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## **Shelf harpacticoid copepods do not escape into the seabed during winter storms**

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### **ABSTRACT**

Winter storms on temperate shelves frequently rework bottom sediments. When the sediment is put in motion, sediment-dwelling harpacticoid copepods risk being suspended. We tested for evidence that adult harpacticoids move below the layer of reworked sediment to avoid suspension. To do so, we determined the rate at which a moderate storm at a site at 18 m depth in the northern Gulf of Mexico (29° 40.63'N, 84° 22.80'W) exposed subsurface sediment during bed-form development and then subjected intact cores from that site to a similar rate of exposure in a laboratory flume. We found no significant difference in vertical position of the population median for adult males of most species and adult females of all species tested between the eroded and control cores. Even the adult males that moved down did not move far enough and were eroded. We conclude that adult harpacticoids do not shelter from winter storms in the seabed. As they are capable of such behavior, being suspended must be more advantageous than living temporarily at depth in the sediment.

### **1. Introduction**

On temperate continental shelves, winter storms occur several times per month, have large spatial scales, and can move sediment at substantial water depths (Sherwood *et al.*, 1994). This sediment motion is likely to be important for small benthic metazoans, particularly meiofauna (Guidi-Guilvard and Buscail, 1995). They live predominantly in the layer of sediment reworked by storms (Huys *et al.*, 1986), and because they are small and have a specific gravity not much greater than that of seawater, they tend to have critical erosion velocities less than those of the sediment they inhabit (see Palmer, 1992). Therefore, when a storm begins to move the sediment, these animals will be suspended unless they move below the layer reworked by the storm. Potential costs and benefits are associated with each alternative. A suspended animal might benefit from access to planktonic food (Decho, 1986), relief from benthic crowding (Service and Bell, 1987), increased dispersal (Palmer, 1988), or increased access to mates (Bell *et al.*, 1988, 1989). Potential costs of suspension include expatriation (Palmer and Gust, 1985), mortality from pelagic predators (D'Amours, 1988), and a negative balance between energy

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use and energy acquisition (Thistle *et al.*, 1995). An animal that moved into the seabed to avoid being suspended might have to live for days in a region of reduced food (Joint *et al.*, 1982) or inimical sediment chemistry.

Although some studies have investigated the responses of meiofauna to flow (Palmer, 1984; Palmer and Molloy, 1986; Foy and Thistle, 1991), their responses to reworking by winter storms are not known. If a meiofaunal species capable of avoiding suspension is in fact suspended, then, for that species, the net cost of suspension must be less than the net cost of living at depth in the sediment during the storm, and storm-related processes occurring in the water column are likely to play a direct role in its ecology. For example, storm transport might be an important component of the species' dispersal. Suspension would also obliterate patches of individuals, while deposition into regions of decreased shear stress as the storm abated could create new patches. In contrast, movement of a meiofaunal species into the seabed to avoid suspension would suggest that the net cost of suspension is greater than the cost of weathering the storm at depth in the seabed, and storm-related processes in the water column would be unlikely to play a direct role in its ecology (although erosional and depositional events could still be important because of effects on the sediment, food, or other species in the system).

As a first step in determining the consequences of winter storms for the ecology of shelf meiofauna, we devised an experiment to determine whether harpacticoid copepods move below the reworked layer of sediment during a simulated winter storm.

## 2. Materials and methods

*a. Establishment of simulation parameters.* A field site at 18 m depth in the northern Gulf of Mexico (29° 40.63'N, 84° 22.80'W) (Fig. 1) was defined by two 10-m-long lines separated by 3 m. The seabed consisted of unvegetated, moderately sorted, medium sand with <1% silt-clay by weight (Table 1). In this region during winter (Dec–Mar), the passage of atmospheric fronts caused strong local winds several times per month (Weatherly and Thistle, in prep.) that rippled the sediment. The range of ripple crest-to-trough heights during interstorm intervals was 2.5–6.5 cm ( $Md = 3.0$  cm). The range of wavelengths was 10–50 cm ( $Md = 40$  cm). We determined the depths to which storms reworked the seabed by means of erosion posts (Ray and Miller, personal communication), each consisting of a 1.59-mm-diameter, stainless-steel wire and a stainless-steel washer (0.64 mm thick, 9.60 mm in diameter, with a 3.76-mm-diameter hole). Posts were inserted normal to the sediment surface until both the washer and a mark painted on the wire were coplanar with the sediment surface. From observations of the posts in unidirectional flow in a flume and in oscillatory, reworking flow in a water tunnel (see below), we determined that, during periods of erosion, the washer followed the sediment surface; during periods of deposition, it remained in position and was buried. At the field site, 10 deploy-

