Limnol. Oceanogr., 28(2), 1983, 241–257

Hydrodynamic processes affecting benthic recruitment[1]

James E. Eckman[2]
School of Oceanography WB-10, University of Washington, Seattle 98195

Abstract

Recruitment of animals into initially defaunated sites containing simulated stalks of a marsh grass was studied on an intertidal sandflat. Laboratory flume experiments were used to predict the effects of these structures on near-bed flow, the sediment size-frequency composition, and the patterns and rates of benthic recruitment. The effects of simulated stalks on both rates of fluid transport near the bed and boundary shear stress change profoundly with their numerical density. Patterns of sedimentation in the field and patterns and rates of recruitment of several taxa depended strongly on the presence and numerical density of these structures, in agreement with a priori predictions assuming passive (i.e. purely hydrodynamic) dispersal. Hydrodynamic (or other physical) effects of manipulation are important and form an additional, but infrequently posed, null hypothesis against which biological effects such as substrate selection, competition, predation, or disturbance should be tested.

Marine soft-bottom environments have distinct communities among arrays of seagrasses (e.g. O'Gower and Wacasey 1967; Santos and Simon 1974; Stoner 1980) or of structures such as animal tubes (e.g. Sanders et al. 1962; Jumars 1975; Woodin 1981; Bailey-Brock 1979). Various mechanisms have been invoked to explain these associations. Woodin (1974) suggested that tube dwellers act to exclude motile, burrowing infauna by monopolizing space in the substratum. Seagrasses (e.g. Young et al. 1976; Orth 1977) and animal tubes (Woodin 1978; Wilson 1979) may provide refuge from predation or disturbance. These structures also provide substrata for the growth of bacteria, algae, and fouling organisms (e.g. Mills 1967), all of which may be eaten by deposit feeders.

Protruding structures (roughness elements in hydrodynamic terms) also affect the hydrodynamic environment near the bed. Their size, geometry, and numerical density will determine the properties of near-bed flow, including the magnitude of the shear stress exerted on the bed (and hence its propensity to erode, or stability); the rate of fluid transport; and the production of turbulence (Wooding et al. 1973; Nowell and Church 1979; Raupach et al. 1980; Eckman et al. 1981; Nowell et al. 1981). These hydrodynamic processes, alone, may produce the distinct infaunal assemblages noted among arrays of tubes or grasses. For example, the rate of fluid transport near the bed will affect immigration rates of animals dispersed passively by lateral advection. The shear stress exerted on the bed will affect the emigration of established individuals and the composition of the surface sediments, the latter important because many benthic invertebrates can select for sediment grain size and organic content (e.g. Wilson 1937, 1948, 1955, 1968; Wieser 1956; Meadows 1964*a*,*b*; Gray 1967). Recruits may also select sites actively on the basis of local patterns of flow (Eckman 1979*a*).

I describe here experiments designed to test the influence of hydrodynamic processes on benthic recruitment. I studied recruitment of larvae, juveniles, and adults into initially defaunated sites on an intertidal sandflat. A range of hydrodynamic environments was created by simulating, with plastic straws, three different numerical densities of shoots and stalks of the bulrush *Scirpus americanus*. At the study site, *S. americanus* dominates the upper intertidal zone (Smith 1980). Laboratory flume experiments

[1] Contribution 1251 from the School of Oceanography, University of Washington. This research was funded by Office of Naval Research contract N00014-80-C-0252 Mod. P00001.

[2] Present address: Marine Science Research Center, SUNY, Stony Brook, New York 11794.

were also conducted to measure the effects on near-bed flow of these straw spacings and heights. Results of the flume experiments are used to predict patterns of recruitment in the field.

Specifically, I propose a compound alternative hypothesis against which I test the null hypothesis that there are no treatment effects on animal recruitment and sediment composition. First, arrays of simulated marsh grass dense enough to reduce boundary shear stresses (i.e. establish a skimming flow, sensu Morris 1955) will accumulate greater proportions of fine sediments and both temporary and permanent meiofauna than will arrays which do not reduce boundary shear stresses. Sediment entrainment and transport occur frequently at the study site. Animals which remain near the sediment surface (e.g. recently settled larvae, most meiofauna) and finer sediments should be less easily eroded from sites experiencing reduced boundary shear stresses. Second, if more than one of the arrays create a skimming flow, then fine sediments will accumulate and animal abundance will increase most rapidly at the site experiencing a higher rate of fluid transport near the bed. Immigration rates of animals dispersed passively will be correlated positively with fluid flux.

These a priori predictions assume a completely passive dispersal of recruits by lateral advection. Lateral advection is likely to dominate recruitment in environments subjected to frequent sediment entrainment and transport, at least among organisms inhabiting surficial sediments. Furthermore, this assumption of passive dispersal ensures the most conservative test possible of the importance of hydrodynamic processes to recruitment: alternative processes (e.g. active site selection, biological interactions) render less likely detection of the trends predicted.

I thank the director and staff of the Friday Harbor Laboratories for providing laboratory facilities and support. This manuscript has benefited from critical reviews by P. A. Jumars, A. R. M. Nowell, G. Taghon, A. C. Charters, E. D. Gallagher, C. A. Hannan, D. Miller, R. F. L. Self, D. D. Trueblood, and two unidentified reviewers.

Methods

Field experiments—Separate recruitment experiments were initiated on 16 April and 18 September 1980 on an extensive intertidal sandflat in Skagit Bay, Washington (48°21′N, 122°29′W). The tidal flat is broad and wide (several kilometers in both dimensions) and of extremely low slope (of order 10^{-3}). On the comparatively small scale of my experiments the tidal ebb and flood currents dominating fluid and sediment transport may thus be considered uniform ($\partial/\partial x = 0$) and two-dimensional ($\partial/\partial y = 0$) to a first approximation.

Both experiments were conducted at +2 m above MLLW, about 50 m seaward of the edge of the fringing bulrush marsh. At this level the exposed flats look homogeneous except for many small (≈5-cm diam) feeding pits created by ducks and demersal fishes, shallow pools (≈2-cm depth, diverse sizes) which retain water throughout the tidal cycle, and widely scattered, distinct tidal streams (cf. Smith 1980).

In each experiment, six contiguous sites, each 4–5 m square, were aligned approximately normal to the direction of tidal flow (Fig. 1). All sites were within a large, shallow pool and were >50 m from the nearest tidal channel, so that conditions of flow and exposure were expected to be essentially identical. The control site (termed A) received no treatment. A circular corer (30-cm diam) was inserted to 12-cm depth at the center of each of the other five sites, all sediments within it were removed, and the hole was filled with foundry sand which had been washed with ambient seawater filtered through a 61-μm mesh. The corer was then removed carefully, leaving a defaunated, circular island 30 cm across. The two end sites in the line of six (Fig. 1) received no further treatment and served as defaunated controls (termed sites $\emptyset_1$ and $\emptyset_2$). Their separation by the largest possible distance permitted an estimate of the spatial heterogeneity in recruit-

