grant and Madsen (1986).

General characteristics of boundary layers

This discussion considers steady, uniform flow over a bottom which is uniform over large horizontal distances, relative to the height off the bed. In theory, the bottom boundary layer may be laminar or turbulent, depending on the relative importance of viscous versus inertial forces in the flow, as characterized by the flow Reynolds number, $Re_f = LU/\nu$ (where L = the characteristic length scale for the flow, U = the characteristic reference velocity of the flow, and ν = the kinematic viscosity of the fluid). Laminar boundary layers occur at low Re_f where turbulent fluctuations are relatively unimportant. Laminar boundary layers have pronounced stream-wise stability; any disturbance to the layer will be quickly dissipated by viscosity downstream, restoring the profile to the predisturbance case. Thus, only horizontal velocities are present in laminar boundary layers in steady, uniform flows. Turbulent boundary layers occur at high Re_f . Here, velocities have both a mean and a fluctuating component; fluctuations are due to turbulent eddies, which can have velocity components in all directions. Transfer of mass and momentum within the layer occurs due to products of coherent velocity fluctuations associated with these eddies. Near the bottom, the energetic eddies scale with height above the bed. The turbulence is produced by the product of vertical shear and Reynolds stress due to the presence of the boundary.

The Re_f is a good predictor of laminar or turbulent boundary layers for flows over smooth flat plates, but other factors are important to this prediction in ocean flows traveling over sediments or bumpy seabeds. Turbulence may be generated in the flow by a source away from the bed (e.g., wave breaking) or turbulence may be "tripped" at the seabed by a relatively large flow disturbance on the bottom. For turbulent flows, the roughness Reynolds number, $Re_* = u_* k_b / \nu$ (where k_b = the hydrodynamic bed roughness scale), is a better predictor of bottom boundary layer characteristics. However, turbulence is such a pervasive feature of ocean flows that even if local Re_* are in the laminar range, the flows often are turbulent (see Yaglom, 1979). In essence, laminar boundary layers are rare in the ocean.

Turbulent boundary layers

Turbulent flows are classified as smooth, rough, or transitional (e.g., see Schlichting, 1979), depending on Re_* of the flow. In the immediate vicinity of the boundary, viscous forces dominate the flow. A pronounced viscous sublayer (see Fig. 5) may develop in the case of flow over hydrodynamically smooth bottoms (e.g., see Eckelmann, 1974) occurring at relatively low Re_* . The viscous sublayer has characteristics of laminar boundary layers. Over hydrodynamically rough bottoms, viscosity still acts at the boundary, but no

distinct well-behaved sublayer forms comparable to the smooth case and eddies may penetrate to within tenths of millimeters of the bed; thus, in rough-turbulent flow the velocity structure close to the bed is complicated (e.g., see Yaglom, 1979) and not well-known. For intermediate Re_* , transitional flow occurs, with characteristics intermediate between smooth- and rough-turbulent. For pipes, flows are shown to be smooth-turbulent for $Re_* < 5$ and rough-turbulent for $Re_* > 70$ (see Schlichting, 1979); for open-channel or geophysical flows, these values may be more like 3.5 and 100, respectively (e.g., see review of Nowell and Jumars, 1984).

Based on empirical studies and scaling arguments (see Clauser, 1956), turbulent boundary layers in the laboratory can be divided into three regions (refer to Fig. 5). Adjacent to the boundary, in the viscous sublayer (for smooth-turbulent flows), velocity varies linearly with distance from the boundary according to $u/u_* = u_*z/\nu$, the scaling parameters for this flow region. The outer region of flow is called the log-deficit layer because the deficit velocity, $(u-U)/u_*$, is logarithmically related to z/δ . Between these two layers (and overlapping with the lower portion of the log-deficit layer) is the log layer, a major feature of steady, uniform flows. The velocity profile in the log layer is described by:

$$\frac{u}{u_*} = \frac{1}{\kappa} \ln \frac{z}{k_b} + B \quad (1)$$

(where B = the empirically defined constant of integration). The velocity scale of eddies (i.e., the root-mean-square of the velocity fluctuations) in the log layer is about 10 percent of the free-stream velocity, U (see Hinze, 1975). For smooth-turbulent flows, the shape of the velocity profile in the log layer depends on u_* and ν . For fully rough-turbulent flows, the velocity profile depends on u_* , ν and bed geometry. From empirical studies of smooth-turbulent pipe flows (see Schlichting, 1979), the lower limit of the log layer is approximated by $11.6\nu/u_*$ and the upper limit of the viscous sublayer by $5.0\nu/u_*$. Between these heights, there is a complicated wake layer that cannot be described simply. In channel flows and geophysical boundary layers, the wake region may be larger (see reviews of Nowell, 1983; Grant and Madsen, 1986).

