YALE
PEABODY
MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research,* one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
https://creativecommons.org/licenses/by-nc-sa/4.0/

Journal of Marine Research, 46, 797–813, 1988

Effects of bivalve siphonal currents on the settlement of inert particles and larvae

by Stephen C. Ertman[1] and Peter A. Jumars[2]

ABSTRACT

Dye studies in a flume revealed that the strong exhalent siphonal current of an individual cockle, *Clinocardium nuttallii,* behaved much like a cylinder held in the flow, shedding vortices downstream. The inhalent flow was much slower and more diffuse, its effects being limited to the lowermost few centimeters above the bottom. Flume experiments with inert particles having settling velocities similar to those of polychaete larvae revealed that the vortex shedding from the excurrent jet led to variability in deposition of the particles a few centimeters downstream of the jet, and that neither the jet nor the incurrent flow substantially changed the mean number of particles depositing per unit area of bed. Field observations within a few days after settlement of *Hobsonia florida,* an ampharetid polychaete, using ecologically similar but nonplanktonically recruiting oligochaetes as an internal control, showed similarly enhanced variability in recruitment within a few centimeters of the siphon of resident *Mya arenaria* (soft-shelled clam). We could find no evidence that isolated clams impede settlement in their immediate surroundings and found, instead, some indication of local settlement being enhanced by the flow convergence toward the incurrent siphon. We thus suggest that any negative influence of suspension-feeding bivalves upon settlement is a larger-scale phenomenon caused by depletion of recruits through the integrated filtering activities of individuals upstream of the settlement site. Hence manipulation of bivalve density in small plots may not be very informative regarding influences upon larval settlement.

1. Introduction

Dense beds of infaunal suspension-feeding bivalves have been suggested to prevent the settlement of planktonic larvae via inhalation and ingestion or entanglement in pseudofeces (reviewed by Woodin, 1976). A quantitative definition of "dense" has never been provided, however, and in some exceedingly dense, manipulated aggregations of bivalves (e.g. Williams, 1980) settlement was still quite successful, albeit somewhat reduced over controls. Similarly, although larvae are ingested by many tube builders (Gallagher, 1983), abundances of recruits are often enhanced by their presence (Gallagher *et al.,* 1983). This paradox may be explained by a fluid-dynamic enhancement of recruitment rate (Eckman, 1983; Gallagher *et al.,* 1983) that exceeds the mortality rate due to ingestion. Observation of this phenomenon with tube builders

---

[1] Department of Oceanography, Florida State University, Tallahassee, Florida, 32306, U.S.A.
[2] School of Oceanography, WB-10, University of Washington, Seattle, Washington, 98195, U.S.A.

led us to question what the effects of isolated bivalves might be on recruitment. Additionally, we originally thought that quantifying the region of influence of isolated siphonal currents could provide one objective definition of a dense assemblage; i.e., one in which such regions of influence overlap.

Based on our experience with tube builders and an increasing appreciation for the role of even very small-scale water motions on larval settlement (Butman, 1986), we conjectured that the effects of isolated bivalves might actually be the reverse of those postulated for dense assemblages. Namely, convergence of flow toward an incurrent siphon would draw a greater flux of particles, including larvae, past the surrounding area of bed than would otherwise pass over the same patch of bottom in the slowly moving fluid of the bottom-most part of the benthic boundary layer. Depending on the geometries and velocities of the siphonal currents and the local flow conditions, it was also conceivable that filtering of larvae from the water would reduce recruits in some small, proximal region just downstream of the incurrent siphon. Yet a third possibility was that the siphonal effect was so weak or broadly acting as to have no detectable influence on local settlement. Without data, one could argue any of these points of view.

We thus set out to test three alternative hypotheses concerning the effects of isolated bivalves on local recruitment: settlement increases, decreases, or is unchanged with increasing proximity to an incurrent siphon.

2. Methods and materials

a. Rationale. Experiments were organized into three distinct phases: a flow visualization study to identify and describe the pattern and spatial extent of siphonal currents under the controlled flow conditions of a laboratory flume, a second flume study of siphonal effects on the settlement of inert particles, and a study of field samples taken around an infaunal, suspension-feeding bivalve and analyzed for the abundance of newly-settled polychaete larvae. Both flume studies were conducted with a cockle, *Clinocardium nuttallii.* Cockles have been implicated in effects on settling larvae (Kristensen, 1957; Hancock, 1970; Woodin, 1976), and their shallow and rapid reburrowing and comparative insensitivity to light and mechanical stimuli of the laboratory environment make them convenient experimental animals. For several reasons, we selected a different bivalve for the field component of this work. Because of the subtleness of the effects revealed by the laboratory studies, we needed a field site in which topography was not complex (i.e., not extensively rippled) on 1–10 cm scales. Furthermore, we needed the locations of siphon openings to be apparent and to remain in one place. *Clinocardium nuttallii* and its habitats near Seattle or Friday Harbor, Washington, failed to meet these criteria. We, instead, selected *Mya arenaria,* the soft-shelled clam, at Skagit Flats (between the mouths of the north and south forks of the Skagit River), Washington. Additionally, we selected this site because we could predict the availability of the larvae of *Hobsonia florida* and could thus sample within days of settlement.

Skagit Flats offer a relatively simple and well known benthic community for investigation. The bed consists of a dense mat of tube-building infauna interspersed with large numbers of the infaunal, suspension-feeding bivalve *Mya arenaria*. Because of its wide expanse and extremely low slope [of order 10^{-3} (Eckman, 1979)], the study area allows us to approximate the equations of tidal fluid transport as being uniform ($d/dt = 0$) and one-dimensional ($d/dx = d/dy = 0$), conditions that can be adequately modeled in a simple flume.