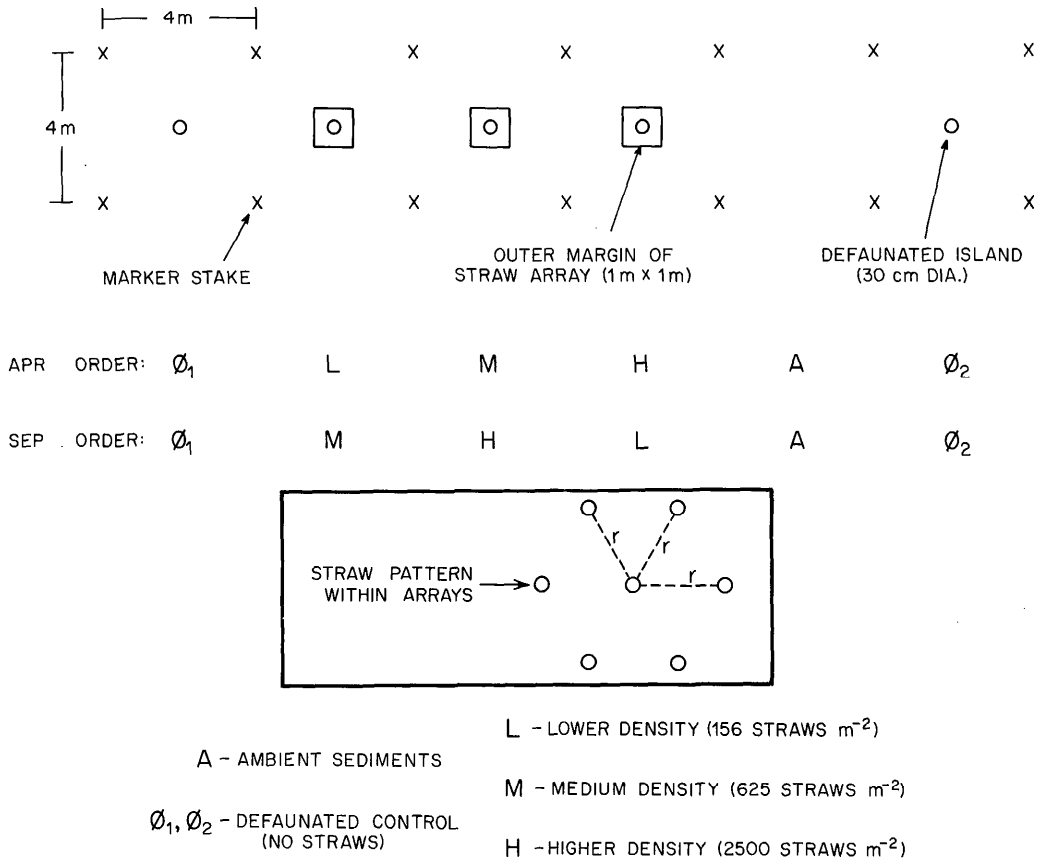

Fig. 1. Schematic diagram of field sites. Six contiguous sites (4 × 4 m) were oriented normal to tidal flow. Five sites contained an initially defaunated island (30-cm diam). Three of these sites contained straw arrays (1 × 1 m). Code letters at base describe site treatments and give their order in both experiments. Straw spacings were: site L, r = 8 cm; site M, r = 4 cm; site H, r = 2 cm. Roughness densities (i.e. proportion of plan area of the bed occupied by straws) were: site L, 1/226; site M, 1/57; site H, 1/14.

ment and in measures of sediment composition.

Locations of the ambient control site (A) and the three treatment sites of various straw densities were assigned randomly to the four inner sites. The three treatment sites (termed L, M, and H) each consisted of arrays (1 × 1 m) of plastic straws (6-mm diam) centered over the 30-cm defaunated island. Straws were inserted vertically so that they protruded 1–2 cm above the bed in a hexagonally packed pattern (Fig. 1). The 1- × 1-m plots were the largest that could be constructed during a single tidal emersion. This size helped ensure that the new boundary layer created by the straws on the incoming and outgoing tide would be as fully developed (i.e. flow uniform in the longstream direction: *see* Schlichting 1968, p. 40; Tritton 1977, p. 85) as possible over the area sampled.

The experiment initiated on 16 April was sampled after 2, 5, 14, and 30 days; the experiment initiated on 18 September was sampled after 2, 6, 16, and 32 days. On each date and in each of the six sites infauna were sampled with 15 cores (1.1-cm diam) inserted to 5 cm. Core locations were chosen randomly without replacement and separately for each date. The same core locations were used for each of the six sites in a paired design. No core was taken >14 cm from the cen-

ter of the initially defaunated island (or from the center of the 4- × 4-m ambient control site). All samples were preserved immediately in 10% buffered Formalin in seawater containing rose bengal.

On each sampling date four (April) or six cores (September) were also taken for analysis of the size composition of the sediments. These cores were taken with plastic straws (6-mm diam) inserted 3–5 cm into the sediments, also in a paired design, at random coordinates within 14 cm of plot centers. Cores were capped, labeled, and frozen immediately on Dry Ice. In the laboratory the top 5 mm of each frozen core was carefully removed, placed in a crucible, baked at 600°C for 3 h to oxidize all organic matter (carbonates comprising a trivial fraction of both foundry sand and ambient, riverborne sediments), and analyzed for size distribution by standard dry-sieving techniques. The weight percentage of particles <88 μm in diameter (i.e. >3.5ϕ) was chosen as a measure of fine sediments (median particle diameter of the open flat = 120 μm). This size limit was a practical compromise: sieves of smaller mesh (larger ϕ) did not consistently retain measurable quantities of sediment from all sites.

Samples for determining infaunal abundances were processed with a technique developed by Feller (1977, 1980). A sample is placed in a 500-ml beaker, sediments are suspended with a jet of water, the suspension is allowed to settle for 3–4 s, and the supernatant is decanted through a 61-μm mesh. This procedure was repeated four times. The remaining sediment was then sieved through a 250-μm mesh. All material retained on both sieves was sorted under a dissecting microscope (6–25×). The efficiency of the method was estimated by examining material passing through the 250-μm mesh from six randomly selected samples. In the April experiment the processing technique resulted in 100% retention of each group counted; in the September experiment there was 100% retention of each except nematodes (96 ± 2.4%) and *Mayunkia aestuarina* (89 ± 21%) (95% C.L. for the normal approximation of the binomial distribution).

For each taxon, and for sediment samples, differences among sites were tested with a parametric, one-way ANOVA. Means and standard errors for sediments and all taxa enumerated, within each experimental site, on each date sampled, are available on request. A Kruskal-Wallis nonparametric ANOVA was substituted if assumptions of homoscedasticity continued to be violated (F_{max} test: Sokal and Rohlf 1969) after transformation. Data were square-root transformed if they were Poisson distributed (χ^2 goodness-of-fit test: Dixon and Massey 1969); a log transform was used otherwise. Adjustment was made for multiple testing by using a lower individual α level according to the highly conservative Bonferroni equation (Miller 1966). The proper individual α level was calculated on an experimentwise $\alpha = 0.05$. If the ANOVA was significant at $\alpha = 0.05$, experimentwise, individual differences among treatments were tested using the Student-Newman-Keuls test (parametric ANOVA) or the multiple comparisons test of Miller (1966, as described by Hollander and Wolfe 1973) for the nonparametric equivalent of ANOVA.

Sample coordinates were used to test for "edge" effects—spatial inhomogeneities in recruitment induced by the experimental design. Organisms which recruit by burrowing or crawling, instead of by passive lateral advection, may show such edge effects. Correlations of abundance with distance from the center of the initially defaunated site were evaluated using a nonparametric correlation coefficient (Spearman's ρ or Kendall's τ).

Flume experiments—Experiments were conducted in a recirculating seawater flume (2.5 m × 50 cm) fitted with a constant-head tank (Nowell et al. 1981). Hexagonal patterns and densities of straw arrays like those tested in the field were simulated by gluing 1-cm × 6-mm plastic straws onto the flat, Plexiglas flume bed. In the flume, straw arrays 35 cm (longstream) by 14 cm (cross-stream) were

Table 1. Nondimensionalized rates of near-bed fluid transport for three arrays, each tested at three shear velocities and total depths of flow. To produce nondimensional values, each of three separate measures of fluid transport rate within 1 cm of the bed (Eq. 4) is divided by the transport rate under identical flow conditions with no straw array present (unobstructed flow). Results of one-way ANOVA appear at the end of each row (density effect) and at the base of each column (shear velocity-depth effect): symbols are ordered from lowest (left) to highest (right) mean transport rate. Symbols underlined are not significantly different ($\alpha = 0.05$). Symbols explained in legend to Fig. 1.

	Array L	Array M	Array H	
$u_* = 0.524$ cm·s^{-1}	1.028	0.740	0.432	$P = 0.0008$
Depth = 5 cm	0.865	0.924	0.477	H M L
$Re_s = 307$*	0.884	0.814	0.501	
$u_* = 1.08$ cm·s^{-1}	0.996	0.703	0.398	$P < 0.00005$
Depth = 3 cm	0.997	0.626	0.325	H M L
$Re_s = 508$*	0.915	0.591	0.359	
$u_* = 1.67$ cm·s^{-1}	0.875	0.664	0.315	$P = 0.0002$
Depth = 1.75 cm	0.888	0.699	0.486	H M L
$Re_s = 958$*	0.844	0.718	0.448	
	$P = 0.1988$	$P = 0.031$	$P = 0.1586$	
	(NS)	$\underline{M_3\ M_{1.75}}\ M_5$	(NS)	

* The Reynolds number (Re_s) is calculated for tops of 1-cm-high straws (6-mm diam). Flow velocity is that for unobstructed flow at $z = 1$ cm; $\nu = 0.01$ cm^2·s^{-1}.

centered 2 m downstream of the flume entrance. Straw arrays occupied 28% of total flow width. Ideally, one would test the full 1-m^2 array in a flume much wider than 1 m; however the dimensions were chosen to allow for possible lateral deflection of flow about the arrays in the flume, such as that likely to occur in the field.

