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Active and passive processes associated with initial settlement and post-settlement dispersal of suspended meiobenthic copepods

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ABSTRACT

Settlement by suspended meiofaunal copepods into shallow depressions was investigated in a large, recirculating laboratory flume. Initial settlement was examined under various near-bottom flow regimes, and the interaction of flow with post-settlement behavior was investigated. Cylindrical depressions of constant depth were constructed with a range of aspect ratios (diameter and depth combinations) to mimic natural microtopographic features. Copepods were released into the flume (at nominal flows of 2, 5 and 7 cm sec^{-1}), and settlement/distribution in the mimic pits was observed. Four experiments were conducted using a total of five species. The first tested for copepod substrate preferences in still water. The second tested for passive settlement into azoic sediment using predictions, based on hydrodynamics, of the ability of depressions of different aspect ratios to act as passive collectors. The patterns of initial settlement of living, freeze-killed and bead-mimic meiofauna were compared. Algal-enriched sediment (to test for active habitat selection) was used in two experiments; one to test for active choice upon initial settlement and the other to test for active habitat selection via post-settlement dispersal into closely-paired pits. Although copepods were capable of active habitat selection in still water, no species tested was able to initially select the preferred habitat in moving water. Moreover, the same copepod species tested in moving water were generally deposited among depressions in the same manner as passive particles. Post-settlement behavior influenced copepod distribution at a low nominal current velocity (2 cm sec^{-1}) as more individuals of both species located (and remained in) algal-enriched depressions after four hrs. Under high flow (8 cm sec^{-1}), copepods were unable to select enriched over non-enriched depressions, either because they did not re-emerge from non-enriched pits or because shear velocity was too high to permit active habitat selection.

1. Introduction

Increasing evidence suggests that the abundance of meiofauna, especially meiobenthic copepods, is influenced by the near-bottom flow regime (Palmer, 1988). Hydro-

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dynamic effects are known to directly influence the sediment density of meiofauna. Flows above critical erosion velocity have been shown to erode surface-dwelling meiofauna into the water column (Palmer and Gust, 1985), and several reports have found the lowest sediment densities of meiofauna either during or immediately after high-flow events (Palmer and Brandt, 1981; Fleeger *et al.,* 1984; Coull and Feller, 1988; Thistle, 1988). Alternatively, sediment-dwelling meiofauna may enter the water column by active emergence usually at slack tide or at dusk (Armonies, 1988; Walters, 1991). Another direct hydrodynamic influence on distribution may occur when suspended meiofauna are redeposited to sediments (Palmer, 1988). Field studies have consistently found increased abundances of copepods in areas surrounding objects that protrude from the bed such as grass culms (Thistle *et al.,* 1984) or biogenic structure (Eckman and Thistle, 1991; Thistle and Eckman, 1990; Thistle *et al.,* 1993), and in pits and depressions (DePatra and Levin, 1989; Kern and Taghon, 1986; Sun *et al.,* 1993; Sun and Fleeger, 1994) that interrupt flow (reduce shear stress) and concentrate small particles. In a review on meiofauna dispersal, Palmer (1988) stated that a key unstudied factor in distribution analysis is the interaction of flow with the return of meiofauna to the sediments after they enter into the water column. Indirect effects of flow are also possible. For example, Eckman and Thistle (1991) suggest that increased abundances of harpacticoid copepods may be associated with increased flux of O_2 in areas of high shear stress.

   Settlement of other small organisms (i.e. larvae of macrofauna) in relation to hydrodynamic regime has recently been the subject of intense study (Butman, 1987; Butman *et al.,* 1988a, b; Pawlik *et al.,* 1991; Butman and Grassle, 1992; Grassle *et al.,* 1992). The larvae of some species are unable to choose the habitat in which they settle, and are passively deposited in areas of low shear velocity (Wethey, 1986; Butman, 1987; 1989), while others are able to select settling sites (Pawlik and Butman, 1993; Turner *et al.,* 1995). The problem of settlement by suspended meiofauna is conceptually related because the size, swimming ability and fall velocities of adult meiofauna and macrofaunal larvae are similar (Butman, 1987), and most studies suggest meiofauna are deposited as passive particles (Eckman, 1983; Eckman and Thistle, 1991; Savidge and Taghon, 1988; DePatra and Levin, 1989). Nevertheless, Palmer (1992) found evidence that freshwater copepods are able to actively select settling sites.

   While erosion and deposition may establish initial sediment densities of meiofauna, post-depositional processes can modify these primary distributional patterns. Species associations (both positive and negative) among meiofauna have been observed in laboratory studies (Chandler and Fleeger, 1987; Decho and Fleeger, 1988). In still water, harpacticoid copepods are able to select areas favorable to them (Hicks and Coull, 1983; Decho and Fleeger, 1988). Field studies often suggest that hydrodynamic processes are unable to completely explain distributional patterns (Kern and Taghon, 1986; Kern, 1990; Fegley, 1988). The relative contributions of

hydrodynamically-driven settlement and post-settlement behavior of meiofauna have yet to be resolved, but may well explain much of the distribution of epibenthic meiofauna.

The purpose of this report is to examine the roles of habitat selection, passive deposition, and post-settlement movement in establishing meiobenthic copepod abundance in small depressions that mimic microtopographic features common on mudflats (Sun *et al.*, 1993; Sun and Fleeger, 1994). We investigated these processes through a series of four experiments. First, we asked if copepods demonstrate habitat selection in still water by choosing algal-enriched over non-enriched sediment (following Decho and Fleeger, 1988). Secondly, we explored the possibility that copepods are deposited as passive particles in moving water. Thirdly, we tested for habitat selection in moving water. Finally, we tested for post-settlement dispersal to preferred habitats under different flow regimes.

2. Materials and methods

a. Overview. The first of the four experiments tested for habitat selection between algal-enriched and non-enriched sediment in standing water. Although previous results indicate that copepods are capable of habitat selection in still water (Decho and Fleeger, 1988), we repeated this work to assay preference for the specific habitat that we intended to employ in flume experiments. The remaining experiments were all conducted in flowing water in a flume, and investigated the contributions of habitat selection, passive deposition, and post-settlement movement in establishing copepod distribution patterns under different flow rates. The second experiment tested for passive deposition of copepods into depressions differing in hydrodynamic characteristics (Passive Expectations Test, hereafter PET). The third experiment tested for habitat selection during settlement in flowing water (utilizing the same two substrata tested in still water) and passive deposition (Active-Passive Experiment I, hereafter APE I). PET and APE I were conducted for one hour to allow time for initial settlement, but with a restricted opportunity for dispersal. Finally, the last experiment tested for habitat selection via post-settlement dispersal in flowing water (APE II). APE II was conducted over four hours to allow for an increased opportunity for dispersal after initial settlement.

All experiments in moving water were conducted in a recirculating flume at the Louisiana University Marine Consortium (LUMCON) Marine Education Center in Cocodrie. This race-track, paddlewheel-driven flume, modelled after a similar facility at the Woods Hole Oceanographic Institution (see Butman and Grassle, 1992), is composed of an acrylic channel 731.5 cm long on a side, 81.3 cm wide, and 61 cm deep. The flume was filled to 25 cm in depth with ambient brackish water (10‰) at 25°C during each experiment. A square deep box, 75 cm long and 30 cm deep, was located about 450 cm from the upstream end, and an acrylic tray (60 cm long, 46 cm wide, and 7 cm deep) was fitted into the deep box to serve as the

settlement area. Depressions of various sizes were built into the settlement box (described below). Defaunated sediment (following Chandler, 1986) was added to each depression to produce pits of a desired, but constant, depth. Pits were positioned at least 18 cm from the outer wall of the flume to avoid possible wall effects generated by a water width/depth ratio <5 (Nowell and Jumars, 1987).

The flume facility is equipped with a TSI Laser Doppler Velocimeter (LDV) that was used to measure horizontal and vertical components of flow. The LDV has a two dimensional backscatter probe, using fiber optic technology, which is mounted on a 3-dimensional traversing system. The probe is automatically positioned using the TSI software and can be moved at increments of less than 1 mm in the x, y or z direction. Profile co-ordinates can be set within the software at predetermined intervals. The LDV was used to measure flow rates in all experiments. Flow visualizations were made to determine flow pattern inside depressions because detailed quantitative velocity profiles for each of the differently-sized pits were not attempted. A fine stream of fluorescein dye was introduced 10 cm upstream from the depressions with a syringe and pipette. The flow pattern downward into and upward out of the depressions was videotaped with a Sony Hi8 camcorder. In the APE II experiment, a vertical velocity profile in front of the tray was measured by LDV under two flow conditions at 2-mm intervals. Shear velocity was calculated by equation $\bar{u}(z) = u_* / k$ $\ln(z/z_0)$, where $\bar{u}(z)$ is the mean velocity at height z, k is Von Karman's constant (0.4) and z_0 is the bottom roughness (Clauser, 1956; Gross and Nowell, 1983).

Meiobenthic copepods were collected from mudflats surrounding the LUMCON laboratory. Air-exposed mud (top 2 cm) was scooped into buckets and washed through a 0.125 mm sieve. In order to separate copepods from the large volume of organic material, we used an intense fiberoptic beam of light to attract animals into the water column. From 50,000 to 300,000 meiobenthic copepods were used in individual flume trials (Table 1). For some experiments we conducted trials with dead copepods to generate a pattern of passive deposition. Live copepods collected as above were frozen in seawater overnight, and thawed prior to use. Polystyrene DVB microspheres (Duke Scientific Corp., Palo Alto, CA) of a size range (500–710 μm) and calculated to have fall velocities corresponding to the observed fall velocities of living, unanesthetized copepods (2.7 to 5.1 mm sec^{-1}; unpublished data) were also used as passive particles to mimic copepods.

Copepods and mimic beads were released in the flume 2.8 m upstream of experimental settlement trays. Entry of copepods into the flume was accomplished via a pivoting, leveled trough mounted above the water surface that distributed animals evenly across the width of the flume. Copepods were allowed to circulate in the flume for 1 hr in PET and APE I experiments; in APE II they were allowed to circulate for 4 hr (Table 1). Bead mimic experiments were conducted (in separate trials from live copepods) for 30 min. At the termination of each experiment, the settlement tray was covered with an acrylic cap and carefully removed from the deep

Table 1. Experimental conditions in each flume trial. All trials were conducted in 10‰ salinity water at 25°C. See Figure 1 for orientation and design information.

Trial	Date	Experiment	Velocity (cm/sec ± S.E.) Nominal	Measured	Particles Number	Type	Orientation/ Design	Duration (hr)
1	5/27/92	PET	5	4.97 ± 0.04	300,000	Live	1	1
2	5/27/92	PET	2	2.22 ± 0.03	330,000	Live	1	1
3	5/28/92	PET	7	7.33 ± 0.11	120,000	Live	2	1
4	5/28/92	PET	5	4.42 ± 0.07	120,000	Live	2	1
5	5/28/92	APE I	7	7.19 ± 0.06	150,000	Live	A	1
6	5/28/92	PET	7	7.18 ± 0.14	150,000	Live	1	1
7	5/28/92	APE I	2	1.81 ± 0.09	200,000	Live	B	1
8	5/29/92	PET	2	1.96 ± 0.10	150,000	Live	1	1
9	5/29/92	PET	5	5.07 ± 0.05	120,000	Dead	1	1
10	6/1/92	APE I	7	7.28 ± 0.09	120,000	Live	B	1
11	6/1/92	APE I	2	2.33 ± 0.14	200,000	Live	A	1
12	6/1/92	APE I	5	4.77 ± 0.09	200,000	Live	A	1
13	6/2/92	PET	7	7.24 ± 0.06	160,000	Dead	2	1
14	7/27/92	APE II	2	2.68 ± 0.09	50,000	Live	—	4
15	7/27/92	APE II	2	2.52 ± 0.11	50,000	Live	—	4
16	8/7/92	APE II	8	8.59 ± 0.12	50,000	Live	—	4
17	8/7/92	APE II	8	8.48 ± 0.14	50,000	Live	—	4
18	12/6/93	PET	7	7.26 ± 0.10	100,000	Beads	1	0.5
19	12/6/93	PET	5	4.39 ± 0.07	100,000	Beads	2	0.5
20	12/6/93	PET	2	1.73 ± 0.04	100,000	Beads	1	0.5

box. All sediment and water in each depression was evacuated into a beaker via a vacuum pump and washed through a 125 μm sieve. Meiofauna were rinsed into a 100 ml jar and preserved in buffered formalin with Rose Bengal. All meiobenthic copepods in the samples were identified to species and enumerated.