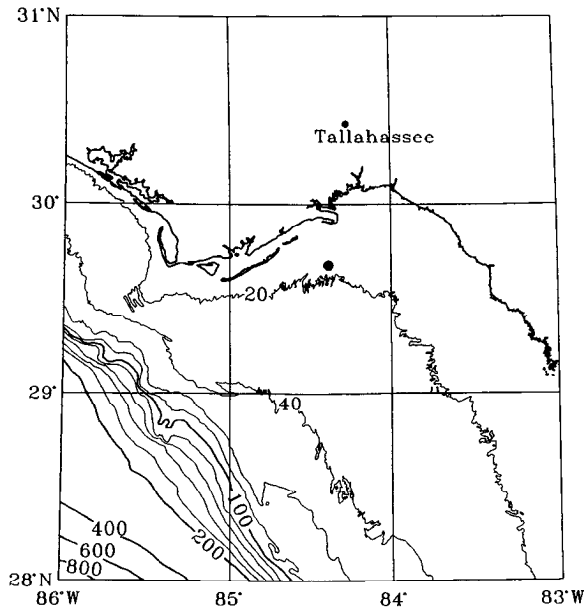


Figure 1. Chart of the study area; contours are in meters. The filled circle offshore marks the study site.

ments of greater than seven days' duration were made over three winters. On each deployment, divers placed 10 posts at random locations and, on a subsequent visit, took 15.5-cm<sup>2</sup> cores over each post found. We exposed the post and washer and estimated the maximum reworking depth by measuring the distance from the mark on the wire to the position of the washer.

To determine the usual vertical distribution of the harpacticoids at the site, divers took two 15.5-cm<sup>2</sup> cores at random in January, February, and March of 1990. Upon recovery and until processed, the cores were kept in a water bath under approximately *in situ* temperature and light conditions. Processing began within 1 hr and was

Table 1. Parameters of the sediment at the site. All values determined graphically (Folk, 1968).

Layer (mm)	Mean ( $\Phi$ )	Inclusive std. dev. ( $\Phi$ )	Inclusive skewness	Kurtosis
0-2	1.06	0.83	-0.08	1.05
2-4	1.08	0.85	-0.14	1.00
4-6	1.20	0.78	-0.13	1.08
6-8	1.18	0.81	-0.13	1.04
8-10	1.12	0.84	-0.16	1.07
10-20	1.15	0.85	-0.13	1.08
20-30	1.21	0.83	-0.14	1.08
30-40	1.04	0.77	-0.14	1.22

Table 2. Because the harpacticoid fauna of our site was largely undescribed, individuals were assigned to working species whose taxonomic affinities were determined with the aid of Wells' (1977) key and the primary literature. Ectinosomatidae were omitted because of taxonomic difficulties. Four other species were omitted for reasons described in the text. The species whose adult males were tested individually for a response are indicated by an asterisk. The species whose adult females were tested individually for a response are indicated by "†."

Family	Species
Laophontidae	<i>Paralaophonte brevis</i> *†
Cletodidae	<i>Enhydrosoma</i> cf. <i>littorale</i> †
Thalestridae	<i>Paradactylopodia</i> sp.
Ameiridae	<i>Nitocra</i> sp.
Parasthenelidae	<i>Parasthenelia</i> cf. <i>ornatissima</i>
Diosaccidae	<i>Robertgurneya</i> sp.*†
Longipediidae	<i>Longipedia</i> sp.
Canthocamptidae	cf. <i>Mesochra</i> *†
Canuellidae	<i>Coullana canadensis</i> *
Diosaccidae	<i>Robertsonia</i> cf. <i>knoxii</i>
Tetragonicipitidae	<i>Phyllopodopsyllus</i> sp.*†
Diosaccidae	<i>Robertsonia</i> sp. A†
Canthocamptidae	cf. <i>Mesochra</i>
Diosaccidae	cf. <i>Robertgurneya</i> *†
Thalestridae	cf. <i>Dactylopodia</i>
Cylindropsyllidae	new genus*
Laophontidae	<i>Pholenota</i> cf. <i>spatulifera</i> *†
Ameiridae	<i>Praeileptomesochra</i> sp.
Diosaccidae	<i>Amphiascoides</i> sp.*†
Ameiridae	<i>Ameira</i> cf. <i>listensis</i>
Ameiridae	cf. <i>Nitocra</i> *
Diosaccidae	<i>Actopsyllus</i> sp.
Ameiridae	<i>Leptomesochra</i> sp.
Diosaccidae	<i>Bulbamphiascus</i> cf. <i>minutus</i> *
Cylindropsyllidae	<i>Paraleptastacus</i> sp.

