J. Exp. Mar. Biol. Ecol., 1989, Vol. 134, pp. 37–88
Elsevier

JEMBE 01353

Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters

Cheryl Ann Butman *
Applied Ocean Physics and Engineering Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, U.S.A.

(Received 20 January 1989; revision received 18 September 1989; accepted 26 September 1989)

Abstract: The hypothesis that planktonic larvae of benthic invertebrates sink through the water like passive particles in turbulent flows near the seabed was tested in the field by exploiting biased sampling characteristics of sediment traps. Traps of several designs were calibrated in a laboratory flume using passively sinking larval mimics having fall velocities similar to those measured on nonswimming polychaete larvae. A priori predictions regarding the rank order in which various trap designs would collect passively sinking larvae in the field were specified by the rank order in which the traps collected larval mimics in the flume. Field experiments were conducted at two sites, 10- and 14-m depth, in Buzzards Bay, Massachusetts, U.S.A., and traps were moored 0.4–1.6 m above the seabed. In experiments during four field seasons, with deployments lasting from several hours to 11 days, trap collections of *Mediomastus ambiseta* (Hartman) polychaete postlarvae, total bivalve larvae and postlarvae, spionid/sabellariid polychaete larvae (individuals too small to identify definitively to family), spionid polychaete larvae, enteropneust larvae, and gastropod larvae nearly always corresponded to a priori predictions for passive particle collections between sediment-trap designs. Results were statistically more significant during some collection intervals than during others, but the rank order of larval collections within each group of traps (deployed simultaneously) corresponded to the rank order of passive particle collections by the traps in the flume, with a couple exceptions. Collections of a polychaete, *Pectinaria gouldii* (Verrill), were more similar between trap designs (i.e., not biased, as predicted for passive particle collections) than the organisms mentioned above. Competent *Pectinaria* larvae may sink more quickly because of their larger size and reduced surface area (due to construction of a parchment tube while still suspended). There may be no trapping bias for particles sinking this fast. Collections of metamorphosing seastar larvae also were not in the predicted passive rank order, which may be due, in part, to larvae adhering to solid trap surfaces during metamorphosis. The passive sinking hypothesis could not be falsified in most of the field experiments, indicating that hydrodynamical processes may determine distributions of larvae in very near-bottom waters. Passive sinking by larvae is not, however, an explicit result of this study. Other processes that may have produced observed collections, such as chemical, sedimentary or biological differences among trap environments, must be tested against the passive sinking alternative hypothesis. If larvae sink like passive particles to within 0.4-m of the seabed, as results of this study suggest, then it is possible that larvae initially reach the seafloor at sites where particulates, with fall velocities similar to larvae, initially settle. Passive deposition may thus determine the relatively large-scale distribution of larvae, with active or passive redistribution of larvae, post-settlement selection, or post-settlement mortality determining localized distributions.

Key words: Hydrodynamics; Invertebrate; Larva; Passive; Selection; Settlement

Correspondence address: C.A. Butman, Applied Ocean Physics and Engineering Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

* Previously published as Cheryl Ann Hannan.

This is Contribution 6950 from Woods Hole Oceanographic Institution.

INTRODUCTION

In temperate latitudes, dispersal of most soft-sediment marine invertebrates occurs during a planktonic larval stage (Thorson, 1946). Larvae drift with ocean currents for variable periods of time (hours to months) before settling onto the sediment surface and assuming a benthic existence. Defining the physically and biologically controlled phases to the larval settlement process is necessary for determining the relative importance of larval settlement in establishing, maintaining and regulating benthic communities. In particular, the role of small-scale (≤ 10s of meters) hydrodynamical processes must be evaluated because sediment types and benthic biological assemblages are distinguished at these scales (Butman, 1987). While large-scale (≥ 10s of kilometers) larval dispersal has been assumed to be primarily a passive process controlled by general oceanic circulation (e.g., Crisp & Southward, 1953; Thorson, 1961; Scheltema, 1971; Kraeuter, 1974; Levin, 1983), there is considerable evidence that larval settlement over very small spatial scales (≤ 10s of centimeters) is primarily an active process where larvae choose the substratum most suitable for settlement (reviews of Crisp, 1974; Gray, 1974; Scheltema, 1974; Strathmann, 1978; also subsequent studies of Oliver, 1979; Williams, 1980; Gallagher et al., 1983; Watzin, 1986; Woodin, 1985, 1986). However, the relationship between small-scale hydrodynamical processes and patterns of initial larval settlement is largely unknown (Butman, 1987).

Recent experimental field studies posing hydrodynamic null hypotheses for the distribution of infauna have focused on patterns generated during early recruitment, not settlement, either because the species lacked a planktonic larval stage (Eckman, 1979, 1983; Gallagher et al., 1983) or because of the difficulty in sampling initial settlers (Peterson, 1986). Likewise, studies of the role of hydrodynamics in determining benthic dispersion patterns of meiofauna (Hogue & Miller, 1981; Thistle et al., 1984; Kern & Taghon, 1986; also reviews of Fleeger & Decho, 1987, and Palmer, 1988a) involve species which, strictly speaking, lack a planktonic phase. Since a small percentage (e.g., ≈ 1% in Palmer & Gust, 1985) of surface-dwelling meiofauna enter the water column due to hydrodynamical (Bell & Sherman, 1980; Hagerman & Rieger, 1981; Hogue, 1982; Eskin & Palmer, 1985; Palmer & Gust, 1985) and/or biological (Palmer, 1984, 1986, 1988b) processes, however, meiofauna recruitment is not entirely a benthic phenomenon. Field studies of the role of hydrodynamical processes at the time larvae or meiofauna initially settle out of the plankton are extremely difficult, because they require sampling of distributions resulting from temporally and spatially unpredictable and very short-lived events – patterns of larval or postlarval distributions at the time the organisms first reach the seabed, before interference from postsettlement phenomena (Butman, 1987).

HYPOTHESIS TESTED

The hypothesis tested in the present study is that competent (to settle, see definitions reiterated in Butman, 1987) planktonic larvae fall through the water like passive particles in turbulent flows as close as 0.4 m from the seabed. If larvae act like passive particles in near-bottom flows, then larvae may be initially deposited on the bottom at sites where sediments that are hydrodynamically similar to larvae initially settle. Testing the passive-sinking hypothesis is a first step toward determining the plausibility of passive deposition.

The experimental approach used here for testing the passive-sinking hypothesis involves exploiting biased sampling characteristics of sediment traps to collect both particles and larvae falling toward the seabed. Traps differentially collect sediments because of trap-induced local disturbances to the flow field, which are trap-geometry dependent, such that collectors with various shapes will retain passive particles in different relative abundances (reviews of Bloesch & Burns, 1980; Blomqvist & Hakanson, 1981; Butman et al., 1986). If larvae act like passive particles in near-bottom flows, then larvae and particles that are hydrodynamically similar to larvae should be collected by traps in the same relative abundances. If larvae are not collected according to predictions for passive particles, then other processes (e.g., behaviors or physiological responses of larvae) are governing the way in which larvae fall toward the seabed and are collected by traps.

The specific null hypothesis in this study is that larvae and particles that are hydrodynamically similar to larvae will be collected in the same rank order of abundance by different sediment-trap designs. To test this hypothesis in the field involved the following. (1) Relevant hydrodynamic characteristics (fall velocity, in particular) of sinking larvae were determined in order to select passive particles that behaved similarly to passively sinking larvae. (2) Relative particle collection efficiencies of a variety of sediment trap designs were determined in a laboratory flume using the selected particles (i.e., larval mimics) and maintaining dynamic- and geometric-similarity to conditions at the intended field study sites. These results are presented in detail in Butman (1986a); collection efficiencies of traps eventually deployed in the field are reviewed here. (3) Field experiments were conducted where selected trap designs (e.g., those having significantly different particle-collection efficiencies relative to each other) were deployed simultaneously over short time periods and trap contents processed for abundances of larvae and postlarvae. Results for one set of trap geometries and for the most abundant polychaete species collected in the study were presented as a note in Hannan (1984a). Results for several other sets of trap geometries and for all abundant infauna collected in the traps are discussed in detail here. A series of field experiments with traps also was conducted prior to (1) and (2), before the author was aware of the complexity of this research problem, using trap designs selected and based on results of the trap-calibration study of Gardner (1980). Because of what was later learned about the limitations to Gardner's study (Butman et al., 1986) and hydrodynamical issues involved in rigorously testing the passive-sinking hypothesis, results of this first series of field tests can be discussed only in terms of a posteriori predictions.

CONCEPTUAL FRAMEWORK FOR EXPERIMENTS

For the field experiments, it is important to distinguish between "random" collections, "passive" collections, and "biological" collections of larvae by traps. It has been suggested (e.g., review of Thorson, 1957) that an alternative hypothesis to active habitat selection by larvae is that organisms are deposited "at random" onto the seabed. Random deposition explicitly states that there is an equal probability that individual larvae will fall onto any given location on the bed. The random-deposition hypothesis has been suggested as a null hypothesis against which biological effects can be tested, in that initial settlement sites for larvae are expected to be similar to initial settlement sites for passive particles only if biological processes have a negligible effect on larval deposition. Thus, an alternative hypothesis to random deposition is referred to here as "biological" deposition.

The random-deposition hypothesis is synonymous with the passive-deposition hypothesis for a well-mixed (i.e., homogeneous) suspension of larvae falling in still water. The initial distribution of passive particles on the seabed also would be random in moving water if the water mass was essentially infinite, if there was a uniform particle supply distributed homogeneously in the water column, if the physical regime did not vary, and for flow over a smooth bottom that is invariant in the horizontal. For temporally and/or spatially varying flow regimes, however, and for variable particle abundances and distributions in the water column, particles will not fall at random onto the seabed; instead, initial settlement sites are determined by hydrodynamical processes and particle characteristics.

For the physical regime of interest in this and most other ocean studies, random deposition is not the appropriate null hypothesis to test against biological effects. The null hypothesis that larvae will track with passive particles in the flow, if biological processes are unimportant in distributing the organisms, still applies; however, random settlement of passive particles is not expected. Rather, particles will fall at locations determined by local flow processes and particle characteristics. This is the "passive-deposition" hypothesis, which is more general than the random-deposition hypothesis, the latter applying only for a small subset of physical conditions.

The important point is that a statistical (e.g., random) null distribution of particle settlement onto the seabed cannot be generated theoretically for the field environment of interest: the null (passive) distribution must be generated empirically, using particles with hydrodynamic characteristics similar to larvae and within a dynamically similar flow regime. Thus, because experiments in the present study test whether or not larvae track with particles in the flow, the null distribution for passive particle collection by traps also must be generated empirically. This information was obtained from the flume experiments of Butman (1986a). It would have been more ideal to generate the null distribution directly for traps collecting passive particles in the field, but this was not possible because it requires knowledge of the fall-velocity distribution of natural particulates at the time they enter the traps. The flume experiments described in Butman

(1986a) are limited in that they are only for one flow speed, and thus, do not cover the range of conditions occurring in the field. Because of this, and other limitations to the field experiments (see Discussion), collections of larvae by traps in the field were only qualitatively compared to collections of particles by traps in the flume.

The experimental design involves simultaneous deployments of several trap geometries having significantly different relative particle collection efficiencies. If relative larval fluxes through the trap mouth openings are significantly different from predictions generated from the flume experiments, then the null hypothesis is falsified. Furthermore, even if the null hypothesis cannot be falsified, it only implies that larvae behave in the flow like passive particles, since the significance level for acceptance of a null hypothesis is unknown. Naturally, the most powerful result is rejection of the null hypothesis at a reasonable significance level.

MATERIALS AND METHODS

LARVAL FALL VELOCITY MEASUREMENTS

Fall velocities of nonswimming polychaete larvae were determined by allowing anesthetized or freshly killed organisms (Table I) to sink through a temperature-controlled column of water (called a "settling chamber"). Details of the methods are given in Hannan (1984b). The precision of this technique was >90% using inert, passive particles (polystyrene or glass spheres). Furthermore, comparisons of fall velocities of spheres measured in the chamber and calculated from Stokes' equation for particle Reynolds numbers (R_p) < 1 and Rubey's (1933) formula (as modified by Grant, 1977) for R_p > 1, agreed to within 11% of the calculated value.

TABLE I

Anesthetizing treatments for larval fall velocities plotted in Fig. 1.

Chemical	Concentration in sea water	Immersion time (min)
MS222	0.7–0.8% by weight	10–40
Chloretone	58.3%, by volume	10
KCL	(a) full-strength 0.1 M	10
	(b) 0.33%, by weight	60
Ethanol	80%	10
Formalin	10%	5–15
Freshwater	full-strength	5

FLUME CALIBRATIONS OF SEDIMENT TRAPS

The flume-calibration study of sediment traps is described in detail in Butman (1986a) and only a brief summary of the methods and results is presented here. Particle collection efficiencies of a variety of sediment trap designs were determined in a large, freshwater flume located in the Ralph M. Parsons Laboratory for Water Resources and Hydrodynamics at Massachusetts Institute of Technology, Cambridge, Massachusetts, U.S.A. The full-scale traps deployed in the field were tested in the flume to maintain aspect-ratio and geometric similarity (Butman et al., 1986). For dynamical similarity, a turbulent flow of ≈ 10 $\mathrm{cm \cdot s^{-1}}$ was used, representing intermediate flow conditions for the range of speeds (0–20 $\mathrm{cm \cdot s^{-1}}$) expected at the selected field site.

The flow was continuously seeded with spherical glass beads (Ferro Class IVA

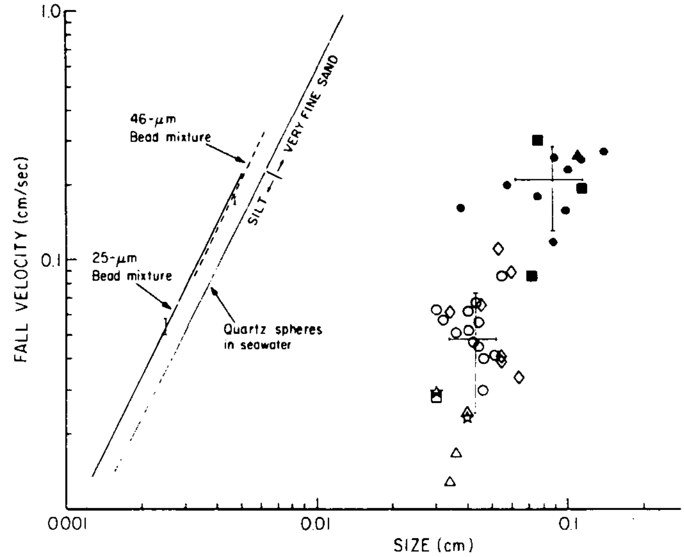

Fig. 1. Relationship between fall velocity and size for all larvae tested, for the glass bead mixtures used in the flume and for quartz spheres. The larval dimension plotted on the abscissa is the narcotized length. Chemical treatment concentrations and immersion times are given in Table I. Values are plotted for Mission Bay *Streblospio benedicti* larvae tested in the "small chamber" (described in Hannan, 1984b) and treated with MS222 (open triangle), KCl (stars) and formalin (open square); for Narragansett Bay *S. benedicti* larvae tested in the small chamber and treated with MS222 (open circles) and Chloretone (open diamonds); and for all larvae tested in the "large chamber" (described in Hannan, 1984b) and treated with MS222 (solid circles), formalin (solid squares), and ethanol (solid triangle). The mean fall velocity (± SD) and mean narcotized length (± SD) are plotted as a cross, separately, for all larvae tested in the small chamber (open symbols) and all larvae tested in the large chamber (closed symbols). For comparison to sediments, the size distribution is plotted of quartz ($\rho_p = 2.65\ \mathrm{g \cdot cm^{-3}}$) spheres having theoretical fall velocities (30‰ seawater, atmospheric pressure, 20 °C) within the range of the measured larval fall velocities. The size separating "silt" from "very fine sand" particles also is indicated. Theoretical fall velocities for ≈94% of the beads in the "25-μm Mixture" (solid line) and for ≈97% of the "46-μm Mixture" (dashed line) used in the flume experiments are plotted for conditions during the trap tests (freshwater, atmospheric pressure, 24 °C; see also Butman, 1986a).

Uni-spheres, density = 2.42 $g \cdot cm^{-3}$). Two mixtures were used, called the "25-μm beads" and the "46-μm beads", indicating mean bead diameters in each mixture. Theoretical (Stokes') fall-velocity distributions of bead mixtures span the range of measured larval fall velocities (Fig. 1). Bead concentrations in the flume during trap collections was monitored upstream and at the height of the trap mouth, using a peristaltic pump sampler.

Particle collection efficiencies of each trap design were calculated by dividing the weight of material collected in the trap by a predicted estimate of the material collected, based on bead concentrations in the oncoming flow. All efficiencies were calculated for the trap mouth area, and were normalized to mean collections by a "standard" trap design (tall cylinder, Table II) that was tested in all series.

FIELD STUDY SITE

The site chosen for the bulk of the field experiments was "Sta. 35", located in northeastern Buzzards Bay, Massachusetts, U.S.A. (41°37.8′N, 70°40.5′W, 14-m depth; Fig. 2). This site was selected because infaunal species composition and abundance were well-documented (Sanders et al., 1980), providing baseline data on the fauna. One set of trap experiments also was conducted at "Sta. NBH", located in outer New Bedford Harbor, eastern Buzzards Bay (41°35.1′N, 70°53.1′W, 10-m depth; Fig. 2), because of other experiments taking place there at the time and because the infaunal community is dominated by the same species that dominate Sta. 35 (see below).