Hobsonia florida is a tube-brooding ampharetid polychaete. *Hobsonia* larvae are released from the top of the tube at about the three-setiger stage (Zottoli, 1974) and are briefly planktonic. Their recruitment at Skagit begins in late April or early May (Smith, 1980; Eckman, 1983; Gallagher *et al.*, 1983) and in fields of artificial tubes is consistent with predictions based entirely on passive transport and deposition (Eckman, 1983). An investigation of their distribution around the siphon openings of *Mya* could thus be expected to provide field evidence of the fluid-dynamic influence of siphonal currents on larval recruitment.

Of the other taxa common to Skagit Flats, the oligochaetes are useful in an *a priori* comparison to *Hobsonia*. Two of the three species present comprise roughly 90% of the oligochaete population (Gallagher, 1983). These two naidid oligochaetes (*Paranais littoralis* and *Amphichaeta sp.*) reproduce by asexual fission within the sediment. Their recruitment, concurrent with that of *Hobsonia* but primarily through the sediment rather than through the water column (based on observations in laboratory aquaria), does not conform to predictions of passive transport and deposition (Eckman, 1983). Successional studies on Skagit Flat have further demonstrated that juveniles of *Hobsonia* are strong competitors with oligochaetes (having Lotka-Volterra competition coefficients nearly equal to one), apparently for diatoms (Gallagher, 1983). Since, by virtue of their life cycle, oligochaete juveniles are insulated from processes occurring beyond the sediment-water interface, we selected oligochaete distribution to help separate resource effects from effects of passive larval settlement. Although Eckman (1983) has already demonstrated the apparently passive deposition of *Hobsonia* larvae around animal-tube mimics, we recognize that a result in which the distribution of *Hobsonia* is fluid-dynamically consistent with the results of flow visualization and passive settlement of inert particles, but is also indistinguishable from the distribution of the oligochaetes, would not resolve the issue of passive settlement versus behavioral selection around infaunal, suspension-feeding bivalves. Eckman (1985) has demonstrated that flow perturbations near the bed may influence bacterial colonization, and similar effects are likely with diatoms. Chemical gradients associated with the bivalve may also affect microbial populations (Aller and Yingst, 1985). The oligochaetes, then, provide a convenient (if not perfect) internal control for the case where *Hobsonia* larval distribution is influenced by the availability of this shared resource.

b. Flume studies. The flume studies were conducted in the 2.5-m by 50-cm recirculating flume described by Nowell *et al.* (1981). A more detailed description of a flume based on this design is given by Muschenheim *et al.* (1986). The leading edge of the 25-cm by 25-cm working area is located 1.75 m downstream of the flume entrance. Work was confined to within 8 cm of the flume midline because preliminary analysis of inert particle deposition indicated that induced secondary circulation from the sidewall boundary layer can have a significant effect over the remainder of the bed when dealing with particles of very low settling velocities. *Clinocardium* were collected subtidally from False Bay, San Juan Island, Washington.

A thin (approx. 4–6 mm) bed of sieved (1-mm mesh), defaunated marine sand taken from False Bay was deposited in the flume and was used to fill the deeper (25 cm) sediment box. The sediment was defaunated by having been collected and air dried for several months. Seawater was allowed to wash over the bed for 30 min to 1 h prior to introduction of a cockle. There was no indication that using defaunated sediment adversely affected the bivalves. When placed on the bed, cockles burrowed in readily. After burrowing, the bed was smoothed. All flume observations were taken under conditions of steady imposed flow in the flume and continuous pumping by the cockles.

c. Laboratory flow visualization. Flow visualization studies were begun in June 1985. A neutrally buoyant dye was injected into the flow through the tapered tip of a 2-mm diameter, glass probe. The effect of the probe on the ambient flow was minimal, as observed by watching the dye streak in its wake. Dye was injected into the flow 5 cm upstream of the bivalve at 1-cm vertical intervals from directly on the bed to 4 cm above the bed and at 1-cm horizontal intervals from 0 to 4 cm (in both directions) from a midline passing over the center of the fused siphons of the cockle. (The probe tip thus occupied 45 separate "stations.") Two video cameras were positioned so as to record the horizontal and vertical deviations of the dye streak, and velocity profiles were calculated by analyzing particle trajectories recorded on videotape. One video camera was focused through the side of the flume on a segment of metric ruler placed just behind the midline of the flume and just forward of the cockle, the edge of the ruler being placed into the flow. The ruler consisted of both a vertical segment and a horizontal segment. A slurry of very fine, oxic marine sediment was released by micropipette into the flow at the head of the flume, and the cockle was induced to cease ventilating by brief teasing with a wooden applicator. The pipette itself was not inserted into the flow. Neutrally buoyant particles were carried into the field of view, and a short segment (approx. 5 min) of videotape was then recorded. The ruler was removed, and the cockle was allowed to acclimate in the flume until its siphons were fully dilated and ventilation appeared normal. These bivalves appear to ventilate continuously if left undisturbed.

Instantaneous downstream velocities were calculated from the particle trajectories recorded on videotape, and the velocity measurements were plotted on a scatter diagram of velocity versus the natural log of the height of the measurement above the bed, velocity being the dependent variable. A regression line can be drawn through these points using the equation for the "law of the wall":

$$U(z) = u_*/k \ln (z/z_o),$$

where $U(z)$ = mean downstream velocity at height z above bottom (cm s^{-1})
k = von Karman's constant (=0.41),
z_o = roughness height (cm), and
u_* = boundary shear velocity (cm s^{-1}).

The maximum turbulent boundary layer that theoretically could develop over the segments of metric ruler was on the order of 5 mm, and was deemed to have an insignificant effect on particle trajectories. This lack of influence was confirmed in the video data. Parallax presents a potentially more serious problem with regard to the apparent velocities of particles at different distances within the depth of field of the camera. Sufficient numbers of trajectories were analyzed so as to provide an adequate estimate of the velocity profile of each run ($r^2 > 0.75$).