completed in < 1 hr. The top 4 cm of each core was sliced into 2-mm layers with the aid of a precision extruder (Fuller and Butman, 1988). (Before slicing, the water overlying the core was removed and passed through a sieve of 50- $\mu$ m aperture; the sieve contents were added to the 0–2-mm-layer sample.) The samples were preserved in sodium-borate-buffered seawater formaldehyde (9:1, v:v) and stained with rose Bengal. The harpacticoids were quantitatively concentrated by washing of the sample in a Barnett (1968)-style trough. Harpacticoids were sorted under a dissecting microscope; adults were identified to working species and sex. To maintain comparability with Thistle *et al.* (1995), we studied the same species (Table 2), except that four species that may have some ability to avoid suspension other than by moving

into the seabed were omitted. Following Thistle *et al.* (1995), we analyzed adult males separately from adult females and omitted egg-carrying females.

We determined the rate at which subsurface sediment layers were exposed to the flow by an indirect approach. First, we deployed a pressure sensor that sampled at 4 Hz for 7.6 min once each hour on the seabed at the site for 10 days in January. During the deployment, a moderate storm occurred (Thistle *et al.*, 1995). From spectra of each detrended, 7.6-min pressure time series, we estimated the amplitudes and periods of the near-bottom pressures caused by the passage of surface gravity waves. From linear wave theory (Denny, 1988), we inferred the amplitude of the corresponding near-bottom wave motions. Measurable vertical fluid excursions due to wind-generated waves were confined to periods of 4–11 s (6-s and 7-s period waves dominated during the storm). We converted the pressure-sensor data into peak horizontal speeds in the water just above the seabed by solving

$$U_b = (2\pi/T)A_b$$

where  $U_b$  is the peak horizontal fluid speed just above the wave boundary layer,  $T$  is the mean wave period over the range of 4–11 s, and  $A_b$  is the combined 4–11-second vertical excursion amplitude. The mean wave period was calculated as a weighted mean based on the individual amplitude contributions of the individual wave periods. During storm onset,  $U_b$  increased from a “quiescent” value of  $\approx 2 \text{ cm s}^{-1}$  ( $T = 8 \text{ s}$ ) to a “storm” value of  $\approx 35 \text{ cm s}^{-1}$  ( $T = 7 \text{ s}$ ). Thistle *et al.* (1995) give statistics on storm frequency and duration.

Using these  $U_b$  estimates, we conducted studies in an oscillatory water tunnel (see Turner and Miller, 1991, and Miller *et al.*, 1992), which we filled with sediment from the study site. The water tunnel’s controls made it impractical to match both the vertical excursion amplitudes and the oscillation periods of the storm waves that we wished to mimic. Instead, a single excursion amplitude (21.7 cm) was selected (a value intermediate between quiescent and storm conditions), and the oscillation period was adjusted to obtain the desired peak horizontal fluid speed. The periods used (5–7 s) encompassed the most energetic periods during the storm (6–7 s).

Preliminary runs revealed that only a peak horizontal velocity comparable to the maximum  $U_b$  measured during the storm created bed forms of a size comparable to those observed at the site. Rather than model the storm by applying only this maximum value, we also included peak horizontal velocities that approximated conditions during the storm during the hour before the maximum  $U_b$  occurred. Thus, a simulation run (60 min) consisted of creating four peak horizontal velocities in the water tunnel for 15 min each: 24, 27, 30, 33  $\text{cm s}^{-1}$ . We noted the change in sediment height at 12 erosion posts (without washers) placed in a stratified random manner along the centerline of the working section every five minutes during a simulation.