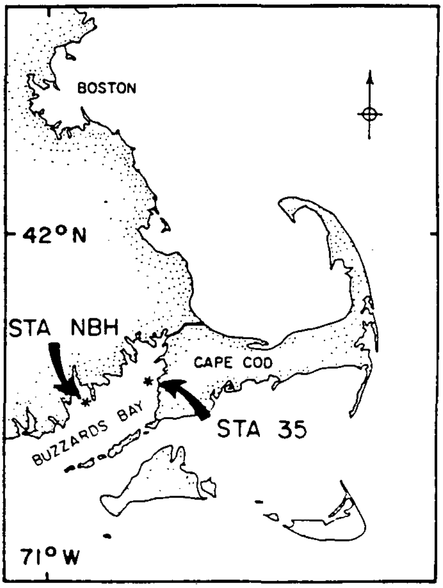

Fig. 2. Chart showing location of study sites, Sta. 35 and Sta. NBH, in Buzzards Bay, Massachusetts, U.S.A. The two stations are ≈ 20 km apart.

TABLE II

Trap dimensions and relative particle collection efficiencies.

Trap code[a]	Designations used in text	Wall thickness (cm)	Height (cm)	Inside mouth diameter (cm)	Relative particle collection efficiency[b] ($\bar{x}$ ± 1 SD)
OPC7.7–1.1	Short, unscreened cylinder	0.1	8.7	7.7 (n = 3)	88.5 ± 10.5[c]
OPC7.7–1.1S	Short cylinder	0.1	8.7	7.7 (n = 3)	88.5 ± 10.5[c]
OPC7.7–2.1S	Medium cylinder	0.1	16.0	7.7 (n = 3)	97.1 ± 8.5[d]
OPF8.9–2.0S	Small funnel	0.1	17.8	8.9 (n = 3)	26.6 ± 7.9[e]
OPF12.2–1.7S	Medium funnel	0.1	20.7	12.2	Not determined
OPF15.8–1.4S	Large funnel	0.1	22.1	15.8	Not determined
CPC11.0–1.2S	Clear cylinder	0.2	13.6	11.0	Not determined
BPC11.6–1.5S	Black cylinder	0.2	17.2	11.6[f]	Not determined
OPC8.5–2.7S	Tall cylinder[g]	0.1	22.8 ± 0.2[h]	8.5 ± 0.1[h] (n = 3)	122.5 ± 24.8
OPG8.3–3.0S	Gallon jar	0.1	24.9 ± 0.1[h]	8.3 ± 0.1[h,i] (n = 2)	240.0 ± 76
OPP8.3–2.7	Cylinder with plate	0.1[j]	22.9 ± 0.3[h]	8.3 ± 0.1[h,k] (n = 3)	43.9 ± 5.2
TBC14.7–1.6	Large cylinder	0.4	23.6 ± 0.2	14.7 (n = 3)	85.5 ± 1.6
TBF14.7–1.6S	Large cylinder with funnel	0.4	24.0 ± 0.2	14.7 (n = 3)	80.6 ± 12.2[l]

[a] These codes correspond to those used in Butman (1986a). The first two letters refer to the material the trap is made of (OP = opaque plastic, CP = clear plastic, BP = clear plastic wrapped in black electrical tape, TB = tenite butyrate plastic); the next letter refers to the geometry (C = cylinder, F = funnel, G = gallon jar [a small-mouth, wide-body trap], P = plate surrounding trap mouth); the number before the hyphen refers to the inside mouth diameter (cm) and the number following the hyphen refers to the aspect ratio (height/inside mouth diameter); S = screened with fine filament (<0.25 mm diameter) plastic mesh with 16-mm^2 openings.

[b] From Hannan (1984b) and Butman (1986a).

[c] For trap OPC8.5–1.0, which was identical to OPC7.7–1.1, only the inside rim at the mouth was cut off (see Butman, 1986a), slightly increasing its mouth diameter.

[d] For trap OPC8.5–1.9, which was identical to OPC7.7–2.1, except the rim was cut off (see footnote c).

[e] For trap OPF8.5–1.9, where the funnel-washings are not included as part of the trap collections (see Butman, 1986a). This trap is similar to trap OPF8.9–2.0, the only difference being that a slightly smaller funnel was used in OPF8.5–1.9, so that it was completely contained within the cylinder (see Butman, 1986a).

[f] This cylinder tapered slightly with an inside diameter at the trap bottom of 11.0 cm.

[g] Called the "standard cylinder" in Hannan (1984a) and Butman (1986a).

[h] Inside of rims of mouth were shaved off these traps, so there was slight variability in height and inside mouth diameter.

[i] Maximum body diameter = 15.2 cm.

[j] Plate thickness = 0.5 cm.

[k] Plate diameter = 15.2 ± 0.1 cm.

[l] Not including funnel washings.

The numerically dominant infaunal organism at both Sta. 35 and Sta. NBH is the small polychaete worm *Mediomastus ambiseta* (Hartman). Densities range from 10^4 to 10^5 individuals per square meter (organisms retained on a 300-μm sieve) at both sites, with peak abundances during larval recruitment in August and September at Sta. 35 and September and October at Sta. NBH (Sanders et al., 1980; Butman et al., in prep.). Several other polychaete species are relatively abundant at Sta. 35, but with densities one to two orders-of-magnitude lower than densities of *Mediomastus*. Recruitment peaks of these organisms generally occur during summer (July and August). At Sta. NBH, two gastropod and several polychaete species follow *Mediomastus* in numerical abundance, having lower densities by one to two orders of magnitude.

In sediment cores from Sta. 35 and Sta. NBH that were sectioned and processed at 2-mm intervals (wet-sieving, without a dispersant, as described in Fuller & Butman, 1988), the top 1 cm of material is similar between the two sites, with mud (<63 μm) dominating ($\leq 70\%$ by weight; author's unpubl. data). Deeper sediments (to ≥ 4 cm) at Sta. 35 are dominated by "moderately well to poorly sorted" sands, with a small ($\leq 7\%$), but persistent gravel fraction (Sanders et al., 1980). Sediments to 2-cm depth at Sta. NBH are dominated (55–60%) by mud year-round, although much of this material is bound in fecal pellets of *Mediomastus ambiseta* (Butman et al., in prep).

Buzzards Bay is a depth- and time-limited boundary layer, where the entire water column is sheared (Signell, 1987; B. Butman et al., 1988). Low-frequency currents in Buzzards Bay are driven by tides, local wind forcing and density stratification, in that order of importance in terms of current magnitude. Tidal elevations are ≈ 1 m and surface current speeds range between 15 and 50 $\text{cm} \cdot \text{s}^{-1}$ throughout the Bay. Flow direction of surface tidal currents is well-described by the main axis of the tidal ellipse, which generally parallels the coastline. Flows along the minor axis of the tidal ellipse are relatively small.

FIELD EXPERIMENTS

Field experiments were conducted at Sta. 35 during summer of 1980, summer and fall of 1982 and fall of 1984, and at Sta. NBH during summer of 1986. Geometries and dimensions of traps deployed in these experiments, as well as their particle collection efficiencies when known from flume studies (Hannan, 1984b; Butman, 1986a), are listed in Table II. The specific traps deployed, the expected rank order of larvae collections for organisms behaving like passive particles (hereafter called "passive rank order"), and other relevant information is listed in Table III for the four research years. Experiments conducted during each year are discussed below, following a description of trapping methodologies.

TABLE III

Traps tested, collecting intervals and expected passive rank order for field experiments.

Experiment	Traps tested[a]	Mean post height[b] (cm)	Number replicates	Collecting interval (duration)	Expected passive rank order[c]
1980 experiments					
80–1	Short, unscreened cylinder	99	3	7.18.80–7.24.80	Unscreened = screened
	Short cylinder	99	3	(6 days)	
80–2	Short cylinder	42,99,161	3,3,3	8.14.80–8.25.80	Short cylinder = medium cylinder > small funnel medium funnel large funnel
	Medium cylinder	42,99,161	3,3,3	(11 days)	
	Small funnel	42,99,161	3,3,3,		
	Medium funnel	42	3		
	Large funnel	42	3		
80–3	Clear cylinder	42	3	8.25.80–9.4.80	Clear = black
	Black cylinder	42	3	(11 days)	
1982 experiments					
82–1	Tall cylinder	94	4	7.23.82–7.27.82	Gallon jar > tall cylinder
	Gallon jar	94	4	(4 days)	
82–2	Tall cylinder	94	3	8.16.82–8.20.82	Tall cylinder > large cylinder = large cylinder with funnel
	Large cylinder	94	3	(4 days)	
	Large cylinder with funnel	94	3		
82–3	Tall cylinder	94	3	9.14.82–9.15.82	Gallon jar > tall cylinder > large cylinder
	Gallon jar	94	3	(26 h)	
	Large cylinder	94	3		
82–4	Tall cylinder	94	3	9.15.82–9.20.82	Gallon jar > tall cylinder > cylinder with plate
	Gallon jar	94	3	(5 days)	
	Cylinder with plate	94	3		

82-5	Tall cylinder	94	3	9.20.82-9.21.82	Gallon jar > tall cylinder > large cylinder
	Gallon jar	94	3	(22 h)	
	Large cylinder	99	3		
82-6	Tall cylinder	94	3	9.21.82-9.22.82	Gallon jar > tall cylinder
	Gallon jar	94	3	(23 h)	
1984 experiment					
84-1	Tall cylinder	95	3	10.23.84-10.26.84	Gallon jar > tall cylinder
	Tall cylinder (WGS)[d]	95	3	(3 days)	Gallon jar (WCS) tall cylinder (WGS)
	Gallon jar	95	3		
	Gallon jar (WCS)[e]	95	3		
1986 experiment					
86-1	Tall cylinder	≈95	3	7.21.86[f]	Gallon jar > tall cylinder
	Gallon jar		3	1317-1751	
	Tall cylinder		3	(4 h 34 min)	
	Gallon jar		3	1751-1929	
	Tall cylinder		3	(1 h 38 min)	
	Gallon jar		3	1325-1932	
				(6 h 7 min)	

---

[a] Refer to designations used in Table II.

[b] Post height variability ($\bar{x}$ ± 1 SD) was 42 ± 6 (n = 15), 99 ± 3 (n = 9), 161 ± 3 (n = 9) in 1980; 94 ± 1 in 1982; 95 ± 2 in 1984; posts not measured in 1986, but placed at same height as in 1982 and 1984.

[c] Based on flume results (see Table II and Hannan, 1984b; Butman, 1986a).

[d] WGS = with gallon-trap sediment added (see text).

[e] WCS = with cylinder-trap sediment added (see text).

[f] Times at midpoint of period of deployment and retrieval of replicate traps.

Trap deployment, recovery and processing

All field experiments were conducted by scuba divers. Each trap was placed in a "basket" that screws onto a 1.9-cm diameter PVC post (refer to Fig. 3). The basket was a threaded PVC flange with four stainless steel struts to hold the trap vertical. Struts screwed onto the flange, so they could be easily changed to accommodate different trap diameters. Posts were hose-clamped against "earth anchors" (steel posts with an eye at the top and a screw plate at the bottom) down to the level of the plate, and this anchor-and-post-assembly was screwed into the sediment to the level of the eye on the post.

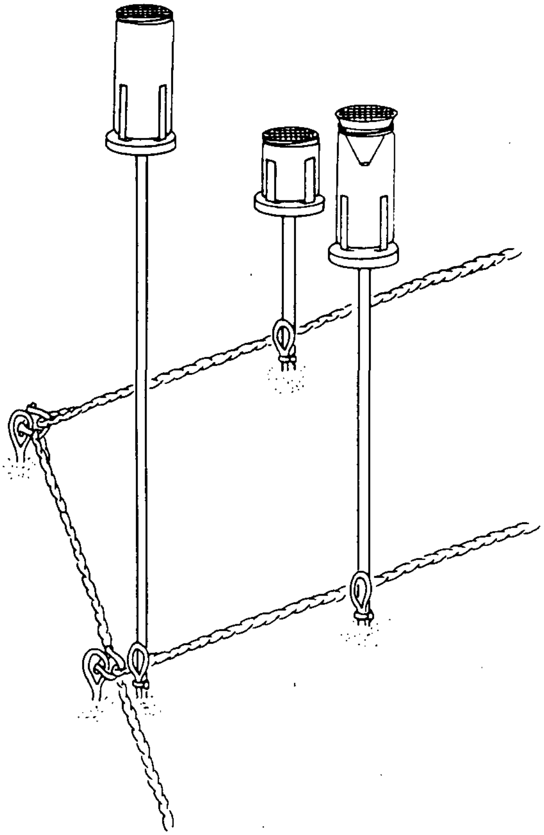

Fig. 3. Diagram showing trap mooring design and floating polypropylene transect lines used to mark the positions of post along the lines. Drawing not to scale.

The distance between individual posts along transect lines was selected so that flow disturbances from an upstream or cross-stream trap would be dissipated before reaching downstream or adjacent traps, respectively (Hannan, 1984b). Transects were generally rectangular arrays laid out on compass courses so that the long leg of the rectangle was perpendicular to the main axis of the tidal ellipse. Posts were placed an arm's length from transect lines, removed from potential disturbances to the bottom created by the lines and divers swimming along the lines.

For the 1980 experiments at Sta. 35, three posts of each of three heights (Table III) were arranged, in random order, along three parallel (±5°) transect lines. A fourth transect was added later and contained six of only the shortest post height. The transect lines were oriented northeast/southwest (60° magnetic) to parallel the major axis of the tidal ellipse in this portion of the Bay. Parallel lines were ≈6.0-m apart and adjacent traps along a transect were 3.3-m apart. For the 1982 experiments at Sta. 35, only the intermediate post height (Table III) was used and there were two different transect arrangements. The first (for Expt. 82–1 only, Table III) consisted of two transect lines forming a right (90°) angle from the surface mooring line, with one line at 60° magnetic and the other at 330° magnetic. Four posts were placed 3.3-m apart along each line. The second was a modification of the first, where two lines, parallel (±2°) to the original 60° transect, were added along the 330° transect. The center of the three parallel lines was ≈3.3-m from the northern line and ≈5.0-m from the southern line. Three posts were placed 3.3-m apart on each line. For the 1984 experiment at Sta. 35 and the 1986 experiment at Sta. NBH, the intermediate post height was used and three lines were arranged in parallel, ≈4.5-m apart, as in the second transect arrangement used in 1982. The lines were at 56° magnetic (±6°) and four posts were placed 4.5-m apart along the lines.

Before placing traps on posts in the 1980 experiments, traps were shaken vigorously to exchange water collected on the way down with near-bottom water. During all other years, water collected by traps on descent was voided by compressed air just prior to placing traps on posts. On recovery, first screens were carefully removed and then traps were capped in place, before transport to the surface. By the time traps were returned to the laboratory for processing, visible suspended sediment had fallen to the bottom of the trap. For the 1980 traps, about half of this "clear" water was discarded before processing, but during all other years, the entire contents of the traps were processed.

Trap contents from the 1980 and from most of the 1982 experiments (those collections exceeding one day) were split twice, using a standard plankton splitter. Half of the total sample was fixed in 10% buffered formalin and processed for "larvae" (see below) and the other two quarters were processed, separately, for particulates. These particulate fractions were allowed to sit for ≈24 h in a cold room (6 ± 1 °C) and then clear water overlying settled material was carefully removed by pipette. Remaining particulate material was frozen and stored for later processing (see below). Entire contents of traps deployed during 1984 and 1986 and those deployed for 1 day during 1982 (Table III) were treated and processed for larvae (i.e., there were no sediment splits).

All larvae fractions were fixed in formalin for 2–7 days and then sieved through nested 500-, 300-, 100- and 63-μm screens into 80% ethanol. All polychaete, mollusc, echinoderm and enteropneust larvae and postlarvae were sorted from all but the 63-μm fraction. Spot checking of this smallest size fraction indicated that very few infaunal larvae or postlarvae passed through the 100-μm screen (Hannan, 1984b). All polychaetes were identified to lowest possible taxon.

The particulate fractions were processed only for Expt. 80–2 (Table III). The frozen material was thawed and dried at 55–60 °C to a constant weight (± 0.005 g) and then wet-sieved through a 63-μm screen. The material retained on the 63-μm screen (the "sand" fraction) was dried and reweighed for calculations of percentage of sand and "mud" (silt plus clay) in suspended particulates.

1980 experiments

During seven trap-collecting intervals in 1980, 12 trap geometries were deployed, as well as various screen and baffle configurations on these traps. A priori hypotheses for trap collections during 1980 were originally based on results of trap calibrations by Gardner (1980). I later realized that Gardner's study was for trap Reynolds numbers that were at least an order-of-magnitude too low for the environment at Sta. 35 (Butman et al., 1986), which necessitated the trap calibration study discussed here and in Butman (1986a). Thus, for the most part, results of the 1980 experiments are uninterpretable because of insufficient information on collection characteristics of traps, including effects of the baffle and screen arrangements. Furthermore, trap collecting intervals were so long (6–14 days) that organisms collected generally could not be considered newly settled larvae or postlarvae, and postsettlement phenomenon (e.g., mortality resulting from competition or predation inside traps) may have been significant. Results from the 1980 experiments are reported for three experiments – those for which there is sufficient information on trap collection efficiencies to allow interpretation of results.