Ocean bottom boundary layers

Typical oceanic bottom boundary layers vary between smooth-turbulent and fully rough-turbulent. For example, the detailed velocity profiles measured in a laboratory flume by Grant et al. (1982) over an area of uniform intertidal sands taken from Barnstable Harbor, Massachusetts, typified a classical smooth-turbulent boundary layer. Other examples include the profiles measured in the laboratory flume studies of Nowell and Church (1979), Nowell et al. (1981),

Eckman et al. (1981), Eckman (1983) and see also the review of Jumars and Nowell (1984). In the ocean, smooth-turbulent profiles were measured by Chriss and Calowell (1982), transitional by Grant et al. (1985), and rough-turbulent profiles by Gross and Nowell (1983), Grant et al. (1984); many other examples exist. Note that, at a given study site, a flow can be smooth-turbulent under one flow condition and rough-turbulent under another condition, for example, due to changes in z_0 (a parameterization of the bed roughness length scale, k_b) or in other sediment properties caused by bioturbation, sediment transport or bedform development (see Grant and Madsen, 1979, 1982).

PROFILE CALCULATIONS AND RESULTS

Profiles of current speed within the log layer at a site can be calculated, given the following assumptions. (1) There is quasi-steady, uniform, neutrally stratified flow over the bed. (2) The bed is uniform over large horizontal distances, relative to the height above the bed of the calculated velocities. (3) Bottom roughness is small, compared to the boundary-layer thickness. In addition, information must be available on velocities occurring at some height above the bed within the log layer and on bottom roughness characteristics. These assumptions periodically are met at Station 35; for example, during flood or ebb tide when near-bed flows are only tidally driven and there are no complications from wind-driven circulation, density-driven circulation or surface waves. Thus, the profiles calculated here accurately represent near-bed flow conditions only a certain percentage of the time. The rest of the time, the velocity profiles resulting from unsteady or non-uniform flows are imposed on the steady-flow case (e.g., the log layer profile), so composite profiles of flows that would be measured over the bed are difficult to predict (for a discussion of these features, see Grant and Madsen, 1986). Some of these complicated boundary-layer flows have been modeled (e.g., Smith and McLean, 1977; Grant and Madsen, 1979, 1982), but such calculations are not necessary for the first-order approach of this paper (see GENERAL DESCRIPTION OF BOUNDARY-LAYER FLOWS...).

Smooth-turbulent profiles

Smooth-turbulent velocity profiles were calculated for everyday flow conditions at the study site. Smooth-turbulent profiles were indicated by the estimated range in ke_* (see Table 1) for the range of measured near-bed flows (Fig. 4), by the observed seabed roughness and because of the preliminary results of detailed velocity measurements near the bed, made by Dr. William D. Grant (WHOI). Current speed and direction were measured over a 6-hr period, during non-storm conditions at Station 35 in October 1982, using four vertically

TABLE 1

Parameter values for velocity profiles shown in Figs. 6, 7 and 8.

	u_{50}^a (cm/sec)	u_* (cm/sec)	C_D^b ($\times 10^{-3}$)	z_0 ($\text{cm} \times 10^{-3}$)	Re_*^c	$(0.1)(\delta)$ (cm)
Smooth-Turbulent						
A.	15.3	0.60	1.53	1.8	1.2	165
B.	9.8	0.40	1.66	2.8	0.8	111
C.	4.6	0.20	1.89	5.6	0.3	55
Rough-Turbulent						
D.	15.3	0.98	4.14	100	294	270
E.	15.3	0.82	2.90	30	74	226

^a $u_{50} = u$ at $z = 50$ cm.^bFor $z = 50$ cm.^cFor smooth-turbulent flow, $k_b = 200 \mu\text{m}$ and for rough-turbulent flow, $k_b = (30)(z_0)$.

stacked acoustic-time-travel current meters (described in Grant et al., 1984) mounted at distances of approximately 30-, 50-, 100- and 200-cm above the bed. From these direct flow measurements, if the velocity profile is logarithmic, it is possible to estimate u_* from equation (1) using the profile technique (Grant et al., 1984), since u_*/κ is given by the slope of the velocity profile. Thus, it is possible to calculate Re_* to determine if flows are smooth-turbulent, rough-turbulent, or transitional. The preliminary results indicate that, during non-storm conditions, the flow is smooth-turbulent to transitional (W.D. Grant, personal communication).