Each of the three arrays was tested at three combinations of flow depth and shear stress (τ_b) (9 combinations total). Boundary shear stress, the drag exerted by a fluid moving over a stationary bed, produces a velocity gradient near the bed (e.g. Komar 1976). Consequently, boundary shear stress, and not mean fluid velocity or velocity measured at an arbitrarily chosen height, best describes the effects of flow on the modes and rates of sediment transport (cf. Graf 1971; Middleton and Southard 1978). The creation in the flume of boundary shear stresses representative of field conditions, therefore, is essential.

Boundary shear stress (τ_b) is expressed commonly as a shear velocity (u_*):

$$u_* = (\tau_b/\rho)^{0.5} \quad (1)$$

where u_* is shear velocity (cm·s^{-1}), τ_b is boundary shear stress (dyn·cm^{-2}), and ρ is fluid density (g·cm^{-3}). Shear velocities tested range from 0.52 to 1.67 cm·s^{-1} for unobstructed flow (Table 1), a range characteristic of the study site: in situ values of u_* go from essentially zero at slack tide (after flood) to at least 1.15 cm·s^{-1}. The latter is the critical entrainment velocity (u_{*cr}) for noncohesive, well sorted sediments of 120-μm median diameter (Miller et al. 1977). Observations of sediment ripples indicate that this critical entrainment velocity is exceeded frequently at the Skagit flats.

Vertical profiles of flow velocity and turbulence intensity were measured within arrays at three separate cross-stream locations 25 cm downstream from the leading edge of the straw array and also at the same locations after all straws were removed (unobstructed flow). Any instantaneous velocity (u) can be expressed as a sum of two terms

$$u = \bar{u} + u' \quad (2)$$

where $\bar{u}$ is a mean velocity and u' an instantaneous velocity fluctuation. Both mean velocity, $\bar{u}$, and turbulence intensity, $[\overline{u'^2}]^{0.5}$, were measured using a Thermo-Systems TSI 1231 W conical quartz

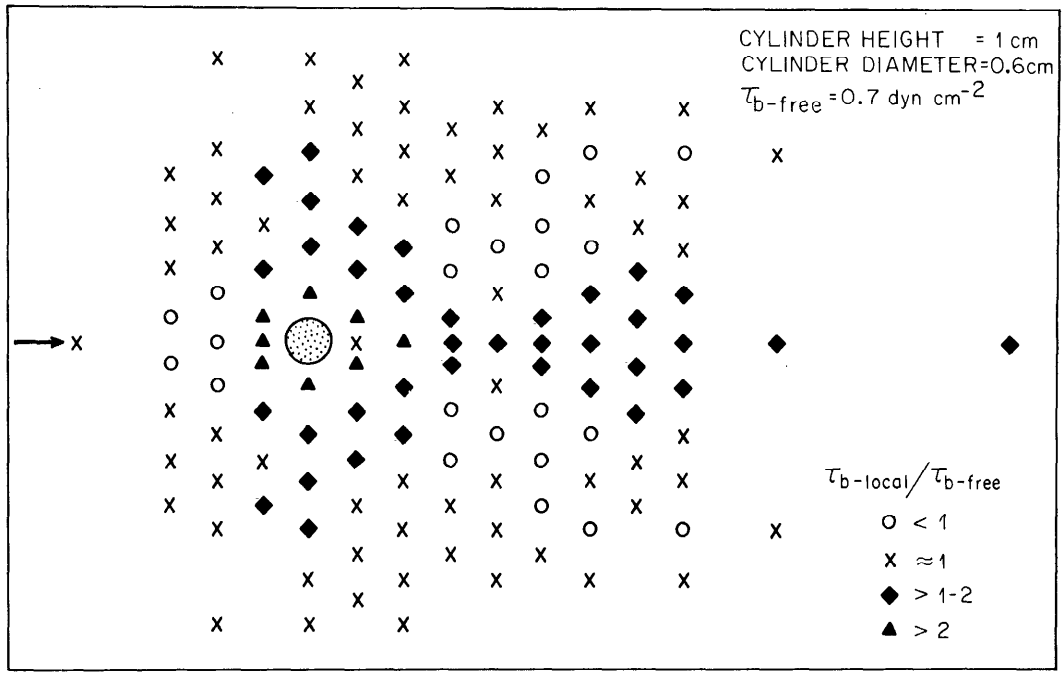

Fig. 2. Distribution of boundary shear stress (τ_b) about a single, rigid cylinder on an otherwise smooth flume bed. In this plan view of the bed the cylinder is represented by a stippled circle. The figure is scaled to cylinder diameter (0.6 cm). Flow is from left to right (arrow). Various symbols represent ratios of locally measured shear stress ($\tau_{b\text{-local}}$) to that exerted on the bed in the absence of the cylinder ($\tau_{b\text{-free}}$). Cylinder creates local regions of both greatly increased and decreased τ_b, resulting simultaneously in both sediment deposition and entrainment. Further details are given elsewhere (Eckman 1979*b*, 1982).

film probe (*see* Nowell et al. 1981; Eckman et al. 1981).

Shear velocity (u_*) for unobstructed flow was determined from the log-profile relationship

$$u(z) = \frac{u_*}{\kappa} \ln(z/z_o) \qquad (3)$$

where $u(z)$ is the velocity at height z above the bed, κ is von Karman's constant (=0.4), and z_o is the roughness height. A plot of $\bar{u}(z)$ vs. ln z produces a straight line of slope u_*/κ for the near-bed region of a steady, uniform boundary-layer flow. Four to seven points (usually five) from within the log layer were used in each regression.

The magnitude of boundary shear stress within straw arrays will be both straw-density dependent and spatially heterogeneous. Even a single, isolated cylinder on an otherwise smooth bed produces regions of both local sediment deposition (low shear stress) and entrainment (high shear stress) (Fig. 2). Furthermore, it is not possible to calculate the average skin friction within straw arrays from velocity profiles because the spatial heterogeneity in flow about such structures violates the assumptions used to derive the log-profile relationship. Consequently, an alternative parameter is required.

Within straw arrays flow near the bed can be characterized by calculating rates of fluid transport or discharge (q_s) per unit width of flow, given by

$$q_s = \int_{z=0}^{z=z_t} u(z)\, dz \qquad (4)$$

where q_s (cm·s^{-1}), $u(z)$ is streamwise velocity at height z (cm·s^{-1}), and z_t is tube height (1 cm). Each of the three vertical profiles of flow velocity within an array was integrated to estimate fluid discharge