Experiment 80–1 (Table III) was designed to test the influence of fine-mesh screens (≤0.25-mm diameter plastic filaments, 16-mm^2 openings) on trap collections, since traps were screened to keep out large predators or disturbers (e.g., fish, crabs, starfish and shrimp). Screened and unscreened versions of the short cylinder were not tested in the flume, but I did test screened and unscreened versions the tall cylinder and gallon jar (Table II). While within-trap-design variability was greater for screened versus unscreened traps, mean particle collection efficiencies of the tall cylinder and gallon jar were not significantly different (Butman, 1986a), prompting the prediction that screens would have no effect on passive particle collections by short cylinders. Effects of screens on particle collection efficiency are not expected to be trap-design dependent because screens interfere with water flow only at the trap mouth (as opposed to baffles, for example, that extend into the trap interior). Screens may enhance sedimentation, but the magnitude of this effect depends on screen configuration (vertical or horizontal), screen opening, flow regime and particle environment. The screen results reported in Butman (1986a) likely differ from results for screens used in predator-exclusion cages (e.g., Virnstein, 1978; Hulberg & Oliver, 1980) because the cage artifact is due largely to screening on the sides of the cages, which interferes with the horizontal transport and deposition of fine sediments (i.e., a "snow fence" effect).

Particle collection efficiencies of traps very similar to three of the five trap designs deployed in Expt. 80–2 (Table III) were determined in the flume, producing the expected passive rank order that larval collections by the two cylinders (short and medium) should not be significantly different, but that the small funnel should collect significantly fewer passively sinking organisms. Because of the physical mechanism that accounts for relative undercollection of particles by funnel traps (Butman, 1986a; Butman et al., 1986), medium and large funnels were expected to collect larvae in relative abundances similar to those of the small funnel. The influence of post height on trap collections also was evaluated in Expt. 80–2.

Experiment 80–3 (Table III) tested two cylindrical trap designs which were similar in dimensions; neither of these traps were tested in the flume. These traps were not deployed to test a biased-trapping hypothesis. The two trap types were made of clear plastic, but three replicates of one trap (black cylinder) were wrapped in black electrical tape. Thus, this experiment tests for the influence of side and bottom lighting on trap collections. This was important because in some of the subsequent trap comparisons, certain trap geometries were opaque while others were clear (Table II), making light a potential confounding factor in data interpretation.

1982 experiments

A priori hypotheses for the passive rank order of larval collections by traps used during all of the 1982 experiments were dictated by results of the laboratory flume experiments (Table III and Hannan, 1984b; Butman, 1986a). During these experiments, a bottom-moored, instrumented tripod (described in Butman & Folger, 1979) was deployed at Sta. 35 for two contiguous intervals. Current measurements were taken at the height of the trap mouths to determine if flow speeds were within the range ($0–20\ \mathrm{cm \cdot s^{-1}}$) expected during trap collections such that $\approx 10\ \mathrm{cm \cdot s^{-1}}$ flow used in the flume study was representative of intermediate flow conditions in the field.

The first tripod (5 July 1982–20 August 1982) was located 30 m east ($\approx 80^\circ$ magnetic) of the surface mooring line. The second tripod (20 August 1982 through end of trap collections) was located 46 m southeast ($\approx 150^\circ$ magnetic) of the surface mooring line. Tripods had instruments for measuring current speed and direction, pressure, light transmission, and temperature. Savonius rotors for measuring current speed were located 0.5 and 1.0 m above the seabed, but the top rotor fouled on the first tripod, so only speeds from the 0.5-m rotor are reported. Sampling programs for the physical measurements are described in Butman & Folger (1979) and more specifically for this study in Butman (1986b) and B. Butman et al. (1988), where relevant tripod data are also reported.

1984 experiment

The 1984 experiment was designed to test the influence of the "sediment environment" in the traps, versus hydrodynamic effects (i.e., passive collection), in explaining results obtained in the 1980 and 1982 experiments. Trap designs with significantly different efficiencies collect suspended particulates at different rates. The null hypothesis predicts that traps with relatively higher particle collection efficiencies will also have relatively higher larval collection efficiencies, if larvae are collected like passive particles. Because higher-efficiency traps also collect more total particulates, however, organisms also could actively select for (or against) this "sediment environment". Experiment 84–1 was an attempt to experimentally separate passive larval collection by traps from active selection by larvae for the trap sediment environment.

Three traps of each of two trap designs (tall cylinder and gallon jar) were first deployed for 44 h (17–19 October 1984) to collect particulates. Contents were sieved through a 63-μm screen to remove any infaunal larvae and postlarvae; water and particulates passing through the sieve were saved. Material from replicates of the tall cylinders was placed into replicates of the gallon jars and visa versa. The sieving process generally resulted in more water than traps could hold, however, and the "overflow" from each trap was allowed to settle in a separate container for three days; then the clear, overlying water was removed by pipette and the remaining settled material was washed into the appropriate trap design. During this process, all trap contents were held in a cold (6 ± 1 °C) room. The procedure described above was an effort to switch the sediment environment between the two trap designs. On 23 October 1984, the traps with the "switched" sediments, referred to as tall cylinder (WGS) and gallon jar (WCS), where WGS = with gallon jar sediment and WCS = with tall cylinder sediment (Table III), as well as three replicates of the tall cylinder and gallon jar, were placed in the field. Unfortunately, this experiment is lacking an important control, tall cylinders refilled with tall cylinder sediment and gallon jars refilled with gallon jar sediment, so results are potentially confounded by the process of putting sediment in traps. Without adequate controls, results cannot be tested statistically, and thus are only discussed qualitatively.

1986 experiment

The 1986 experiment was originally designed to determine variability in trap collections as a function of current speed. Trap contents from experiments during 1980, 1982, and 1984 integrated collections over several tidal cycles (minimum of two, for 1-day experiments; Table III), and thus, very low or no-flow periods (i.e., slack water) were sometimes (i.e., in the absence of other flow forcing, such as wind- or density-driven circulation) interspersed with flow periods where current speeds were generally within a factor of two of the $10\,\mathrm{cm}\cdot\mathrm{s}^{-1}$ flow tested in the flume (Butman, 1986a,b). Tests of the passive-sinking hypothesis rely on trap biases which are hydrodynamic effects (i.e., result when there *is* flow), so traps must show biased collections of larvae *during flows* to test this hypothesis. The original plan for this experiment was to deploy traps for four consecutive, $\approx$3-h intervals during a 12-h tidal cycle, with the intervals selected based on in situ monitoring of current speed. Two of the intervals would occur during slack water (low-flow periods) and two would occur during the ebbing and flooding tides (high-flow periods). In addition, one set of traps would be left in place throughout the entire 12-h period. The two trap designs chosen for these experiments were the tall cylinder and gallon jar, because they yielded consistent results during 1982 and 1984 (see Results).

The experiment was actually conducted for only half of the tidal cycle (Table III), due to various logistical and mechanical problems at first, and then nightfall. Current speed at the height of the trap mouths was monitored with a Savonius rotor mounted on a small tripod that was positioned by divers, and that was tethered to the surface vessel by an electrical cable. Data were accessed, in real time, on the surface. Three, successive 1-min readings were taken every 15 min. Even though the experiment was conducted on a windless day, and during a period of relatively large tides during daylight hours, the current-meter data indicated a mean flow (probably density-driven; W. R. Geyer, pers. comm.) in addition to the tidal flow. Speeds rarely dropped below 5 $\text{cm} \cdot \text{s}^{-1}$ during the entire 6-h period, and only decreased to a minimum of $\approx$2 $\text{cm} \cdot \text{s}^{-1}$ during what must have been slack water. We did two, sequential trap deployments, one for $\approx$4.5 h and the other for $\approx$1.5 h, and one additional set of traps was left out for the entire period (Table III). This experiment thus addressed variability in trap collections between consecutive, very short-term deployments, where flow speed varied only between 5 and 9 $\text{cm} \cdot \text{s}^{-1}$. Because flow speeds during collections were within a factor of two of the 10 $\text{cm} \cdot \text{s}^{-1}$ flume flow tested and never dropped to zero, biased collections are expected due to hydrodynamic effects during *all* collecting intervals.

Statistics

The null hypothesis (H_0) for the trap experiments was that there was no difference in collections between trap designs during a given collecting interval. For Expts. 80–1, 80–3, 82–1 and 82–6, where only two trap designs were deployed simultaneously, a t test (two-tailed) was used to compare the mean density of organisms in the two trap designs. For Expts. 82–2, 82–3, 82–4 and 82–5, where more than two trap designs were deployed, a one-way ANOVA was used. For all tests, data were log- or square-root-transformed, when necessary, to homogenize variances. When the ANOVA was significant, Tukey's a posteriori, multiple comparisons test was used to test all pair-wise combinations of the means. The expected passive rank order specified a priori predictions for the alternative hypothesis (H_A) in each experiment during 1982, 1984 and 1986, so an a priori contrast test (e.g., a Linear Contrast; Sokal & Rohlf, 1981) would have been justified. An a posteriori test was used, instead, because differences among trap designs in ways other than those predicted for hydrodynamic reasons may be biologically meaningful.

For Expt. 80–2, where three trap designs were placed on posts of different heights (Table III), a two-way ANOVA was used, with trap design (short cylinder, medium cylinder and small funnel) and post height as main effects and a design × height interaction. Tukey's multiple comparisons test was performed to test which means differed. For the short post height, a one-way ANOVA also was performed for all five trap designs, followed by Tukey's test when the ANOVA was significant.

A two-way ANOVA was also performed for Expt. 86–1, where two trap designs were tested at three time intervals. In this case, trap design and collecting interval were main effects, with a design × interval interaction. If collecting interval was significant, differences between means were analyzed using Tukey's test.

For all statistics, each faunal group was treated separately. The underlying assumption in using a univariate approach to analyze these data is that faunal groups are independent (e.g., settling worms and clams do not interact).

RESULTS

FALL VELOCITIES OF NONSWIMMING LARVAE

Fall velocities were measured for 14 spionid larvae (species not identified, but several species present) and one phyllodocid larva (*Eteone longa* Claparede), ranging from 375 to 1400 μm in narcotized length. Fall velocities (W_n) normalized to 20 °C, 30‰ seawater varied between 0.16 and 0.38 $\mathrm{cm \cdot s^{-1}}$ for the MS222 treatment (Fig. 1, Table I). For those larvae treated with formalin, ethanol or freshwater, W_n was 0.085–0.26 $\mathrm{cm \cdot s^{-1}}$, overlapping the range for MS222 treatments and indicating that "worst case" treatments may enhance variability by only a factor of two. Superimposed on treatment effects, however, is variability in fall velocity with larval size (Fig. 1). Fall velocity was positively correlated with narcotized length; r_s (Spearman's rank correlation coefficient) was 0.58 for larvae treated with MS222 (n = 9) and 0.54 if larvae killed in formalin or ethanol are included (n = 12). These correlations are significant at $P \leq 0.05$.

Fall velocities were also measured for six east-coast (from two broods) and 20 west-coast (from four broods) *Streblospio benedicti*, 300–640 μm in narcotized length (differences in larvae from east and west coasts are described in Levin, 1984a). Normalized fall velocities were 0.013–0.086 $\mathrm{cm \cdot s^{-1}}$ (n = 16) for larvae treated with MS222, 0.018–0.111 $\mathrm{cm \cdot s^{-1}}$ (n = 8) for larvae treated with Chloretone, 0.023–0.030 $\mathrm{cm \cdot s^{-1}}$ (n = 2) for larvae treated with KCl and 0.027 $\mathrm{cm \cdot s^{-1}}$ for the one larva fixed in formalin after treatment with KCl. Normalized fall velocity was not significantly correlated with narcotized length ($r_s = 0.14$); however, the size range for larvae tested in the small chamber was only a third of the range tested in the large chamber. The best correlation ($r_s = 0.65$, $P \leq 0.01$) between W_n and narcotized length results if the larvae tested in both chambers, spanning almost an order-of-magnitude in size, are included in the analysis.

A visual inspection of the data (Fig. 1) indicates that the range in fall velocities measured for all larvae treated with MS222 encompass measurements for larvae treated otherwise (with KCl, Chloretone, formalin or ethanol). Statistical analyses of these data were limited by the small sample sizes for most of the alternative (to MS222) treatments. In addition, statistical tests of the effects on fall velocity of parental origin (east or west coast), genetic affinity (brood), and larval age for the *Streblospio benedicti* larvae indicated significant parental origin and age effects (Hannan, 1984b), so these factors complicate analyses of treatment effects alone. In the one case where the H_0 of no difference in fall velocity between MS222- and Chloretone-treated larvae could be tested (for west coast *Streblospio benedicti* from a single brood, where n = 4 for each treatment), however, it could not be rejected ($P \leq 0.171$, Mann–Whitney *U* test).

For less than an order-of-magnitude variability in size (narcotized length), larval fall velocity varied by just over an order-of-magnitude, between ≈0.015 and 0.30 $\text{cm} \cdot \text{s}^{-1}$. This corresponds to fall velocities of coarse silt-sized quartz sediments (Fig. 1). Fall velocities of particles in two glass-bead mixtures used for calibrating sediment traps (Butman, 1986a) show close correspondence to the range in measured larval fall velocity.

TRAP COLLECTIONS – GENERAL COMMENTS

Trap collections are reported for organisms from four invertebrate phyla (Annelida, Mollusca, Echinodermata, and Enteropneusta). For each experiment, collections are reported only for organisms that were sufficiently abundant to permit meaningful statistical analyses. Only organisms collected in the 500-, 300- and 100-μm fractions of trap samples are reported. Examination of several of the 63-μm fractions indicated that, except possibly for some straight-hinge larval bivalves, very few individuals from the groups reported were small enough to pass through the 100-μm screen. Percentages of organisms retained on the two larger screen sizes generally increased with increasing length of the trap-collecting interval (Hannan, 1984b), suggesting that the organisms collected fed and grew in traps during the longer intervals.

Two polychaete species were consistently collected at Sta. 35 in numbers large enough to permit meaningful statistical analyses: *Mediomastus ambiseta* (Family Capitellidae) and *Pectinaria gouldii* (Verrill) (Family Pectinariidae, also called *Cistenides gouldii*, e.g., Whitlatch & Weinberg [1982], referring to the subgenus identified in Hartman [1941]), hereafter referred to as *Mediomastus* and *Pectinaria*. All *Mediomastus* were metamorphosed postlarvae, and individuals in the > 1-day collections were found inside mucus sheaths, with sand grains attached. These were newly settled individuals, however, because > 90% of the individuals collected passed through the 300- and were retained on the 100-μm screen (Hannan, 1984b). *Pectinaria* individuals were also metamorphosed postlarvae. Most individuals were found inside their characteristic cone-shaped tubes. In traps left out for only one day, *Pectinaria* tubes consisted only of opaque, parchment-like material that the worms in this genus evidently secrete while still in the plankton (Lacalli, 1980); however, sand grains were attached to the anterior ends of tubes when traps were exposed for several days. *Pectinaria* were divided about evenly between the combined 500- and 300-μm fractions and the 100-μm fraction.

Polychaetes from a group referred to here as "spionids/sabellariids" were also relatively abundant in trap samples at Sta. 35. These were very small individuals (with 1–4 setigers, but most individuals had only 1 or 2 segments), confined almost exclusively to the 100-μm fraction, and were always collected as unmetamorphosed pelagic larvae. All larvae possessed the long, "serrated", larval setae characteristic of the planktonic larval stage in spionids (e.g., in the genus *Polydora*; Blake, 1969), which are indistinguishable from the provisional bundles of "barbed" setae protruding from only the head region (or "episphere") of sabellariid larvae (e.g., Eckelbarger, 1975). In fact, larval spionids could be distinguished from larval sabellariids only by the presence of "spatulate" setae, beginning on segment three, in sabellariids. Thus, for larvae with 1–2 segments, the two families are indistinguishable. The sabellariids are likely larvae of *Sabellaria vulgaris* Verrill, the only sabellariid species previously collected in bottom samples at Sta. 35 (Sanders et al., 1980), which do not metamorphose until they are $\approx$550-μm and $\approx$6-setigers long (Eckelbarger, 1975). Adult spionids were rarely found at Sta. 35 during the study of Sanders et al. (1980), but several *Polydora* species and *Streblospio benedicti* are abundant in the shallower, more estuarine regions of Buzzards Bay.

Bivalves were nearly always abundant in traps at both Sta. 35 and Sta. NBH. Most individuals were small (87% were collected in the 100-μm fractions; Hannan, 1984b) and some were collected as veligers, in the relatively undifferentiated "straight-hinge" larval stage. The straight-hinge larvae were enumerated in all experiments but 82–1, 82–4 and 82–5. These were the first samples to be sorted and the straight-hinge larvae were inadvertently missed. Preserved larval bivalves are notoriously difficult to identify, even to family in some cases (Rees, 1950; Chanley & Andrews, 1971), and they were not separated into lower taxonomic units in this study.

Two other taxa were occasionally abundant in traps at Sta. 35, enteropneusts (or acorn worms) and seastars. Both groups were found primarily in the 100-μm fractions (94% of the enteropneusts and 98% of the seastars). The enteropneusts were metamorphosed tornaria larvae, possessing postlarval characteristics – constrictions dividing proboscis from collar region and collar from trunk. Enteropneusts were occasionally collected by Sanders et al. (1980) in bottom samples at Sta. 35 and, although they are probably in the genus *Saccoglossus* (J.F. Grassle, pers. comm.), they were not definitively identified to genus. Most seastars were undergoing metamorphosis from the brachiolaria larval stage. Generally, the stalk (three brachiolar arms and the sucker for attachment) and primordium of the definitive star could be seen. Both structures were in various stages of development among specimens collected; however, none of the individuals were completely metamorphosed since the stalk was always present in some form. These metamorphosing larvae are probably in the genus *Asterias* because postlarval and adult *Asterias* were occasionally collected by Sanders et al. (1980) (J.F. Grassle, pers. comm.), but they are reported here simply as "seastars".