b. *Habitat selection.* To determine if meiobenthic copepods actively select or avoid different types of sediment, we conducted a preference experiment in still water. Two treatments were utilized: heat treated and non-heat treated, but algal-enriched sediment. The purpose was to identify a sediment that copepods would distinctly prefer. The putative non-preferred sediment was washed through 0.5 mm sieve with distilled water and heated at 100°C for 24 hr to kill and remove meiofauna. The putative preferred sediment was collected from the field the day before the experiment and sieved through 0.125 mm sieve with filtered sea water. After settling for one night and removing standing water, sediment was mixed with the freeze-killed planktonic alga, *Isochrysis galbani.* Preference experiment chambers were circular (20.5 cm i.d.) and 18 cm in depth. The bottom of the chamber was covered with sand (an undesirable substrate for mud-dwelling copepods) to about 10 cm. Three pairs of vials (14 mm inner diameter) were buried into the sand with tops flush with the

surface at three different locations (at equal distances between locations) close to the wall of chamber. Each depression of the pair was filled with one sediment type (either algal enriched or non-enriched), and located next to each other. The meiobenthic copepods *Coullana sp.* (formerly called *Scottolana canadensis* in Louisiana citations) and *Cletocamptus deitersi* (Richard) were collected from a local mudflat. Two replicate trials were conducted by releasing about 1000 copepods in the center of the chamber by first adding them to a plastic cylinder touching the bottom and then gently pulling the cylinder away. Vials were collected after 2 hr, and the number of copepods enumerated.

c. Passive Expectations Test (PET). We tested the hypothesis that copepods are deposited in flow as passive particles by comparing the distribution of live copepods and passive particles among pits expected to differ in hydrodynamic characteristics. Depressions were constructed of acrylic cylinders inset in an acrylic plate with the top of each cylinder flush with the plate surface. The acrylic cylinders were 4 cm deep and were filled with 3 cm of azoic sediment, yielding 1 cm deep pits. Four different cylinder diameters (1.9, 2.5, 4.4, and 5.7 cm, hereafter referred to as Pits A, B, C, and D respectively) were employed to generate depressions that varied in aspect (depth to diameter) ratio (0.53, 0.40, 0.23, and 0.18 respectively). The four pit diameters were deployed in a Latin-square design with four rows and four columns with rows oriented with the direction of flow (Fig. 1a). Trials were conducted at nominal flow velocities of 2, 5, and 7 cm sec^{-1} (Table 1) in May and June 1992.

The randomization procedure chanced to produce a distribution in which each pit diameter was non-randomly associated with the pit diameter of upstream and downstream neighbors (a close inspection of Figure 1a reveals a consistent neighboring of pit diameter on both up- and downstream sides). This distribution of pit diameters could lead to inaccurate conclusions about the particle trapping characteristics of a given pit size if trapping characteristics are effected by a turbulent eddy behind upstream depressions. To test for this possible effect, we repeated two of the trials in this experiment with the entire array of pits in both of the two possible orientations with respect to flow (Fig. 1a; Table 1), thus reversing the up/downstream relationship of the pits.

Our *a priori* expectations, based on the particle trapping characteristics of free-standing cylinders (Lau, 1979; Yund *et al.*, 1991), were that higher aspect ratio depressions would trap more passive particles per pit surface area than would lower aspect ratio pits. Eddies associated with high aspect-ratio cylinders are less likely to remove settled particles. To generate actual rankings of pits, we conducted flume trials with two different types of passive particles; freeze-killed copepods and polystyrene DVB microspheres. At nominal flow velocities of 5 and 7 cm sec^{-1}, one passive particle trial was conducted with each pit array orientation. One orientation was tested with dead copepods, while the other was tested with beads (Table 1). At
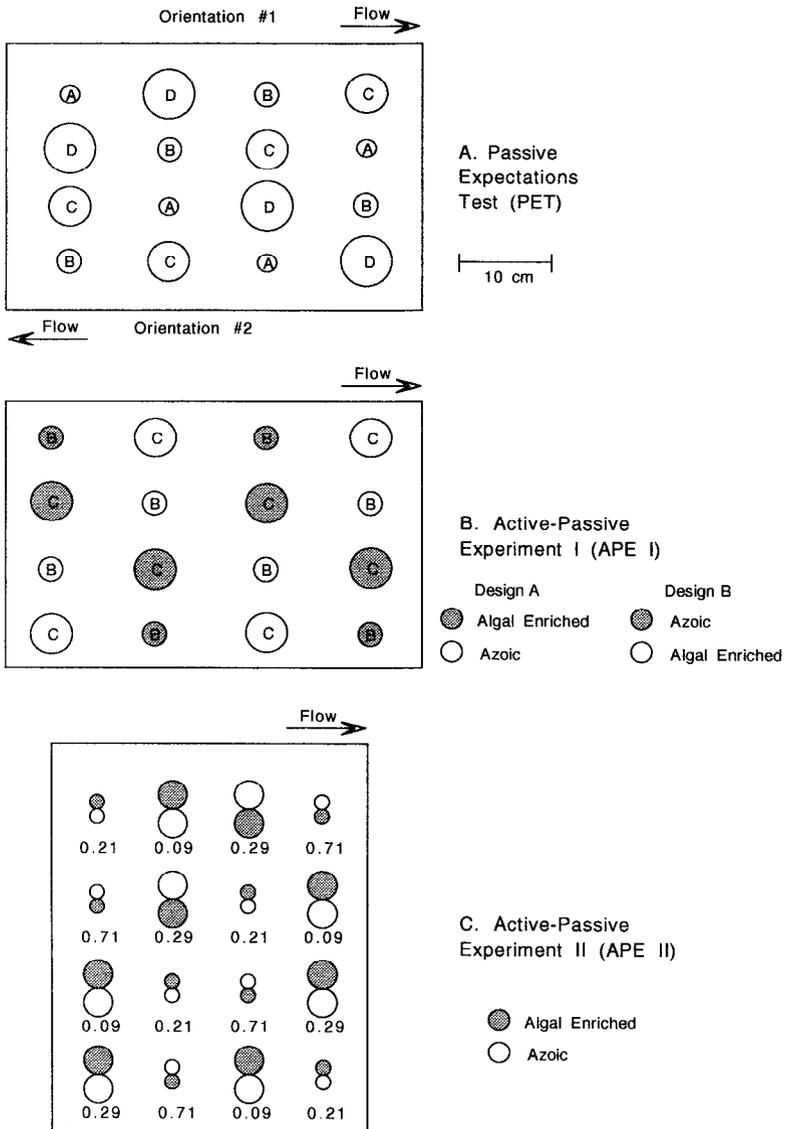
Figure 1. Experimental design for the arrangement of pits in the (A) Passive Expectations Test (PET), (B) Active-Passive Experiment I (APE I) and (C) Active-Passive Experiment II (APE II). Pit diameters are drawn to scale and designated as follows: A, 1.9 cm; B, 2.5 cm; C, 4.4 cm; D, 5.7 cm (except in APE II where aspect ratios are provided). PET trials were conducted with the array of pits oriented in two different directions with respect to the direction of flow (A). APE I trials were conducted with non-enriched vs. algal enriched sediment treatments distributed among pits in two different patterns, as indicated by hatched pits and design keys A and B. APE II was conducted with only one orientation and utilized closely-paired pits with and without algal enrichment.

the nominal flow velocity of 2 cm sec^{-1}, only a single polystyrene-bead passive-particle trial was conducted.

Data from this experiment were analyzed via a series of linear models (ANOVA). Separate analyses were conducted within live and dead trials for each of the four most abundant species and for all copepods grouped. Identical analyses were conducted for trials utilizing beads. For each of these dependent variables, raw counts in each pit were divided by pit surface area to yield a measure of copepods or beads per unit area. The model for each dependent was a Latin-square design with row, column, and pit size (aspect ratio) as main factors. The four levels within the two factors, row (1, 2, 3, and 4) and pit aspect ratio (A, B, C, and D), were ranked by the mean number of each dependent variable captured per unit area. Although column was included as a factor in each model, the relative ranking of column capture efficiency is not presented because column effects were rarely significant and no consistent patterns were detected (suggesting that wall effects were minimal). These analyses test only the two-tailed hypothesis that capture rates varied as a function of any of the three factors. To increase the precision of our hypothesis testing in the live-animal analyses, we also converted the results of these nondirectional heterogeneity tests to one-tailed, ordered heterogeneity tests (hereafter OH tests; Rice and Gaines, 1994a, b) in which expected pit-size rankings were based on the observed ranks of passive particles (either dead meiofauna or beads, depending on the passive particle trial that matched the flow speed and array orientation of the live-animal trial). This approach allowed us to explicitly test for deviation from an expected ranking among pit aspect ratios, rather than just testing the less specific "two-tailed hypothesis" that pit aspect ratio had some unspecified effect on captures.

d. Active-Passive Experiment I (APE I). We tested for habitat selection in flowing water by presenting copepods with pits containing non-enriched and algal-enriched sediment produced as in the habitat selection experiment above. We simultaneously incorporated a test for passive deposition by utilizing two different pit sizes that were expected to differ in their propensity to trap particles (as described in PET above). Pits were again constructed of acrylic cylinders inset in an acrylic plate so that the top of each cylinder was flush with the plate surface. Two different cylinder diameters (2.5 and 4.4 cm, Pits B and C) alternated in an offset blocked design of four rows and columns (Fig. 1b). Cylinders were filled with three cm of either algal-enriched or non-enriched sediment producing 1-cm deep pits. The two sediment treatments were paired with their neighboring equal-sized pit (a distance of several cm) in two different designs (Fig. 1b). Trials were conducted at three different flow velocities (2, 5, and 7 cm sec^{-1} nominal velocity) concurrent with PET trials. Trials with both treatment position designs were conducted at 2 and 7 cm sec^{-1} flow velocities, while only the A design was run at 5 cm sec^{-1} (Table 1).

We analyzed this experiment as a randomized block design, where rows served as blocks on the settling grid (Fig. 1b). The model also allowed us to examine the effect of algal treatment (algal-enriched or non-enriched sediment) and aspect ratio (of the two pit sizes used) as main effects on the number of live copepods collected in each pit type. Flume run replication was also a main effect in the model, except at 5 cm sec^{-1} when only one replication was performed. The analysis was conducted on total copepods and the four most abundant species. *A posteriori* tests were conducted using Tukey's Studentized Range test.

e. Active-Passive Experiment II (APE II). The role of post-settlement behavior in habitat selection in flowing water was examined by presenting copepods with closely-paired pits containing non-enriched and algal-enriched sediment over a 4-hr period. We again incorporated a test for passive deposition by utilizing different pit sizes that were expected to differ in their ability to trap particles (as described in PET and APE I above). Depressions in APE II were again constructed of acrylic cylinders except that two pit diameters, 1.4 and 3.2 cm, and two pit depths, 0.3 and 1 cm were used. Pit aspect ratios were 0.09, 0.21, 0.31, and 0.71, and represent a slightly larger range than those used in PET and APE I. Sixteen locations, four rows and four columns, were selected in the tray. A multiple Latin-square design was employed. Rows and columns were randomized and each row and column had four different diameter and depth combinations (Fig. 1c). At each location, two depressions of the same diameter and depth were paired and adjacent (2 mm distant). Before the experiment, the paired depressions in each location were randomly filled with algal-enriched or non-enriched sediments to the appropriate depth. The remaining area of the tray was filled with defaunated sediment. The flume settlement ex-periment was conducted at two different but constant nominal velocities (2 and 8 cm sec^{-1}) in July and August, 1992. For each flow rate, two replications were performed.

Data were standardized to pit surface area for each observation. Residual analyses for normality were performed after data transformation, $\ln(x + 1)$. The result indicated approximate normality for all data analyzed ($W > 0.96, P > 0.2$, Shapiro and Wilk, 1965). A split-plot model was adopted as the experimental design. The main effect was pit size (aspect ratio) with a multiple Latin square arrangement. The subplot effect was algal treatment (enriched vs. non-enriched). The two replications at each flow velocity served as multiple square effects, and row and column effects were modeled such that effects were nested within replicates. Error I and II are pooled error terms to test main effects (main plot, pit size) and subplot (algal treatment). A Tukey multiple comparison test was also used to detect aspect-ratio effects within each treatment-sediment type.

3. Results

Flow visualizations clearly showed that dye entered pits at its downstream edge before entering a gyre that carried it toward the upstream edge. Then, depending on the pit depth and water velocity, dye was either carried out of the top of the pit or back around within the pit. In the deepest pits and at the lowest velocity flows, some dye remained in the bottom of the pits. Although residence time varied among pits, the qualitative pattern did not, closely resembling the circulation pattern in free-standing cylinders presented in Butman *et al.* (1986) in that dye stayed for a much longer time at the slower velocities in smaller and deeper depressions.

a. Habitat selection. In standing water, the algal-enriched sediment was clearly preferred over the heat-treated, non-enriched sediment. Copepod mean abundance in treatments with algal-enriched sediment was 250 and 194 individuals per vial in two trials, while only 55 and 24 were found in treatments with non-enriched sediment. The average density in preferred sediment was highly significantly greater than in non-preferred sediment ($P < 0.001$, t-test).

b. Passive Expectations Test (PET). In the concurrent PET and APE I experiments, four copepod species were abundant enough to warrant analysis. Life history information (from Sun and Fleeger, 1994) suggests that *Coullana* sp. is an epibenthic harpacticoid species, with adult females about 1.2 mm in length, that freely moves into the water column, especially as copepodites. *Pseudostenhelia wellsi* Coull and Fleeger is a tube-dwelling, strongly infaunal harpacticoid about 0.5 mm in length (see Chandler and Fleeger, 1984), *Cletocamptus deitersi* is an epibenthic harpacticoid species about 0.8 mm in length and *Nannopus palustris* Brady is a harpacticoid infaunal burrower about 0.75 mm in length; all four were abundant in PET and APE I trials. In APE II, conducted several weeks later, *Coullana* sp. and *Halicyclops coulli* Herbst (an epibenthic cyclopoid species about 0.7 mm in length) were abundant and examined in detail. Total copepods were also examined in all experiments.