For smooth-turbulent laboratory pipe flows, empirical results show that the general log-layer equation given in (1) has the specific form of:

$$\frac{u}{u_*} = \frac{1}{\kappa} \ln \frac{z u_*}{\nu} + 5.5 \quad (2)$$

(see Schlichting, 1979); note that the constant differs slightly for channel flows and geophysical flows. To calculate a profile from this relationship requires estimates of ν , $u(z)$ measured inside the log layer, and u_* ; also, some iteration is necessary. For all calculations, $\nu = 0.01 \text{ cm}^2/\text{sec}$ was used.

To choose $u(z)$ requires an estimate of the thickness of the log layer. This thickness can be approximated by $(0.10)(\delta)$ (Clauser, 1956; Grant and Madsen, 1986), where $\delta =$ the boundary-layer thickness. For a tidal flow, $\delta = \kappa u_*/\sigma$, where $\sigma =$ the tidal frequency ($2\pi/P$, where P is the tidal period of ~ 12 hr, in this case). For log-layer thicknesses estimated here (see Table 1), velocities measured at 0.5-m above the bed will always be in the log layer; for slower flows at the site, measurements at $z = 1.0$ m may be above the log layer. To be

conservative, u_{50} (i.e., u at $z = 50$ cm) was used in calculations here. The difference in mean velocities measured at $z = 0.5$ m and $z = 1.0$ m was consistently between 1 and 2 cm/sec (B. Butman, personal communication), and thus, for $z = 50$ cm, the range of velocities (4.6 to 15.3 cm/sec, see Table 1) used to calculate profiles here seems reasonable based on the flow measurements at $z = 1.0$ shown in Fig. 4.

The choice of values for u_* needed to calculate smooth-turbulent profiles was constrained by the requirement that C_D , the bottom drag coefficient ($\sqrt{C_D} = u_*/u_{50}$), must be about 1×10^{-3} to 2×10^{-3} (typical values measured for smooth-turbulent flows). Some iteration was required to obtain the values

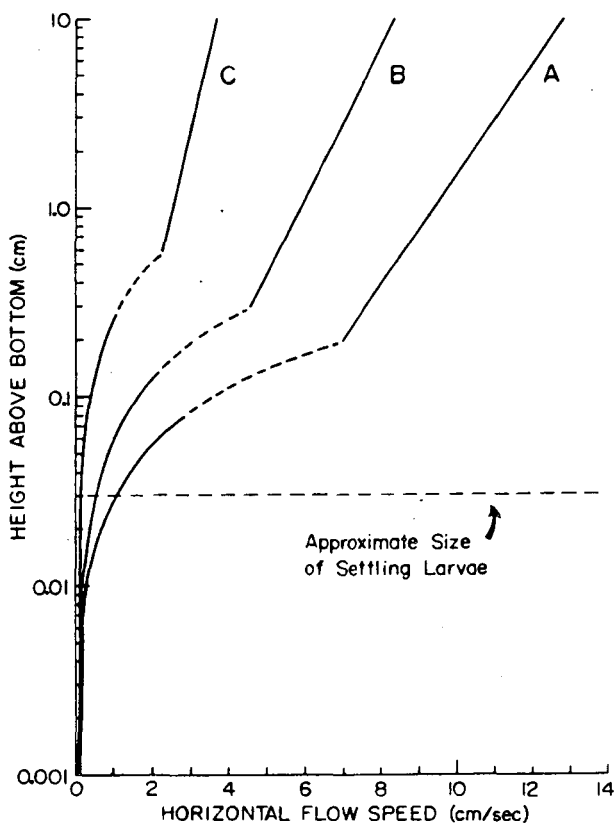


Fig. 6. Smooth-turbulent velocity profiles on a semi-log plot, calculated for a range of near-bottom flow speeds measured at Station 35. Parameter values are listed in Table 1. The log layer is the straight-line portion of each curve. Below this, the dashed curves indicate approximately the region of the wake layer, where velocities are difficult to estimate (see GENERAL DESCRIPTION OF BOUNDARY-LAYER FLOWS ...).

listed in Table 1.

To determine Re_* for the profiles, $k_b = 200 \mu\text{m}$ was used for the smooth-turbulent case (see Table 1). This value was chosen because, while sediments at the study site are primarily sands (250-500 μm , see STUDY SITE AND FLOW MEASUREMENTS), surface sediments are heavily pelletized by the dominant infaunal organism, Mediomastus ambiseta (a small polychaete worm). This organism occurs in abundances of up to 2×10^5 per square meter (Sanders et al., 1980); it feeds below the sediment surface and deposits discrete cylindrical fecal pellets ($\sim 80 \mu\text{m} \times 200 \mu\text{m}$) on the sediment surface. Note, however, that k_b as large as 830 μm still would result in $Re_* < 5.0$ for even the largest value of u_* listed in Table 1 for smooth-turbulent flows.