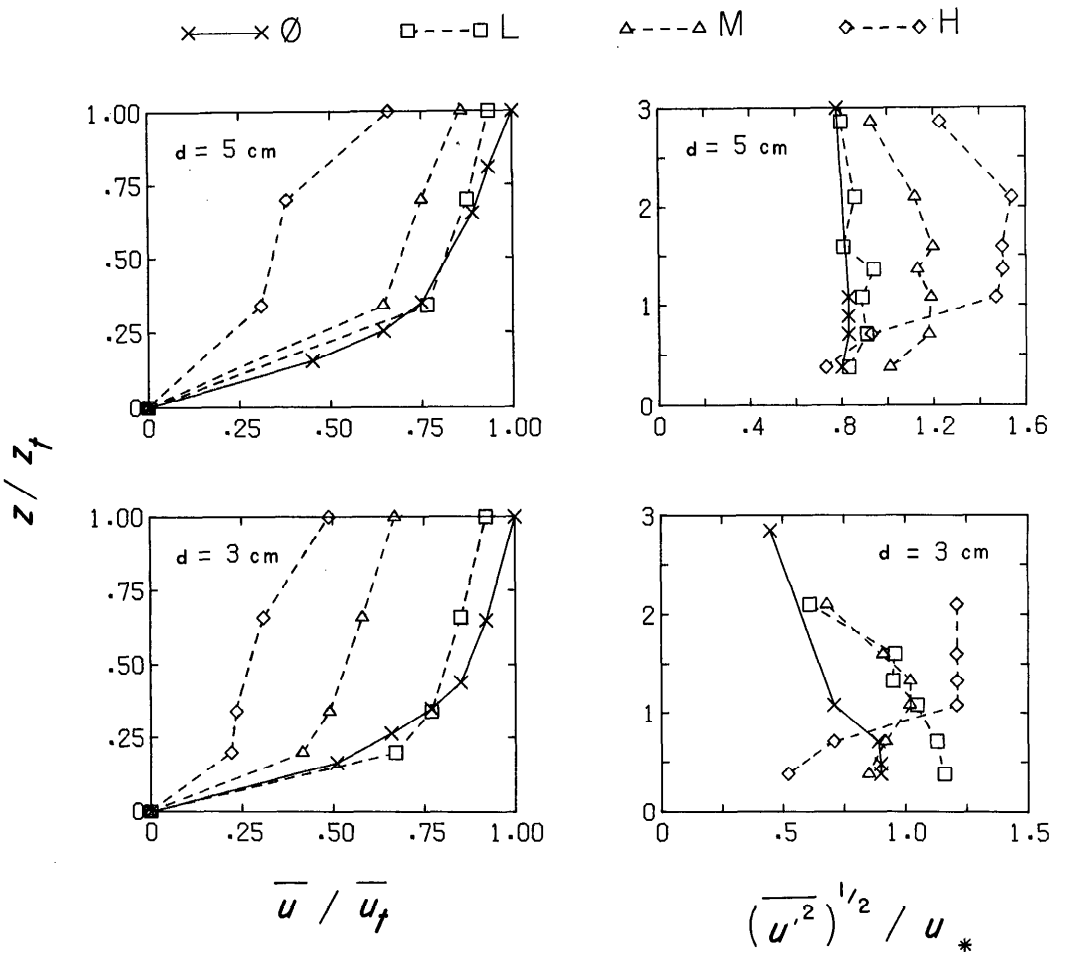

Fig. 3. Nondimensionalized vertical profiles of mean flow velocity ($\bar{u}$) and turbulent kinetic energy ($\overline{u'^2}$) among straw arrays tested in the flume at flow depths of 5 and 3 cm. Mean flow velocity at each height is normalized to the mean velocity at z = 1 cm (i.e. tops of straws) ($\bar{u}_t$), measured for unobstructed flow. For 5-cm depth flow, $\bar{u}_t$ = 5.17 cm·s^{-1}; for 3-cm depth flow, $\bar{u}_t$ = 8.47 cm·s^{-1}. Turbulent kinetic energy is normalized to shear velocity (u_*) for unobstructed flow. Values of height above the flume bed (z) are normalized to straw height (z_t = 1 cm). Symbols as in Fig. 1.

rate, and statistical comparisons among experiments were made by using these estimated rates expressed as a proportion of the average fluid discharge rate for unobstructed flow (estimated from profiles measured over the flat flume bed). Differences among experiments were tested using a one-way ANOVA. In addition, the signature of a bed-averaged reduction in boundary shear stress among arrays (i.e. establishment of a skimming flow sensu Morris 1955) was sought from shapes of velocity profiles (Plate and Qurashi 1965; Petit et al. 1976) and turbulent kinetic energy profiles (Mulhearn and Finnigan 1978; Nowell and Church 1979).

Results

Flume experiments—Table 1 summarizes results of the flume experiments. In all combinations tested, the high-density array exhibited a significant (average of 52–63%) reduction in fluid discharge among straws, while the low-density array showed no strong effect. The nondi-

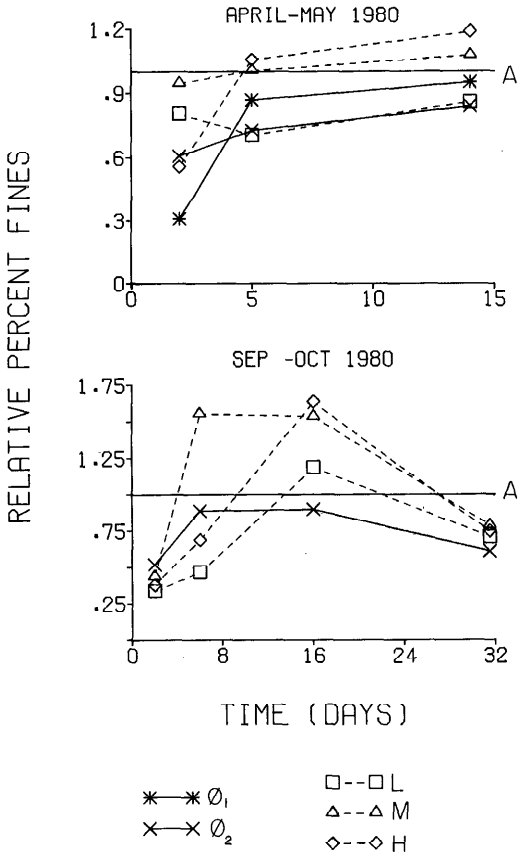

Fig. 4. Temporal trends in the composition of surficial sediments for both April and September experiments. For each treatment site, relative percentage of fine particles (ordinate) is calculated by dividing mean percentage by weight of fine particles (i.e. d < 88 μm) by mean percentage of fine particles measured concurrently at the ambient site A. Symbols as in Fig. 1.

mensionalized discharge rates within arrays H and L exhibited no detectable shear velocity dependence (column ANOVAs: Table 1). Within array H velocity profiles were sigmoidal below the tops of straws, and the region of maximum turbulent kinetic energy production was above the tops of straws (Fig. 3). These properties each indicate that a skimming flow was established (Plate and Qurashi 1965; Mulhearn and Finnigan 1978; Nowell and Church 1979). Consequently, within array H the boundary shear stress was reduced below that of unobstructed flow at all shear velocities and flow depths tested.

The pattern exhibited by array M was more complex. At the greatest flow depth (d = 5 cm) and lowest shear velocity (u_* = 0.524 cm·s^{-1}) tested the discharge rate was not significantly different from that measured within array L: there was no obvious reduction in fluid discharge rate near the bed (Table 1, Fig. 3). However, as flow depth decreased and shear velocity increased, a statistically significant reduction (average of 30–37%) in discharge rate became apparent. Turbulent kinetic energy was again greatest above the tops of straws (Fig. 3), characteristic of skimming flow. Consequently, at greater shear velocities and lesser flow depths the shear stress exerted on the bed within array M was also reduced from that of unobstructed flow. The discharge rate within array M was always significantly greater than within array H (Table 1).

Array L exhibited no detectable reduction in discharge rate (Table 1). Turbulent kinetic energy near the bed exceeded that of unobstructed flow at lower depths and higher shear velocities (Fig. 3). Consequently, it is likely that at these greater shear velocities the *average* boundary shear stress within array L increased slightly (*see also* Eckman et al. 1981). However, because of the relatively large spacings within array L (8 cm or 13 straw diameters) the spatial distribution of τ_b likely resembled the complex pattern shown by an isolated cylinder (Fig. 2).

Field experiments: April–May 1980—The implanted foundry sand was covered by natural sediment at all of the treatment sites within 1 day, so that organisms moved into natural sediment particles. Results are reported from samples taken 2, 5, and 14 days after the start of the experiment. After day 14 strands of filamentous green algae began to accumulate on the tidal flat and became trapped by the protruding straws at all sites. By day 30, sites M and H were covered by a dense mat of algae.

By day 2, site M contained more fine particles (d < 88 μm) than any of the other treatment sites (Table 2, Fig. 4), al-

Table 2. Composition of surficial sediments for April and September experiments. Values listed for each site are mean percentages (by weight) of particles <88 μm in diameter (% > 3.5φ). Significance of the one-way ANOVA and results of multiple comparisons tests appear at the end of each row: site symbols are ordered from lowest (left) to highest (right) mean percentage. Symbols underlined are not significantly different ($\alpha = 0.05$).

	Site							
	A	$Ø_1$	$Ø_2$	L	M	H	*P*	
April 1980								
Day 2*	24.8	7.61	15.2	20.2	23.5	13.8	0.002†	$Ø_1$ H $Ø_2$ L M A
Day 5	15.4	13.4	11.3	11.0	15.6	16.3	0.0003†	L $Ø_2$ $Ø_1$ A M H
Day 14	13.4	12.7	11.2	11.5	14.5	16.0	0.1124	
September 1980								
Day 2	22.7	15.5	11.7	7.76	10.0	8.62	<0.00005†	L H M $Ø_2$ $Ø_1$ A
Day 6*	22.7	—	20.2	10.6	35.4	15.7	0.023‡	L H $Ø_2$ A M
Day 16	19.2	—	17.2	22.9	29.6	31.4	0.0001†	$Ø_2$ A L M H
Day 32	34.0	—	20.7	24.3	27.0	25.6	<0.00005†	$Ø_2$ L H M A

* Kruskal-Wallis test.
† $P < 0.01$ experimentwise.
‡ $P < 0.05$ experimentwise.

though in general differences are not statistically significant. By day 5, both sites M and H contained more fine particles than did ambient sediments, and a significantly greater percentage than site L. This trend of relatively high proportions of fine particles at sites H and M was still apparent on day 14 (Fig. 4, Table 2), although the ANOVA is not significant.