At Sta. NBH, spionid polychaete larvae and postlarvae and gastropod postlarvae were abundant in traps, in addition to *Mediomastus* and bivalves. Most spionids possessed 4–8 setigers, with a few having as many as 12 setigers. In these size classes, they could be clearly distinguished from larval sabellariids. The lack of a modified 5th setiger (e.g., Blake, 1969) for individuals with ≥5 setigers, suggests that these older individuals may be *Streblospio benedicti*, rather than a *Polydora* species. Most gastropods were found in the 100-μm fraction and were too small to identify even to family.

1980 EXPERIMENTS

Results of Expt. 80–1 indicate screened traps collect more organisms than unscreened traps (Fig. 4). For total bivalves, mean collections by screened and

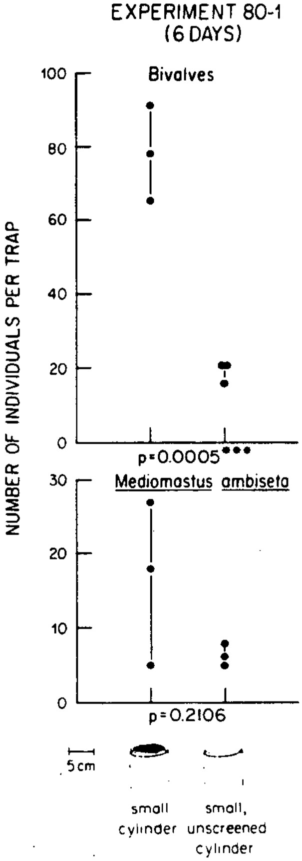

Fig. 4. Collections of *Mediomastus ambiseta* and bivalves (including straight-hinge larvae) in Expt. 80–1 (Table III). Plotted are the number of organisms collected in half the contents of each replicate trap and normalized to 46.57-cm² trap mouth area. Scale drawings of the traps are shown below the graphs, as are the probabilities of rejecting the H_0 (t test; $\log(x+1)$-transformed data). $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

unscreened traps differed by a factor of 4.0 and for *Mediomastus*, mean collections differed by a factor of 2.6. The H_0 could be rejected ($P = 0.0005$) for bivalves, but not for *Mediomastus* ($P = 0.2106$), because the variance was high for the screened trap. Because the screens did not significantly affect passive particle collections by other trap designs tested in the flume (Butman, 1986a), reduced numbers in the unscreened traps may be attributed to effects of predators or "disturbers" that cannot get through screens. Variances were also higher for screened versus unscreened traps collecting passive particles in the flume (Butman, 1986a).

For Expt. 80–2, collections of *Mediomastus* by the short cylinder, medium cylinder and small funnel supported the expected passive rank order (Table III) at all three post heights (Fig. 5, Table IV). Mean collections by the small funnel were significantly lower

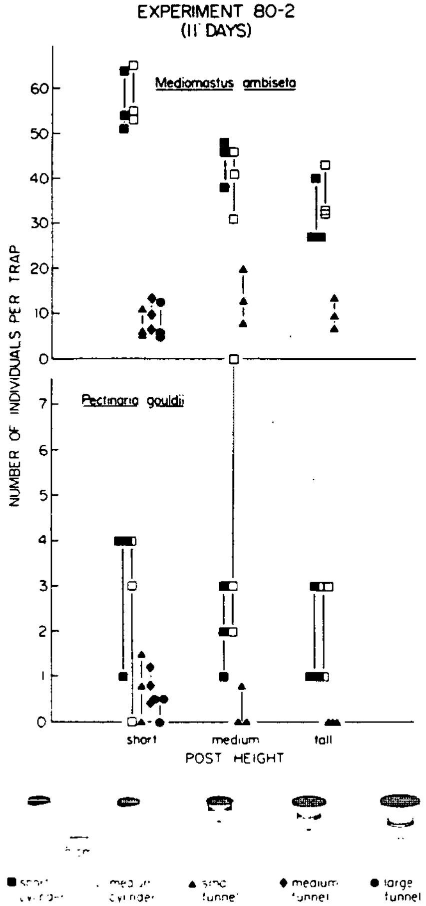

Fig. 5. Collections of *Mediomastus ambiseta* and *Pectinaria gouldii* in Expt. 80–2 (Table III). Plotted are the number of organisms collected in half the contents of each replicate trap and normalized to 46.57-cm^2 trap mouth area. Scale drawings of the traps are shown below the graphs. Results of statistical tests are given in Tables IV and V.

TABLE IV

Results of two-way ANOVAs and Tukey's multiple comparisons tests for collections by the short cylinder (SC), medium cylinder (MC) and small funnel (SF) on short (S), medium (M) and tall (T) posts during Expt. 80–2 (data shown in Figs. 5 and 6). For Tukey's tests, means are arranged in order, with highest value on left; horizontal bars connect means that are not significantly different at $P \leq 0.05$.

Source	df		SS		F		P		
Mediomastus ambiseta[a]									
Trap Design	2		76.97		147.70		0.0001***		
Post Height	2		4.811		9.23		0.0017**		
Trap × Height	4		5.361		5.14		0.0061**		
Error	18		4.690						
Tukey's test									
Trap Design	MC	SC	SC	MC	MC	SC	SF	SF	SF
Post Height	S	S	M	M	T	T	T	M	S
Pectinaria gouldii[b]									
Trap Design	2		5.332		11.23		0.0007***		
Post Height	2		0.356		0.75		0.4869		
Trap × Height	4		0.755		0.79		0.5441		
Error	18		4.274						
Tukey's test									
Trap Design	MS	SC	FS						
Total Particulates									
Trap Design	2		6.121		130.59		0.0001***		
Post Height	2		7.572		161.53		0.0001***		
Trap × Height	4		1.997		21.30		0.0001***		
Error	18		0.422						
Tukey's test									
Trap Design	SC	MC	MC	SC	MC	SF	SF	SF	SC
Post Height	S	S	M	M	T	S	M	T	T
Percent Mud									
Trap Design	2		58.423		2.87		0.0831		
Post Height	2		52.921		2.60		0.1022		
Trap × Height	4		52.073		1.28		0.3156		
Error	18		183.480						

[a] $\sqrt{x + 0.5}$-transformed data.
[b] log $(x + 1)$-tranformed data.
$*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$.

than collections by the two cylinders, which were not significantly different (Table IV). Post height was significant only for collections by the short and medium cylinders on tall posts versus the medium cylinder on short post. Collections by the two other funnel traps (medium and large), tested at the short post height only, were not significantly different from those of the small funnel trap (Table V), as predicted from theory (Butman et al., 1986).

For *Pectinaria*, trap design, but not post height, was significant in comparisons of collections by the short cylinder, medium cylinder and small funnel (Fig. 5, Table IV). The trap effect supported the a priori predictions. When collections by the two larger funnels are included in the analyses (short posts only), then there are no significant differences among trap designs (Table V).

TABLE V

Results of one-way ANOVAs and Tukey's multiple comparisons tests for collections by the short cylinder (SC), medium cylinder (MC), small funnel (SF), medium funnel (MF) and large funnel (LF) at the short post height during Expt. 80–2 (data shown in Figs. 5 and 6). For Tukey's tests, means are arranged in order, with highest value on left; horizontal bars connect means that are not significantly different at $P \leq 0.05$.

Source	df		SS		*F*	*P*
Mediomastus ambiseta						
Trap Design	4		8524.943		84.38	0.0001***
Error	10		252.587			
Tukey's test						
Trap Design	MC	SC	MF	LF	SF	
Pectinaria gouldii						
Trap Design	4		15.957		2.45	0.1141
Error	10		16.280			
Total Particulates						
Trap Design	4		10.042		92.45	0.0001***
Error	10		0.272			
Tukey's test						
Trap Design	SC	MC	MF	SF	LF	
Percent Mud						
Trap Design	4		49.117		1.53	0.2657
Error	10		80.140			

*$P \leq 0.05$, **$P \leq 0.01$; ***$P \leq 0.001$.

The total weight of particulates collected in the short cylinder, medium cylinder and small funnel agreed with a priori predictions for all but the tall post height (Fig. 6, Table IV). On the tall posts, the small funnel and short cylinder collected similar amounts of particulates. Post height was significant for the short cylinder, where less material was collected with increasing height above bottom. Medium cylinders and small funnels also collected significantly less material on tall posts than on short posts. When collections by all three funnel types and the two cylinders are compared for the short post height only, trap design was significant, but the results do not support the a priori predictions (Table V). The large funnel collected significantly less than the small funnel, which collected significantly less than the medium funnel; collections by the two cylinders and medium funnel were not significantly different.

The percentage of mud (i.e., the <63-μm fraction) was not significantly different among all trap designs and at all post heights (Fig. 6, Tables IV, V), although there tended to be more sorting of the sediments among trap designs at the tall post height.

The mean number of *Mediomastus* and bivalves in the clear traps versus black traps deployed in Expt. 80–3 were not significantly different ($P = 0.2990$ for *Mediomastus*, $P = 0.5304$ for bivalves; t test, $\log(x + 1)$-transformed data). There is no variance for

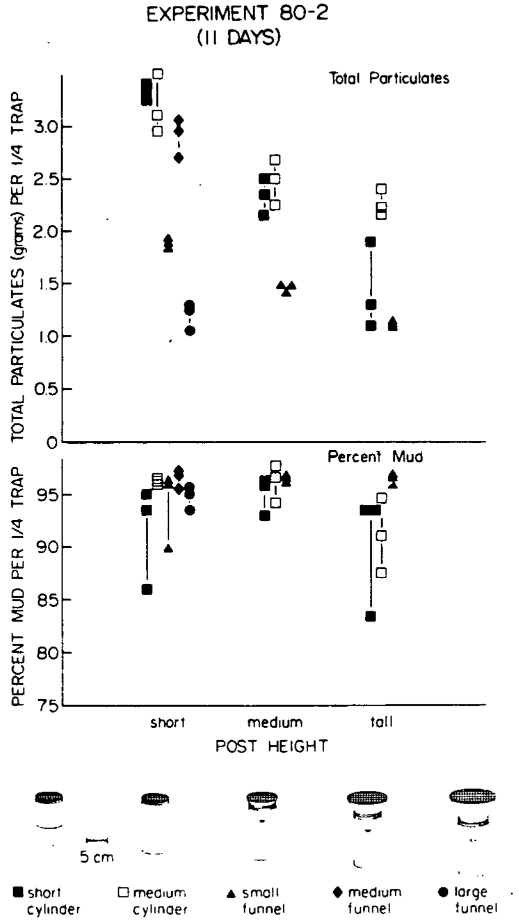

Fig. 6. Collections of Total Particulates and Percent Mud in Expt. 80–2 (Table III). Plotted are the mean total weight of particulates and the mean percentage of mud in two subsamples from each trap (each subsample = 1/4 trap contents). Particulate weights were normalized to 46.57-cm^2 trap mouth area. Scale drawings of the traps are shown below the graphs. Results of statistical tests are given in Tables IV and V.

the black traps, however, since only two of the three traps were successfully recovered. Mean collections (± 1 SD) per 95.03 cm^2 trap mouth area were 36.9 ± 0 in the black traps (n = 2) and 47.7 ± 11.2 in the clear traps (n = 3) for *Mediomastus*, and 35.4 ± 0.6 in the black traps (n = 2) and 43.0 ± 11.8 (n = 3) in the clear traps for bivalves. These results suggest that side and bottom lighting has little effect on trap collections during this trap collecting interval.

1982 EXPERIMENTS

For the six experiments conducted in 1982, collections strongly supported the hypothesis that sinking organisms and passive particles are collected in the same rank order by various sediment-trap designs, but the statistical significance of the results varied between deployments, organisms, and groups of traps tested. For Expts. 82–1 (Fig. 7) and 82–6 (Fig. 8), where only two trap designs were deployed, mean collections by the gallon jar were always greater than mean collections by the tall cylinder, as predicted (Table III). Results are statistically significant ($P \leq 0.05$) for *Mediomastus* (Expt. 82–1), bivalves (Expt. 82–6), spionids/sabellariids (both experiments) and enteropneusts (Expt. 82–1, but not collected in Expt. 82–6). Statistical significance was greater in the 4-day (Expt. 82–1) than in the 1-day (Expt. 82–6) deployment, where fewer individuals were collected.

For the two 1-day experiments (Expts. 82–3 and 82–5, Figs. 9 and 10), where the large cylinder was tested with the gallon jar and tall cylinder, the overall ANOVA was significant for *Mediomastus* (both experiments), bivalves (Expt. 82–3) and *Pectinaria* (Expt. 82–5). In these cases, the rank order of mean collections by the three trap designs followed the a priori prediction (Table III), but Tukey's test revealed that collections by the gallon jar differed significantly from those by the tall cylinder, the large cylinder, or both, but collections by the two cylinders did not differ significantly from each other.

In the remaining two experiments (82–2 and 82–4, Figs. 11 and 12), three trap designs were deployed for 4 or 5 days, and the overall ANOVA was significant for seastars in Expt. 82–2 (seastars were not collected in Expt. 82–4) and for *Mediomastus*, bivalves and spionids/sabellariids in Expt. 82–4. For Expt. 82–2, the tall cylinder was expected to collect more organisms than the large cylinder and large cylinder with funnel, which were not expected to differ (Table III). The bivalve data support this prediction, but the result is significant only at $P = 0.0699$. For seastars, Tukey's test revealed that collections by all three trap designs differed significantly. Contrary to a priori predictions, the large cylinder with funnel collected more larvae than the large funnel. For Expt. 82–4, the cylinder with plate was expected to collect fewer organisms than the tall cylinder (Table III), but Tukey's test revealed that collections by these two trap designs did not differ significantly. Significant ANOVAs were due to differences between the gallon jar and the tall cylinder, the cylinder with plate, or both.

Mean collections by the two trap designs (gallon jar and tall cylinder) that were deployed in five of the six 1982 experiments were in the direction predicted for passive particles in $^5/_5$ tests for *Mediomastus* and *Pectinaria* and in $^4/_5$ tests for bivalves and spionids/sabellariids, even though the result is not always significant at $P \leq 0.05$ (Figs. 7, 8, 9, 10 and 12). The probability of obtaining the expected rank order in larval collections by these two trap designs in $^5/_5$ trials is 0.031 and in $^4/_5$ trials is 0.078 (Mosteller's test of predicted rank order; Lienert & Sarris, 1968), suggesting that for *Mediomastus* and *Pectinaria*, the passive rank order occurred significantly ($P \leq 0.05$) more often than predicted for random assortment.

Traps deployed during Expt. 82–1 contained a potential fish predator, juvenile

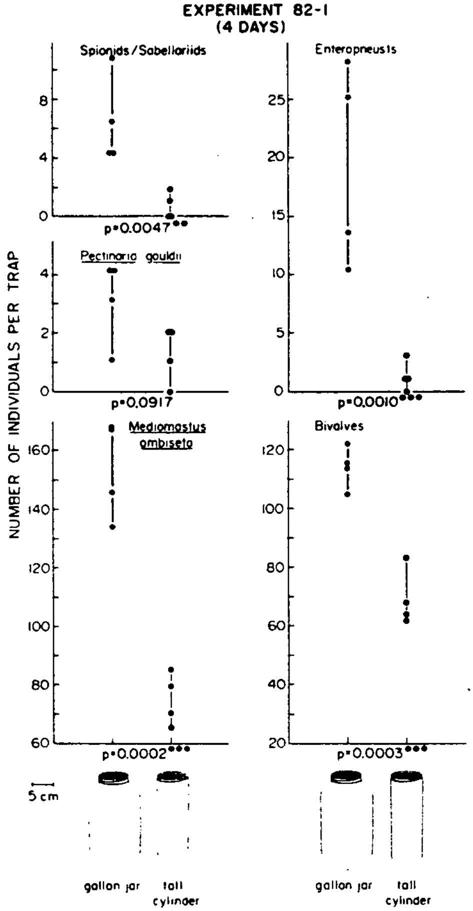

Fig. 7. Collections of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids, bivalves (not including straight-hinge larvae) and enteropneusts in Expt. 80–1 (Table III). Plotted are the number of organisms collected in three quarters of the contents of each replicate trap and normalized to 56.74-cm^2 trap mouth area. Traps are arranged in the expected passive rank order (Table III). Scale drawings of the traps are shown below the graphs, as are the probabilities of rejecting the H_0 (t test; *Mediomastus* data were $\log(x + 1)$-transformed and *Pectinaria*, spionids/sabellariids, and enteropneust data were $\sqrt{x + 0.5}$-transformed). $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

cunners in the Family Labridae, probably *Tautogolabrus adsperus* (Walbaum). More fish were collected in tall cylinders than in gallon jars (Fig. 13). There is a significant negative correlation between number of cunners and number of *Mediomastus* (Pearson's correlation coefficient, $r = -0.974$, $P = 0.026$), but not number of bivalves ($r = -0.443$, $P = 0.557$) in the tall cylinder. A correlation is not meaningful for the gallon jars since only zero or one fish were collected. The significant correlation between *Mediomastus* and fish in the cylinders may account for differences between replicates in larval collections, but it cannot account for the approximately two-fold difference in collections between the two trap designs. For example, a replicate of the tall cylinder with one fish contained 85 *Mediomastus*, but two replicates of the gallon jar, with one fish each, contained 128 and 129 *Mediomastus* (Fig. 13).