Smooth-turbulent velocity profiles are shown in Fig. 6 for z between 0.001 and 10 cm. Also shown by a horizontal dashed line on the figure, is the approximate size (300 μm) of a settling polychaete larva; however, in temperate latitudes, settling larvae can vary in size by approximately an order-of-magnitude (from 100 to 1000 μm). Below this height, a 300 μm larva would not have room to maneuver in a flow by horizontal swimming. It would be sitting on the bottom or crawling along the bed and, at most, the flows would cause it to roll. For a more detailed look at velocities very near the bed (i.e., at

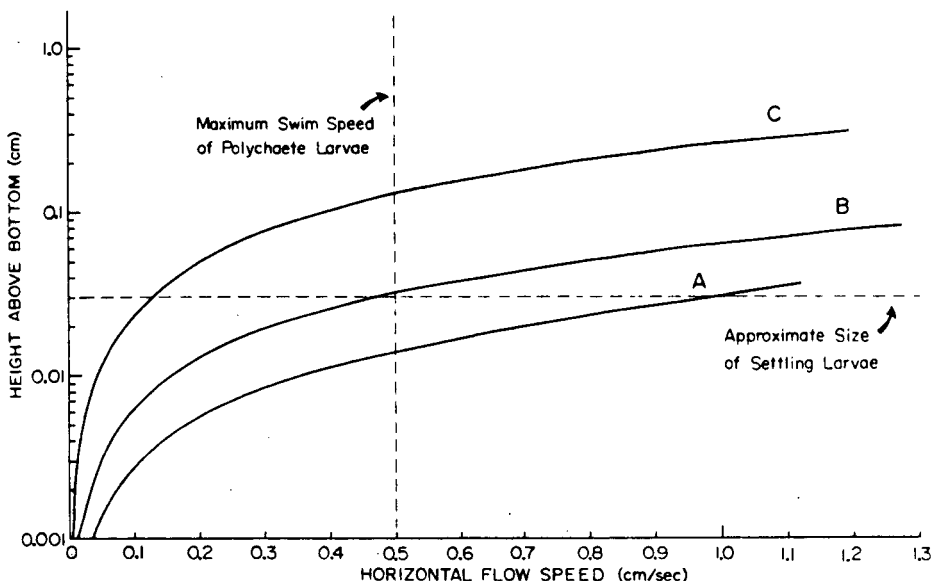


Fig. 7. Smooth-turbulent velocity profiles in the viscous sublayer on a semi-log plot, calculated for a range of near-bottom flow speeds measured at Station 35. Parameter values are listed in Table 1.

distances relevant to settling larvae), the same smooth-turbulent profiles (see Table 1) are plotted for z between 0.001 and 0.2 cm in Fig. 7. In addition to the approximate size of settling larvae (horizontal dashed line), the maximum measured swim speed of a polychaete larva (from the review of Chia et al., 1984) is shown as a vertical dashed line on the figure. Flow speeds to the right of this line would advect larvae; larvae may effectively maneuver by horizontal swimming in flows to the left of this line. Thus, larvae would be expected to effectively maneuver by horizontal swimming only for flows occurring in the upper left-hand quadrant of the figure.

The results indicate that larvae can horizontally swim only in the slowest profile plotted (see C in Fig. 7) and only to a height of about 0.1-cm above the bed. Above this height in profile C and for velocities at $z > 300 \mu\text{m}$ in profiles A and B, larvae essentially would be advected by the flow. The velocities plotted in Fig. 7 all lie within the viscous sublayer (see Fig. 6), and thus, mean flow components occur only in the stream-wise (horizontal) direction. While they are being advected horizontally, larvae could still swim vertically to heights of at least 0.1-cm above the bed and face no opposed velocity. However, even in smooth-turbulent flows, the viscous sublayer periodically is subject to turbulent eddy penetration so vertical velocities, of-the-order $(0.1)(U)$, could be present from time-to-time.

rough-turbulent profiles

In addition to the smooth-turbulent case for everyday flows, it is possible to construct rough-turbulent profiles at the site for conditions following a major storm with sufficient bottom stress to move sediments. It is observed at the site that storm winds oriented down the long axis of the bay (see Fig. 1) generate sufficient bottom stress to cause ripples to form on the seabed. After the storm, the ripples persist until they are obliterated by benthic biological processes. Because ripples set a much larger bottom roughness scale than grain roughness or fecal pellet roughness, rough-turbulent flows can result for the same range of everyday forcing conditions that produced smooth-turbulent profiles for the non-rippled bed.