Table 3 summarizes data on the recruitment of all common taxa (*see also Fig.* 5). All organisms are of meiofaunal size. *Huntemannia jadensis* and other harpacticoids are shallow-dwelling, interstitial crawlers (large adult *H. jadensis* may more accurately be termed burrowers) which swim episodically, at least during slack water (pers. obs.). Juveniles of the ampharetid polychaete *Hobsonia florida* live in surficial sediments only and generally have 3–7 setigers. *Hobsonia florida* is believed to exhibit entirely benthic development (Zottoli 1966, 1974; *see also* Banse 1979.)

Table 3. Summary of multiple comparisons tests for differences in abundances among sites for each of 3 days sampled during the April experiment. Unless noted, each one-way ANOVA was a parametric test significant at $P < 0.01$ experimentwise. Site symbols are ordered from lowest (left) to highest (right) mean abundance. Symbols underlined are not significantly different ($\alpha = 0.05$).

	Day 2	Day 5	Day 14
Hobsonia florida juveniles	$Ø_1$ H $Ø_2$ L M A	H $Ø_1$ $Ø_2$ L A M	$Ø_2$ $Ø_1$ H L A M*
Huntemannia jadensis	$Ø_1$ H $Ø_2$ M L A†	NS	$Ø_2$ A H $Ø_1$ L M‡
Total harpacticoids (excluding *H. jadensis*)	$Ø_2$ H L $Ø_1$ M A	L M $Ø_1$ $Ø_2$ H A	L H $Ø_2$ $Ø_1$ A M
Nematodes	§	M $Ø_2$ H L $Ø_1$ A†	L H $Ø_2$ M $Ø_1$ A
Oligochaetes	§	H $Ø_1$ M $Ø_2$ L A	H M L $Ø_2$ $Ø_1$ A

* $P < 0.10$ experimentwise.
† Kruskal-Wallis test.
‡ $P < 0.05$ experimentwise.
§ Not counted, this date.

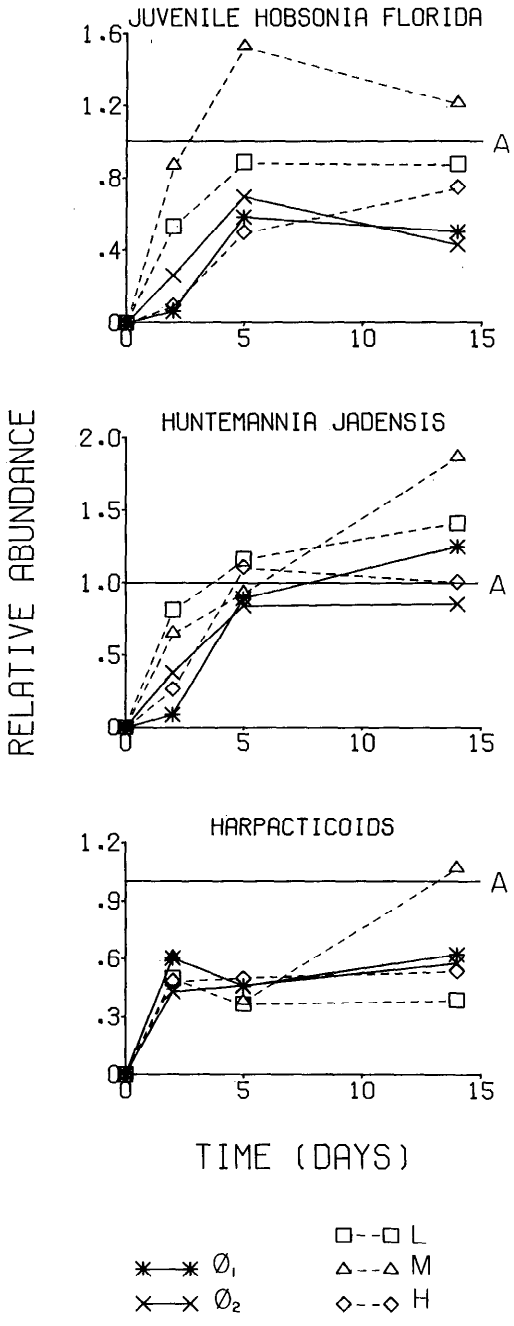

Fig. 5. As Fig. 4, but of temporal trends in relative abundances of juvenile *H. florida*, *H. jadensis*, and other harpacticoids during the April experiment. For each treatment site, relative abundance is calculated by dividing mean abundance by mean abundance measured concurrently at the ambient site A.

Throughout this experiment several groups exhibited enhanced recruitment to site M (Table 3, Fig. 5). By day 2, site M alone had predisturbance abundances of *H. florida* juveniles and rapid accumulation persisted through day 5. High abundances were still apparent on day 14, although site M was then distinguishable, statistically, only from defaunated control sites $Ø_1$ and $Ø_2$.

Early recruitment of *H. jadensis* was slowest to sites H, $Ø_1$, and $Ø_2$ (Fig. 5): on day 2, sites $Ø_1$ and H had abundances significantly lower than ambient levels (Table 3). There were no detectable differences among sites on day 6. By day 14, however, abundances of *H. jadensis* at site M were distinguishable from ambient levels, but not significantly different from those at sites L and $Ø_1$.

Other harpacticoids recovered more slowly than *H. jadensis*, and independently of treatment, initially (Table 3, Fig. 5). By day 14 site M alone had recovered to predisturbance abundances of harpacticoids and had significantly greater numbers than all other treated sites. Site L had the lowest abundances of harpacticoids on day 14.

By day 14 the mean abundances of both nematodes and oligochaetes were still indistinguishable among treatments and were significantly lower than those in ambient sediments (Table 3). Among all treated sites the mean abundances of oligochaetes reached a maximum of 42% of ambient levels, that of nematodes a maximum of 32% of ambient levels.

Few edge effects were noted in this experiment (Table 4), none on day 2. On day 5, only the abundance of nematodes (at site $Ø_2$) and harpacticoids (at site M) were correlated significantly with distance from the center of treated sites. On day 14, a significant trend existed only for nematodes at site M. All these correlations were in the expected direction (i.e. higher abundances near the edge of the plot).

During the course of this experiment an additional effect of the straw treatments became obvious. The tidal flat nor-

Table 4. Summary of significant (i.e. $\alpha < 0.05$ experimentwise) nonparametric correlations between taxon abundance per core and distance from the center of the originally defaunated site. Kendall's τ was used if median abundances were <5 (i.e. many ties existed); Spearman's ρ was used otherwise.

	Site	τ or ρ	P
Apr–May 1980			
a. Day 2			
NS			
b. Day 5			
Nematodes	$Ø_2$	$\rho = 0.8076$	0.001*
Harpacticoids	M	$\rho = 0.6007$	0.009
c. Day 14			
Nematodes	M	$\rho = 0.6502$	0.005*
Sep–Oct 1980			
a. Day 2			
C. salmonis	M	$\tau = 0.6428$	0.001
b. Day 6			
Nematodes	II	$\rho = 0.6972$	0.002
c. Day 16			
NS			
d. Day 32			
Nematodes	L	$\rho = 0.8444$	0.001
Tanais sp.	M	$\tau = 0.6277$	0.001

* $P \leq 0.01$ experimentwise.

Table 5. Median level of contamination of sites (15 samples per site) by plant debris during the September experiment. I assigned ordinal values visually as follows: 0—debris absent; 1—debris present but rare; 2—debris common; 3—debris abundant. Results of Kruskal-Wallis nonparametric ANOVA and multiple comparisons tests appear at end of each row; site symbols are ordered from lowest (left) to highest (right) median level of contamination. Symbols underlined are not significantly different ($\alpha = 0.05$).

	Site				
	L	M	H	P	
Day 2	0	0	1	0.002	L M H
Day 6	0	3	2	<0.0005	L H M
Day 16	0	1	1	<0.0005	L M H
Day 32	0	0	1	0.001	L M H

mally contains many small pits created by the foraging activities of ducks and demersal fishes. Smith (1980) estimated that an annual average of almost 1% of the substratum is disturbed per day by ducks, and that 18–31% of the tidal flat is detectably in some stage of recovery from waterfowl foraging. I never saw any such foraging pits in any of the 1- × 1-m straw arrays: in one instance I observed an approximately straight line of more than 10 pits change direction by 90° at the margin of site M. All arrays seemed to be equally effective in preventing this kind of disturbance of the substratum.

Field experiments: September–October 1980—As in the April experiment, recruitment after day 1 was into surfaces composed of natural sediment particles, and few edge effects were noted (Table 4). There was a similar absence of foraging pits created by ducks and demersal fishes in all straw arrays.

On day 6, I found a large pit (≈50 cm in diameter and ≈5 cm deep) at the treated control site $Ø_1$. This pit persisted through the rest of the experiment. Because precise location of the defaunated island was impossible after this disturbance, site $Ø_1$ was not sampled reliably after day 2. During the experiment the straw-treatment sites were contaminated temporarily by plant debris consisting mainly of small pieces (several millimeters long) of decayed bulrush and broken fragments of brown and red macroalgae. This debris was abundant only in samples taken on day 6 (Table 5) and was most pronounced at site M.