To estimate critical shear velocity ( $U_{*cr}$ ), we also made observations of initial

sediment motion in the water tunnel. The maximum shear stress in the presence of waves was estimated with the formula from Jonsson (1966) cited by Nielsen (1986)

$$\tau_{\max} = 0.5\rho f(A\omega)^2,$$

where  $\rho$  is fluid density,  $A$  is the semi-excursion amplitude just outside the wave boundary layer,  $\omega$  is the wave angular frequency  $2\pi/T$ , and  $T$  is the wave period. The friction factor ( $f$ ) was calculated from

$$f = \exp \left[ 5.213 \left( \frac{2.5D}{A} \right)^{0.194} - 5.977 \right],$$

where  $D$  is the diameter of the modal sediment grain size. The critical shear velocity ( $U^*_{cr}$ ) is related to the shear stress of initial sediment motion under waves by

$$U^*_{cr} = \sqrt{\tau_{\max}/\rho}$$

*b. Simulation experiment.* The experiment was designed to determine whether harpacticoids responded to sediment reworking by a storm by moving below the reworked layer. For each run, two 15.5-cm<sup>2</sup> cores collected at random from the field site were kept in a water bath at approximately *in situ* temperature and light until mounted in a laboratory flume (described by Foy and Thistle, 1991). The tops of the core tubes were coplanar with the flume bed. (The water overlying the sediment was removed and added to the 5-min sample (see below).) We used a precision extruder to bring the surface of the sediment flush with the surface of the flume bed. To fill the flume without disturbing the sediment, we placed a plastic tube with a vertical array of 50- $\mu$ m-mesh-covered holes temporarily over the location of each core.

The cores were then exposed to one of two flow speeds. During low-speed runs, which were designed to simulate conditions between storms, the flow was nonnegligible (see below) but well below the erosion threshold of the sediment. Once the flow was established, we removed the plastic tubes. After 5 min, we brushed the flume bed downstream of the cores (to ensure that any harpacticoids no longer in the cores were collected) and changed the 50- $\mu$ m-aperture sieve that intercepted the water flowing out of the flume. We then allowed 75 min to elapse before again brushing and changing sieves. The 5-min sample contained harpacticoids that were in the water overlying the cores, any that may have been washed from the sediment surface as the flow speed changed from 0 to the low-speed value, and any that emerged before the run began. The 75-min sample contained harpacticoids that eroded from the sediment surface or actively entered the flow during the run. We then repositioned the plastic tubes over the core locations and drained the flume. The cores were then removed from the flume and sliced at 2-mm intervals to 4 cm.

During high-speed runs, which simulated conditions during the moderate storm modeled above, the cores were exposed to the low flow speed for 5 min before the

flume was brushed, the sieve changed (to capture any harpacticoids that emerged or were eroded), the high flow speed (see below) established, and 2 mm of sediment extruded from each core. (At the high flow speed, 2 mm of sediment eroded in 5 min, mimicking reworking rates during storms at the site, see Results.) After 5 min, the flume was brushed, the sieve was changed (and its contents were collected), and 2 mm of sediment was extruded from each core. Every 5 min for 75 min, we repeated the procedure, giving a total of 3 cm of sediment extruded per core per run. At the end of a high-speed run, the fourth centimeter of sediment of each core was sliced into 2-mm layers.

A high-speed and a low-speed run were conducted on each of six occasions. Run order was randomized. Runs were begun at twilight or later and were completed during the night. The laboratory was illuminated with red light. All of the samples were processed as described for the vertical-distribution study.

To characterize the two flow regimes, we measured the speed in the working section at eight heights between 0.5 and 4.0 cm above bottom with a hot-bead anemometer that had been calibrated ( $r^2 > 0.99$ ) in a rotating tank. To obtain the friction velocity ( $U^*$ ), we averaged three velocity measurements (10-Hz sampling rate integrated over 40 s) from each height and used the Law of the Wall to estimate  $U^*$  from the slope of the mean-flow-versus-in(depth) regression (Eckman *et al.*, 1981).

For hypothesis testing, we used parametric  $t$ -tests. For unpaired tests, the  $F'$  statistic (SAS, 1989) was used to test for heterogeneity of variances. A species abundances in the layers of a core may not be independent, so we used the median depth of the parameter of interest (e.g. abundance of males of a species) as the dependent variable in statistical analyses.