Two rough-turbulent profiles were calculated here (see Table 1), using $u_{50} = 15.3 \text{ cm/sec}$ and two different ripple heights, h , of 0.5 and 0.15 cm. In both cases, a ripple steepness (h/l , where l = the distance between ripple crests) of 0.2 was used. This corresponds to the maximum ripple steepness observed under waves (see Grant and Madsen, 1982). For a rippled bed, the bottom roughness parameter, z_0 , can be estimated by $z_0 = h (h/l)$ (Grant et al., 1984), so $z_0 = 0.1 \text{ cm}$ and 0.03 cm for the 0.5-cm and 0.15-cm tall ripples, respectively.

For rough-turbulent flow, empirical results show that the general log-layer equation given in (1) has the form:

$$\frac{u}{u_*} = \frac{1}{\kappa} \ln \frac{z}{z_0} \quad (3)$$

Again, u_* can be calculated once z_0 and a reference value for $u(z)$ are known. For the same $u(z)$ used in the smooth-turbulent case, C_D is expected to be higher for rough-turbulent flows, i.e., $C_D > 2 \times 10^{-3}$ (see Table 1).

The two rough-turbulent profiles are plotted, along with a smooth-turbulent profile, for the same u_{50} , in Fig. 8. The slopes of the curves for the log

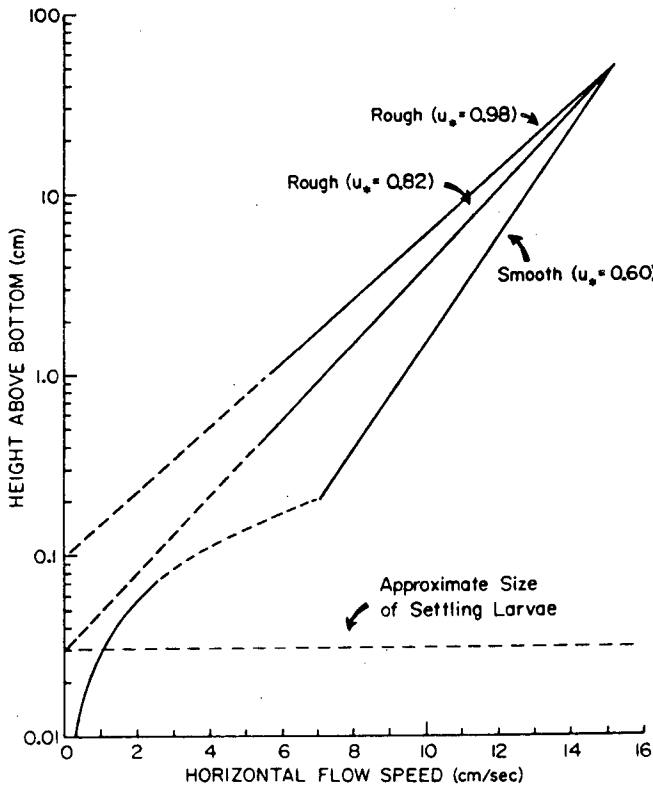


Fig. 8. Two rough-turbulent velocity profiles and a smooth-turbulent profile, all having the same u_{50} , but different values of u_* and z_0 (see Table 1). A log layer is known to accurately describe a rough-turbulent profile at distances $> (100)(z_0)$ from the bed, and is a reasonable predictor for distances between $(10)(z_0)$ and $(100)(z_0)$. Thus, on the figure, the rough-turbulent profile curves are dashed below $(10)(z_0)$, indicating that velocities in this region may be described by some other wake function. The dashed portion of the smooth-turbulent profile represents the wake layer (see Fig. 6).

layer are smaller in the rough-turbulent cases, than in the smooth-turbulent case. Thus, at a given height above the bed (below $z = 50$ cm), velocities are lower in the rough-turbulent flows. This simply reflects the fact that, in rough-turbulent flows, eddies close to the bed are mixing low-momentum fluid near the bed with higher-momentum fluid away from the bed so that near-bed mean velocities are lower, relative to the smooth-turbulent case.

The rough-turbulent profiles intercept the ordinate at z_0 and, in these cases, z_0 is greater than or equal to the approximate size of settling larvae (see Fig. 8). Thus, it appears that in rough-turbulent flows larvae may have a lot of vertical distance to maneuver by horizontal swimming before flow speeds reach a value that the organisms cannot swim against. However, it is important to realize that z_0 is a roughness parameter, reflecting where the flow effectively goes to zero. The boundary layer actually can attach anywhere between the trough and the crest of the ripples; in fact, internal boundary layers with different profile characteristics form in this complicated flow region close to the seabed (see caption to Fig. 8). Depending on where the larva is situated relative to the roughness elements, the animal could experience relatively high or low velocities. For example, very low flows generally would be expected in the lee of a ripple crest in a steady flow, but eddies also can be shed from these crests.