We first tested our *a priori* expectations of the relative capture efficiency of the four pit sizes for passive particles by assaying the distribution of beads per pit unit surface area at each of the three nominal flow velocities (Fig. 2). Our expectation that higher aspect-ratio pits would capture more particles per unit area was only met at the lowest (2 cm sec^{-1}) nominal flow velocity. There was a significant effect of pit size (Table 2, trial 20, test 11), and the relative capture ranking of the pits was A > B > C > D (Table 2; Fig. 2a). There was also a significant effect of row, with the rows ranked 1 > 2 > 3 > 4 in decreasing order of number of particles trapped (Table 2; trial 20, test 11). At both of the higher nominal flow velocities (5 and 7 cm sec^{-1}), pit size did not significantly affect bead captures (Table 2, trials 19 and 18). A comparison of the relative capture efficiency of the pits across flow velocities reveals an interesting pattern (Fig. 2). As flow velocity increased, the relative capture

Passive Particles

A. 2 cm/s

B. 5 cm/s

C. 7 cm/s

Beads/cm ^{2}

0.53   0.4   0.23   0.18
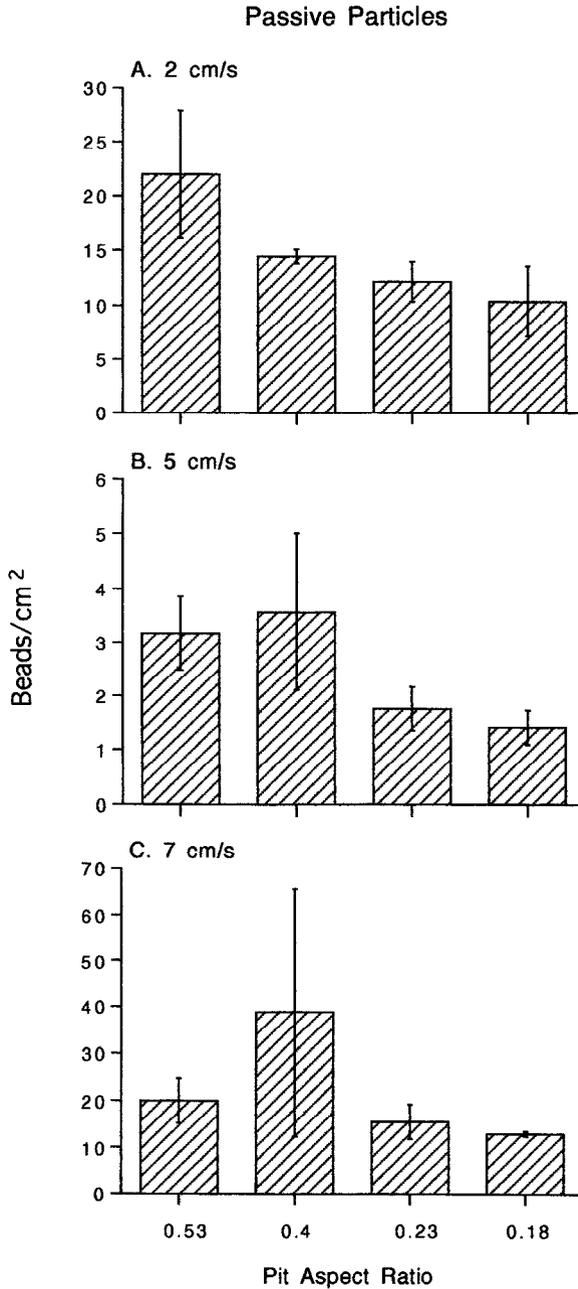
Pit Aspect Ratio

Figure 2. Distribution of beads in the four pit aspect ratios at 2 (A), 5 (B), and 7 (C) cm sec^{-1} flow velocities. Means are reported for $N = 4$ pits and error bars represent one standard error. In the text, pits are labelled A through D to designate the highest through lowest aspect ratio pits respectively.

Table 2. ANOVA results from the PET trials. Each line gives the *F*-ratios, significance levels, and within Row and Pit Size rankings for a single analysis. All models have three effects (Row, Column, and Pit Size), and each effect has 3 d.f. Relevant comparisons are either between the same dependent variables from live vs. dead trials or between the live dependent variables and beads. In both cases, analyses to be compared are separated by single lines and bounded by double lines. Ordered heterogeneity (OH) tests were conducted for pit size effects for each live dependent variable. For each OH test, the data set employed to generate the expected pit size ranking via passive deposition is indicated by the 'versus' test number.

Nominal Velocity	Orient.	Trial	Dependent	Test #	Effect F-ratio's			Within Effect Ranks		OH Test
					Row	Column	Pit Size	Row	Pit Size	Versus
2 cm/s	1	2 (L)	*Coullana*	1	0.99	0.64	1.70	1 > 4 > 2 > 3	B > A > C > D	#11*
			Pseudostenhelia	2	1.80	13.86***	13.74***	1 > 2 > 3 > 4	B > A > C > D	#11**
			Cletocamptus	3	0.96	4.18	4.94*	1 > 2 > 4 > 3	B > C > A > D	#11 NS
			Nannopus	4	1.68	2.71	4.70*	1 > 2 > 3 > 4	B > A > C > D	#11*
			Total Copepods	5	1.97	7.71*	10.76**	1 > 2 > 3 > 4	B > A > C > D	#11**
		8 (L)	*Coullana*	6	0.90	2.70	0.76	2 > 4 > 1 > 3	A > B > C > D	#11 NS
			Pseudostenhelia	7	1.17	2.75	2.16	1 > 2 > 3 > 4	B > A > C > D	#11*
			Cletocamptus	8	0.95	0.13	0.30	1 > 3 > 4 > 2	B > C > A > D	#11 NS
			Nannopus	9	0.31	1.51	1.38	4 > 2 > 1 = 3	B > A > C > D	#11 NS
			Total Copepods	10	0.30	3.14	2.35	2 > 1 > 4 > 3	B > A > C > D	#11*
		20	Beads	11	5.48*	1.21	4.67*	1 > 2 > 3 > 4	A > B > C > D	NA
5 cm/s	1	1 (L)	*Coullana*	12	4.51	6.12*	1.20	1 > 2 > 4 > 3	B > C > A > D	#17 NS
			Pseudostenhelia	13	6.76*	3.56	1.10	1 > 2 > 4 > 3	B > C > A > D	#18 NS
			Cletocamptus	14	6.43*	2.73	0.95	1 > 2 > 4 > 3	B > C > D > A	#19 NS
			Nannopus	15	7.88*	3.44	1.22	1 > 2 > 4 > 3	B > C > A > D	#20 NS
			Total Copepods	16	6.73*	4.47	1.09	1 > 2 > 4 > 3	B > C > D > A	#21 NS
		9 (D)	*Coullana*	17	6.27*	1.51	0.82	1 > 2 > 3 > 4	B > A > C > D	NA
			Pseudostenhelia	18	7.84*	1.22	1.18	1 > 2 > 3 > 4	B > A > C > D	NA
			Cletocamptus	19	5.68*	1.29	1.92	1 > 2 > 3 > 4	B > A > C > D	NA
			Nannopus	20	8.35*	1.52	2.85	1 > 4 > 3 > 2	A > B > C > D	NA
			Total Copepods	21	6.52*	1.44	0.94	1 > 2 > 3 > 4	B > A > C > D	NA

Table 2. (Continued)

Nominal Velocity	Orient.	Trial	Dependent	Test #	Effect F-ratio's			Within Effect Ranks		OH Test
					Row	Column	Pit Size	Row	Pit Size	Versus
5 cm/s	2	4 (L)	*Coullana*	22	1.53	1.33	4.18	1 > 3 > 2 > 4	A > C > D = B	#27 NS
			Pseudostenheliam	23	0.85	3.79	7.46*	1 > 3 > 4 > 2	C > A > D > B	#27 NS
			Cletocamptus	24	0.48	7.32*	1.10	1 > 3 > 4 > 2	C > A > B > D	#27 NS
			Nannopus	25	0.61	1.35	0.95	4 > 2 > 3 > 1	A > D > C > B	#27 NS
			Total Copepods	26	0.62	5.38*	1.80	1 > 3 > 4 > 2	A > C > D > B	#27 NS
		19	Beads	27	1.45	1.45	1.90	3 > 2 > 4 > 1	B > A > C > D	NA
7 cm/s	2	3 (L)	*Coullana*	28	3.55	0.98	0.22	1 > 2 > 4 > 3	B > C > D > A	#33 NS
			Pseudostenhelia	29	4.19	1.04	0.22	1 > 2 > 3 > 4	C > B > D > A	#34 NS
			Cletocamptus	30	0.90	1.75	0.80	1 > 3 > 2 > 4	C > B > D > A	#35 NS
			Nannopus	31	1.01	0.92	0.89	3 > 1 > 4 > 2	A > B > D > C	#36 NS
			Total Copepods	32	5.12	2.26	0.41	1 > 2 > 3 > 4	B > C > D > A	#37 NS
		13 (D)	*Coullana*	33	7.76*	2.03	0.29	1 > 2 > 4 > 3	C > B > D > A	NA
			Pseudostenhelia	34	8.36*	1.10	0.36	1 > 2 > 3 > 4	C > B > D > A	NA
			Cletocamptus	35	5.85*	0.40	0.37	1 > 2 > 4 > 3	B > C > D > A	NA
			Nannopus	36	10.43*	1.92	0.64	1 > 2 > 4 > 3	B > C > D > A	NA
			Total Copepods	37	10.35*	1.40	0.35	1 > 2 > 4 > 3	C > B > D > A	NA
7 cm/s	1	6 (L)	*Coullana*	38	7.42*	1.90	2.41	1 > 2 > 4 > 3	A > B > C > D	#43*
			Pseudostenhelia	39	9.65*	3.74	2.20	1 > 3 > 2 > 4	B > A > C > D	#43**
			Cletocamptus	40	5.92*	2.22	1.36	1 > 2 > 3 > 4	B > A > C > D	#43*
			Nannopus	41	2.47	1.11	0.26	1 > 3 > 2 > 4	B > C > D > A	#43 NS
			Total Copepods	42	8.97*	2.62	1.91	1 > 2 > 3 > 4	A > B > C > D	#43*
		18	Beads	43	1.40	2.17	1.07	1 > 3 > 2 > 4	B > A > C > D	NA

L = Live, D = Dead; NA = Not Applicable (test not conducted). NS = not significant. *$P < 0.05$ **$P < 0.01$ ***$P < 0.005$

efficiency of Pit A decreased, yielding the highest capture efficiency for Pit B (Fig. 2b, c).

Although our *a priori* expectations of pit trapping characteristics were not met in all flow velocities, the distributions of the two types of passive particles among pits nevertheless yielded a valid capture expectation based on passive deposition. Unfortunately, the reduction in the relative capture efficiency of Pit A also tended to reduce the magnitude of pit size effects and decreased the likelihood for statistically significant effects. It is disconcerting that pits did not always yield significant differences in the capture of passive particles (i.e., we therefore must compare the distribution of live copepods against a non-significant passive pattern). However as shown below, the rankings for live and passive comparisons were quite consistent between replicate runs (even though they may have been very different numerically) adding confidence to our results. In addition, the ANOVA approach tests only the relatively weak, two-tailed hypothesis that pit size affects particle captures, while our hypothesis predicts that the effect of pit size on live copepod capture will coincide with the effect of pit size on passive particle capture. Consequently, we used the observed pit-size rankings for beads and dead copepods as our expected pit-size effect, and converted the pit-size results from our ANOVA's to test directional hypotheses by using the ordered heterogeneity (OH test) method of Rice and Gaines (1994a, b). A P value < 0.05 in these tests indicates that the pit-size effect in the live dependent analysis did not differ significantly from the passive expectation. In addition, given the large number of statistical tests conducted to analyze the PET experiment, our results may have been influenced by type I error.