The quantity u_* is a convenient construct for describing the average boundary shear stress of the flow: $u_* = (\tau_o/\rho)^{1/2}$, where τ_o = boundary shear stress (g cm^{-1} s^{-2}) and ρ = fluid density (g cm^{-3}). From u_* we calculated the roughness Reynolds number of the flow:

$$Re_* = u_* k_s/\nu,$$

where k_s = bed roughness scale (=150 μm; mean grain diameter of False Bay sand);
ν = kinematic viscosity of seawater.

The roughness Reynolds number is used to characterize turbulent boundary layer flow over a flat, granular bed (Nikuradse, 1933), being hydraulically smooth turbulent at $Re_* < 3.5$, fully rough turbulent at $Re_* > 100$, and transitional at $3.5 < Re_* < 100$. All of our experimental boundary layers are characterized as smooth turbulent.

While u_* is the pertinent parameter for describing processes that influence particle settling near the bed, we also provide the value of the free-stream velocity (U_∞), herein defined as the velocity just above the calculated thickness of the turbulent boundary layer, so that the flow may be considered in its tidally driven environmental context.

The above procedure was repeated for the three cardinal orientations of the cockle: incurrent siphon upstream, incurrent siphon downstream, and siphonal axis perpendicular to the flow. Observations were made for two velocities (U_∞ = 16 cm s^{-1}, u_* = 0.79 cm s^{-1} and U_∞ = 2.8 cm s^{-1}, u_* = 0.16 cm s^{-1}). We focussed on the low velocity end of natural flows because there the effects of siphonal flow relative to those of the ambient flow should be greatest. These velocities are in agreement with known current velocities at Skagit Flat. Tidal inflow at the study site begins as a thin "sheet" of water a few centimeters thick approaching at speeds of 10–30 cm s^{-1} (Eckman, 1979).

d. Passive deposition. We tested the influence of an infaunal, suspension-feeding bivalve (*C. nuttallii*) on the passive deposition of polystyrene spheres ($210 < D < 350$ μm; $= 1.06$ g cm^{-3}) in the flume. Sphere diameters were selected such that their Stokes settling velocities ($0.079 < W_s < 0.220$ cm s^{-1}, $\mu = 1.07 \times 10^{-2}$ g cm^{-1} s^{-1}) included nearly the full range of narcotized spionid larvae settling velocities determined by Hannan (1984). We were unsuccessful in obtaining larvae or newly-settled juveniles of *Hobsonia* free of sedimentary gut contents for direct measurement of their settling velocity.

Polystyrene spheres were injected into the flow 1.6 m upstream of the test area by a micropipette inserted to a depth of 4–6 cm. The pipette was drawn slowly across the entire width of the flume to create a line of injected spheres. Spheres were redistributed throughout the water column by turbulence in the head region of the flume. Most of the spheres were washed from the flume before they could settle to the bed. Repeated injections were performed until it was likely, based on pretests, that enough spheres had settled in the test area to meet the acceptance criterion described below. Repeated small injections also minimized the possibility of a pattern of deposition determined by injection geometry.

Samples were taken with a 6-mm diameter plastic drinking straw at 4 logarithmically increasing radial distances (2.0, 3.2, 5.0, 7.9 cm) from the center of the *Clinocardium* siphon. The straw was inserted to a depth of 1.0 cm, and it consistently removed a 0.5-cm long plug of sediment. For purposes of sampling, the region around the cockle was considered as comprising 4 quadrants, the quadrant axes running with and perpendicular to the flow (Fig. 1). Four samples were taken within each quadrant along separate random bearings (5° increments). Thus, 16 random samples were taken around each cockle per run. The samples were ejected into small vials for counting under a dissecting microscope (6–12×). After a run, the entire sediment bed was removed from the flume, and the flume was rinsed repeatedly with seawater to remove all spheres. Thirteen runs were completed before the supply of spheres was exhausted. Free-stream flow velocities ranged from 3.3 to 16 cm s^{-1} ($u_* = 0.19$ to 0.78 cm s^{-1}).

Because of the method of particle injection, there was some concern that a given sample might not contain a polystyrene sphere simply because enough spheres had not been injected and allowed to settle in the test area. An acceptance criterion was established after the second run, such that at least half of the 16 samples collected from a given run must contain at least 1 sphere for the run to be considered satisfactory. Runs 2, 8, and 9 were discarded based on this criterion.

e. Field sampling. Prior to sampling, dye observations were used to investigate the qualitative similarity of siphonal circulation in *Mya* and *Clinocardium*. In order to avoid the confounding influence of multiple siphonal currents, isolated *Mya* (those separated by at least 30 cm from their nearest neighbor) were chosen for sampling. Because of the high density of this bivalve at Skagit, considerable search time was

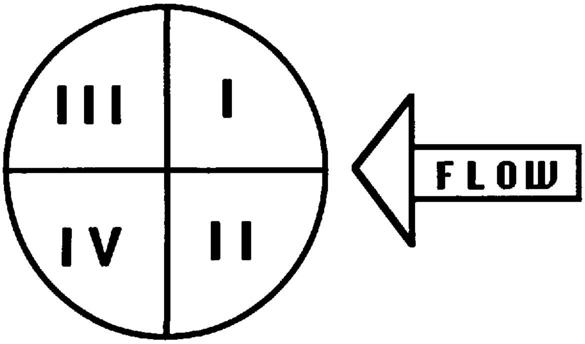

Figure 1. Orientation of sample quadrants to direction of ambient flow around *C. nuttallii* in a flume.

spent in locating acceptable animals. Field samples were taken with a 6-mm diameter plastic drinking straw at 5 logarithmically increasing radial distances (1.8, 3.3, 6.0, 11.0, 20.0 cm) from the center of a *Mya* siphon opening. Samples were taken along separate random bearings (5° increments) oriented by magnetic north. The straw was inserted to a depth of 1.5 cm and consistently removed a 1-cm long plug of sediment. The sediment plug was ejected into a small vial and was fixed in the field with a 10% formaldehyde solution buffered with sodium borate and containing Rose Bengal stain.