Even though, for a given z , mean horizontal velocities are lower in the rough-turbulent flows than in the smooth-turbulent flow plotted in Fig. 8, eddies regularly reach to within tenths of millimeters of the seabed in rough-turbulent flows (see GENERAL DESCRIPTION OF BOUNDARY-LAYER FLOWS ...). As previously mentioned, the most energetic eddies in the flow have velocities of about 10 percent of the free-stream velocity, U . For example, if U was 15.3 cm/sec (at $z = 50$ cm) for the flows in Fig. 8, then eddy velocities are a maximum of 1.5 cm/sec at this level above the bed, easily exceeding values required to prohibit effective swimming by a larva in any direction (see Fig. 6); eddy velocities closer to the bed are smaller and less energetic.

In summary, under most flow conditions analyzed here, horizontal flow speeds exceed maximum larval swim speeds even to within one body diameter of the organism from the seabed. If larvae actively maneuver in a flow, then vertical swimming to get into higher or lower horizontal flows seems most likely. These kinds of behaviors often have been proposed for planktonic organisms in the water column, for example, to account for vertical migrations of copepods (see reviews by Longhurst, 1976; Pearre, 1979; and also the recent collection of papers in Angel and O'Brien, 1964). Mileikovsky (1973) also proposed that "high" vertical swim speeds of soft-sediment invertebrate larvae may account for their retention in near-shore and estuarine waters; retention of, especially,

crustacean and bivalve larvae in estuaries by active vertical movements of the organisms has a burgeoning literature (e.g., see symposium on this subject in Kennedy, 1982). However, previous to the present study, the relative effectiveness of horizontal versus vertical swimming for organisms in flows very close to the seabed has never been investigated quantitatively.

Other calculations

As with other particles, larvae have mass so they always are sinking through the water at a speed specific to their size, shape and density. Fall velocities of anesthetized polychaete larvae were measured directly by the author (see Hannan 1984a, b) and span about an order-of-magnitude, from 0.01 to 0.3 cm/sec,

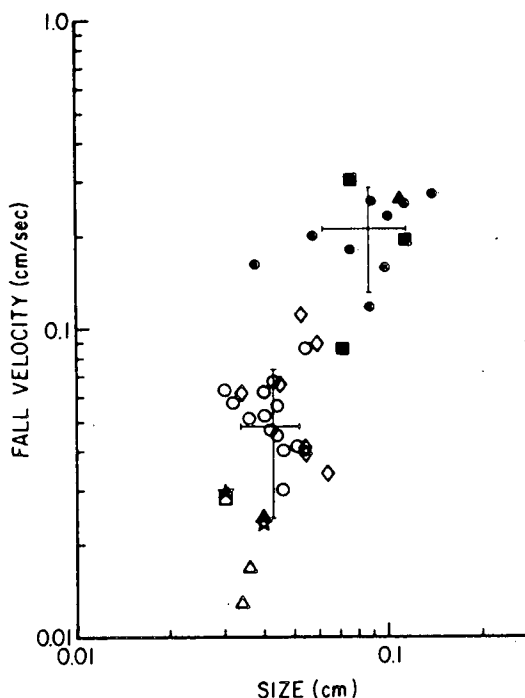


Fig. 9. Relationship between fall velocity and size for polychaete larvae tested in the study of Hannan (1984a, b). The length of the organisms, after they were anesthetized, is plotted against their measured fall velocity. Fall velocities were measured in two different settling chambers for two different groups of larvae, indicated by the closed versus the open symbols. The different symbols represent different anesthetizing treatments, but there were no significant differences in fall velocity that could be attributed to treatment (see Hannan, 1984b). The crosses represent mean fall velocity (\pm SD) and mean length (\pm SD) for the two groups of organisms tested. Details of the methods are given in Hannan (1984b).

roughly increasing with increasing body size (Fig. 9). It is interesting that this range overlaps the range of measured swim speeds for polychaete larvae (0.05 to 0.52 cm/sec, see review of Chia et al., 1984). Thus, even when larvae are swimming vertically it is possible that they are capable only of standing still!