### 3. Results

*a. Simulation parameters.* We determined the thickness of the sediment layer that winter storms put in motion at the site as follows. From theory and from direct observation of sediment motion under storm conditions as modeled in the oscillatory water tunnel, we knew that, although the small amount of fine sediment present goes into suspension, most of the grains moved as bed load. The erosion-post data revealed that reworking to  $\geq 1.0$  cm occurred in 9 of 10 deployments, to  $\geq 2.0$  cm in 7 of 10 deployments, and to  $\geq 3.0$  cm in 5 of 10 deployments. Over the 10 deployments, a median of 55% of the washers were covered by  $\geq 1.0$  cm of sediment, 20% by  $\geq 2.0$  cm, and 10% by  $\geq 3.0$  cm. These depths (estimates of half the ripple height) are consistent with measurements of ripple heights at the field site. Figure 2 shows that the bulk of the adult harpacticoids inhabited the reworked layer.

The erosion rate used in the flume experiment caused reworking rates no greater than those at the field site during a winter storm as estimated from our studies in the oscillatory water tunnel. In the tunnel, ripples formed only when peak horizontal



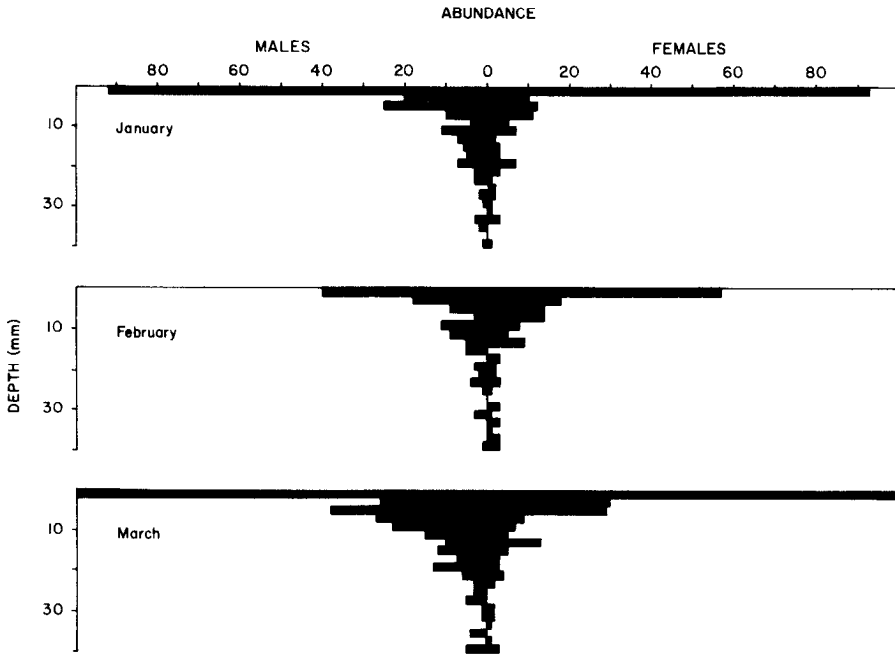


Figure 2. Abundances of adult harpacticoids by sex for January, February and March 1990. The data are sums by 2-mm layer of adult harpacticoids from two 15.5-cm<sup>2</sup> cores taken at random from the study site during nonstorm intervals. In March, the 0–2-mm-layer abundance of males was 145 and of females was 143.

velocity approached the maximum  $U_b$  inferred from the pressure-sensor data, so we examined only the last 15-min interval of each run. For each interval, we omitted the first 5 min because the bed was adjusting to the new (higher) peak horizontal velocity. At the end of the 5-to-10-min interval for each of three replicates, 36%, 40%, and 27% of the reworking rates were  $\geq 2$  mm per 5 min (Table 3). For the 10–15-min interval, we found 33%, 40%, and 25% of the measurements were  $\geq 2$  mm per 5 min (Table 3). (Because adjacent measurements may not have been independent, we treated instances where adjacent measurements were both  $\geq 2$  mm per 5 min as single measurements.)

In a subsequent water-tunnel experiment, we exposed an initially flat bed to a peak horizontal velocity of 33 cm s<sup>-1</sup> for 45 min. At 2 of 11 locations, the reworking depth was  $\geq 2.5$  cm, showing that the observed reworking rates were not confined to the surface few millimeters. Because the ripple heights formed in the tunnel were less than those observed in the field, the reworking rate we used in the flume experiment should be no greater than rates common at the site near the peak of a storm as severe as the one we mimicked. Current-meter records (Thistle *et al.*, 1995) show that the storm we used as a model was a moderate one because storm duration was positively correlated with storm intensity at the study site (unpublished data), and 62% of the

Table 3. Change in sediment height (mm) at 12 locations in the working section of the oscillatory water tunnel. “-” = erosion; “+” = deposition.