For trials conducted at nominal velocities of 5 and 7 cm sec^{-1}, we have matching data sets for live and dead copepods (Table 2, trials 1 and 9 and 3 and 13 respectively). Across all dependent variables (except live *Coullana* sp.) in the 5 cm sec^{-1} trials there was a significant effect of row (Table 2, trials 1 and 9). Rows 1 and 2 displayed the sequentially highest captures in 9 out of the 10 analyses (Table 2). The single exception (dead *Nannopus palustris*) showed a row ranking of 1 > 4, but was based on exceedingly small sample sizes (*N. palustris* was consistently the rarest copepod in all PET and APE I trials). Pit-size effects were not significant in any of the 10 analyses. Nevertheless, the relative ranking of pits was strikingly consistent across analyses. Pit B captured the most copepods in 9 out of the 10 analyses, followed by either Pit A or C (Table 2; Fig. 3). The sole exception was again for the dependent variable dead *N. palustris,* for which Pit A was ranked highest (Fig. 3c). None of the OH tests comparing pit-size effects for each live dependent with the pit ranking generated by the corresponding dead dependent were significant. However, with the exception of *N. palustris* (tests 15 and 20), all pairs of runs differed in pit-size rankings by no more than two positions (either A/C or A/D inversions in the second through fourth ranked positions; Fig. 3). Similarly, row rankings differed by only one position (inversion of the 3rd and 4th ranked rows; Table 2).

PET, 5 cm/s, Orientation 1
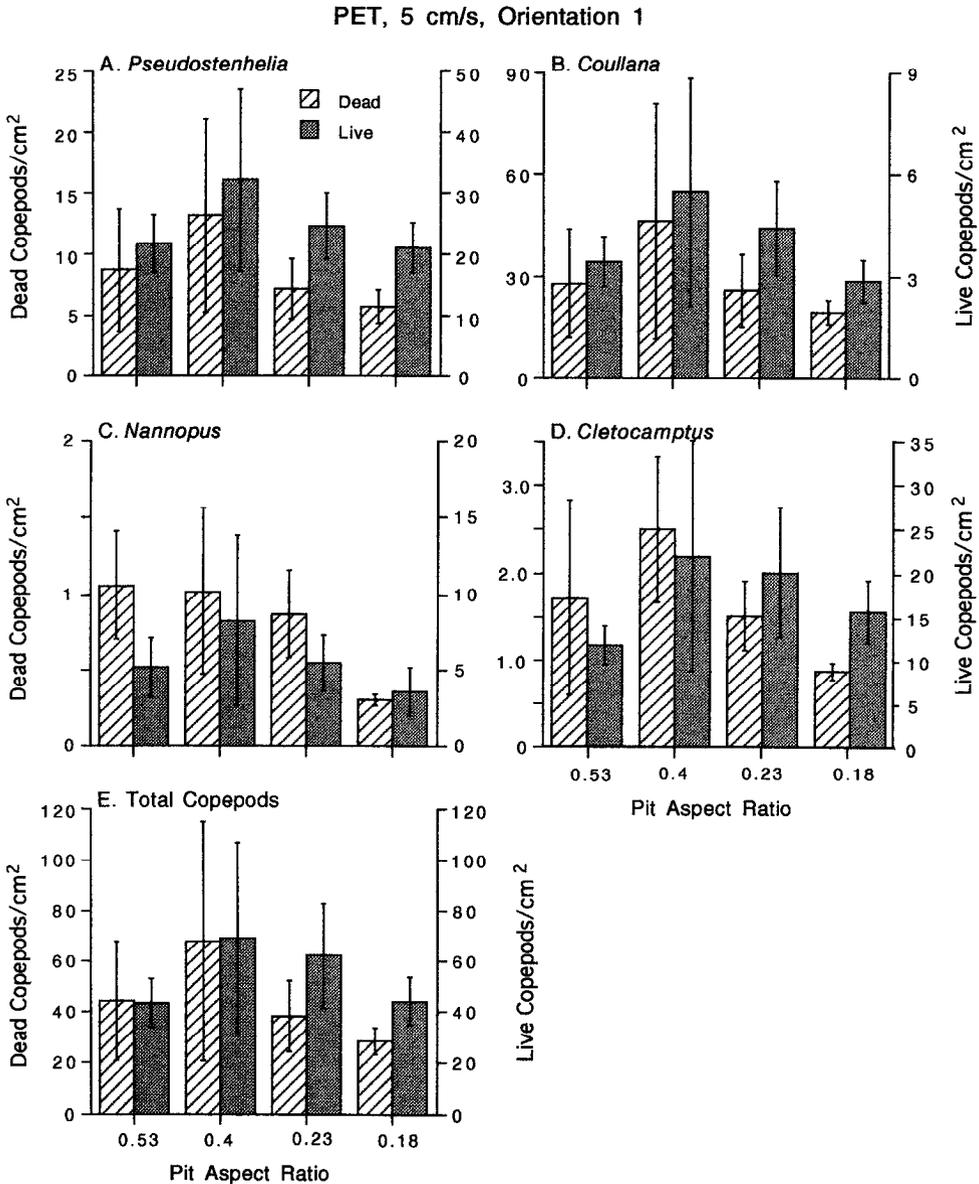
Figure 3. Distribution of live and dead copepods in the four pit sizes in the two trials conducted at a nominal flow velocity of 5 cm sec^{-1} and with the pits in orientation 1 (trials #1 and 9). Means for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D), and the total number of copepods (E) are reported for $N = 4$ pits. Error bars represent one standard error. The distribution of live copepods within each panel should be compared to the distribution of dead copepods, which generate an expected distribution based on passive deposition. In the text, pits are labelled A through D to designate the highest through lowest aspect ratio pits respectively.

The 7 cm sec^{-1} trials comparing live and dead copepods showed a similar pattern (Table 2; Fig. 4). Row effects were significant for all dead dependents and none of the live dependents (Table 2; trials 3 and 13). However, Row 1 had the highest captures for all dependents except live *N. palustris,* and live/dead dependent pairs either had identical row rankings (*Coullana* sp. and *Pseudostenhelia wellsi*) or differed in the ranking of only one row (*C. deitersi* and total copepods; Table 2). Pit-size effects were not significant in any analysis (Table 2), but with the exception of live *N. palustris,* pit rankings were all either B > C > D > A or C > B > D > A (Fig. 4). Pit rankings thus differed only in the relative position of Pits C and B, which had mean captures that were exceedingly close for all dependents (Fig. 4). In spite of the similar patterns, all OH tests comparing pit-size effects for live dependents with the pit rankings of corresponding dead dependents were not significant. Thus, while we cannot statistically exclude the possibility that the distribution of live dependents differed from that of the passive dead dependents, the magnitude of the deviations appears to be very small.

The remaining live copepod trials were all compared to bead trials conducted at the same nominal velocities and pit array orientations. At 2 cm sec^{-1}, bead deposition was significantly affected by row and pit size, with rows ranked 1 > 2 > 3 > 4 and pit sizes ranked A > B > C > D (Table 2, trial 20, trial 11). The distribution of live copepods in both trials 2 and 8 can be compared to these passive expectations (Fig. 5). ANOVA pit-size effects were significant for 4 out of the 10 live dependent variables (Table 2, tests 2–5). More importantly, pit-size effects did not differ significantly from the expectations generated by passive bead deposition in 6 out of the 10 OH tests (Table 2, tests 1, 2, 4, 5, 7, and 10). For 8 out of 10 of the live dependents, Row 1 had the highest captures (exceptions are *Coullana* sp. and *N. palustris* in trial 8). Three out of the 10 dependents had rows ranked 1 > 2 > 3 > 4 (the same as the bead row ranking), while the remainder each had one row displaced from this ranking by either one or two positions (except *N. palustris* in trial 8, which had a 4 > 2 > 1 = 3 row ranking).

At 5 cm sec^{-1}, bead counts were not significantly affected by row or pit size (Table 2, trial 19). Inexplicably, row rankings differed dramatically from all others in this study (3 > 2 > 4 > 1). Pit-size ranking were B > A > C > D (Figs. 2b and 6f). In contrast, live copepod data (tests 22–26) show row rankings of either 1 > 3 > 4 > 2 or 1 > 3 > 2 > 4 (except for *N. palustris:* 4 > 2 > 3 > 1), and pit-size rankings with C and A ranked higher than B and D (again, *N. palustris* differs slightly from this pattern). The OH tests indicate that all live dependent variables exhibit a pit-size effect that differs from the bead deposition pattern (Table 2, trial 2). Only in this one set of comparisons did passive beads and live copepods appear to respond to the hydrodynamics of the pit array in rather different ways.

At the nominal flow velocity of 7 cm sec^{-1}, bead counts were not significantly affected by row or pit size (Table 2, trial 18). Row rankings were 1 > 3 > 2 > 4 while

PET, 7 cm/s, Orientation 2
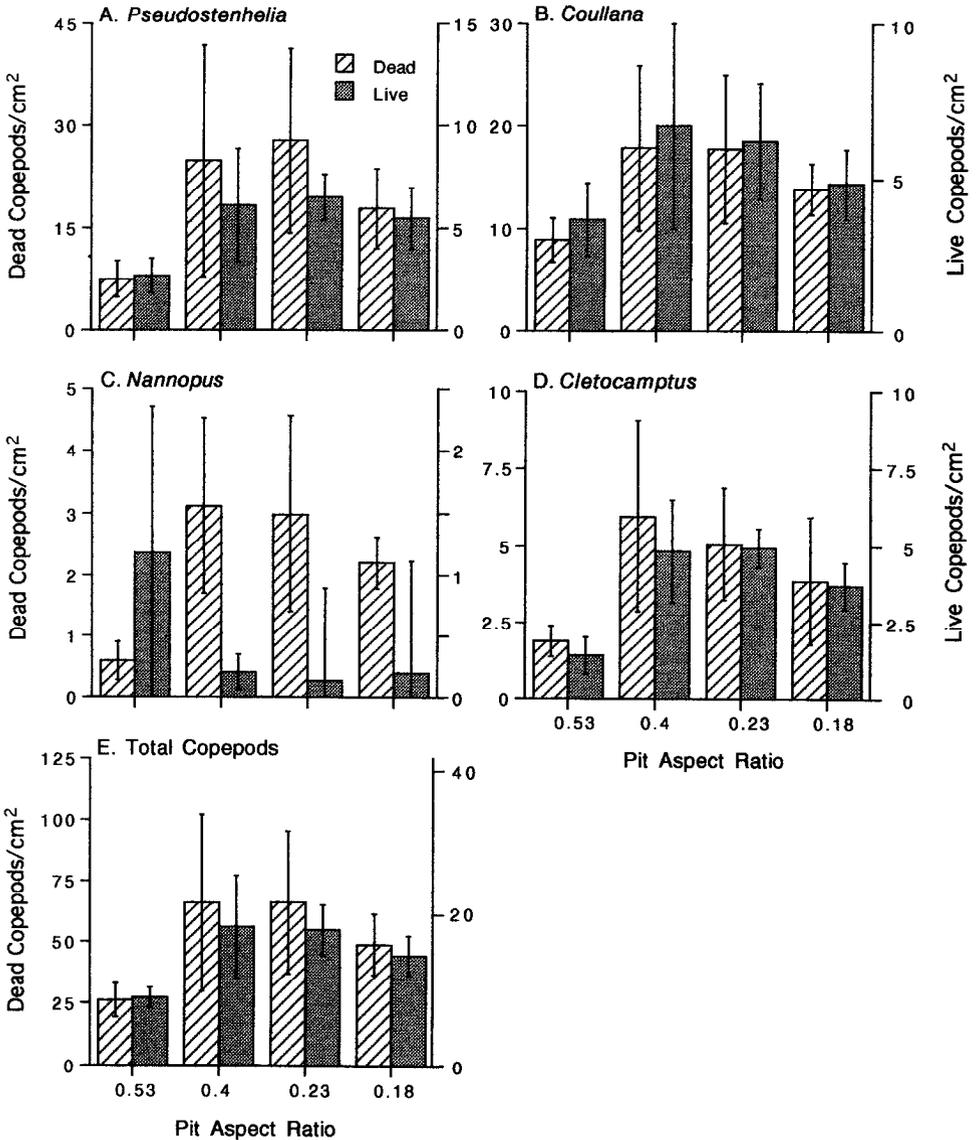
Figure 4. Distribution of live and dead copepods in the four pit sizes in the two trials conducted at a nominal flow velocity of 7 cm sec^{-1} and with the pits in orientation 2 (trials #3 and 13). Means for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D), and the total number of copepods (E) are reported for $N = 4$ pits. Error bars represent one standard error. The distribution of live copepods within each panel should be compared to the distribution of dead copepods, which generate an expected distribution based on passive deposition. In the text, pits are labelled A through D to designate the highest through lowest aspect ratio pits respectively.