The previous analyses have focused on how very near-bottom flow velocities may limit or allow active larval movements near the bed. It also is fruitful to look at the other extreme. Assuming that larvae only sink toward the bed like passive particles (see Hannan, 1984a, b), I have calculated the horizontal distance they would be carried by specific flows before reaching the bottom, given various starting heights above the bed (see Fig. 10). These results are useful, for example, in predicting distances between habitats where larvae would be able to test the substrate. Once deposited, if larvae are carried to a certain distance above the bed (i.e., by resuspension or by vertical swimming), then profile characteristics determine the horizontal advection distance (i.e., where the next test location would be) from that height. For the flows

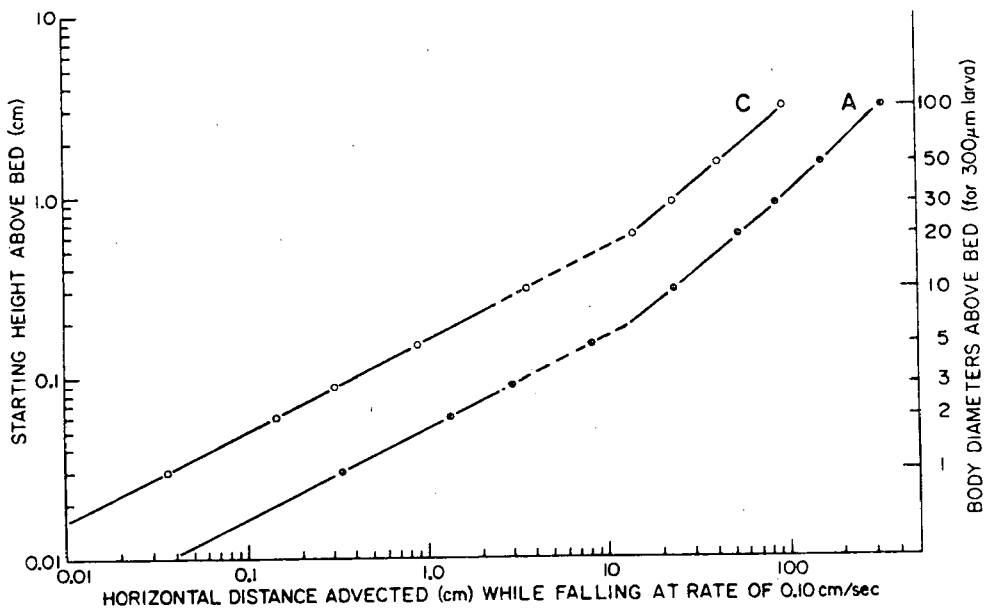


Fig. 10. Horizontal distances that passively sinking larvae would be advected given various starting heights above the bed. Larval fall velocities were taken as 0.1 cm/sec (see Fig. 9) and horizontal velocities for various starting heights above the bed were taken from smooth-turbulent profiles A and C in Fig. 6.

considered, larvae may be carried from tenths of millimeters to meters, for starting heights up to 3 cm (or about 100 body diameters of a 300 μm larva) above the bed. If this were the mechanism of habitat selection by larvae, then these spatial scales apply.

DISCUSSION AND CONCLUSIONS

Biologists have observed and quantified swimming in planktonic organisms for over half a century (see review of Chia et al., 1984). With the exception of vertical migrations, it is usually assumed that the organisms have little control of their position in the water column through swimming, since horizontal flow speeds greatly exceed their swim speeds (Mileikovsky, 1973). In fact, technically this distinguishes between plankton, "the drifters", and nekton, "the swimmers" (see Hardy, 1965). Likewise, larval dispersal in the plankton usually is assumed to be physically controlled (e.g., see Scheltema, 1971; Ducourt, 1982; Levin, 1983). However, until recently, settlement of larvae onto the seabed was assumed to be biologically controlled, through active habitat selection by the animals (see reviews cited in INTRODUCTION). An underlying assumption to this tenet is that the organisms can exert some control over their position close to the seabed, in order to select habitats. The precise mechanisms involved (e.g., horizontal or vertical swimming, hopping or crawling) have never been clear, but for an organism to choose a habitat, it seems necessary for the animal to be able to peruse the available sites (but see also the "threshold stimulus" hypothesis of Doyle, 1975, 1976).

It seems reasonable to expect that there will be some limiting height above the seabed, below which flow speeds would be low enough to allow organisms to maneuver effectively. This follows from the "no-slip condition" in fluid dynamics; flow speed must go to zero at the boundary. The rate at which velocity decreases with distance from the bed (i.e., the shape of the velocity profile) determines this "limiting maneuvering height". If larvae are choosing habitats by swimming around near the bed, it should be possible to constrain the limiting maneuvering height, for a given mean-stream flow. This was a goal of the present study.