The samples were processed with a technique developed by Feller (1977). A sample was placed in a 250-ml beaker, and the sediment was suspended with a jet of water. The suspension was allowed to settle for 3–4 s, and the supernatant was decanted through a 63-μm mesh. This procedure was repeated 4 times. The remaining sediment was then sieved through a 125-μm mesh. All material retained on both sieves was sorted under a dissecting microscope (6–25×). The efficiency of this method was estimated by examining the material passing through the 125-μm mesh for one randomly preselected sample out of every ten counted. The processing method resulted in 100% retention of both target taxa (*Hobsonia* juveniles and oligochaete buds).

Field sampling began on the last day of March, 1986, and continued sporadically through mid-July, as weather permitted. Asexual oligochaete buds were present from the first day of sampling, but *Hobsonia* larvae were not discovered until a sample taken on April 26th. Based on previous records of the onset of larval availability, samples were being taken nearly every other day during this period. The early and frequent sampling ensured that we would catch *Hobsonia* just after settlement. All *Hobsonia* juveniles were less than 7 setigers long, and most appeared to be newly settled, 3- to 4-setiger recruits. Even at the 3-setiger stage, post-settlement motility is probably limited since tube construction has already begun. Seventy-five samples taken from 15 *Mya* were counted and analyzed.

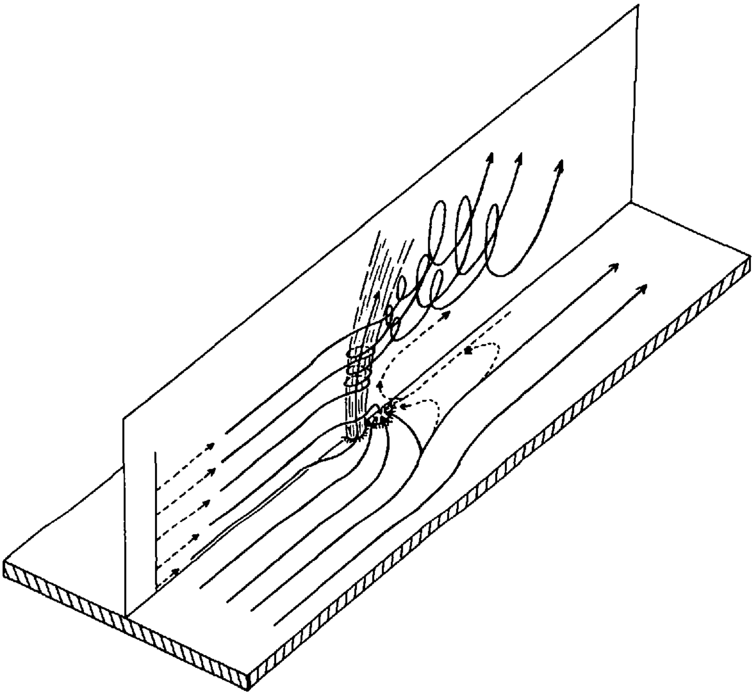

Figure 2. Schematic representation of mean flow about the fused siphons of a ventilating *C. nuttallii*, as indicated by dye-injection studies. Half the (symmetric) flow pattern is hidden by the (opaque) vertical plane, except for an indication of spiraling upward entrainment about the exhalent jet. (Dye trace spacing ≈ 1 cm).

3. Results

a. Flow visualization. The flow field around the siphonal currents of *Clinocardium* (Fig. 2) was similar at both flow velocities. We have chosen to illustrate the orientation with the incurrent siphon downstream because it demonstrates best the strong separation of influence between excurrent jet and incurrent sink. The siphons of neither *M. arenaria* nor *C. nuttallii* protrude appreciably from the bed; the observed perturbations in the flow field are due to the fluid-dynamic effects of the siphonal currents.

High flow velocities were produced by the excurrent jet. At a flume free-stream velocity of 2.8 cm s^{-1} ($u_* = 0.16$ cm s^{-1}) an upwelling from the excurrent jet could be observed at the free surface, 13 cm above the bed. Using a hot-film anemometer, Price and Schiebe (1978) measured excurrent siphon exit velocities of 11–14 cm s^{-1} for the freshwater clam *Anodonta*. We estimate the excurrent exit velocity of one of our *Clinocardium* as 9–11 cm s^{-1}, based on the angle of deflection of the excurrent jet 3 cm above the bottom in a flow with a known velocity profile. Because of the strong velocity difference between the excurrent jet and the boundary layer flow, the jet acts very much like a solid object in the near-bed region of importance to larvae settling around the bivalve. The dye streaks generally diverged around the jet, although at low flow velocities fluid entrainment caused a curious spiralling of those dye streaks passing close enough to get caught in the low-pressure boundary layer around the jet itself. The patterns of flow around the excurrent jet are strongly reminiscent of patterns described by Eckman and Nowell (1984) for flow around animal-tube mimics. Thus, we would expect the jet wake to demonstrate roughly the same patterns of boundary shear stress as those that occur around a solid cylinder. The strong lateral shear due to the "horseshoe vortex" will be absent, however, since the ambient flow deflects the siphonal jet and is not directed toward the bed as in the case of a rigid cylinder. An important unsteady component will be superimposed on the downstream flow by periodic shedding of vortices from the excurrent jet.