On day 2, the treated sites all contained relatively low mean percentages of fine particles (Table 2, Fig. 4). Immediately thereafter sediments <88 μm in diameter accumulated rapidly at site M (Fig. 4), which on day 6, contained a greater mean percentage of fine particles than all other sites (including ambient sediments), and a significantly greater percentage than site L. At site H the accumulation of fine particles was more gradual (Fig. 4), and by day 16, sites M and II had significantly higher percentages than all others (Table 2). Between days 16 and 30, relative percentages declined at all treated sites (Fig. 4) due primarily to a large increase in the mean percentage of fine particles at the ambient site A (Table 2).

Table 6. Summary of multiple comparisons tests for differences in abundances among sites for each of 4 days sampled during the September experiment. Unless noted, each one-way ANOVA was a parametric test significant at $P < 0.01$ experimentwise. Site symbols are ordered from lowest (left) to highest (right) mean abundance. Symbols underlined are not significantly different ($\alpha = 0.05$).

	Day 2	Day 6	Day 16	Day 32
Eogammarus confervicolus	NS*	Ø$_2$ A L H M*	NS*	NS*
Tanais sp.	M Ø$_2$ L H Ø$_1$ A	Ø$_2$ L H A M†	NS	NS
Corophium salmonis	L H M Ø$_2$ Ø$_1$ A*	M L H Ø$_2$ A	M H L Ø$_2$ A	M H L Ø$_2$ A
Manayunkia aestuarina	L M H Ø$_2$ Ø$_1$ A*	L M H Ø$_2$ A*	H L M Ø$_2$ A*	L M H A Ø$_2$
Pseudopolydora kempi japonica juveniles	H L M Ø$_1$ Ø$_2$ A	L H M Ø$_2$ A	H M A L Ø$_2$	NS
Harpacticoids (excluding *H. jadensis*)	Ø$_2$ M H Ø$_1$ L A	Ø$_2$ L H A M	Ø$_2$ A M L H	A Ø$_2$ H M L
Huntemannia jadensis	L Ø$_2$ Ø$_1$ H M A*	NS	H Ø$_2$ A M L	NS
Nematodes	L H M Ø$_2$ Ø$_1$ A*	H L M Ø$_2$ A*	M H L Ø$_2$ A	H L M Ø$_2$ A*
Foraminifera	L H M Ø$_2$ Ø$_1$ A	H Ø$_2$ L M A	H L Ø$_2$ M A	NS*
Oligochaetes	L M H Ø$_2$ Ø$_1$ A*	NS	NS	NS

* Kruskal-Wallis test.
† $P < 0.05$ experimentwise.

Table 6 summarizes data on the recruitment of all common taxa. The gammarid amphipod *Eogammarus confervicolus* is a highly motile, epifaunal omnivore. Many field and laboratory observations indicate that it is extremely thigmotactic (*see also* Pomeroy and Levings 1980). *Tanais* sp. is a tube-dwelling tanaid which feeds on both filamentous algae and smaller fauna (unpubl. obs.). The tube-dwelling gammarid amphipod *Corophium salmonis* is a surface deposit feeder which frequently explores new sites both by walking and by swimming. *Manayunkia aestuarina* is a small (0.5–3 mm), tube-dwelling sabellid polychaete which inhabits only surficial sediments and the burrows of larger animals. The spionid polychaete *Pseudopolydora kempi japonica* disperses via pelagic larvae (Myohara 1979). Pertinent life-history traits of the other groups counted have been described above.

The abundances of two species were related strongly to the ephemeral contamination of some sites by plant debris. *Eogammarus confervicolus* was essentially absent except on day 6, when it was abundant only at sites M and H (Table 6). Even among cores within sites, the abundance of this amphipod is strongly correlated with ordinal measures of debris content (data not shown). Similarly, only on day 6 was the mean abundance of *Tanais* sp. significantly greater at site M than at other sites (Table 6). On day 6, site M was the most heavily contaminated by plant debris (Table 5).

On day 2, all treated sites contained relatively low and statistically indistinguishable numbers of harpacticoids (Table 6, Fig. 6). Immediately thereafter, harpacticoids increased most rapidly at site M, and on day 6, site M contained significantly greater numbers than all other treated sites. By day 16, however, the abundances of harpacticoids at all sites containing straw arrays were indistinguishable statistically, and each contained significantly greater mean numbers than did the treated site Ø$_2$. By day 32, site L had the most harpacticoids. *Huntemannia jadensis* also was most common at site L on days 16 and 32 (Fig. 6, Table 6).

In contrast, the mean abundances of several taxa were consistently low at all sites containing arrays of straws. In the

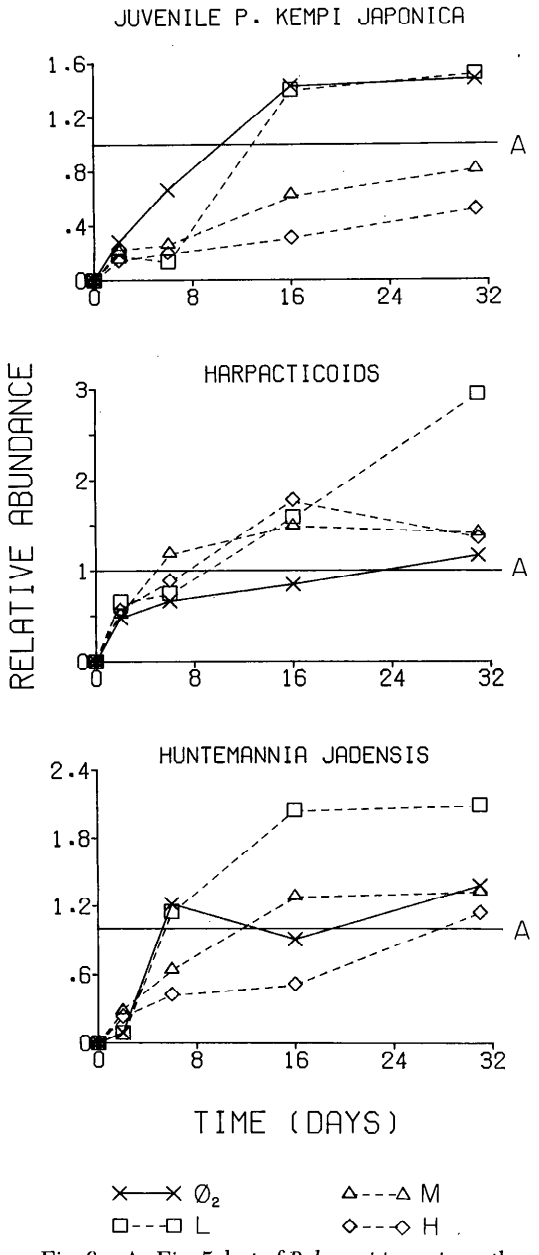

Fig. 6. As Fig. 5, but of *P. kempi japonica,* other harpacticoids, and *H. jadensis* during the September experiment.

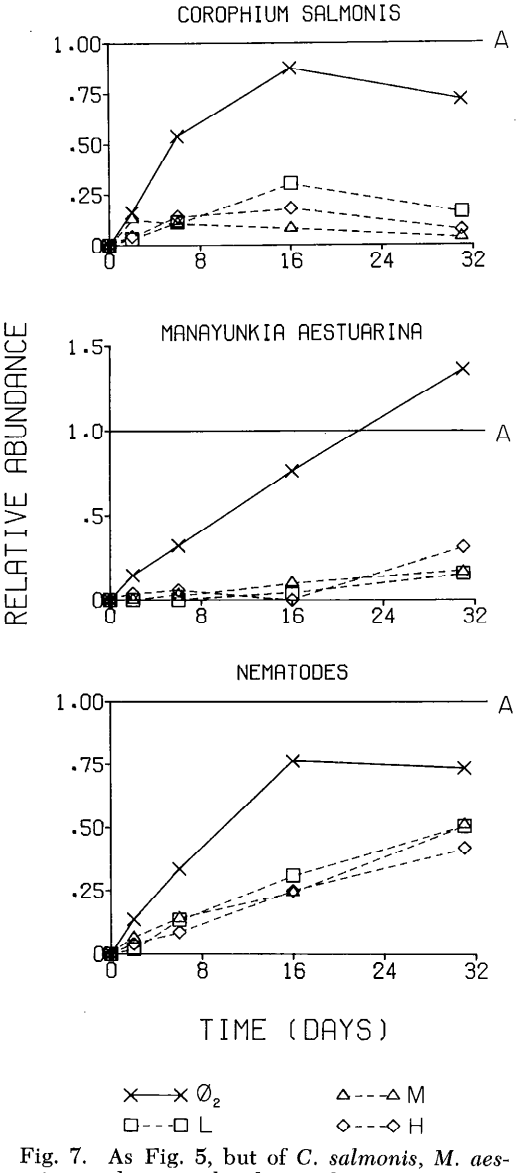

Fig. 7. As Fig. 5, but of *C. salmonis, M. aestuarina,* and nematodes during the September experiment.

defaunated control (i.e. no straws), site $Ø_2$, mean abundances of *C. salmonis, M. aestuarina,* and nematodes eventually attained ambient levels (Fig. 7, Table 6). However, the mean abundances of these three taxa were consistently lower at all sites with straws. Juveniles of *P. kempi japonica* also recruited most slowly to sites M and H (Fig. 6, Table 6).