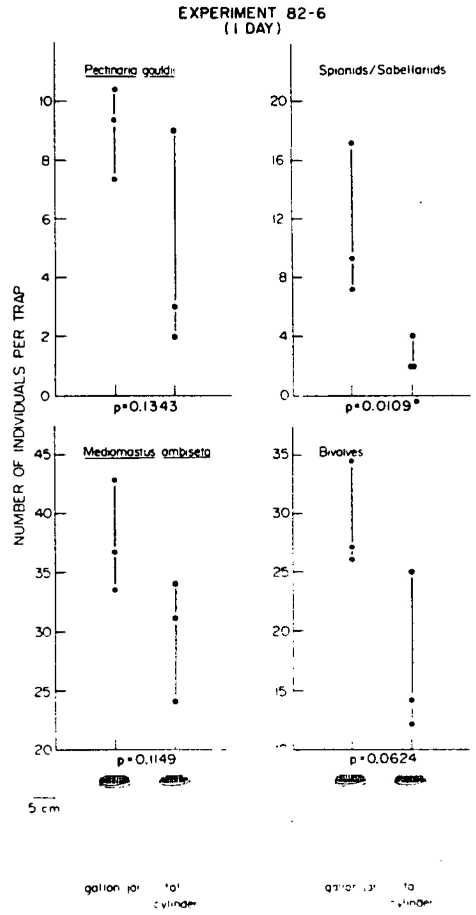

Fig. 8. As for Fig. 7, but for collections of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids and bivalves (including straight-hinge larvae) in Expt. 82–6 (Table III). Spionid/sabellariid data were log (x + 1)-transformed for the t test.

During the 1982 field season, the near-bottom current measurements confirmed that flow speeds within 1.0 m of the bottom were between 0 and 20 cm · s^{-1}, as predicted (Table VI, Fig. 14C). A typical example of the bottom tripod data during a trap collecting interval (Expt. 82–1) is given in Fig. 14. The correspondence between the regular, semidiurnal fluctuations in the pressure record (Fig. 14F) and the north–south component of the current (Fig. 14E) indicates that the flows are primarily tidally driven and approximately parallel the shoreline, again, as expected. Temperature varied little

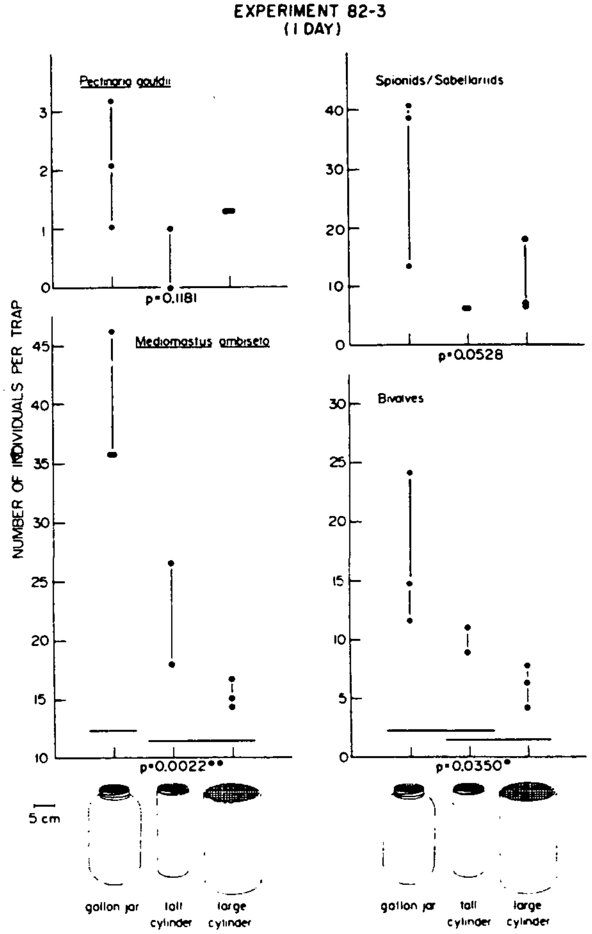

Fig. 9. Collections of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids and bivalves (including straight-hinge larvae) in Expt. 82–3 (Table III). Plotted are the number of organisms collected in three quarters of the contents of each replicate trap and normalized to 56.74-cm^2 trap mouth area. Traps are arranged in the expected passive rank order (Table III). Scale drawings of the traps are shown below the graphs, as are the probabilities of rejecting the H_0 in the overall ANOVA (all data were log $(x + 1)$-transformed). Horizontal bars below the data connect means that are not significantly different in Tukey's multiple comparisons tests. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

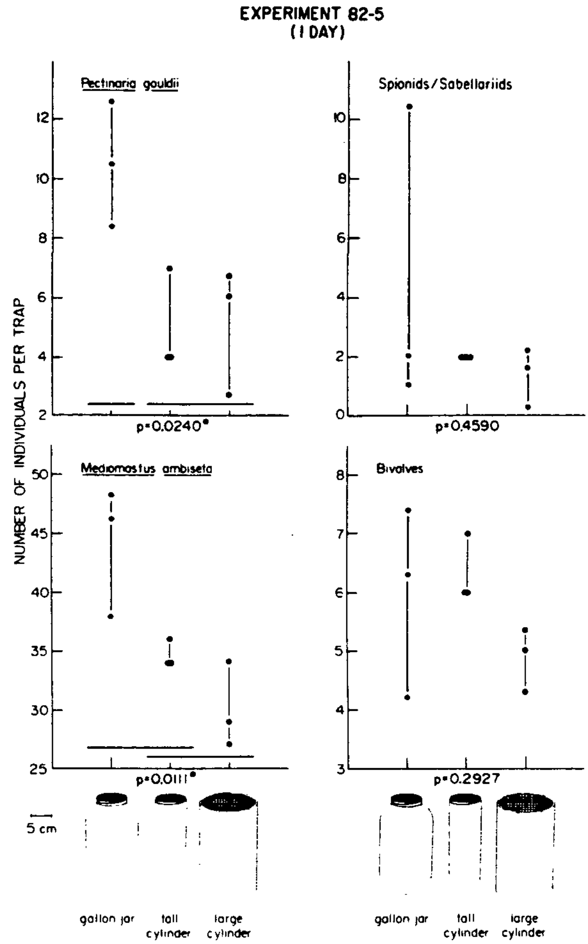

Fig. 10. As in Fig. 9, but for collections of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids and bivalves (not including straight-hinge larvae) in Expt. 82–5 (Table III). *Mediomastus* data were log $(x + 1)$-transformed for the ANOVA.

TABLE VI

Summary of near-bottom water temperatures and current speeds during the 1982 experiments.

Experiment	Number of observations[a]	Near-bottom water temperature (°C)[b]			Distance above bottom (m)	Near-bottom current speed (cm · s⁻¹)		
		Range	Mean	1 SD		Range	Mean	1 SD
82–1	1569	21.3–23.0	21.9	0.3	0.5	0–20.7	5.9	3.3
82–3	425	20.1–20.7	20.4	0.1	1.0	0–15.3	7.7	3.2
					0.5	0-15.0	5.6	2.6
82–4	1833	19.4–20.7	19.9	0.4	1.0	0–15.4	8.0	4.1
					0.5	0-16.7	5.4	3.8
82–5	345	19.1–19.6	19.4	0.1	1.0	0–14.6	5.7	3.7
					0.5	0–12.0	4.8	2.6
82–6	369	18.1–19.1	18.9	0.1	1.0	0–13.1	5.6	3.7
					0.5	0–10.4	3.8	2.9

[a] Measurements were taken every 3.75-min during the collecting intervals (Butman, 1986b).

[b] Temperature was recorded at a distance ≈ 1.5-m above the bottom.

over a given collecting interval and only by a few °C over the entire field season (Table VI). The maximum and mean flow speeds varied among the collecting intervals by a maximum of 7.6 and 2.4 cm · s^{-1}, respectively (Table VI).

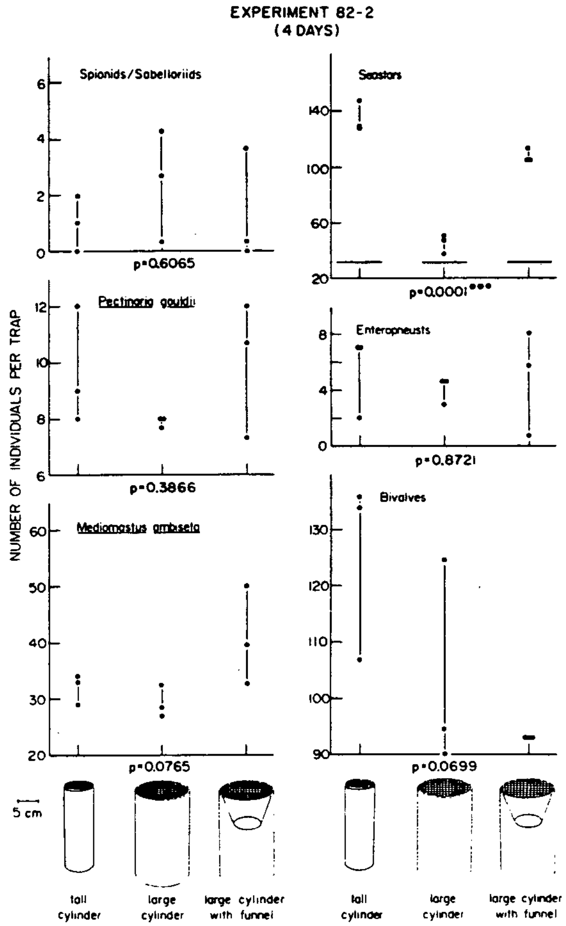

Fig. 11. As in Fig. 9, but for collections of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids, bivalves (including straight-hinge larvae), enteropneusts and seastars in Expt. 82–2 (Table III). *Mediomastus* and bivalve data were $\log(x + 1)$-transformed, and seastar data were $\sqrt{x + 0.5}$-transformed for the ANOVA.

1984 EXPERIMENT

Expt. 84–1 was done very late in settlement season (October) and few organisms were collected (Fig. 15). *Mediomastus* results for the tall cylinder and gallon jar were similar to those in the 1982 experiments (e.g., Figs. 7 and 8), following the expected passive rank order (Table III). In contrast, the tall cylinder (WGS) and gallon jar (WCS), traps with the "switched sediment environment", contained only zero or one *Mediomastus* postlarva per replicate, so the trap sediment environment may have had an effect on collections. For the bivalves, however, collections by the two trap designs followed the predicted rank order whether or not their sediment environments were switched.

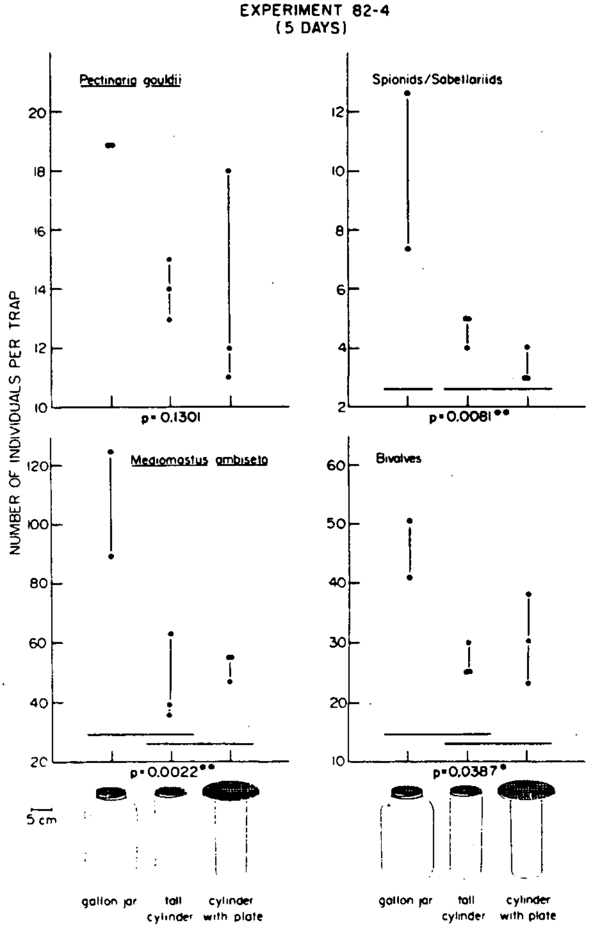

Fig. 12. As in Fig. 9, but for collection of *Mediomastus ambiseta*, *Pectinaria gouldii*, spionids/sabellariids and bivalves (not including straight-hinge larvae) in Expt. 82–4 (Table III). Spionid/sabellariid data were log $(x + 1)$-transformed for the ANOVA.

1986 EXPERIMENT

As described earlier (Materials and Methods), the original design of this experiment was to deploy traps for ≈ 3-h intervals during relatively high- and low-flow periods over

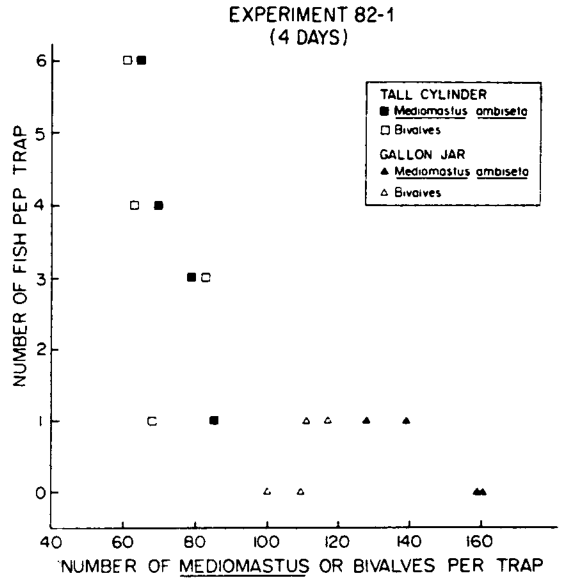

Fig. 13. Collections of *Mediomastus ambiseta* and bivalves plotted as a function of the number of juvenile cunners collected in each replicate of the traps deployed in Expt. 82–1.

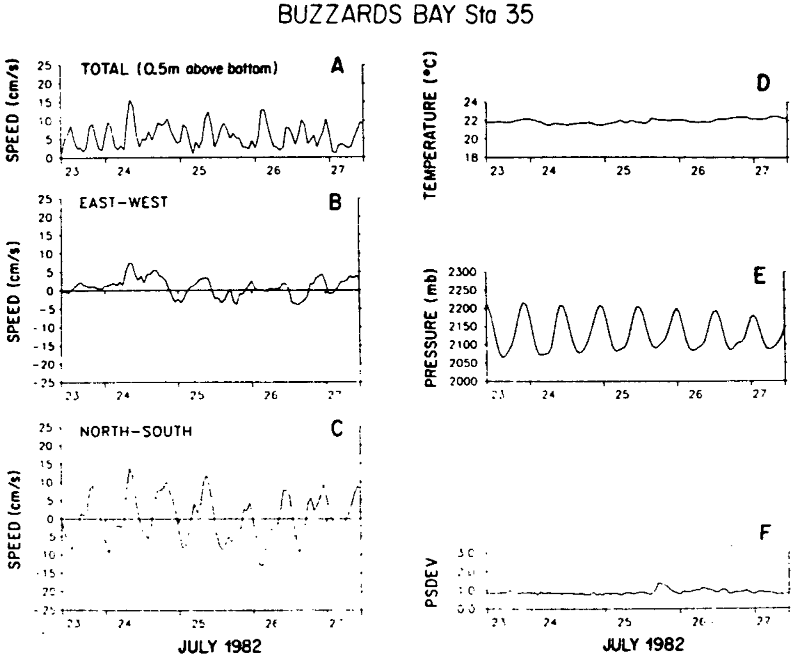

Fig. 14. Physical measurements (1-h averages) from the bottom tripod during Expt. 82–1 (Table III), including current speed (A, B and C), temperature (D), pressure (E) and pressure standard deviation, PSDEV (F). Statistics of temperature and speed measurements are given in Table VI.

half of a tidal cycle (refer to Fig. 16), but this plan could not be executed because current speed at Sta. NBH did not drop below ≈5 cm · s^{-1} during trap collections. Speeds were 2–3 cm · s^{-1} immediately after the tripod was positioned on the bottom at

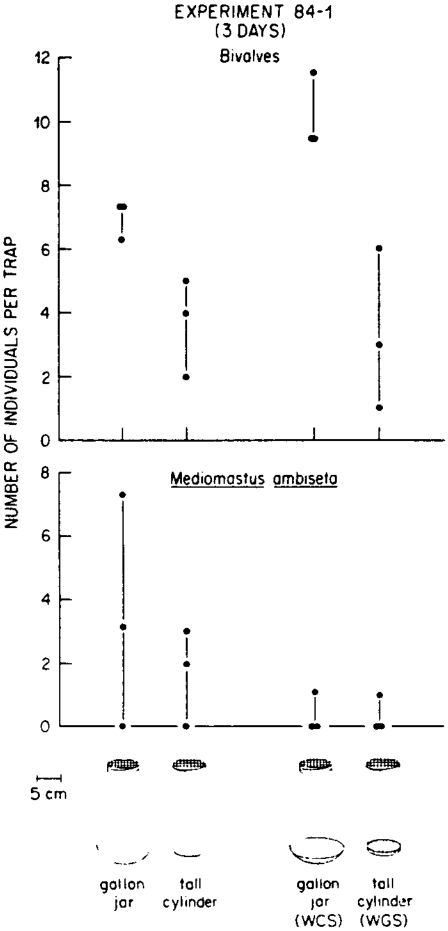

Fig. 15. Collections of *Mediomastus ambiseta*, and bivalves (including straight-hinge larvae) in Expt. 84–1 (Table III). Plotted are the number of organisms collected in the entire contents of each replicate trap and normalized to 56.74-cm^2 trap mouth area. Scale drawings of the traps are shown below the graphs, arranged in the expected passive rank order (Table III).