At a low free-stream velocity of 2.8 cm s^{-1} ($u_* = 0.16$ cm s^{-1}), the incurrent siphon entrained fluid close to the bed up to 3–4 cm laterally, but its vertical influence extended only 1–2 cm. With increasing height the lateral influence was sharply reduced. At the higher free-stream velocity of 16 cm s^{-1} ($u_* = 0.79$ cm s^{-1}), the lateral and vertical influences of the incurrent siphon both extended no further than about 1 cm. These observations were consistent for all 3 orientations of the cockle; thus the inhalant siphon appears constrained to draw in relatively slow-moving fluid near the bed.

We have drawn the region of recirculation downstream of the cockle with dotted lines because we are unable to accurately describe a mean pattern of flow. Conservation of mass requires that recirculation exists, but the weak and fluctuating recirculatory flow interacts with diffuse exchange along the edges of the region. Vortices shed episodically from the siphon jet repeatedly entered this region from higher in the water column and reached the bed. Thus, patterns of flow in this region are variable and temporally complex, with the strongest flows produced by shed vortices. We have, however, observed particles close to the bed enter this region and move several millimeters *upstream* before depositing.

b. Passive deposition. In general, polystyrene spheres were drawn into the bivalve with no observable effect on its behavior. Those spheres vented by the excurrent jet were carried up into the water column and out of the region of study. For the sake of comparing polystyrene spheres with larvae, those spheres that were removed from the region of study by the excurrent jet may be considered mortalities. Although planktonic larvae have been reported to pass alive through the mantle cavities and even digestive tracts of some adult bivalves, subsequent mortality is very high due to entrapment in mucus of the adults (see Mileikovsky, 1974, for review).

Figure 3 is a graph of raw abundance for the deposition of polystyrene spheres plotted against radial distance from the *C. nuttallii* siphon. The data are presented as paired graphs, illustrating upstream data (quadrants I and II) and downstream data

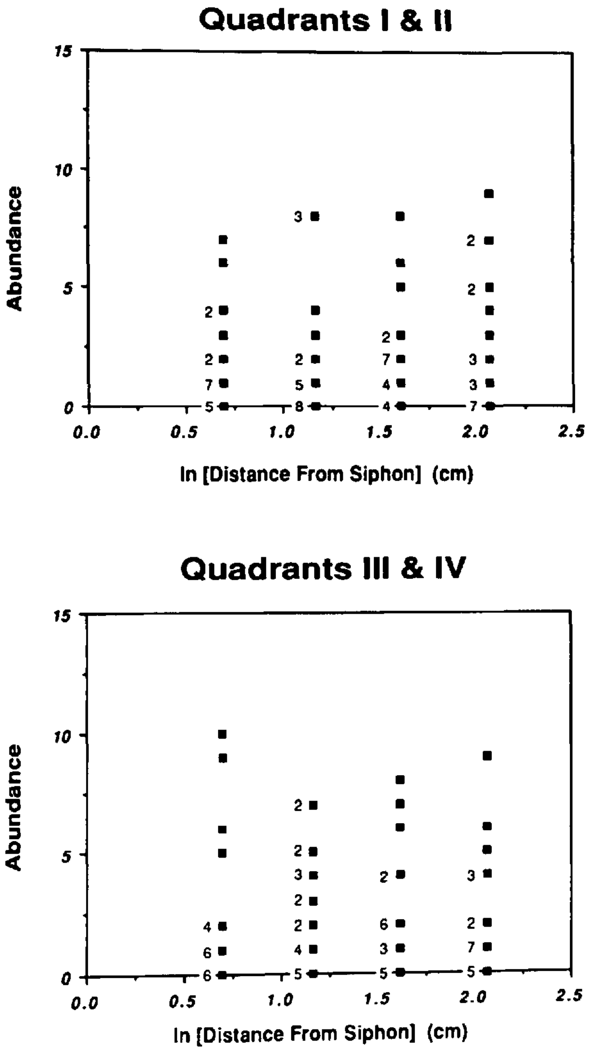

Figure 3. Abundance of polystyrene spheres versus radial distance from *C. nuttallii*, showing upstream data (quadrants I & II) and downstream data (quadrants III & IV) separately. Two outliers are not plotted (quadrant II—abundance equals 19 at 2.0 cm; quadrant III—abundance equals 32 at 5.0 cm).

(quadrants III and IV) separately. Two outliers (out of 160 data points) lie beyond the range of these graphs and are not plotted. They are probably due to clumping of spheres, perhaps in the initial dispersal or perhaps in pseudofeces. These data are *not* omitted from our statistical analyses.

We employed Jonckheere's nonparametric, distribution-free test for ordered alternatives (Hollander and Wolfe, 1973) to test two *a priori* hypotheses:

(1) There is a *decrease* in polystyrene sphere abundance with increasing proximity to the *Clinocardium* (due to inhalation and entrapment in pseudofeces or ejection from the region of study),

(2) There is an *increase* in polystyrene sphere abundance with increasing proximity to the *Clinocardium* (due to entrainment of fluid past the bivalve by the incurrent and excurrent siphons),

against the null hypothesis that polystyrene sphere abundance was the same at all distances sampled. We also tested the *a posteriori* hypothesis that the inhalation of polystyrene spheres was a "near-field" phenomenon:

(3) There is a *decrease* in polystyrene sphere abundance with increasing proximity over the three sample distances nearest the *Clinocardium* (2.0, 3.2, 5.0 cm)

against the similarly shortened null hypothesis. These tests were made separately for upstream and downstream data. We were unable to reject the null hypothesis for any of these six tests ($P > 0.20$). We also performed a series of Wilcoxon Paired-Sample tests (Zar, 1984) to determine if there was a significant difference between upstream and downstream abundance at any of the 4 ranges sampled. The data were paired by run, range, and side of flume sampled (quadrant I with III; quadrant II with IV). There were no significant differences ($P > 0.30$).