PET, 2 cm/s, Orientation 1
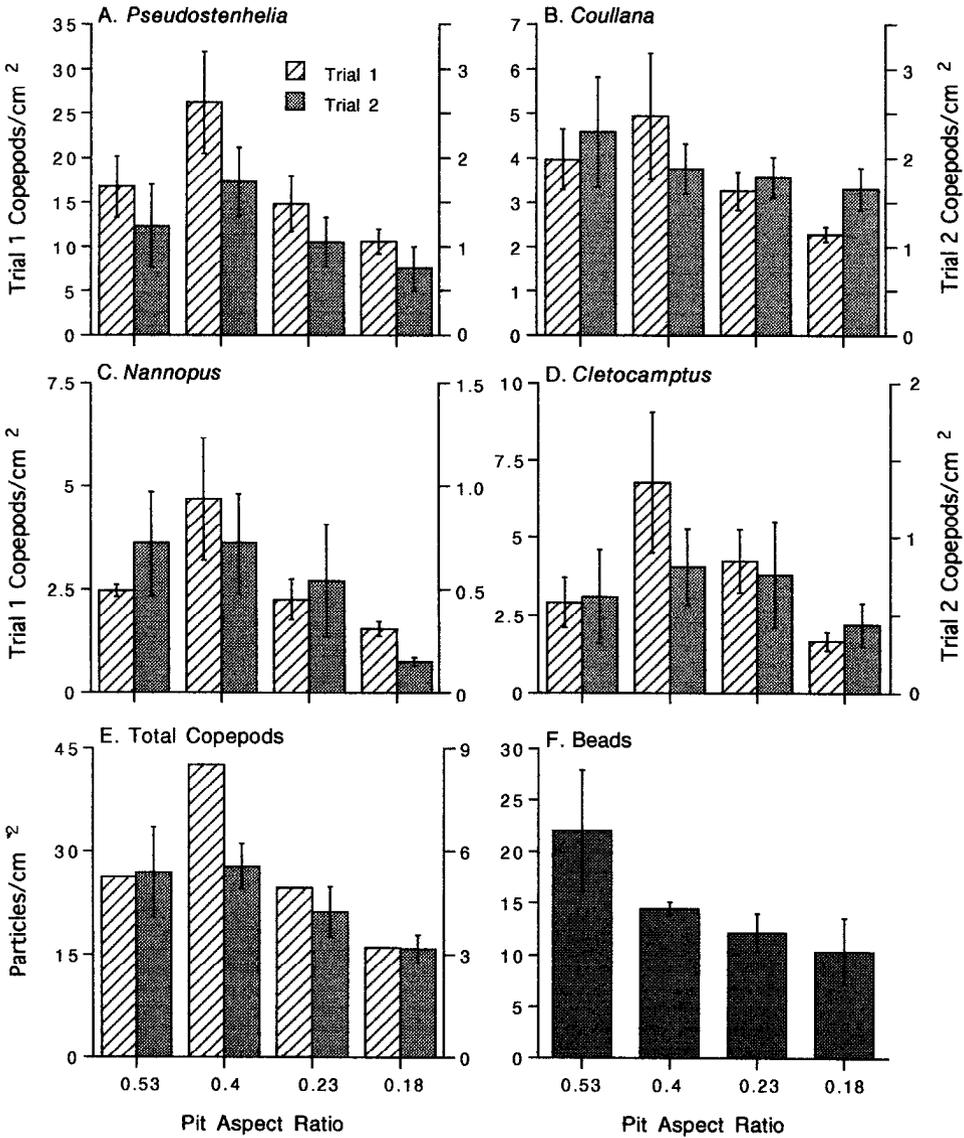
Figure 5. Distribution of live copepods and beads in the four pit sizes in the three trials conducted at a nominal flow velocity of 2 cm sec^{-1} and with the pits in orientation 1 (trials #2, 8, and 20). Means for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D), the total number of copepods (E), and the number of beads (F) are reported for $N = 4$ pits. Error bars represent one standard error. The distribution in both trials with live copepods (A–E) should be compared to the distribution of beads (F), which generate an expected distribution based on passive deposition.

pit-size rankings were B > A > C > D (Table 2; Fig. 7f). None of the live copepods exhibited a significant pit-size effect in the ANOVA analyses (Table 2, tests 38–42). Moreover, pit-size effects on live copepods did not differ from bead deposition patterns in 4 out of the 5 OH tests (Table 2, tests 38–40, 43).

Since our randomization procedure chanced to produce an experimental design in which pits were non-randomly associated with their up- and downstream neighbors (Fig. 1a), we conducted live copepod trials at nominal velocities of 5 and 7 cm sec^{-1} with the array of pits in two different orientations (reversed 180°) with respect to flow. These trials also varied in the total number of copepods released (Table 1), and probably in the relative abundance of different species as well. Consequently, we could not analyze pairs of trials with one model, with orientation as a main effect, because orientation and species abundance were not independent. Hence to assess possible orientation effects, we have to compare results between pairs of trials. At 5 cm sec^{-1} nominal velocity, the live copepod trial conducted in orientation 2 resulted in a markedly different pit aspect ratio ranking than the trial conducted in orientation 1 (Table 2, trials 4 and 1). Indeed, the results from this trial contrast strongly with all of our other results, and are not easily explainable. It is therefore tempting to conclude that orientation had an effect (due to interference among pits). However, the bead trial conducted in orientation 2 produced a pit ranking of B > A > C > D, consistent with the deposition of dead copepods in orientation 1 and similar to the B > C > A > D ranking of live copepods in orientation 1. If orientation affected depositional processes, passive particles should be affected as much as live copepods. At 7 cm sec^{-1} nominal velocity, orientation does appear to have had an effect on deposition patterns. In trials conducted in orientation 1, both live copepods and beads exhibit a A > B > C > D or B > A > C > D pit ranking (Table 2, trials 6 and 18), while in trials conducted in orientation 2, both live and dead copepods exhibit a B > C > D > A or C > B > D > A pit ranking (Table 2, trials 3 and 13). The possible existence of an orientation (or interference) effect does not negate our evidence of passive deposition. It does, however, dictate that comparisons be limited to trials conducted in the same orientation.

c. Active-Passive Experiment I (APE I). Analyses were conducted on the four most abundant copepods and total copepods (same species as PET) to test for active choice upon initial settlement and for passive settlement. The randomized-block ANOVA indicates that replicate flume runs differed in copepod abundance in 4 out of the 10 analyses. This is most likely due to differences in initial numbers of copepods added to the flume (see Table 1), but could have been related to the reversal of the pit array followed in each trial. Block (row position) effects were significant in 5 out of the 15 experimental trials (Table 3). When row positions varied, the first row always displayed the highest density. Aspect-ratio effects were significant in a total of 6 out of the 15 tests conducted over all species and flow rate

combinations (Table 3). All significant aspect ratio effects were at 2 and 5 cm sec^{-1}. Total copepod abundance was highly significantly related to pit size (aspect ratio) at 2 and 5 cm sec^{-1}, and of the species tested, only *C. deitersi* did not show an aspect-ratio effect at some velocity. Tukey's Studentized range test revealed that when a difference was indicated by ANOVA, B pits contained significantly more copepods per pit surface area than the larger C pits, and Figures 8–10 shows that the Pit B contained more copepods in 14 of the 15 trials for the various species and flow conditions. Thus, the smaller pit was the better collector, as would be predicted from hydrodynamic expectations, if copepods settle as passive particles.

Initial habitat selection was examined by comparing the abundance of copepods in algal-enriched and non-enriched pits. Abundances in enriched and non-enriched pits were nearly identical in all experimental trials, flow conditions and species (Figs. 8–10). Algal enrichment did not influence settlement intensity in any treatment or species (no significant algal-treatment effects, Table 3), clearly indicating the absence of active habitat selection upon initial settlement.

d. Active-Passive Experiment I (APE II). Boundary layers were well developed at both the 2 and 8 cm sec^{-1} nominal flow velocities (Fig. 11). At 1 cm above the bottom, the mean velocity increased from 0 to about 1.8 cm sec^{-1} under low flow while velocity increased from 0 to 6.6 cm sec^{-1} under high flow. At low flow, shear velocity (u_*) (0.2 cm sec^{-1}) was about one third of the high-velocity condition (0.6 cm sec^{-1}).

Significant differences in numbers of settled copepods were found between replicate flume runs under the same flow condition (Table 4). In non-enriched sediment, the results of ANOVA and Tukey multiple comparisons consistently indicated a significant aspect-ratio effect on the densities of *Coullana* sp., *H. coulli*, and total copepods under both low- and high-flow conditions (Tables 4 and 5). The densities of these species significantly increased with increasing depression aspect ratio under both flow conditions (Table 5 and Fig. 12) as would be predicted by passive hydrodynamic capture expectations. However, in algal-enriched sediment, the densities of the two species and total copepods did not show significant differences among different aspect-ratio depressions at the low velocity (Table 5). Significant density differences were found only at the high velocity. The range of aspect ratios for pits was greater in APE II (from 0.09 to 0.71) than in PET (0.18 to 0.53).

Highly significant differences were detected between the closely paired-pits containing algal-enriched or non-enriched sediment under the low-flow condition, suggesting post-settlement habitat selection over the 4-hr hour experiment (see algal enrichment effects, Table 4). *Coullana* sp., *H. coulli*, and total copepods were significantly greater in density in pits with algal-enriched sediment. The mean density of copepods in algal-enriched pits was about twice that of adjacent non-enriched pits in low-flow trials (Fig. 12). However, under a high-flow condition, no significant