On day 6, site H had very low mean abundances of Foraminifera (Table 6), but by day 32, there were no significant differences among sites.

Oligochaetes recovered quickly in

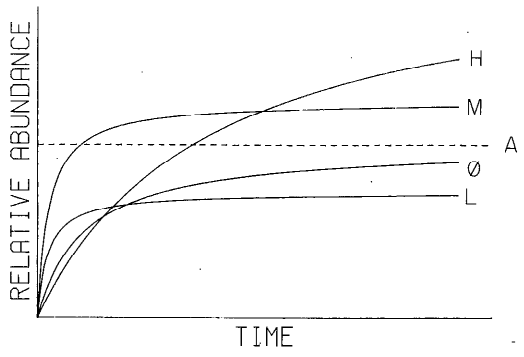

Fig. 8. Temporal patterns in relative composition of surficial sediments and relative abundances of any passively dispersed taxon as predicted from results of flume experiments. Relative abundances are raw abundances normalized to abundances at the ambient site A.

September, in contrast to April. There were no significant differences among sites on or after day 6 (Table 6).

Discussion

Results of the flume experiments indicate that both sites M and H should experience a net reduction in boundary shear stress during periods of active sediment transport on the Skagit flats (i.e. for $u_* > 1.15$ cm·s^{-1}). Both fine sediments and animals which live in surficial sediments and are likely to be dispersed passively by sediment transport should therefore be less easily eroded from these sites. Consequently, sites M and H ultimately should accumulate greater proportions of fine sediments and passively dispersed animals than other sites, including ambient site A (Fig. 8). The flume experiments also indicate that rates of fluid transport near the bed should be greater at site M than at site H. Since fluid flux should determine the immigration rates of animals dispersed passively, site M should accumulate them, and fine particles, more quickly than site H (Fig. 8).

The prediction of patterns of sediment accumulation and animal recruitment at site L is more difficult. Increases in turbulence intensity near the bed (Fig. 3) are likely to increase slightly the bed-averaged boundary shear stress. Consequently, site L may ultimately contain lower percentages of fine sediments and fewer animals than all other sites (Fig. 8). This prediction is tenuous, however. The widely spaced straws at site L are each likely to create the complex, local pattern in τ_b characteristic of an isolated cylinder (Fig. 2). Recruitment among such structures, therefore, may be highly variable spatially (cf. Eckman 1979*a*).

The a priori predictions summarized in Fig. 8 apply to sediment composition and to all animals dispersed passively. The surface-dwelling organisms likely to be dispersed passively by the frequent sediment transport at Skagit include *M. aestuarina*, juveniles of *H. florida*, and *P. kempi japonica* (after settlement from the plankton), and other members of the permanent meiofauna. In comparing recruitment patterns of these animals with the predictions summarized in Fig. 8, we must note that their susceptibility to entrainment and lateral transport (as well as larval availability) is likely to vary. Consequently, differences may be expected in the periods needed for development of the pattern exhibited in Fig. 8. For some groups, the pattern may not have developed in a month. Therefore the signature of any groups conformance to the predictions is a preferential accumulation at site M.

Trends in the composition of the sediments support these predictions. In both April and September, site M accumulated rapidly a relatively high percentage of fine particles (Fig. 4). The accumulation at site H was more gradual, but fine particles ultimately also surpassed site A there in both of my experiments. The frequent lack of significant differences among sites (Table 2) is likely due to the low power of the ANOVA at small sample sizes (4 per site in April, 6 in September) rather than to the absence of real differences. If there were no differences in sediment composition among treatment sites, it is highly unlikely ($P = 0.00273$, binomial test) that sites M and H would have had the two highest percentages of fine particles on four or more of seven times sampled.

The patterns of recruitment of several

of the taxa also support the predictions, assuming passive dispersal by lateral advection. In April, *H. florida* juveniles were recruited most rapidly to site M, and on day 5 were significantly more abundant there than at all other sites (Fig. 5, Table 3). Mean abundances of harpacticoids at site M were significantly greater than at other treated sites by the end of the experiment. Early recruitment of *H. jadensis* was slowest to sites H, $\emptyset_1$, and $\emptyset_2$; on day 14, abundances of *H. jadensis* were distinguishable from ambient levels only at site M. In September, harpacticoids were significantly more common at site M than at other treated sites on day 6 (Table 6, Fig. 6). On day 6, site H had extremely few Foraminifera. This is consistent with the low rates of fluid discharge here (Table 1): on day 6, the percentage of fine particles at site H was also far below the higher values later attained (Table 2).

Some patterns of recruitment cannot be explained by differences among sites in rates of fluid transport and in boundary shear stress. Throughout the September experiment, *C. salmonis, M. aestuarina,* and nematodes all showed greatly reduced abundances at all sites containing straw arrays (Fig. 7, Table 6). Juveniles of *P. kempi japonica* were similarly slow to recover at sites M and H (Fig. 6, Table 6). It is unlikely that the consistently more rapid recoveries of these four taxa at site $\emptyset_2$ were due to anomalously high rates of fluid transport there, since other animals showed no such rapid recoveries there or at other sites (e.g. at site M; *see also* H. jadensis, *Fig. 6*). These trends also could not have been related to the early and ephemeral contamination of sites M and H by decaying plant debris (Table 5): three groups were recruited as slowly to site L, and the trend persisted beyond day 6.

I suggest that the lower abundances of these taxa at sites containing straw arrays are due to behavioral responses. The straws resemble the stalks of bulrush, which are abundant about 50 m landward, in the upper marsh. During fall, the avoidance of bulrush stalks by these animals, and, consequently, the avoidance of the higher intertidal zone, would reduce the exposure of overwintering individuals to physical stresses. Ice cover frequently corresponds to that of the marsh plants (J. E. Smith, E. D. Gallagher, and P. A. Jumars pers. comm.). *Corophium salmonis, M. aestuarina,* and *P. kempi japonica* all reproduce during late summer and early fall (Smith 1980; pers. obs.).

The patterns of recruitment of harpacticoids after day 6 in September also cannot be explained by the hydrodynamic arguments. On day 14, harpacticoids were significantly more abundant at all three sites with straw arrays than at the defaunated control site $\emptyset_2$ (Fig. 6, Table 6). By day 32, site L had extremely large numbers of harpacticoids. A possible explanation is that during September harpacticoids benefited especially from the refuge (sensu Woodin 1978) offered by straw arrays. During my experiments all straw arrays appeared effective in preventing the intrusion of ducks and demersal fishes. Smith (1980) reported that disturbance of the Skagit tidal flat by ducks is greatest in September, and that the most important fish predator, the staghorn sculpin, *Leptocottus armatus,* which eats these estuarine harpacticoids, emigrates from permanent tidal streams into tidal areas in early fall.

Conclusions

Animal tubes and seagrasses exert important and complex effects on near-bed flow. The hydrodynamic effects of such structures are determined, in part, by their scales, geometries, and numerical densities. In accord with a priori predictions, sediment composition and patterns and rates of recruitment of several kinds of animals were affected by the numerical density of simulated marsh grass stalks.

The important hydrodynamic effects of tubes or seagrasses are not induced only by dense arrays; even isolated tubes produce complex patterns of fluid circulation, sediment scour, and local deposition (Fig. 2; Eckman 1979*b*, 1982). The ability of even a single simulated tube to

enhance recruitment on an intertidal sandflat (Eckman 1979*a*) may be caused by such effects. Among arrays of tubes at lower densities, then, local flow effects may create a patchwork pattern of animal abundances. Such a pattern may differ from that produced by the provision of refuge (sensu Woodin 1978, 1981) from larger predators. The careful selection of sample location and core size may permit testing of the importance of hydrodynamic vs. refuge effects in tube arrays or grass meadows.