The results from the flow visualization study suggested that the region of the bed downstream of *Clinocardium*'s siphonal currents would be subject to a complex pattern of boundary shear stress due, predominantly, to turbulent flow around the exhalent jet. Turbulence and variation of boundary shear stress would be greatest near the siphon, decreasing to some ambient level farther away. Since boundary shear stress correlates with the flux of fluid and particles to and from the bed (Jumars and Nowell, 1984), we predicted that polystyrene sphere abundance would reflect this variability. In other words, there would be patches of increased and decreased polystyrene sphere deposition downstream of the siphon jet. The averaged result of this downstream patchiness in deposition would be reflected as an increased variability in polystyrene sphere abundance for samples taken near the bivalve. We defined our *a priori* test parameter, the "deviation from 2-quadrant mean," as the difference between polystyrene sphere abundance in any 6-mm diameter sample taken at a specific range around the *Clinocardium* siphon and the mean abundance of all 8 samples taken in the same upstream or downstream semicircle (1 sample at each of 4 ranges from each of 2 quadrants). We then plotted this parameter against radial distance from the *C. nuttallii* (Fig. 4). Using Jonckheere's test, we evaluated the absolute value of this test

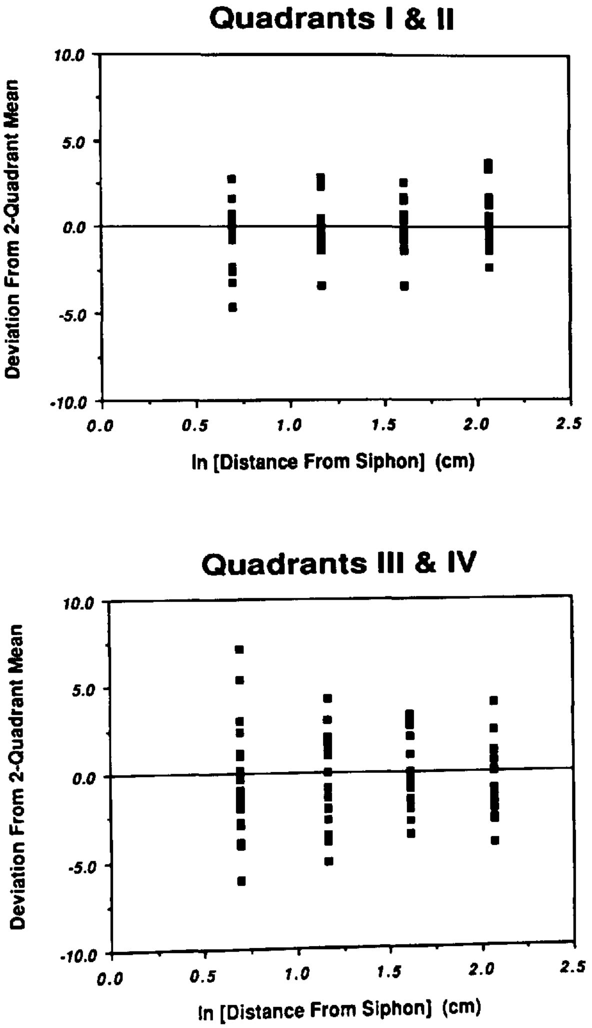

Figure 4. Deviation of sample abundance of polystyrene spheres from 2-quadrant mean abundance versus radial distance from *C. nuttallii*, showing upstream data (quadrants I & II) and downstream data (quadrants III & IV) separately. Two outliers are not plotted.

parameter (i.e., $|x-\bar{x}|$) for the predicted trend:

(4) There is an *increase* in the deviation of polystyrene sphere abundance from the 2-quadrant mean abundance with increasing proximity to the *Clinocardium* (due to variation in downstream boundary shear stress),

against the null hypothesis that the deviation of polystyrene sphere abundance from the 2-quadrant mean abundance was the same for all distances sampled. The upstream results were hydrodynamically consistent; the null hypothesis could not be rejected ($P > 0.35$). The downstream data are also hydrodynamically consistent, supporting the predicted trend ($P < 0.03$); there is an increased variability in the deposition of spheres just downstream of the bivalve.

c. Field sampling. Field dye studies confirmed the qualitative similarity of flow geometry around *Mya* and *Clinocardium* siphonal currents. The quantitative procedures used in the field study mirror the passive deposition procedures, and the results are displayed in a similar manner so that comparisons may be made. Raw abundance data for *Hobsonia* and the oligochaetes were plotted against radial distance from the *Mya* siphon (Fig. 5), and we employed Jonckheere's test (Hollander and Wolfe, 1973) to test abundances of each taxon for the alternate hypotheses already presented: larval abundance increases, decreases, or is unchanged with increasing proximity to a bivalve siphon. As in the passive deposition study, we also tested the *a posteriori* hypothesis that inhalation of larvae is a "near-field" phenomenon, using Jonckheere's test over the 3 sample ranges nearest to the *Mya* (1.8, 3.3, 6.0 cm). We were unable to reject the null hypothesis for any of these tests ($P > 0.20$).

The passive deposition study demonstrated a detectable fluid dynamic effect of siphonal currents (i.e., spatial variability of flow effects) on the deposition of inert polystyrene spheres downstream of a bivalve in a unidirectional flow, resulting in an increased variability ("patchiness") in polystyrene sphere abundance near the bivalve. Direction of tidal flow on Skagit Flats is highly variable due to bi-directional tidal currents and variable winds across the open expanse of Skagit Bay. If *Hobsonia* settlement is dominated by passive deposition; however, the spatially and temporally averaged result of this *downstream* patchiness should still be reflected as an increased variability in larval abundance for samples taken near a *Mya*.