PET, 5 cm/s, Orientation 2
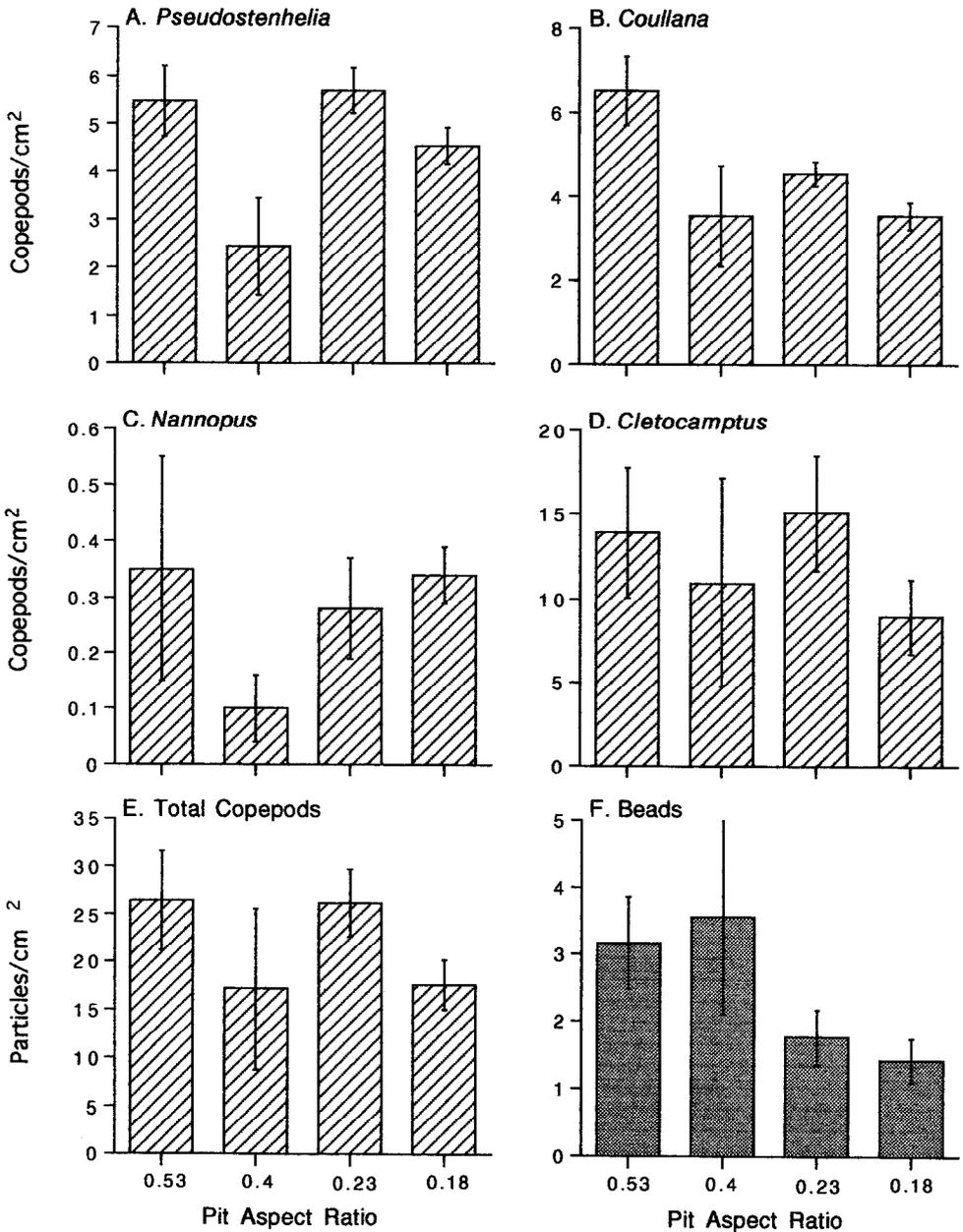
Figure 6. Distribution of live copepods and beads in the four pit sizes in the two trials conducted at a nominal flow velocity of 5 cm sec^{-1} and with the pits in orientation 2 (trials #4 and 19). Means for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D), the total number of copepods (E), and the number of beads (F) are reported for $N = 4$ pits. Error bars represent one standard error. The distribution of live copepods (A–E) should be compared to the distribution of beads (F), which generate an expected distribution based on passive deposition.
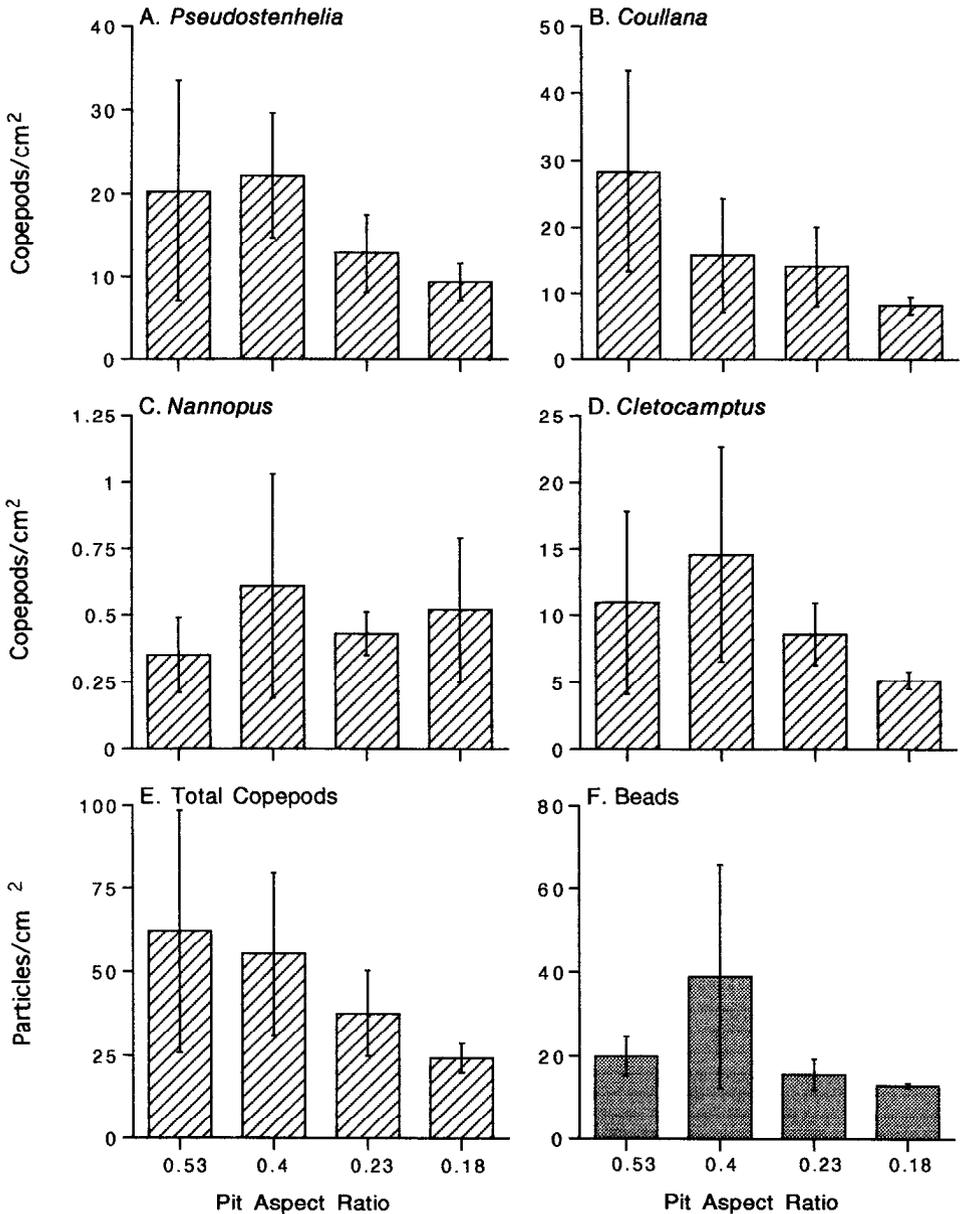
Figure 7. Distribution of live copepods and beads in the four pit sizes in the two trials conducted at a nominal flow velocity of 7 cm sec^{-1} and with the pits in orientation 1 (trials #6 and 18). Means for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D), the total number of copepods (E), and the number of beads (F) are reported for $N = 4$ pits. Error bars represent one standard error. The distribution of live copepods (A–E) should be compared to the distribution of beads (F), which generate an expected distribution based on passive deposition.

Table 3. Randomized-block ANOVA results from the APE I experiment. F-statistics are presented for four species and total copepods. REP refers to flume run (only one replicate run was performed at 5 cm sec^{-1}), ROW to the row position (block) and ALG to algal enrichment treatment.

	Flow (cm sec^{-1})		
	2	5	8
Coullana sp.			
REP	0.28		45.44**
ROW	0.70	1.35	2.27
PIT SIZE	0.71	7.96*	3.19
ALG	1.39	1.66	0.04
PIT SIZE * ALG	3.69	0.27	0.55
Pseudostenhelia wellsi			
REP	28.80**		0.03
ROW	1.59	5.17*	7.22**
PIT SIZE	14.51**	16.35**	2.20
ALG	0.01	5.20	0.03
PIT SIZE * ALG	1.70	0.51	0.02
Cletocamptus deitersi			
REP	48.76**		72.11**
ROW	0.41	2.48	6.57**
PIT SIZE	3.58	0.39	0.65
ALG	0.98	1.22	0.24
PIT SIZE * ALG	1.15	0.01	0.97
Nannopus palustris			
REP	1.21		2.94
ROW	0.46	1.09	3.79*
PIT SIZE	2.50	6.34*	0.04
ALG	0.82	0.02	1.09
PIT SIZE * ALG	0.49	1.26	0.57
Total copepods			
REP	0.43		3.40
ROW	1.14	5.36	6.48**
PIT SIZE	12.94**	19.40**	2.54
ALG	1.53	3.48	0.05
PIT SIZE * ALG	1.68	0.43	0.06

*$P < 0.05$; **$P < 0.01$.

difference in density was detected between the closely paired enriched and non-enriched pits (Fig. 12).

4. Discussion

As demonstrated by Decho and Fleeger (1988) and this study, meiobenthic copepods exhibit a significant preference for algal-enriched sediment over non-enriched sediment in still water. However, none of the four species (or total

APE I, 2 cm/s
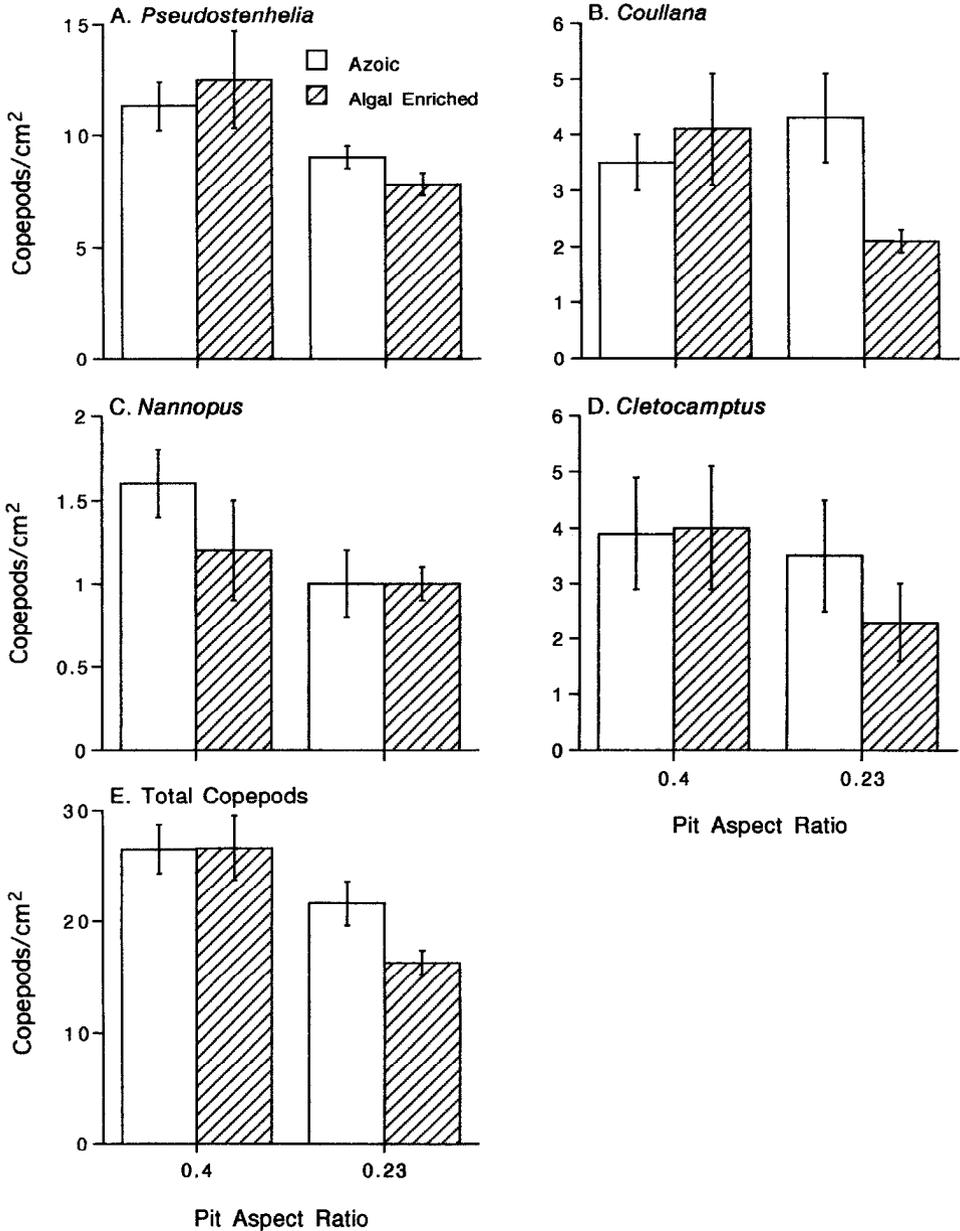
Figure 8. Distribution of copepods in two pit sizes in the APE I experiment conducted at a nominal velocity of 2 cm sec^{-1}. Mean densities for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D) and total copepods (E) are reported for two pit sizes. Error bars represent one standard error. Striped bars are algal-enriched pits and open bars, non-enriched pits.

copepods) tested in this study were able to exercise initial habitat selection in moving water (Active-Passive Experiment I, APE I, Figs. 8–10, Table 3). Similarly, many marine invertebrate larvae have been shown to be unable to select habitats in moving water, presumably because chemical cues from preferred habitats are diluted and dispersed in flowing water, and due to their inability to maneuver horizontally against high flow (Butman *et al.*, 1988b).

Moreover, the same copepods tested in moving water were generally deposited among pits in the same manner as passive particles. When we tested for passive deposition alone (Passive Expectation Test, PET), we found that in most cases at 2 and 7 cm sec^{-1} nominal flows, copepods and polystyrene beads exhibited the same deposition pattern among pits varying in aspect ratio (Table 2, ordered heterogeneity, OH, tests 1–10, 38–42). The two cases that differed from this pattern (Table 2, OH tests 3 and 41) did so only because of minor reversals between pairs of pits. The results of the OH tests against passive expectations based on dead copepods (Table 2, OH tests 12–16, 28–32) are less compelling, but differences between pit-size rankings are again generally only due to reversals in rank between single pairs of pits. The lack of statistically significant results in these tests is probably largely due to the low power induced by the small sample size dictated by the Latin square design, and due the unexpectedly poor capture efficiency of the smallest (A) pits, resulting in similar captures in the A and C Pits. In only one set of tests did we obtain results that differed strikingly from passive expectations. At 5 cm sec^{-1} flows, live copepods were distributed among pit sizes in a manner quite different from beads (Table 2, OH tests 22–26). In most of these cases there was a complete reversal of the highest- and lowest-ranked pit sizes. We have no explanation for this result, but it is possible that copepods may exhibit some flow-related settlement preferences under very specific sets of conditions. However, the contrast between this result and the passive deposition patterns exhibited under all other conditions in the PET experiment (and APE I and Active-Passive Experiment II, APE II) suggests that under most flow conditions, the deposition of meiobenthic copepods is predominately passive.