≈ 1200 EDT (Eastern Daylight Time), ≈ 2 h before predicted low water. Six replicates of the two trap designs (tall cylinder and gallon jar) were deployed between 1308 and 1331 with the intent of retrieving and replacing three replicates of each design ≈ 3 h later, at the end of slack low water. Current speed was ≈ 5 cm · s^{-1} within 30 min of the initial trap deployment, but did not drop again until ≈ 1930, however, after ensuing darkness

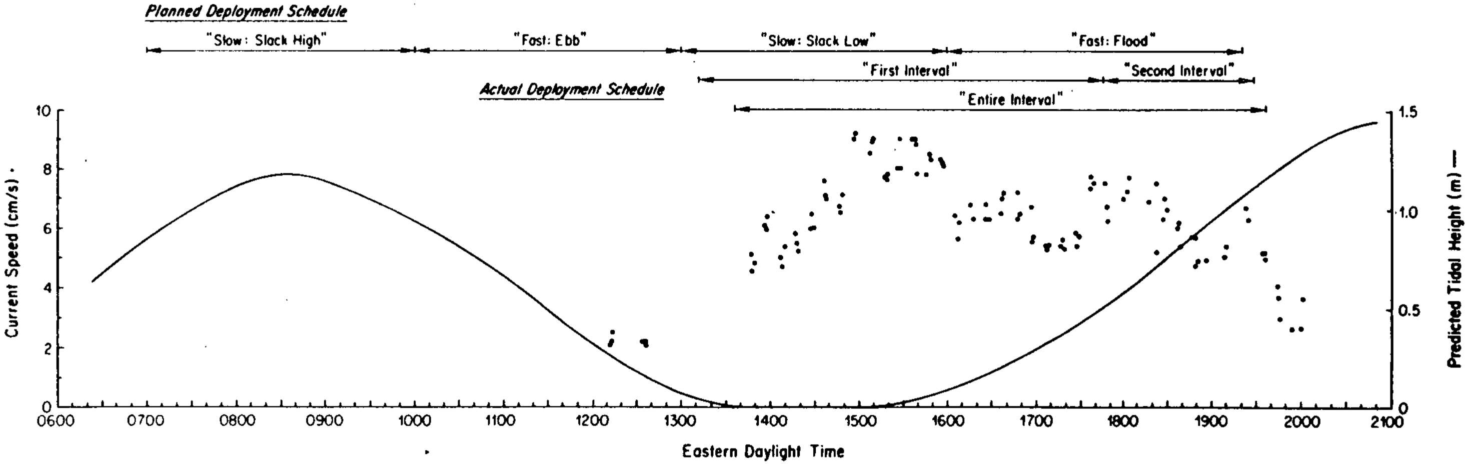

Fig. 16. Current-speed record and predicted tidal height during Expt. 86–1, showing the planned trap-deployment schedule and when traps were actually deployed and retrieved (Table III).

forced the retrieval of all of the traps (between 1920 and 1943). Three replicates of the tall cylinder and two replicates of the gallon jar (others were lost, spilled or otherwise useless) were retrieved and replaced between 1738 and 1804, resulting in the three trap collecting intervals: (1) 1317–1751 ("First Interval"; times at midpoint of period of deployment and retrieval of replicate traps), (2) 1751–1929 ("Second Interval"), and (3) 1325–1932 ("Entire Interval"). Mean (± 1 SD) flow speeds during these intervals

TABLE VII

Results of two-way ANOVAs and Tukey's multiple comparisons tests for collections by the tall cylinder (TC) and gallon jar (GJ) during the First (F), Second (S) and Entire (E) collecting intervals in Expt. 86–1 (data shown in Fig. 17). For Tukey's tests, means are arranged in order, with highest value on left; horizontal bars connect means that are not significantly different at $P \leq 0.05$.

Source	df		SS		*F*		*P*
Mediomastus ambiseta[a]							
Trap Design	1		6.733		8.48		0.0172*
Collecting Interval	2		9.023		5.68		0.0253*
Design × Interval	2		9.573		6.03		0.0218*
Error	9		7.145				
Tukey's test							
Trap Design	GJ	TC	GJ	GJ	TC	TC	
Collecting Interval	F	E	E	S	F	S	
Bivalves[b]							
Trap Design	1		6.741		39.75		0.0001***
Collecting Interval	2		6.192		18.85		0.0006***
Design × Interval	2		3.376		9.95		0.0052**
Error	9		1.526				
Tukey's test							
Trap Design	GJ	GJ	TC	GJ	TC	TC	
Collecting Interval	E	F	F	S	E	S	
Spionids							
Trap Design	1		7159.192		180.02		0.0001***
Collecting Interval	2		628.196		7.90		0.0105**
Design × Interval	2		249.476		3.14		0.0926
Error	9		357.912				
Tukey's test							
Collecting Interval	F	T	S				
Gastropods[b]							
Trap Design	1		0.862		14.24		0.0044**
Collecting Interval	2		2.968		54.52		0.0002***
Design × Interval	2		4.104		33.90		0.0001***
Error	9		0.545				
Tukey's test							
Trap Design	GJ	GJ	TC	TC	TC	GJ	
Collecting Interval	F	S	F	E	S	E	

[a] $\sqrt{x + 0.5}$-transformed data. [b] Log (x + 1)-transformed data. $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

were 7.0 ± 1.3 cm · s^{-1} (n = 57) for the First Interval, 5.8 ± 1.6 cm · s^{-1} (n = 37) for the Second Interval, and 6.6 ± 1.2 cm · s^{-1} (n = 94) for the Entire Interval.

During all three intervals and for all organisms collected (*Mediomastus*, spionids, bivalves and gastropods), mean collections by the gallon jar were much greater (up to a factor of five) than by the tall cylinder, supporting the passive-sinking hypothesis (Table III). Trap design and collecting interval were significant in the two-way ANOVAs (Table VII) for all four faunal groups, and the design × interval interaction was significant for all but the spionids. Gallon jars collected significantly more *Mediomastus* only during the First Interval and more bivalves only during the Entire Interval. For spionids and gastropods, results were statistically significant during all intervals.

One of the most curious results in this series of trap deployments is that collections

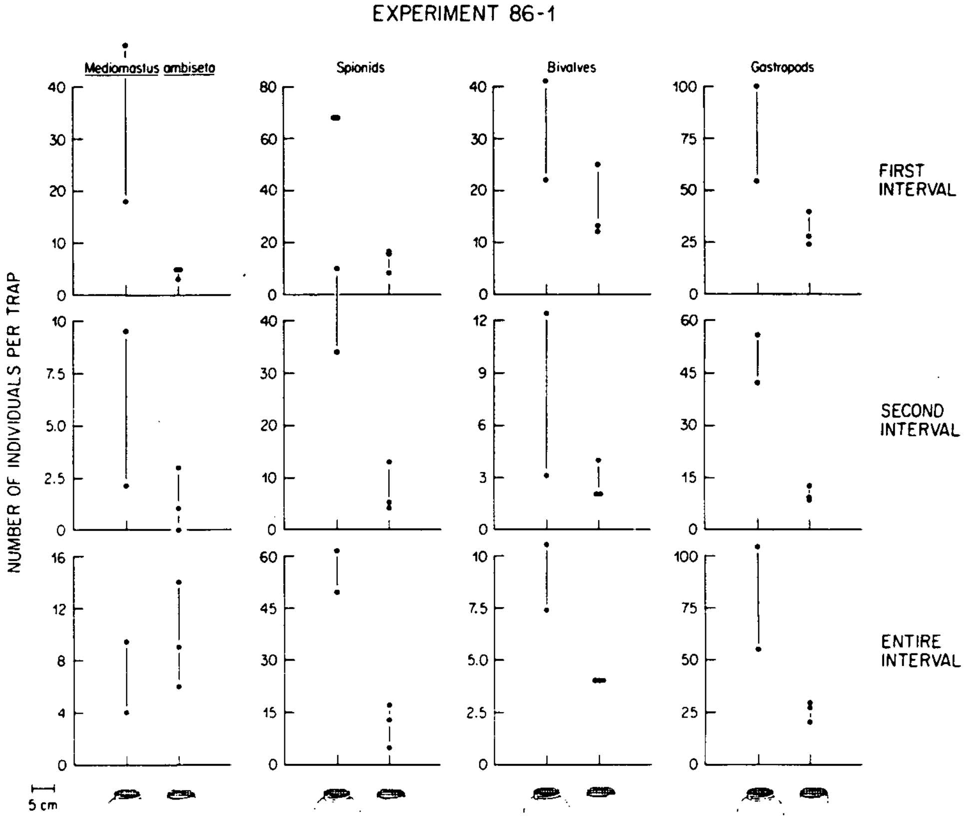

Fig. 17. Collections of *Mediomastus ambiseta*, spionids, bivalves (including straight-hinge larvae) and gastropods in Expt. 86–1 (Table III). Plotted are the number of organisms collected in the entire contents of each replicate trap and normalized to 56.74-cm^2 trap mouth area. Traps are arranged in the expected passive rank order (Table III). Scale drawings of the traps used in the experiment are shown below the graphs. Results of statistical tests are given in Table VII.

of all four groups in traps deployed over the Entire Interval were *not* the sum of collections between the First and Second Intervals, but were much lower, especially for the gallon jars (Fig. 17). Tukey's tests generally showed that both trap designs collected significantly more organisms during the First Interval than during the Second and/or Entire Intervals (depending on trap design and faunal group, Table VII). In no case were collections during the Entire Interval significantly greater than those during both the First and Second Intervals. A possible explanation for this result is that larval availability changed over the 6-h period of the experiment. If trap contents are sometimes removed by occasional, strong eddies, then traps may not integrate larval availability over the collecting interval, but reflect the most recent "depositional" event inside the traps.

DISCUSSION

LIMITATIONS TO EXPERIMENTAL DESIGN

In this study, falsification of the null hypothesis that various trap designs will collect passive particles in a laboratory flume and sinking larvae in the field with similar relative efficiencies could mean either that (1) the processes determining larval abundances in traps are not solely hydrodynamical (i.e., biological and chemical processes are exclusively or additionally important), or that (2) passive particle collection efficiencies of traps in the field deviated significantly from collection efficiencies measured in the flume. The success of testing the biological hypothesis central to this study depends on how accurately the flume study mimicked conditions in the field.

The flume study using passive larval mimics was designed to maintain dynamic- and geometric-similarity to conditions during larval collections in the field. This involved matching between the flume and field the trap aspect ratio, trap geometry, trap Reynolds number ($R_t = u_f D/\nu$, where u_f = horizontal flow speed at height of trap mouth, D = trap mouth diameter and ν = fluid kinematic viscosity) and u_f/W (Butman et al., 1986). Full-scale traps were tested in the flume, so similarity in trap aspect ratio and trap geometry was maintained exactly. Because of the inherent variability in the field flow regime, R_t and u_f/W were not matched exactly; flume experiments were conducted only at values of R_f and u_f/W that were expected to be within the range of those occurring in the field. The tripod measurements (Table VI) confirmed that these values were, in fact, representative of field conditions during trap collections. A steady, turbulent, unidirectional mean flow of $\approx 10\ \mathrm{cm \cdot s^{-1}}$ was used in the flume, however, whereas during the field collections mean tidal flows were between 0 and $20.7\ \mathrm{cm \cdot s^{-1}}$ (at least during 1982, Fig. 14), and varied in direction as described by the tidal ellipse.

The robustness of the measured trap collection efficiencies in the flume study to variability in flows occurring during field collections is unknown. Furthermore, larval availability is unpredictably variable. To minimize variability in both flow and larval availability, when possible (i.e., weather permitting) trap deployments were held to one day after 1980. Even so, because hydrodynamical biases in trap collection efficiencies are not expected to occur when there is no flow, traps would be unbiased collectors four times daily, (i.e., during slack water) in a semidiurnal tidal flow. The threshold velocity for the hydrodynamical biases observed in the flume experiments is unknown. Certain biases are also expected to vary with flow speed (e.g., Butman, 1986a, and Baker et al., 1988, for R_t effects). Thus, between-trap differences in field collections of larvae (or inert particles) are not necessarily expected to be *quantitatively* similar to differences in particle collection efficiencies measured for traps in the flume. This is why only the *rank order* of collections by various trap designs was compared between the field and the flume. This requires, however, that the bulk of the larvae was available and collected *when there was flow*, and not during slack water.

The experiment during 1986 was designed to determine if larvae primarily enter traps during relatively slow- (zero or near-zero) or fast-flow periods over the tidal cycle. Unfortunately, this test was not achieved because flow speed did not drop below $\approx 5\ \mathrm{cm \cdot s^{-1}}$ during the time interval when traps could be deployed (Fig. 16), and only dropped to a minimum of $2\ \mathrm{cm \cdot s^{-1}}$ during "slack water", probably due to a density-driven mean flow at the study site (W. R. Geyer, pers. comm.). Results of this experiment confirm, however, that larvae are available and collected when there *is* a mean flow of $5.8–7.0\ \mathrm{cm \cdot s^{-1}}$ (Fig. 16), similar to mean flows measured during longer collecting intervals in 1982 (Table VI).

The experimental design also assumed that matching fall velocity alone was sufficient for dynamical similarity between the particles used in the flume and larvae sinking in the field, based on assumptions of negligible particle-particle interactions and particle inertia (Butman et al., 1986). If trap-induced particle aggregation or particle adhesion to trap surfaces contribute to differences in trap collection efficiencies, then trap collection efficiencies would have to be determined for more realistic larval mimics, since particle surface characteristics of spherical glass beads sinking in freshwater differ significantly from larvae sinking in seawater. The aggregation and adhesion mechanisms, along with effects of resuspension and unequal mouth and bottom area, were presented in Butman et al. (1986) as alternative explanations for observed trap biases. There is, however, little evidence for either the aggregation or the adhesion mechanisms.

Finally, the larval fall velocity measurements are, themselves, limited in specifying particle fall velocities for the flume experiments. Since the larvae were killed so they would remain immobile throughout a run, tissue characteristics (and thus, mass density of the larvae) may have been altered by this procedure. The results for the extreme treatments (e.g., formalin and ethanol) tested in this study indicate that errors due to treatment effects are within the scatter of the data (Fig. 1). Measurements also were made on larvae of only a small number of polychaete species, nearly all of which were in a single family (Spionidae), whereas bivalve, gastropod, enteropneust and seastar larvae were also collected by the traps in the field. Interestingly, subsequent fall velocity measurements using similar procedures on capitellid polychaete larvae (Butman et al., 1988a,b; Grassle & Butman, in press), bivalve larvae (Butman et al., 1988; Webb &

Butman, submitted), and ophiuroid larvae (Webb, in press) indicate fall velocities within the range of those reported here. In fact, gravitational fall velocities span only about one and a half orders of magnitude (between ≈ 0.008 and $0.40\ \mathrm{cm \cdot s^{-1}}$; medium to coarse quartz silts) for a variety of marine organisms with a temporary planktonic stage, including resting copepod eggs (Marcus & Fuller, 1986), dinoflagellate cysts (Anderson et al., 1985) and meiofauna (Palmer, 1984), suggesting that there may be some optimization in nature for this physical characteristic (C.A. Butman & B. Butman, in prep.).

This discussion of the limitations to achieving dynamic similarity between traps collecting passive particles in the flume and collecting sinking larvae in the field indicates that results of the field experiments should be interpreted cautiously. The potentially most serious limitation is the possibility that larvae may have entered the traps during no-flow periods when all trap designs were expected to have similar collection efficiencies. Since the field experiments indicate that biased collections of organisms occur when there is flow, larvae entering traps during no-flow periods interspersed between flow periods would tend to homogenize differences in collections between trap designs, rendering statistical detection of hydrodynamical differences in larval collections more difficult. This may partially explain why trends in the data often supported the predicted rank order, but were not always significant at reasonable confidence levels. Finally, this experimental design cannot distinguish the biologically intriguing case where larvae actively enter traps during no-flow periods, but are passively collected during flow periods.

TESTS OF PASSIVE-SINKING HYPOTHESIS

During four field seasons, collections of *Mediomastus ambiseta* postlarvae, bivalve larvae and postlarvae, enteropneust postlarvae, spionid/sabellariid larvae, spionid larvae and gastropod larvae between trap designs deployed simultaneously generally corresponded to the predicted passive rank order (Figs. 7–12, 15 and 17). Results are statistically more significant during some collecting intervals than during others (Table VIII). The physical mechanism(s) responsible for particular trap biases may partially explain why some experiments support the a priori predictions while others do not, as well as explaining taxon-specific responses.

The process of particle collection by sediment traps was most recently described theoretically in Butman et al. (1986) and is only briefly discussed here. Particles enter traps either by falling directly into the trap mouth opening or by being carried into the trap by the flow. Direct falling applies to particles with relatively large fall velocities for which particle inertia is significant, such that the particles move independently of the flow. The silt-like particles of interest here (Fig. 1) are not in this category (Butman et al., 1986). These relatively slow-falling particles enter the trap with the flow via eddies shed at the trap mouth that circulate through the trap interior. Particles are collected if they settle out of these eddies and remain on the trap bottom (i.e., if they cannot be resuspended). The most commonly used definition of trap collection efficiency is simply

TABLE VIII

Summary of results of 1980 and 1982 experiments indicating probability levels for which the H_0 of no difference in collections between or among trap designs could rejected; $*P \le 0.05$, $**P \le 0.01$, $***P \le 0.001$, MS = marginally significant ($P \le 0.1$), NS = not significant ($P > 0.1$).

Experiment Post Height[b] Duration (days)	80–2[a] Short 11	82–1 Med. 4	82–2 Med. 4	82–3 Med. 1	82–4 Med. 5	82–5 Med. 1	82–6 Med. 1
Mediomastus ambiseta	***	***	MS	**	*	*	NS
Pectinaria gouldii	NS	MS	NS	NS	NS	*	NS
Bivalves		***	MS	*	*	NS	MS
Spionids/sabellariids		**	NS	MS	**	NS	*
Enteropneusts		***	NS				
Seastars			***[c]				

[a] But see Table IV for results of two-way ANOVAs.