The smooth-turbulent velocity profiles constructed here for everyday flow conditions at Station 35 in Buzzards Bay, Massachusetts (see Fig. 1) indicate that only the slowest flow modeled (profile C in Figs. 6 and 7) would permit effective horizontal swimming by larvae near the bed. In this case, the limiting maneuvering height is about 0.1 cm (or about three body diameters of a 300- μm larva), for a maximum swim speed of 0.5 cm/sec. This flow profile was constructed for a measured flow speed of 4.6 cm/sec at $z = 50$ cm. During five larvae experiments in the summer and early fall of 1982, flows < 6.0 cm/sec at

$z = 100$ cm occurred from 24.4 to 56.8 (mean = 43.2) percent of the time (see Fig. 4). These are the flows for which larvae would be expected to effectively maneuver, at least to heights of 0.1-cm above the bed, because flows measured at $z = 100$ cm were 1 to 2 cm/sec faster than those measured at $z = 50$ cm (B. Butman, personal communication).

These results suggest that during about 40 percent of the tidal cycle at this site, it is physically realistic for larvae to swim around near the bed, exploring available habitats for settlement. However, for about half of these flows (those between 4 and 6 cm/sec, see Fig. 4), larval maneuvering would be confined to distances of only 0.1-cm (or three body diameters of a 300- μ m larva) above the bed. Obviously, the larger the settling larva, the smaller the maneuvering height. As mentioned earlier (see PROFILE CALCULATIONS AND RESULTS), larvae would encounter no opposed velocity if they swam vertically to heights of about 0.25 cm above the bed, within the viscous sublayer, in all of the smooth-turbulent profiles plotted (see Fig. 6). However, turbulent eddies, with velocities on-the-order-of 1 cm/sec or less and with components in all directions, are expected above the sublayer and periodically even inside the sublayer, making larval maneuvering in any direction difficult.

Rough-turbulent flows are expected, a priori, to have relatively lower mean velocities close to the bed than smooth-turbulent flows with the same mean-stream velocity, due to turbulent mixing near the bed. This was demonstrated in the cases modeled here (see Fig. 8). The advantages incurred by lower mean velocities near the bed may not outweigh the disadvantages of increased eddy penetration to within larval-body diameters of the bed, however, since larvae would constantly experience fluctuating eddy velocities in all flow directions. On-the-other-hand, larvae may find some refuge in the microtopography in slow-flow regions behind flow obstacles (e.g., see Eckman 1979, 1983).

The profiles calculated here are for quasi-steady (i.e., current) boundary layers, without consideration of possible effects of surface waves. Although wave-generated velocities do not reach the bottom at the study site discussed here, wave effects on the bed are prevalent in many common coastal habitats where larvae settle. Where wave effects extend to the seabed, wave boundary layers can form, in addition to current boundary layers. The combined effects of wave and current boundary layers on near-bed velocity profiles and sediment transport are discussed in Grant and Madsen (1979, 1982). In general, wave boundary layers are thinner than current boundary layers and higher stresses occur closer to the seabed in the wave boundary layer. These higher near-bed velocities have obvious implications to larval settlement.

A conclusion of this study is that, at least at the study site modeled, larvae probably do not search for preferred habitats by active horizontal

swimming near the bed, since the bulk of the flows modeled would not permit such searches even for maximum measured larval swim speeds. The larvae may swim vertically in smooth-turbulent flows, going down to test the substrate and up to be advected to another site downstream. It is curious that measured swim speeds and fall velocities of polychaete larvae are the same order-of-magnitude, suggesting that larvae may only be able to maintain position in the water column while swimming up; measurements of swim speeds and fall velocities for the same individual are required to test this hypothesis.

An estimate was made here of advection distances between substrate tests by a larva that used, for example, the "balloonist technique" (coined by P.A. Jumars, personal communication) where an organism swims or is lifted up off the bottom, is advected with the flow and then passively sinks to a new site downstream. Using this technique, larvae could test substrates separated by scales of millimeters to meters, depending on their starting height above the bed (see Fig. 10).

This first attempt to determine near-bed flow velocities relative to aspects of larval settlement biology has suggested some realistic flow-regime dependent settlement mechanisms meriting further study. The calculations were necessarily idealized, in some cases, but the idealizations do not significantly affect the outcome of the study. The modeled field profiles represent first-order-type solutions for the purposes of hypothesis development; direct measurements are needed to test the ideas presented here. The analyses suggest many important areas for future research on larval biology (i.e., quantifying swim speeds and directions, fall velocities, and excursion heights above the bed during searches) and on larval ecology during settlement (i.e., quantifying habitat selection for a realistic range of field flows modeled in a laboratory flume).

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J.C.J. NIHOUL

University of Liège, B5 Sart Tilman, B-4000 Liège, Belgium



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