Preliminary analysis of the *Hobsonia* abundance data revealed strongly skewed frequency data. Thus, we defined our *a priori* test parameter, the "deviation from local median," in a manner congruous with the passive deposition study, but using the *median* larval abundance of all 5 samples taken from all 5 ranges around a particular *Mya*. We plotted this test parameter against radial distance from the *Mya* siphon for both *Hobsonia* and the oligochaetes (Fig. 6). Again using Jonckheere's test on the absolute value of the test parameter, we evaluated both taxa for the predicted trend of increasing deviation of sample larval abundance from local median abundance with increasing proximity to the bivalve. The *Hobsonia* data revealed a strong trend in the predicted direction ($P < 0.0025$), while the oligochaetes showed no trend ($P > 0.35$). Although statistically nonsignificant ($P > 0.25$; Jonckheere's test of an increase in x-median (x) with increasing proximity to a siphon), Figure 6 also indicates a tendency for enhancement of *Hobsonia* larval abundance (with respect to local median abundance) near the bivalve.

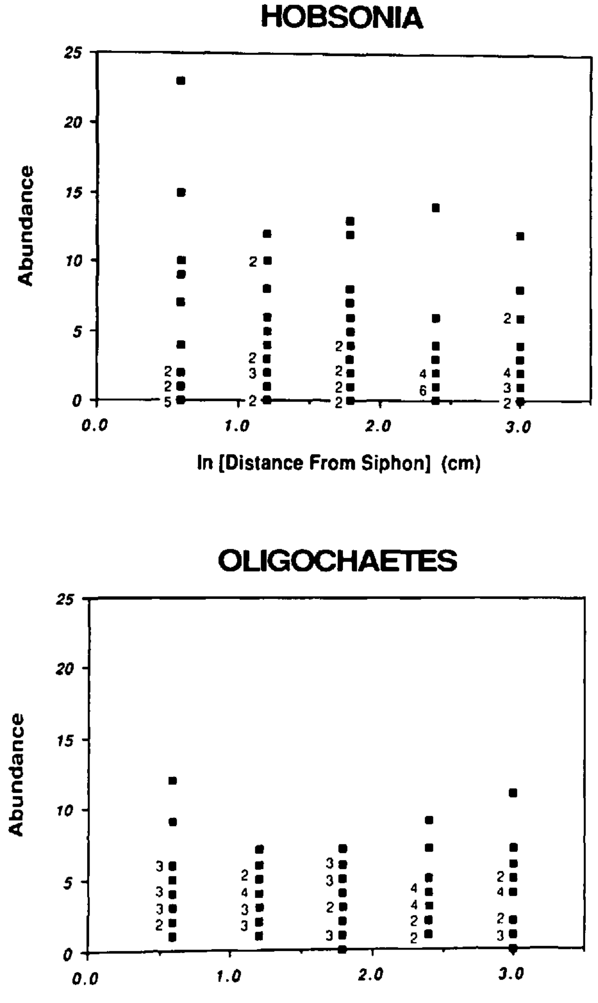

Figure 5. Abundance of *H. florida* larvae and asexual oligochaete buds versus radial distance from *M. arenaria* on Skagit Flat, WA.

4. Discussion

We conclude from all these results that the siphonal circulation produced by the bivalve "pump" (sensu Jørgensen *et al.*, 1986) and induced via interaction of the bottom-boundary-layer flow with the siphonal currents of the two studied bivalves, *Clinocardium nuttallii* and *Mya arenaria,* has only weak and spatially limited effects on near-bed particle exchange. It is difficult to argue from any of our data that the effect of the incurrent siphon on trajectories of passively settling larvae extends beyond 2 cm of the siphon. For isolated bivalves, we have no evidence of any decrease in local

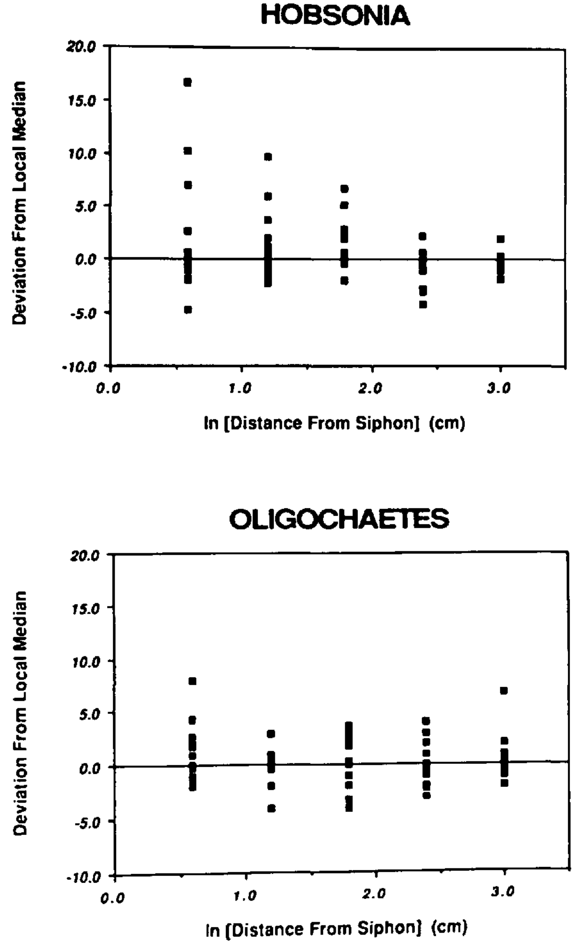

Figure 6. Deviation of sample abundance of *H. florida* larvae and asexual oligochaete buds from local median abundance versus radial distance from *M. arenaria* on Skagit Flat, WA.

deposition or settlement attributable to the siphon. The dominant effect appears to occur downstream, as a result of the ambient flow's interaction with the excurrent jet, and is one of increased variability in deposition and settlement near the bivalve.