Independent evidence of passive deposition of meiobenthic copepods comes from the APE I and APE II experiments where a range of pit sizes were available for settlement. The APE I experiment was also run at a nominal 5 cm sec^{-1} flow and with the same copepod species as PET. Settlement densities in APE I generally conformed to passive expectations, especially at 2 and 5 cm sec^{-1} flows (note the significant aspect ratio effects for 6 out of the 15 analyses, Table 3). Figures 8–10 show that the smaller pit had consistently higher copepod abundance (in 14 of 15 observations) even though aspect ratios (0.40 and 0.23) for the two pit sizes used were very similar. In APE II, passive settlement expectations were met in high-velocity flows for both species abundant enough to warrant testing (and total copepods), and at low velocity in non-enriched pits (Table 4). The range of aspect

APE I, 5 cm/s
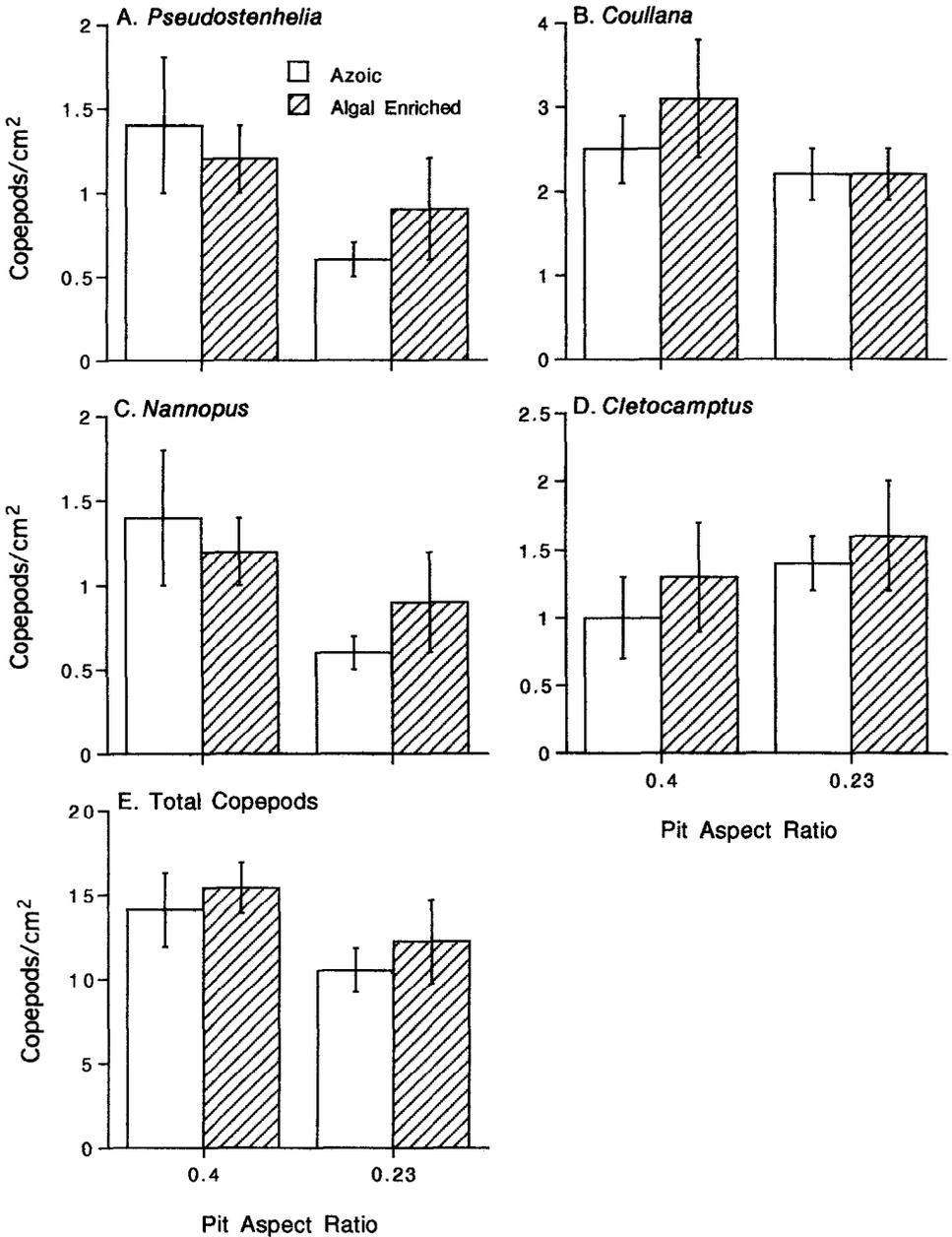
Figure 9. Distribution of copepods in two pit sizes in the APE I experiment conducted at a nominal velocity of 5 cm sec^{-1}. Mean densities for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D) and total copepods (E) are reported for two pit sizes. Error bars represent one standard error. Striped bars are algal-enriched pits and open bars, non-enriched pits.

ratios used in APE II was broader than in PET perhaps enhancing the likelihood of statistically significant results. Most importantly, in APE I and APE II when a difference was noted, the smaller depression (larger aspect ratio) always proved to be the better copepod collector.

We utilized past work with free-standing cylinders (Lau, 1979; Yund *et al.,* 1991) to generate *a priori* expectations of copepod and particle capture efficiency for the pit sizes used in these experiments. Depressions differ from settling traps in that pits are embedded with their tops flush with the surface and, as a result, depressions are likely to experience very different hydrodynamic regimes. The decreased capture efficiency of the smallest pit (aspect ratio of 0.53) in the PET experiment at higher flows (Fig. 2) was a primary example, and may have been caused by an extension of the turbulent eddy formed behind the upstream edge of the pit beyond the back-stream pit edge. Nevertheless, pit sizes used are representative of the natural microtopographic features that we mimicked (Sun and Fleeger, 1994), and our comparisons of live copepods to passive particles permitted valid tests of the hypotheses of interest. It is also possible that flow interference among pits may have taken place. Settlement was observed in the pit array using two orientations (achieved by turning the array 180°) and rather different results were obtained (e.g., see Table 2, trials 1 and 4). The short downstream distances between pits may not have allowed flow recovery between rows of the array (Snelgrove *et al.,* 1993) causing a more complex pattern of flow than anticipated. Nevertheless, our comparisons were always between the patterns of deposition of live copepods and passive particles within a given orientation, and the absence of a major difference between live copepods and passive particles *within* an orientation implies passive deposition. Such interference may also explain the unexpected capture efficiency of the smallest pit.

Our two passive particles (beads and dead copepods) in the PET experiment may have differed in their ability to predict the deposition patterns of live copepods. The two sets of trials in which the OH tests indicate that copepod deposition among pits was largely consistent with passive expectations (Table 2, tests 1–10, 38–42) were based on bead deposition patterns. In contrast, all comparisons to dead copepod deposition patterns yielded results that were not statistically significant, albeit due to generally minor variation in pit rankings (Table 2, tests 12–16, 28–32). Beads were selected to mimic the average fall velocity of living, unanesthetized copepods which slow their overall rate of descent by alternating between passive sinking and upward swimming (B. Sun, personal observation). As a consequence of this swimming behavior, live copepods have a lower fall velocity than dead copepods. Hence, beads should have more closely mimicked the passive behavior of live copepods, and this variation in mimic ability appears to be reflected in our results.

Even if copepods are initially deposited as passive particles in moving water, habitat selection may play an important role in determining distribution patterns if post-settlement movement occurs. Our 1-hr experiments (PET and APE I) were

APEI, 7 cm/s
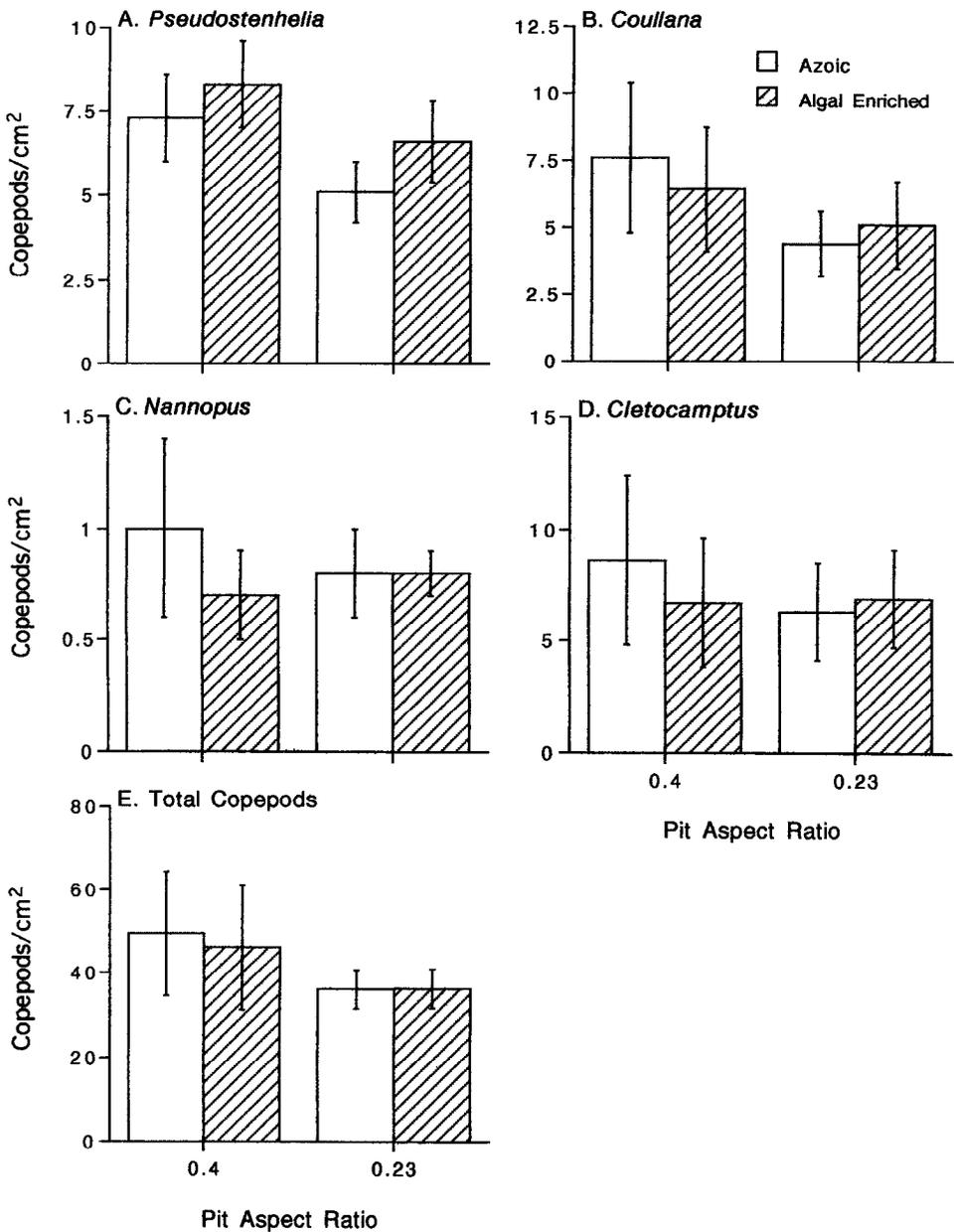
Figure 10. Distribution of copepods in two pit sizes in the APE I experiment conducted at a nominal velocity of 7 cm sec^{-1}. Mean densities for *Pseudostenhelia wellsi* (A), *Coullana* sp. (B), *Nannopus palustris* (C), *Cletocamptus deitersi* (D) and total copepods (E) are reported for two pit sizes. Error bars represent one standard error. Striped bars are algal-enriched pits and open bars, non-enriched pits.
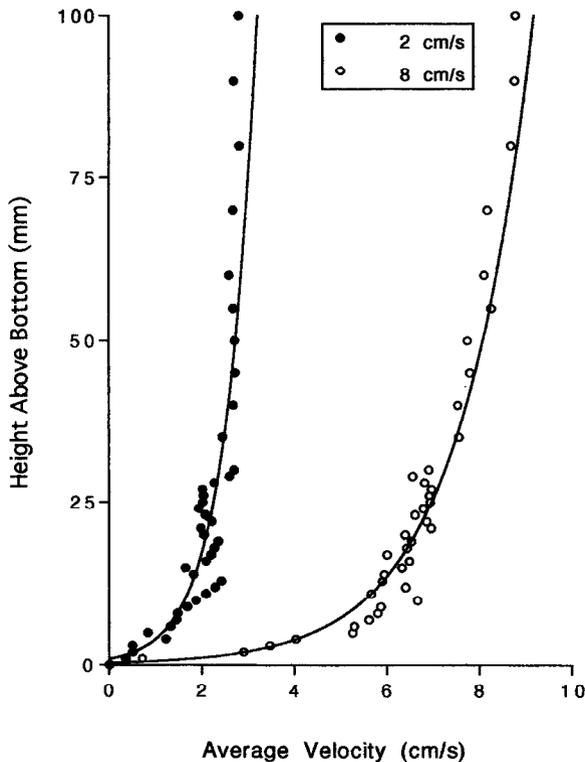
Figure 11. Vertical distribution of mean velocity at 2 and 8 cm sec^{-1} flows in the APE II experiment.