[b] See Table III for post heights.

[c] Collections do not, however, correspond to the preducted passive rank order (see Table II and Fig. 13).

the net deposition (flux) of particles onto the trap bottom divided by the total flux of particles settling through the trap mouth opening.

The pair of traps that most frequently yielded results supporting the passive sinking hypothesis were the tall cylinder and the gallon jar (Figs.7–10, 12, 15 and 17). Relative to the tall cylinder, the gallon jar overcollects particles, in part, because the area of the trap bottom is larger than the area of the trap mouth. The maximum size of the eddy entering the trap is initially constrained by the trap mouth diameter, but in the gallon jar the eddy can expand to fill the larger trap area, thereby increasing the area for particle deposition. In the flume, eddies were observed to penetrate to the trap bottom in both the tall cylinder and gallon jar, indicating that resuspension of particles from the trap bottom may also determine trap collection efficiency. The angular velocity of the eddy is set by the flow speed approaching the trap mouth, but if the eddy size increases between trap mouth and trap interior, the angular velocity of the eddy decreases. Thus, the gallon jar may also retain more particles on the trap bottom than the tall cylinder. Since the field experiments using these two trap designs nearly always supported the a priori predictions, this suggests that the organisms collected tended to move with the flow, are carried into the traps by eddies, and settle out of these eddies over the trap bottom where they may be susceptible to resuspension.

Collections of organisms by the funnel versus cylindrical traps deployed in Expt. 80–2 (Fig. 5) is likely via similar mechanisms. Particle deposition over a trap bottom area much different from the trap mouth area also accounts, in part, for relative undercollection by funnel traps (Butman et al., 1986). In addition, particles may deposit on the funnel walls permanently, or only momentarily, with subsequent resuspension and removal by eddies.

In contrast, relative (to the tall cylinder) undercollections of passive particles by the plate trap in the flume resulted from particle retention in small eddies (of order plate thickness) shed just downstream of the plate leading edge (Hannan, 1984b). Over time, a small mound of particles developed on the plate surface. As in the tall cylinder, an eddy (of order trap-mouth diameter in size) circulated through the plate trap, but the concentration of particles in the eddy was low due to particle removal at the plate leading edge. This situation persisted because of the steady, mean flow conditions in the flume. In the field, however, flows are unsteady (Fig. 14) and it is likely that eddies in the flow could aperiodically sweep any material deposited on the plate surface into the trap mouth. This may explain why larval and postlarval collections by the plate traps were similar to collections by the standard cylinder in Expt. 82–4 (Fig. 12), instead of relative undercollection by the plate traps as predicted by the flume experiments (Table III).

When total suspended particulates, as well as organisms, were analyzed in the trap contents (Expt. 80–2, Figs. 5 and 6), the rank order of collections of *Mediomastus* and total particulates were similar, and corresponded to the predicted rank order (Table III) for the short and medium post heights (Table IV). For traps on tall posts the unusually low (compared to the other heights and to passive predictions) collections of total particulates in the short cylinder may be due to enhanced scouring of the interior of this trap with distance above the seafloor. The tall posts experienced higher flow speeds and also had a greater tendency to flex in the current, which may have resulted in enhanced resuspension of particulates from the short cylinder, and thus, lower collection efficiencies. The organisms may not have been resuspended due to mucus secretions associated with tube-building and burrowing after settlement. *Mediomastus* postlarvae were often found in flimsy tubes stuck to the trap bottom after all the "loose" trap contents had been washed from the containers, especially for relatively long collecting intervals such as Expt. 80–2 (Table III).

The decreased collections of *Mediomastus* postlarvae and total particulates with increasing height above the seabed in the cylindrical traps tested during Expt. 80–2 (Figs 5 and 6, Table IV) lends further support for the passive sinking hypothesis. The largest change was between short and medium posts, where there was a decrease of about 30% in collections of *Mediomastus* and total particulates. This is likely due to resuspended material from the seafloor contributing to collections by traps on the short posts, and for this reason, only the medium post height was used in experiments after 1980 (Table III). Collections in the small funnel of total particulates, but not of *Mediomastus*, however, decreased approximately linearly with height above the bottom (Fig. 6). This is difficult to resolve in terms of the passive sinking hypothesis, but perhaps larvae are more susceptible than particulates to removal from the trap mouth by eddies circulating within the funnel region.

Comparison between collections of total particulates and larvae is crude in that only a fraction of the particulate material (i.e., the coarse silt and very fine sand; Fig. 1) is expected to have fall velocities within the range of passively sinking larvae in the field and the larval mimics used in the flume. The potential for particle-size selection by traps of different geometries and as a function of flow regime was discussed in Butman et al. (1986) and empirical evidence for sorting by size or fall velocity was presented in Blomqvist & Kofoed (1981) and Baker et al. (1988). In general, relatively fine material is expected to be more susceptible to removal by eddies recirculating throughout the trap interior. Even though 95% of the material collected in traps during Expt. 80–2 was in the silt and clay size range (Fig. 6), size analyses alone do not necessarily indicate fall velocities of natural, intact aggregates which, undoubtedly, make up a major proportion of the suspended material. The precise fraction of suspended material expected to track similarly to passively sinking larvae was not resolved in this study.

While the rank order of collections of *Pectinaria gouldii* postlarvae among trap designs was often consistent with a priori predictions for passive particles, the trends were only occasionally significant at $P \leq 0.05$ (Table VIII). Generally, *Pectinaria* postlarvae were more evenly distributed among all trap designs than any other organism. The passive sinking characteristics of this organism may differ from the other polychaetes collected because individuals within the *Pectinaria* genus build tubes during late larval life, while still in the water column. Lacalli (1980), for example, collected *Pectinaria* within their parchment-like tubes in plankton samples. Most *Pectinaria gouldii* collected in the present study were larger than the other organisms collected and were contained in tubes; empty tubes were always found in samples with tubeless *Pectinaria*. The gravitational sinking rate of the relatively large larvae, or of the *Pectinaria*-tube assembly was not measured, but if the larvae fall faster and the tube additionally increases the fall velocity of the larva (i.e., through reduction of surface area), the organisms may no longer move with the flow, and thus, with the eddies circulating through the trap interior. If larvae enter traps only by direct sinking through the trap mouth opening, then collections normalized to mouth area, as reported here, are expected to be similar between all trap designs.

During the one interval when metamorphosing seastars were collected, abundances were higher in the large cylinder with funnel than in the large cylinder (Fig. 11), a pattern significantly different from that predicted for passive particle collections (Table III). Metamorphosing seastars have a morphological adaptation (e.g., a sucker) for attachment to a surface that other larvae collected in this study do not possess (except bivalves, which may have a byssus). The relatively high seastar abundances in the funnel trap may have been due to the larger surface area for attachment afforded by the funnel. Larvae may actively seek such attachment surfaces or, following passive deposition onto the funnel surface, seastar larvae may better resist resuspension because of their attachment capabilities. While this mechanism would increase the relative abundances of seastars on the funnel walls, they must eventually go through the bottom of the funnel to be collected, since funnels were removed from traps prior to capping in the field.

ALTERNATIVE EXPLANATIONS FOR RESULTS

Although observed differential collections of larvae and postlarvae between trap designs generally support the a priori predictions for passive particle collections, there are several alternative explanations for the results. (1) Settling larvae may have actively selected certain trap designs in response to features of the flow or sedimentary environment inside the trap. (2) Settling larvae may have actively avoided certain trap designs, also in response to some physical feature(s) of the trap environment. (3) Larval or postlarval predators may have occurred in different abundances between trap designs such that trap collections reflect differential mortality. These three hypotheses are discussed in more detail below.

The possibility that larvae actively select or avoid a particular trap environment in response to its flow characteristics could not be separated from the null hypothesis of passive deposition in this study, if larvae select for flow characteristics that result in enhanced passive particle collections. The cue to the larvae is difficult to envision. It seems more likely that larvae respond to scalar (rather than dynamical) cues, which reflect flow processes, such as the quality or quantity of sediment collected.

Traps that were relative (to the tall cylinder) overcollectors of passive particles in the flume are, by definition, expected to accumulate relatively more sediment per unit time in the field. This was substantiated for several trap designs in Expt. 80–2 (Fig. 6). Larvae may have thus selected a particular trap design because of features of the sedimentary environment inside the trap. If larvae respond positively to high sedimentation rate, for example, then larval collections would correspond to the predicted passive rank order, but due to biological rather than to physical processes. This explanation was attributed to results of trap experiments by Oliver (1979; Dayton & Oliver, 1980) where two types of containers, having the same geometry and cross-sectional area but different heights, were deployed simultaneously to test settlement responses of polychaete larvae to relatively "depositional" (the "tall" traps) and "erosional" (the "short" traps) environments. *Capitella "capitata"* Hartman, was collected in higher numbers in tall traps, whereas *Armandia brevis* Moore was collected in similar numbers by the two trap designs. Oliver ascribed this to active habitat selection by larvae since the results corroborated field distributions of adults – *Capitella* being preferentially associated with muddy sediments and depositional locales, while *Armandia* was more broadly distributed.

By analogy, *Mediomastus* may have selected the gallon jar over the tall cylinder, for example, in response to enhanced quantity of sediment or sedimentation rate in the gallon jar. Differences between the chemical nature of sediments or the overlying water in the various trapping environments were not assessed in this study. The bulk sediment analyses of particulates collected during Expt. 80–2 indicated that the percentage of mud remained constant among trap designs for which total particulates varied (Fig. 6), suggesting that size selection by traps did not occur at this crude level of assessment. Detailed analyses of specific components of sediments to which organisms are likely to respond (e.g., Whitlatch & Johnson, 1974; Watling, 1988) are required to fully evaluate this possibility.

Even in the absence of sediment sorting by size or composition, if chemical reactions in the collected sediments are quantity-dependent, reactions may proceed differently between trap designs which differ in total material collected. The amount of material collected in the short-term (hours to days, Table III) experiments was small, however, not even covering the bottom of the traps in the one-day experiments. Thus, larvae may have had to perceive differences in sedimentation *rate* among trap designs, and the mechanism by which this may be accomplished is difficult to imagine. Reactions in the water overlying the sediment may also depend on the rate of water exchange within the traps, which is slower in funnel traps than in the cylinders (Gardner, 1980; Butman, 1986a), but probably did not differ substantially between the gallon jar and the tall cylinder.

Experiment 84–1 was an attempt to experimentally evaluate the response of settling larvae to the sediment environment within a trap relative to passive physical processes. The results suggest that bivalve larvae and postlarvae are indifferent to the sediment environment in the traps (Fig. 15), but a flawed experimental design (lack of an important control; see Materials and Methods) renders this experiment inconclusive. The experiment is furthermore limited because the first deployment (to collect particulates) was for 2 days, but the second deployment (to collect larvae) was for 3 days. Thus, even though the sediment environment was switched between the trap designs in the second deployment, particulate material added during the one additional collecting day may have provided a biased sediment signal within a particular trap design. The possibility that larvae actively selected particular trap designs cannot be discounted in this study.

The third alternative hypothesis, that biased collections result from biological processes (predation or competition) within traps, requires that predators or competitors are always differentially collected by traps in trends opposite to the predicted passive rank order, which seems unlikely. Nonetheless, results of Expt. 80–1, where the same trap design was deployed with and without screens, clearly indicates that some organism(s) which cannot get through the screens significantly decreased the number of larvae collected in the unscreened compared to the screened traps (Fig. 4). There may also be organisms smaller than the screen size that are actively or passively collected in the traps and that may result in larval mortality. Collections of juvenile cunners between the gallon jar and tall cylinder during Expt. 82–1, for example, were opposite the predicted passive rank order and their abundance per trap was negatively correlated with the number of *Mediomastus* and bivalves collected (Fig. 13). Visual inspection of the data indicates, however, that the correlation primarily explains differences between replicate collections by the cylinder, rather than differences in collections between trap designs. If the predation effect is a linear function (i.e., if the number of larvae ingested per fish is a constant), then it is unlikely that the predation effect alone accounts for the approximately two-fold difference in larval collections between these trap designs during this collecting interval.

In summary, while the passive sinking hypothesis could not be falsified during most of the field experiments and for most of the organisms collected in this study, there are several alternative hypotheses to explain the results, which have yet to be adequately tested.

IMPLICATIONS FOR SETTLEMENT

Results of this study suggest that planktonic larvae of benthic invertebrates collected in traps deployed over soft sediments in shallow, subtidal regions of Buzzards Bay sink like passive particles to within ≈0.4 m of the seabed. The results further suggest that the larvae respond to small-scale fluid flows and turbulence like passive particles, since small-scale hydrodynamical processes determine biased collection characteristics of a given trap design. Thus, sites where larvae initially come to rest on the seafloor may be stipulated by the boundary-layer flow environment such that larvae are deposited in areas where particulates, with fall velocities similar to larvae, initially settle. The results corroborate those of the recruitment studies of Eckman (1979, 1983), Hogue & Miller (1981), and Savidge & Taghon (1988; but also Kern & Taghon, 1986) which also indicated that small-scale hydrodynamical processes may determine patterns of recruitment into soft sediments.

Fall velocities of nonswimming polychaete larvae measured in this study correspond to those of coarse silt sediments, but this does not necessarily imply that distributions of larvae or adults should be strongly correlated with the distribution of silts in the field. Larvae could come to rest on the seabed during a depositional event, even within a predominantly sandy environment, for example, and once deposited, larvae may burrow into sediments to avoid resuspension, as demonstrated for certain meiofauna taxa (Palmer, 1984). Furthermore, differential postsettlement mortality (e.g., Muus, 1973; Luckenbach, 1984; Watzin, 1986) or postsettlement migrations (e.g., Wilson, 1983; Levin, 1984b; Smith & Brumsickle, in press) may obscure patterns of initial settlement in the field.

The organisms collected in the traps were in various stages of development, including precompetent larvae (spionids/sabellariids and gastropods), metamorphosing larvae (seastars), metamorphosed postlarvae (*Mediomastus*, *Pectinaria* and enteropneusts), and a mixture of stages (bivalves). Since all groups were collected by traps in the predicted passive rank order in at least one case (Table VIII), there is no obvious relationship between developmental stage and susceptibility to passive transport and sinking. Within a taxon, however, differences in collections between trap tests may be due to a preponderance of a certain developmental stage in the water at the time of a given experiment. Bivalves are particularly suspect because traps generally contained a wider range of developmental stages of this taxon than of the others. Certain developmental stages may behave like passive particles while others do not; both increasing and decreasing swimming capabilities over larval development have been reported in the literature (e.g., reviews of Chia et al., 1984; Sulkin, 1984). Resolving developmental stage beyond the gross categories mentioned above was outside the scope of this study, but the intriguing possibility of stage-dependent passive transport merits further investigation.

By using passive particle analogs to represent passively sinking larvae, results of this study indicate that larvae could be passively distributed and deposited at the same spatial scales (of order meters to kilometers) that apply to bulk sediment transport and deposition. This may help to explain the frequent observation that adult distributions of organisms are often well-correlated with particular sediment characteristics, as recently reviewed in Butman (1987). While passive larval settlement is not the only mechanism by which these associations may be maintained, by operating during the early life history of the organism, it is likely of fundamental importance in determining species distributions.

Passive transport and deposition may be viewed as processes exerting hydrodynamical constraints on the habitats available for inspection and settlement by a competent larva. If larvae are passively deposited at relatively large spatial scales, then it is likely that active habitat selection, when it occurs, determines only local distributions within the depositional locale. Active selection mechanisms (e.g., review of Woodin, 1986; also Butman et al., 1988a,b) probably operate at the time the larva first reaches the bottom, such that the organism can opt to remain or leave the depositional locale. The larva is not, however, "free to choose" in the sense of freely inspecting all the options, as the original active habitat selection hypothesis purported (e.g., Meadows & Campbell, 1972, and the eloquent response of Moore, 1975). There is little, concrete support for active selection in response to cues perceived while an organism is in the water column (Butman, 1987; Pawlik, submitted).

The time (pre- or postmetamorphoses) at which and manner in which larvae choose a preferred habitat within a fluid flow is largely unknown. Field measurements combined with theoretical extrapolations indicate that flow speeds, even within several larval body lengths of the seafloor, exceed swim speeds of the larval groups collected in this study by at least an order of magnitude over most of the tidal cycle in Buzzards Bay (Butman, 1986b). Several mechanisms whereby larvae could select sediment within a flow were outlined in Butman (1986b, 1987) and are reiterated here. The larvae may redistribute by actively choosing a preferred microenvironment by crawling or short, hopping excursions within the depositional locale (Butman et al., 1988a,b; Grassle & Butman, in press), by actively swimming above the bottom or remaining on the sediment surface to be resuspended and transported away (Bell & Sherman, 1980; Palmer & Brandt, 1981; Palmer & Gust, 1985), by resuspension only during storm events (Hogue, 1982; Dobbs & Vozarik, 1983), and/or by passively accumulating around microtopographic structures (Eckman, 1979, 1983; Hogue & Miller, 1981; Savidge & Taghon, 1988).