A naive calculation from our results would suggest that there is room for some 10^3 bivalves m^{-2} before most of the bed is affected, and that the effect, if detectable, would be local enhancement of larval settlement. Such a calculation, however, confuses two important effects occurring on two different scales. Suspension-feeding bivalves, and active suspension feeders in general, are in the business of enhancing the local flux of particles to the bed, so one should expect a very local enhancement (of debatable magnitude and importance) in larval settlement. If larvae are inhaled and suffer mortality, then a separate issue is depletion of larvae by upstream bivalves. Depletion of larvae by upstream bivalves in shallow intertidal settings does occur, and these large-scale effects (e.g., Peterson and Black, 1987) can completely overshadow in magnitude the small-scale enhancement of fluxes suggested—and the variability in recruitment documented—by our observations of isolated individuals.

In view of our results, it is thus no surprise that what constitutes a dense assemblage has remained undefined. By our arguments, the upstream edges of even extraordinarily dense assemblages and any small patch (i.e., an experimental density manipulation of the scale produced by most experimentalists; e.g. Williams, 1980) would be readily colonized by larvae and might even show enhanced recruitment due to the circulation produced and induced by the bivalves. At the other extreme is an extensive and dense bed of bivalves with a thin and slow-flowing overlying layer of water containing larvae; few propagules may survive to settle at the center or downstream edge of the bed. The same density of bivalves, with a deeper and more turbulent overlying water column (less susceptible to particle depletion), might readily allow larval recruitment. Moreover, the rate of recruitment will be directly proportional to the supply rate of the larvae. Thus, it is clear that it would be foolish to attempt a definition of a dense assemblage from the standpoint of impending recruitment as simply an areal density of bivalves—without taking fluid dynamics, spatial scale, and larval supply into account.

Acknowledgments. We thank the Director for access to the fine facilities of the Friday Harbor Laboratories of the University of Washington, Seattle. A.R.M. Nowell, C. Smith, D. Thistle, F. Dobbs, and K. Carmen provided valuable comments on earlier drafts. This work was supported by NSF Grants Nos. OCE-81-17397 and OCE-86-08157.

REFERENCES

Aller, R. C. and J. Y. Yingst. 1985. Effects of the marine deposit-feeders *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia), and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates, and microbial distributions. J. Mar. Res., *43*, 615–645.

Butman, C. A. 1986. Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom profiles, *in* Marine Interfaces Ecohydrodynamics, J. C. J. Nihoul, ed., Elsevier Science Publishing Co., NY, 670 pp.

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.

Eckman, J. E. and A. R. M. Nowell. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. Sedimentology, *31*, 851–862.

Feller, R. J. 1977. Life history and production of meiobenthic harpacticoid copepods in Puget Sound. Ph.D. thesis, Univ. of Washington, Seattle, 249 pp.

Gallagher, E. D. 1983. The mechanisms of succession in the Skagit Flat infaunal community. Ph.D. thesis, Univ. of Washington, Seattle, 193 pp.

Gallagher, E. D., P. A. Jumars, and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology, *64,* 1200–1216.

Hancock, D. A. 1970. The role of predators and parasites in the fishery for the mollusc *Cardium edule* L., *in* Proc Adv. Study Inst. Dynamics Numbers Popul. (Osterbeek, 1970), P. J. den Boer and G. R. Gradwell, eds., Pudoc, Wageningen. 419–439.

Hannan, C. A. 1984. Initial settlement of marine invertebrate larvae: the role of passive sinking in a near-bottom turbulent flow environment. Ph.D. thesis, WHOI/MIT Joint Program, 534 pp.

Hollander, M. and D. A. Wolfe. 1973. Nonparametric Statistical Methods. John Wiley and Sons, NY, 503 pp.

Jørgensen, C. B., P. Famme, H. S. Kristensen, P. S. Larsen, F. Møhlenberg and H. U. Riisgård. 1986. The bivalve pump. Mar. Ecol. Prog. Ser., *34,* 69–77.

Jumars, P. A. and A. R. M. Nowell. 1984. Fluid and sediment dynamic effects on marine benthic community structure. Amer. Zool., *24,* 45–55.

Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden sea. Archs. Néerl. Zool., *12,* 351–453.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol., *26,* 303–311.

Muschenheim, D. K., J. Grant and E. L. Mills. 1986. Flumes for benthic ecologists: theory, construction, and practice. Mar. Ecol. Prog. Ser., *28,* 185–196.

Nikuradse, J. 1933. Laws of flow in rough pipes. Nat. Advis. Comm. Aeronaut. Tech. Memo. 1292. 62 pp. (Transl. from German, 1950).

Nowell, A. R. M., P. A. Jumars and J. E. Eckman. 1981. Effects of biological activity on the entrainment of marine sediments. Mar. Geol., *42,* 133–154.

Peterson, C. H. and R. Black. 1987. Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. Limnol. Oceanogr., *32,* 143–166.

Price, R. E. and F. R. Schiebe. 1978. Measurements of velocity from excurrent siphons of freshwater clams. The Nautilus, *92,* 67–69.

Smith, J. E. 1980. Seasonality, spatial dispersion patterns and migration of benthic invertebrates in an intertidal marsh-sandflat system of Puget Sound, Washington, and their relation to waterfowl foraging and the feeding ecology of Staghorn Sculpin, *Leptocottus armatus.* Ph.D. thesis, Univ. of Washington, Seattle, 177 pp.

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.

Zar, J. H. 1984. Biostatistical Analysis, 2nd ed. Prentice-Hall, NJ, 718 pp.

Zottoli, R. A. 1974. Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus.* Trans. Amer. Micros. Soc., *93,* 78–89.

Received: *24 December, 1987;* revised: *22 July 1988.*