intended to primarily examine initial settlement. Copepods could circulate the racetrack flume at most from 3–4 times (depending on if a copepod was traveling on the inside or outside of the flume) at 2 cm sec^{-1}, 8–10 times at 5 cm sec^{-1} and 11–15 times at 7 cm sec^{-1} during an hour. Certainly, copepods could enter and leave pits (and re-enter the water or crawl along the bottom) and then re-enter pits during this time, however the opportunity for such movement would be greatly reduced compared to the 4-hr period in the APE II experiment. In APE II with this increased opportunity for dispersal, at nominal flows of 8 cm sec^{-1}, neither of the two abundant copepod species, *Coullana* sp. and *Halicyclops coulli,* were able to preferentially settle or disperse into algal-enriched pits (Fig. 12, Table 3). But at very low nominal velocity (2 cm sec^{-1}), both species were more abundant in adjacent algal-enriched compared to non-enriched pits. We have interpreted these results as evidence of active selection of algal-enriched sediments. However, the same pattern could be generated if copepods were instead actively avoiding non-enriched sediments. Nevertheless, this finding confirms that post-settlement movement into preferred areas occurs, but this movement is likely limited to small spatial scales (in this case,

Table 4. Two-way ANOVA results under two flow conditions for examining the effects of pit size, aspect ratio, and algal enrichment on two species and total copepods in APE II. The experiment was conducted as a split plot design. Main plot (pit size) was designed as a multiple Latin square and subplot as the algal enrichment treatment (see statistical analysis in methods and materials for details). REP refers to replicate flume run and ALG to the algal enrichment treatment.

| | | | *F*-value | |
Source of variation	DF	*Coullana* sp.	*Halicyclops coulli*	Total Copepods
2 cm sec^{-1}				
REP	1	472.37**	41.39**	363.09**
ROW (REP)	6	2.68	2.70	2.44
COLUMN (REP)	6	3.40*	2.08	2.65
PIT SIZE	3	12.91**	18.53**	13.03**
ERROR I	15	0.68	2.20*	0.65
ALG	1	70.48**	22.56**	84.06**
ALG * PIT SIZE	3	3.23*	1.37	3.32*
ERROR II	28			
8 cm sec^{-1}				
REP	1	101.18**	24.44**	97.77**
ROW (REP)	6	0.43	1.14	0.38
COLUMN (REP)	6	1.13	5.27**	1.84
PIT SIZE	3	4.11*	45.38**	4.27*
ERROR I	15	2.09*	1.95	2.63*
ALG	1	1.94	0.24	1.74
ALG * PIT SIZE	3	1.07	1.26	0.56
ERROR II	28			

*$P < 0.05$; **$P < 0.01$.

pits were adjacent as is often the case in natural microtopography) or regions of low current flow or slack tide.

An important issue concerning meiofaunal dispersal has been the relative importance of passive and active processes in both water-column entry and settlement processes (Palmer, 1988). Studies have suggested that settlement is determined either by passive (hydrodynamic) processes (Eckman, 1979; Eckman, 1983; DePatra and Levin, 1989) or by both active and passive processes (Kern and Taghon, 1986; Savidge and Taghon, 1988; Kern, 1990; Palmer *et al.*, 1992). If an active process is dominant, meiofauna should be aggregated and abundant in favorable microhabitats. However, if passive settlement is important, aggregation and increased abundance should occur only in microhabitats where shear velocity is decreased. Eckman and Thistle (1991) concluded that harpacticoid copepods settle in higher numbers in areas of reduced shear, consistent with passive deposition. Our work confirms that active processes (most important at times of low or slack flow) can modify patterns of

Table 5. Tukey multiple comparisons of *Coullana* sp., *Halicyclops coulli* and total copepod abundance as a function of sediment algal enrichment (enriched and non-enriched) and aspect ratio in two flow conditions in the APE II experiment. For each comparison, means that do not share a letter are significantly different from one another ($P < 0.05$). Data were transformed by $\ln(x + 1)$.

Treatment	Aspect ratio	*Coullana* sp.	*H. coulli*	Total copepods
2 cm sec^{-1}				
Algal-enriched	0.09	2.45 a	0.57 a	2.64 a
	0.21	2.46 a	0.57 a	2.66 a
	0.31	2.68 a	0.69 a	3.00 a
	0.71	2.79 a	0.87 a	3.04 a
Non-enriched	0.09	1.57 a	0.26 a	1.73 a
	0.21	2.04 bc	0.59 ab	2.27 bc
	0.31	1.74 ab	0.22 a	1.98 ab
	0.71	2.36 c	0.74 b	2.47 c
8 cm sec^{-1}				
Algal-enriched	0.09	2.30 a	1.21 a	2.53 a
	0.21	2.48 ab	1.32 a	2.78 ab
	0.31	2.51 ab	1.29 a	2.81 ab
	0.71	2.79 b	1.75 b	3.00 b
Non-enriched	0.09	2.15 a	1.00 a	2.42 a
	0.21	2.44 ab	1.42 b	2.77 b
	0.31	2.58 b	1.29 ab	2.81 b
	0.71	2.55 b	1.75 b	2.82 b

passive settlement, and that both active and passive processes are important to determine distributional patterns.

The results of the APE II study suggest that the interaction between copepod behavior and shear velocity at the benthic boundary layer may be important to determine the relative importance of passive and active processes. Boundary layers were well developed under both flow conditions, but the shear velocity at the lower-velocity flow (0.2 cm sec^{-1}) was one third that of the higher velocity (0.6 cm sec^{-1}). In the field, both *Coullana* sp. and *Halicyclops coulli* have been shown to readily enter the water column (Radziejewska unpublished) and may be abundant in emergence and sediment traps (McCall and Fleeger, 1995). In the low-velocity APE II trials, both species were probably able to cross the benthic boundary layer to select pits containing the preferred sediment from the neighboring non-enriched depressions or even from the local non-depression area. At higher velocities, active habitat selection was inhibited and abundance patterns were explained by the hydrodynamic capture efficiency of the pits. Some meiobenthic copepods have been shown to avoid the water column under conditions of increased flow by burrowing into the sediment (Palmer, 1984; Palmer and Molloy, 1986; Foy and Thistle, 1991), and copepods could
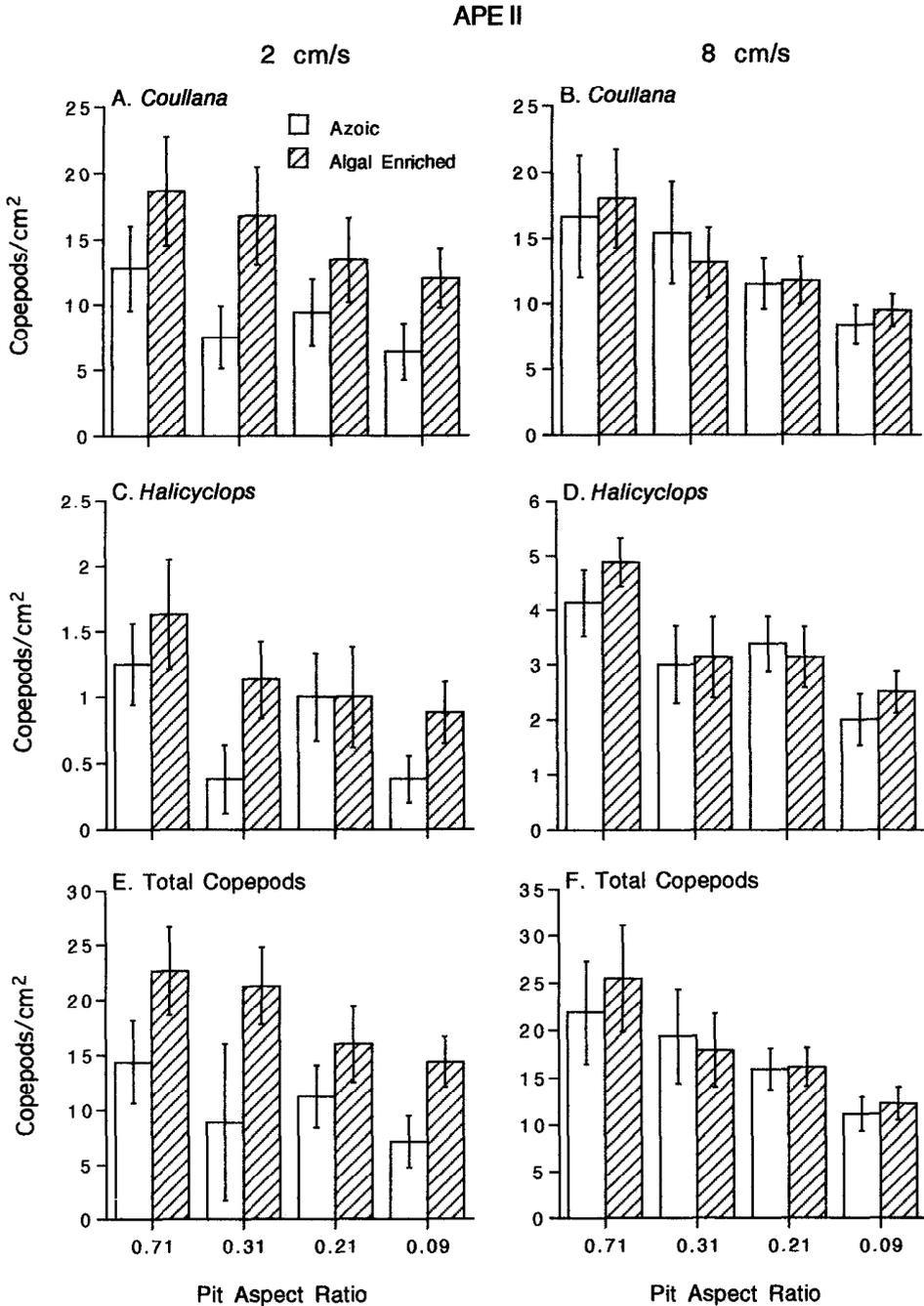
Figure 12. Mean density (± standard error) with different pit sizes at 2 cm sec^{-1} (A, C, E) and 8 cm sec^{-1} (B, D, F) for *Coullana* sp. (A, B), *Halicyclops coulli* (C, D) and total copepods (E, F) in the APE II experiment. The striped bars represents algal-enriched treatments and the open bars, non-enriched treatments.

have burrowed into the sediment in the bottom of our experimental pits in the flume. Under high-shear conditions copepods were either unable to locate algal-enriched pits because they settled passively without re-emergence, or if they did re-emerge, they could not overcome the shear velocity necessary for active habitat selection and consequently re-entered the flowing water. Behavior has been shown to be important to settlement processes in macrofaunal larvae (Pawlik and Butman, 1993), and does differ greatly among meiofaunal groups and species (Palmer, 1984). Behavior is very important in determining how the interaction with flow occurs with different functional groups of meiofauna (Sun and Fleeger, 1994).

It is possible that some of our observed settlement patterns were influenced by biological interactions among copepod species already settled into depressions. For example, Chandler and Fleeger (1987) found that dense patches of *Pseudostenhelia wellsi* facilitate colonization by *Coullana* sp. but inhibit colonization by *Cletocamptus deitersi*. However, when *P. wellsi* colonizes sediment, it builds tubes taking several hours to complete (Chandler and Fleeger, 1984), and it is therefore unlikely that interspecific interactions would alter settlement patterns over the brief time used in the PET and APE I experiments. Also, the maximum patch size of settled copepods and pit aspect ratio were confounded in the PET and APE I experiments by our use of a constant pit depth. The diameter of a settlement pit cannot effect settlement by passive mimics, but might influence settlement of living organisms through biological interactions, especially after densities exceed some threshold associated with patch size. Sun and Fleeger (1991) showed that benthic copepods from the area providing specimens used in the flume experiments have small patch sizes (1–4 cm²) that are smaller than all but the smallest experimental pit diameter used (the 1.9 cm diameter pit has a surface area of 2.8 cm²; other pit surface areas range from 5.3 to 25.5 cm²). Patches within settlement pits could develop, reducing the chance that biological interactions altered settlement patterns.

Several recent studies have emphasized the importance of pits and depressions to sediment processes and fauna. These topographic features enhance larval settlement (Snelgrove *et al.*, 1993, 1994) and particle deposition, thereby concentrating food for deposit feeders (Yager *et al.*, 1993). Meiofauna also respond to pits and depressions (Hogue and Miller, 1981). Sun *et al.* (1993) and Sun and Fleeger (1994) found that epibenthic meiofauna are more abundant in sediment depressions compared to surrounding non-depression areas, and Sun and Fleeger (1991) showed that dispersion patterns are aggregated and dynamic on mudflats. Copepods in our study did not conclusively settle in a way different from that based on passive expectations. Consequently, pits as microdepositional environments should generally be important to aggregation patterns and should be expected to be areas of high abundance of epibenthic meiofauna. Juvenile fish that consume meiofauna may respond to this level of aggregation. McCall and Fleeger (1993) found that juvenile spot (*Leiostomus*

xanthurus) selectively feed in high-density patches of meiofauna, and therefore pits may prove to be important to recruitment processes. Our study also suggests that, under low flow velocities, copepods can re-emerge and either enter flow or move through the boundary layer. Not only is this ability potentially significant to be able to find to favorable locations (Decho and Fleeger, 1988 found that *Microarthridion littorale* is disproportionately abundant in small-scale areas high in potential food concentration), but dispersal may be significant to escape from unfavorable areas such as localized areas of contamination (Fleeger *et al.,* 1995).

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