Results of this study have important implications to interpreting any field manipulative experiment which alters patterns of flow. Experiments designed to identify mechanisms of recruitment or forces that structure communities must account for the hydrodynamic effects of manipulation. As an additional example, cages used to exclude predators from marine soft bottoms frequently have strong sedimentation effects (e.g. McCall 1977; Virnstein 1977; Hulberg and Oliver 1980). Many cage controls (topless, sideless) will not mimic accurately the hydrodynamic environment created by a complete cage (e.g. Woodin 1981: table 10). In light of the demonstrated importance of hydrodynamic processes, such experimental artifacts are difficult to ignore.

The importance of competition, predation, or disturbance can be tested unambiguously only if purely physical forces, such as hydrodynamic ones, are taken into account. Such hydrodynamic effects form an additional null hypothesis against which biological interactions should be tested.

References

BAILEY-BROCK, J. H. 1979. Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. J. Mar. Res. **37:** 643–656.

BANSE, K. 1979. Ampharetidae (Polychaeta) from British Columbia and Washington. Can. J. Zool. **57:** 1543–1552.

DIXON, W. J., AND F. J. MASSEY, JR. 1969. Introduction to statistical analysis, 3rd ed. McGraw-Hill.

ECKMAN, J. E. 1979*a*. Small-scale patterns and processes in a soft-substratum, intertidal community. J. Mar. Res. **37:** 437–457.

———. 1979*b*. Particle deposition in animal-tube wakes: Description, identification of relevant parameters and biological significance. Zool. 533b Publ. Rep. Univ. Washington, Friday Harbor Lab. Library.

———. 1982. Hydrodynamic effects exerted by animal tubes and marsh grasses and their importance to the ecology of soft-bottom, marine benthos. Ph.D. thesis, Univ. Washington.

———, A. R. NOWELL, AND P. A. JUMARS. 1981. Sediment destabilization by animal tubes. J. Mar. Res. **39:** 361–374.

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

———. 1980. Quantitative cohort analysis of a sand-dwelling meiobenthic harpacticoid copepod. Estuarine Coastal Mar. Sci. **11:** 459–476.

GRAF, W. H. 1971. Hydraulics of sediment transport. McGraw-Hill.

GRAY, J. S. 1967. Substrate selection by the archiannelid *Protodrilus rubropharyngeus*. Helgol. Wiss. Meeresunters. **15:** 253–269.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. Wiley.

HULBERG, L. W., AND J. S. OLIVER. 1980. Caging manipulations in marine soft-bottom communities: Importance of animal interactions or sedimentary habitat modifications. Can. J. Fish. Aquat. Sci. **37:** 1130–1139.

JUMARS, P. A. 1975. Environmental grain and polychaete species' diversity in a bathyal benthic community. Mar. Biol. **30:** 253–266.

KOMAR, P. D. 1976. Boundary layer flow under steady unidirectional currents, p. 91–106. *In* D. J. Stanley and D. J. Swift [eds.], Marine sediment transport and environmental management. Wiley.

MCCALL, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. **35:** 221–266.

MEADOWS, P. S. 1964*a*. Substrate selection by *Corophium* species: The particle size of substrates. J. Anim. Ecol. **33:** 387–394.

———. 1964*b*. Experiments on substrate selection by *Corophium* species: Films and bacteria on sand particles. J. Exp. Biol. **41:** 499–511.

MIDDLETON, G. V., AND J. B. SOUTHARD. 1978. Mechanics of sediment movement. Soc. Econ. Paleontol. Mineral.

MILLER, M. C., I. N. MCCAVE, AND P. D. KOMAR. 1977. Threshold of sediment motion under unidirectional currents. Sedimentology **24:** 507–527.

MILLER, R. G., JR. 1966. Simultaneous statistical inference. McGraw-Hill.

MILLS, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Can. **24:** 305–355.

MORRIS, H. M. 1955. A new concept of flow in rough conduits. Trans. Am. Soc. Civil Eng. **120:** 373–398.

MULHEARN, P. J., AND J. J. FINNIGAN. 1978. Tur-

bulent flow over a very rough, random surface. Boundary-Layer Meteorol. **15:** 109–132.

MYOHARA, M. 1979. Reproduction and development of *Pseudopolydora kempi japonica* (Polychaeata: Spionidae) with special reference to the polar lobe formation. J. Fac. Sci. Hokkaido Univ. Ser. 4 Zool. **21:** 355–369.

NOWELL, A. R., AND M. CHURCH. 1979. Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. **84:** 4816–4824.

———, P. A. JUMARS, AND J. E. ECKMAN. 1981. Effects of biological activity on the entrainment of marine sediments. Mar. Geol. **42:** 133–154.

O'GOWER, A. K., AND J. W. WACASEY. 1967. Animal communities associated with *Thalassia, Diplanthera* and sand beds in Biscayne Bay. 1. Analysis of communities in relation to water movements. Bull. Mar. Sci. **17:** 175–210.

ORTH, R. J. 1977. The importance of sediment stability in seagrass communities, p. 281–300. *In* B. C. Coull [ed.], Ecology of marine benthos. Univ. South Carolina.

PETIT, C., M. TRINITE, AND P. VALENTIN. 1976. Study of turbulent diffusion above and within a forest—application in the case of SO_2. Atmos. Environ. **10:** 1057–1063.

PLATE, E. J., AND A. A. QURASHI. 1965. Modelling of velocity distributions under and above tall crops. J. Appl. Meteorol. **4:** 400–408.

POMEROY, W. M., AND C. D. LEVINGS. 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts Banks, Fraser River Estuary. Can. J. Fish. Aquat. Sci. **37:** 1–10.

RAUPACH, M. R., A. S. THOM, AND I. EDWARDS. 1980. A wind-tunnel study of turbulent flow close to regularly arrayed rough surfaces. Boundary-Layer Meteorol. **18:** 373–397.

SANDERS, H. L., E. M. GOUDSMIT, E. L. MILLS, AND G. E. HAMPSON. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. Limnol. Oceanogr. **7:** 63–79.

SANTOS, S. L., AND J. L. SIMON. 1974. Distribution and abundance of the polychaetous annelids in a South Florida estuary. Bull. Mar. Sci. **24:** 669–689.

SCHLICHTING, H. 1968. Boundary layer theory, 6th ed. McGraw-Hill.

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. Washington, 177 p.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman.

STONER, A. W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci. **30:** 537–551.

TRITTON, D. J. 1977. Physical fluid dynamics. Van Nostrand Reinhold.

VIRNSTEIN, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. Ecology **58:** 1199–1217.

WIESER, W. 1956. Factors influencing the choice of substratum on *Cumella vulgaris* Hart (Crustacea, Cumacea). Limnol. Oceanogr. **1:** 274–285.

WILSON, D. P. 1937. The influence of the substratum on the metamorphosis of *Notomastus* larvae. J. Mar. Biol. Assoc. U.K. **22:** 227–243.

———. 1948. The relation of the substratum to the metamorphosis of *Ophelia* larvae. J. Mar. Biol. Assoc. U.K. **28:** 723–760.

———. 1955. The role of microorganisms in the settlement of *Ophelia bicornis* Savigny. J. Mar. Biol. Assoc. U.K. **34:** 531–543.

———. 1968. The settlement behavior of the larvae of *Sabellaria alveolata* (L.). J. Mar. Biol. Assoc. U.K. **48:** 387–435.

WILSON, W. H., JR. 1979. Community structure and species diversity of the sedimentary reefs constructed by *Petaloproctus socialis* (Polychaeta: Maldanidae). J. Mar. Res. **37:** 623–641.

WOODIN, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: The importance of biological interactions. Ecol. Monogr. **44:** 171–187.

———. 1978. Refuges, disturbance, and community structure: A marine soft-bottom example. Ecology **59:** 274–284.

———. 1981. Disturbance and community structure in a shallow water sand flat. Ecology **62:** 1052–1066.

WOODING, R. A., E. F. BRADLEY, AND J. K. MARSHALL. 1973. Drag due to regular arrays of roughness elements of varying geometry. Boundary-Layer Meteorol. **5:** 285–308.

YOUNG, D. K., M. A. BUZAS, AND M. W. YOUNG. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. **34:** 577–592.

ZOTTOLI, R. A. 1966. Life history, morphology, and salinity tolerance of the ampharetid polychaete *Amphicteis floridus* Hartman 1951. Ph.D. thesis, Univ. New Hampshire.

———. 1974. Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus*. Trans. Am. Microsc. Soc. **93:** 78–89.

Submitted: 20 August 1981
Accepted: 16 September 1982