These experiments provide compelling evidence of the potential for hydrodynamical processes to control or constrain mesoscale distributions of pelagic larvae and settled postlarvae. The results must be viewed, however, within the context of other processes known to affect larval and postlarval distributions, for example, behavioral regulation of depth distributions, particularly in the Crustacea (e.g., Sulkin, 1984), and predation (e.g., Young & Chia, 1988). Vertical swimming by larvae can be effective in transporting organisms to preferred water masses because flow speeds in the vertical are much smaller than those in the horizontal (Mileikovsky, 1973). Ontogenetic changes in swimming capabilities and other larval behaviors may render the organisms more or less passive as they develop in the water column. Likewise, physiological constraints to development have behavioral consequences (e.g., Pechenik, 1988) which may ultimately affect distributions both in the water column and on the bottom. This, and other studies (e.g., Eckman, 1979, 1983; Palmer, 1986, 1988a; Palmer & Gust, 1985), indicate that hydrodynamics cannot be ignored in studies of benthic invertebrate settlement and recruitment, urging subsequent studies of, especially, the interactions between biological and physical processes in determining species distributions.

ACKNOWLEDGEMENTS

First and foremost, I thank J.F. Grassle, W.D. Grant (deceased), and K.D. Stolzenbach for their enlightened guidance and support during my doctoral dissertation and beyond. In addition, I thank B. Binder, B. Butman, J.T. Carlton, C.M. Fuller, J.P. Grassle, P.A. Jumars, A.R.M. Nowell, J.S. Oliver, C.H. Peterson, G.L. Taghon, and R.B. Whitlatch. I am grateful to many WHOI divers, particularly C.M. Fuller, for help with the field experiments. I also thank those persons operating or involved with WHOI vessels and support facilities, particularly R.G. Weeks, G.R. Hampson and A.D. Colburn, Jr. I thank A. R. M. Nowell and P. A. Jumars for use of their facilities at Friday Harbor, C.M. Fuller and K.D. Stolzenbach for their creative investment in the flume experiments, R.F. Pectrecca for help with sorting and species identifications, V.R. Starczak for statistical analyses, S.J. Bowman for typing the manuscript and J.H. Doucette for help with graphics. This paper was substantially improved by the careful review of J.E. Eckman and suggestions by an anonymous reviewer.

The research was supported by the Coastal Research Center, Education Program and a PEW Memorial Trust Fellowship at WHOI, the Diving Equipment Manufacturers Association, an Association for Women in Science Predoctoral Award, a National Ocean Survey/Sea Grant Fellowship (NOAA NA80-AA-D00077), a NSF Dissertation Improvement Grant (OCE81-19865), and a NSF grant (OCE85-000875) to C.A. Butman and J.P. Grassle.

REFERENCES

Anderson, D.M., J.J. Lively, E.M. Reardon & C.A. Price, 1985. Sinking characteristics of dinoflagellate cysts. *Limnol. Oceanogr.*, Vol. 30, pp. 1000–1009.

Baker, E.T., H.B. Milburn & D.A. Tennant, 1988. Field assessment of sediment trap efficiency under varying flow conditions. *J. Mar. Res.*, Vol. 46, pp. 573–592.

Bell, S.S. & K.M. Sherman, 1980. A field investigation of meiofaunal dispersal: tidal resuspension and implications. *Mar. Ecol. Progr. Ser.*, Vol. 3, pp. 245–249.

Blake, J.A., 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta : Spionidae). *Ophelia*, Vol. 7, pp. 1–63.

Bloesch, J. & N.M. Burns, 1980. A critical review of sedimentation trap technique. *Schweiz. Z. Hydrol.*, Vol. 42, pp. 15–55.

Blomqvist, S. & L. Hakanson, 1981. A review on sediment traps in aquatic environments. *Arch. Hydrobiol.*, Vol. 91, pp. 101–132.

Blomqvist, S. & C. Kofoed, 1981. Sediment trapping – a subaquatic in situ experiment. *Limnol. Oceanogr.*, Vol. 26, pp. 585–590.

Butman, B. & D.W. Folger, 1979. An instrument system for long-term sediment transport studies on the continental shelf. *J. Geophys. Res.*, Vol. 84, pp. 1215–1220.

Butman, B., R. Signell, P. Shoukimas & R.C. Beardsley, 1988. Current observations in Buzzards Bay, 1982–1986. U.S. Geological Survey Open File Report 88–5, Woods Hole, Massachusetts, 211 pp.

Butman, C.A., 1986a. Sediment trap biases in turbulent flows: results from a laboratory flume study. *J. Mar. Res.*, Vol. 44, pp. 645–693.

Butman, C.A., 1986b. Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom velocity profiles. In, *Marine interfaces ecohydrodynamics*, edited by J.C.J. Nihoul, Elsevier Oceanography Series, Vol. 42, Elsevier, New York, pp. 487–513.

Butman, C.A., 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 25, pp. 113–165.

Butman, C.A., W.D. Grant & K.D. Stolzenbach, 1986. Predictions of sediment trap biases in turbulent flows: A theoretical analysis based on observations from the literature. *J. Mar. Res.*, Vol. 44, pp. 601–644.

Butman, C.A., J.P. Grassle & E.J. Buskey, 1988a. Horizontal swimming and gravitational sinking of *Capitella* sp. I larvae: Implications for settlement. *Ophelia*, Vol. 29, pp. 43–57.

Butman, C.A., J.P. Grassle & C.M. Webb, 1988b. Substrate choices made by marine larvae settling in still water and in a flume flow. *Nature*, Vol. 333, pp. 771–773.

Chanley, P. & J.D. Andrews, 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia*, Vol. 11, pp. 45–118.

Chia, F.-S., J. Buckland-Nicks & C.M. Young, 1984. Locomotion of marine invertebrate larvae: a review. *Can. J. Zool.*, Vol. 62, pp. 1205–1222.

Crisp, D.J., 1974. Factors influencing the settlement of marine invertebrate larvae. In, *Chemoreception in marine organisms*, edited by P.T. Grant & A.M. Mackie, Academic Press, New York, pp. 177–265.

Crisp, D.J. & A.J. Southward, 1953. Isolation of intertidal animals by sea barriers. *Nature*, Vol. 172, pp. 208–209.

Dayton, P.K. & J.S. Oliver, 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In, *Marine benthic dynamics*, edited by K.R. Tenore & B.C. Coull, University South Carolina Press, pp. 93–120.

Dobbs, F.C. & J.M. Vozarik, 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol. Progr. Ser.*, Vol. 11, pp. 273–279.

Eckelbarger, K.J., 1975. Developmental studies of post-settling stages of *Sabellaria vulgaris* (Polychaeta : Sabellariidae). *Mar. Biol.*, Vol. 30, pp. 137–149.

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

Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.*, Vol. 28, pp. 241–257.

Eskin, R.A. & M.A. Palmer, 1985. Suspension of marine nematodes in a turbulent tidal creek: species patterns. *Biol. Bull.* (*Woods Hole, Mass.*), Vol. 169, pp. 615–623.

Fleeger, J.W. & A.W. Decho, 1987. Spatial variability of interstitial meiofauna: a review. *Stygologia*, Vol. 3, pp. 35–54.

Fuller, C.M. & C.A. Butman, 1988. A simple technique for fine-scale, vertical sectioning of fresh sediment cores. *J. Sed. Petrol.*, Vol. 58, pp. 763–768.

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

Gardner, W.D., 1980. Sediment trap dynamics and calibration: a laboratory evaluation. *J. Mar. Res.*, Vol. 38, pp. 17–39.

Grant, W.D., 1977. Bottom friction under waves in the presence of weak current: its relationship to coastal sediment transport. Sc.D. dissertation, Massachusetts Institute of Technology, Cambridge, 275 pp.

Grassle, J.P. & C.A. Butman, in press. Active habitat selection by larvae of the polychaetes, *Capitella* sp. I and II, in a laboratory flume. In, *Proc. 23rd Eur. Mar. Biol. Symp.*, edited by J.S. Ryland & P.A. Tyler, Olsen & Olsen, Fredensborg, Denmark.

Gray, J.S., 1974. Animal–sediment relationships. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 12, pp. 223–261.

Hagerman, G.M., Jr. & R.M. Rieger, 1981. Dispersal of benthic meiofauna by wave and current action in Bogue Sound, North Carolina. *P.S.Z.N.I. Mar. Ecol.*, Vol. 2, pp. 245–270.

Hannan, C.A., 1984a. Planktonic larvae may act like passive particles in turbulent near-bottom flows. *Limnol. Oceanogr.*, Vol. 29, pp. 1108–1116.

Hannan, C.A., 1984b. Initial settlement of marine invertebrate larvae: the role of passive sinking in a near-bottom turbulent flow environment. Ph.D. dissertation, Massachusetts Institute of Technology/ Woods Hole Oceanographic Institution Joint Program, Woods Hole, 534 pp.

Hartman, O., 1941. Polychaetous annelids Part IV. Pectinariidae. *Allen Hancock Pacific Exped.*, Vol. 7, pp. 325–352.

Hogue, E.W., 1982. Sediment disturbance and the spatial distributions of shallow water meiobenthic nematodes on the open Oregon coast. *J. Mar. Res.*, Vol. 40, pp. 551–573.

Hogue, E.W. & C.B. Miller, 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *J. Exp. Mar. Biol. Ecol.*, Vol. 53, pp. 181–191.

Hulberg, L.W. & J.S. Oliver, 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.*, Vol. 37, pp. 1130–1139.

Kern, J.C. & G.L. Taghon, 1986. Can passive recruitment explain harpacticoid copepod distributions in relation to epibenthic structure? *J. Exp. Mar. Biol. Ecol.*, Vol. 101, pp. 1–23.

Kraeuter, J.N., 1974. Offshore currents, larval transport, and establishment of southern populations of *Littorina littorea* Linne along the U.S. Atlantic Coast. *Thal. Jugosl.*, Vol. 10, pp. 159–170.

Lacalli, T.C., 1980. A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. *Can. Tech. Rept. Fish Aquat. Sci.*, Vol. 940, 27 pp.

Levin, L.A., 1983. Drift tube studies of bay-ocean water exchange and implications for larval dispersal. *Estuaries*, Vol. 6, pp. 364–371.

Levin, L.A., 1984a. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. *Biol. Bull.* (*Woods Hole, Mass.*), Vol. 166, pp. 494–508.

Levin, L.A., 1984b. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology*, Vol. 65, pp. 1185–1200.

Lienert, G.A. & V. Sarris, 1968. Testing monotoxicity of dosage-effect relationship using Mosteller's test and its sequential modification. *Methods Inf. Med.*, Vol. 7, pp. 236–239.

Luckenbach, M.W., 1984. Settlement and early post-settlement survival in recruitment of *Mulinia lateralis* (Bivalvia). *Mar. Ecol. Progr. Ser.*, Vol. 17, pp. 245–250.

Marcus, N.M. & C.M. Fuller, 1986. Subitaneous and diapause eggs of *Labidocera aestiva* Wheeler (Copepoda : Calanoida): differences in fall velocity and density. *J. Exp. Mar. Biol. Ecol.*, Vol. 99, pp. 247–256.

Meadows, P.A. & J.I. Campbell, 1972. Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.*, Vol. 10, pp. 271–382.

Mileikovsky, S.A., 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.*, Vol. 23, pp. 11–17.

Moore, P.G., 1975. The role of habitat selection in determining the local distribution of animals in the sea. *Mar. Behav. Physiol.*, Vol. 3, pp. 97–100.

Muus, K., 1973. Settling, growth and mortality of young bivalves in the Oresund. *Ophelia*, Vol. 12, pp. 79–116.

Oliver, J.S., 1979. Processes affecting the organization of marine soft-bottom communities in Monterey Bay, California and McMurdo Sound, Antarctica. Ph.D. dissertation, University of California, San Diego, 300 pp.

Palmer, M.A., 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. *Mar. Behav. Physiol.*, Vol. 10, pp. 235–253.

Palmer, M.A., 1986. Hydrodynamics and structure: interactive effects on meiofauna dispersal. *J. Exp. Mar. Biol. Ecol.*, Vol. 104, pp. 53–68.

Palmer, M.A., 1988a. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Progr. Ser.*, Vol. 48, pp. 81–91.

Palmer, M.A., 1988b. Epibenthic predators and marine meiofauna: separating predation, disturbance and hydrodynamic effects. *Ecology*, Vol. 69, pp. 1251–1259.

Palmer, M.A. & R.R. Brandt, 1981. Tidal variation in sediment densities of marine benthic copepods. *Mar. Ecol. Progr. Ser.*, Vol. 4, pp. 207–212.

Palmer, M.A. & G. Gust, 1985. Dispersal of meiofauna in a turbulent tidal creek. *J. Mar. Res.*, Vol. 43, pp. 179–210.

Pechenik, J.A., 1988. Environmental influences on larval survival and development. In, *Reproduction of marine invertebrates, Vol. IX, General aspects: seeking unity in diversity*, edited by A.C. Giese et al., Blackwood Sci. Publ. and Boxwood Press, Palo Alto and Pacific Grove, California, pp. 551–608.

Peterson, C.H., 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: is pattern fixed during settlement season or altered by subsequent differential survival? *Limnol. Oceanogr.*, Vol. 31, pp. 200–205.

Rees, C.B., 1950. The identification and classification of lamellibranch larvae. *Bull. Mar. Ecol.*, Vol. III, pp. 73–103.

Rubey, W.W., 1933. Settling velocities of gravel, sand, and silt particles. *Am. J. Sci. Fifth Ser.*, Vol. 25, pp. 325–338.

Sanders, H.L., J.F. Grassle, G.R. Hampson, L.S. Morse, S. Garner-Price & C.C. Jones, 1980. Anatomy of an oil spill: long-term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. *J. Mar. Res.*, Vol. 38, pp. 265–380.

Savidge, W.B. & G.L. Taghon, 1988. Passive and active components of colonization following two types of disturbance on an intertidal sandflat. *J. Exp. Mar. Biol. Ecol.*, Vol. 115, pp. 137–155.

Scheltema, R.S., 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull.* (*Woods Hole, Mass.*), Vol. 140, pp. 284–322.

Scheltema, R.S., 1974. Biological interactions determining larval settlement of marine invertebrates. *Thal. Jugosl.*, Vol. 10, pp. 263–296.

Signell, R. P., 1987. Tide- and wind-forced currents in Buzzards Bay, Massachusetts. Master's thesis, Woods Hole Oceanographic Institution, Tech. Rep., WHOI-87-15, Massachusetts Institute of Technology, Cambridge, 86 pp.

Smith, C. R. & S. J. Brumsickle, in press. The effects of post-larval immigration, patch size and substrate isolation on colonization and succession in intertidal sediments. *Limnol. Oceanogr.*.

Sokal, R. R. & F. J. Rohlf, 1981. *Biometry*. Freeman & Co., New York, second edition, 859 pp.

Strathmann, R. R., 1978. Larval settlement in echinoderms. In, *Settlement and metamorphosis of marine invertebrate larvae*, edited by F. S. Chia & M. E. Rice, Elsevier, Amsterdam, pp. 235–246.

Sulkin, S. D., 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Mar. Ecol. Progr. Ser.*, Vol. 15, pp. 181–205.

Thistle, D., J. A. Reidenauer, R. H. Findlay & R. Waldo, 1984. An experimental investigation of enhanced harpacticoid (Copepoda) abundances around isolated seagrass shoots. *Oecologia*, Vol. 63, pp. 295–299.

Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Danm. Fisk. Havunders. Ser. Plankton*, Vol. 4, pp. 1–523.

Thorson, G., 1957. Bottom communities (sublittoral or shallow shelf). In, *Treatise on marine ecology and paleoecology*, Vol. 1, edited by J. W. Hedgepeth, *Geol. Soc. Am. Mem.*, Vol. 67, pp. 461–534.

Thorson, G., 1961. Length of pelagic life in marine bottom invertebrates as related to larval transport by ocean currents. *Oceanography Am. Assoc. Adv. Sci.*, Vol. 67, pp. 455–474.

Virnstein, R. W., 1978. Predator caging experiments in soft sediments: caution advised. In, *Estuarine interactions*, edited by M. I. Wiley, Academic Press, New York, pp. 261–273.

Watling, L., 1988. Small-scale features of marine sediments and their importance to the study of deposit-feeding. *Mar. Ecol. Progr. Ser.*, Vol. 47, pp. 135–144.

Watzin, M. C., 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. *J. Exp. Mar. Biol. Ecol.*, Vol. 98, pp. 65–113.

Webb, C. M., in press. Larval swimming and substratum selection in the brittle star *Ophioderma brevispinum*. In, *Proc. 23rd Eur. Mar. Biol. Symp.*, edited by J. S. Ryland & P. A. Tyler, Olsen & Olsen, Fredensborg, Denmark.

Whitlatch, R. B. & R. G. Johnson, 1974. Methods for staining organic matter in marine sediments. *J. Sed. Petrol.*, Vol. 44, pp. 1310–1312.

Whitlatch, R. B. & J. R. Weinberg, 1982. Factors influencing particle selection and feeding rate in the polychaete *Cistenides (Pectinaria) gouldii*. *Mar. Biol.*, Vol. 71, pp. 33–40.

Williams, J. G., 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *J. Mar. Res.*, Vol. 38, pp. 729–741.

Wilson, W. H., Jr., 1983. The role of density dependence in a marine infaunal community. *Ecology*, Vol. 64, pp. 295–306.

Woodin, S. A., 1985. Effects of defecation by arenicolid polychaete adults on spionid polychaete juveniles in field experiments: selective settlement or differential mortality. *J. Exp. Mar. Biol. Ecol.*, Vol. 87, pp. 119–132.

Woodin, S. A., 1986. Settlement of infauna: larval choice? *Bull. Mar. Sci.*, Vol. 39, pp. 401–407.

Young, C. M. & F.-S. Chia, 1988. Abundance and distribution of pelagic larvae as influenced by predation, behavior and hydrographic factors. In, *Reproduction of marine invertebrates, Vol. IX, General aspects: seeking unity in diversity*, edited by A. C. Giese et al., Blackwood Sci. Publ. and Boxwood Press, Palo Alto and Pacific Grove, California, pp. 385–464.