A. 5- to 10-Minute Interval

Replicate	Position											
	1	2	3	4	5	6	7	8	9	10	11	12
1	-1	-2	-2	+1	+1	-1	-2	+3	-7	0	+6	-2
2	-7	-5	+3	-9	-3	+2	-3	+9	-1	0	0	-4
3	+4	-2	-4	+1	0	+1	+7	+3	-9	+2	-3	-1

B. 10- to 15-Minute Interval

Replicate	Position											
	1	2	3	4	5	6	7	8	9	10	11	12
1	-1	-3	+3	-1	-5	0	0	-2	-1	+11	0	-14
2	+7	-10	-7	+7	-12	+5	-10	-5	+2	-2	+2	+2
3	-2	-1	-8	+2	+2	+2	+6	+2	-2	+6	+8	+1

storms lasted longer. Storms at least as long as our model occurred at the site an average of 8.7 times during winter (Thistle *et al.*, 1995), so reworking rates as great as that we used should be common there.

The critical shear velocity ( $U_{*cr}$ ) estimated in the oscillatory water tunnel was  $2.4 \text{ cm s}^{-1}$  for a modal grain size of  $407 \text{ }\mu\text{m}$ , which is consistent with the  $U_{*cr}$  required to obtain an erosion rate of 2 mm per 5 min during the high-speed flume runs (see below).

*b. The simulation experiment.* For the low-speed condition, the flume settings produced an average  $U^*$  of  $0.6 \text{ cm s}^{-1}$  ( $= 10.6 \text{ cm s}^{-1}$  at 4.0 cm above bottom). For the high-speed condition, they produced an average  $U^*$  of  $1.9 \text{ cm s}^{-1}$  ( $= 46.2 \text{ cm s}^{-1}$  at 4.0 cm above bottom). From equations of Nowell and Jumars (1987), we determined that the flow was turbulent and that the boundary layer extended the full height of the water column in the working section.

As a check on the impact of the experimental procedures on the vertical distribution of harpacticoids, we compared the median depths of adults of the species listed in Table 2 for each sex in cores taken at the study site in January, February, and March 1990 to those in cores from low-speed runs (Table 4). The two cores from each low-speed run were not independent and were pooled. The two cores from each month were pooled to maintain comparability. A *t*-test revealed no significant difference for adult males ( $p > 0.40$ , two tailed) or for adult females ( $p > 0.13$ , two tailed) in median depth between our best estimate of vertical position in the field and the vertical distribution in the low-speed cores at the end of the experiment. For adult males, the test could have detected a difference in median depth  $\geq 2.5 \text{ mm}$  with

Table 4. The 2-mm layer in which the median (Md) depth of the adults (pooled over all species in Table 2) of each sex occurred in the vertical-distribution study by month and in the low-speed flume runs. Note that animals collected in the 5-min sample of the low-speed flume runs were included in the top 2-mm sample for this calculation to maintain compatibility with the vertical-distribution samples.

Females				Males			
Month	Md Depth	Run	Md Depth	Month	Md Depth	Run	Md Depth
Jan	0-2	1	4-6	Jan	2-4	1	2-4
Feb	4-6	2	2-4	Feb	2-4	2	4-6
Mar	0-2	3	2-4	Mar	4-6	3	2-4
		4	6-8			4	4-6
		5	10-12			5	4-6
		6	4-6			6	4-6

a probability of 0.8 (Dixon and Massey, 1969). For adult females, the test could have detected a difference in median depth  $\geq 6.5$  mm with a probability of 0.8.

To test for downward movement in response to our simulated storm, we first examined the adult males of the six species that Thistle *et al.* (1995) had found individually to use significant (no correction for multiple testing) amounts of their energy reserves when suspended in a simulated storm (*Nitocra* sp., *Robertgurneya* sp., *Robertsonia* cf. *knoxii*, *Robertsonia* sp. A, cf. *Robertgurneya*, *Bulbamphiascus* cf. *minutus*). For the adult males of the six species pooled by run, there was no significant increase in the mean of the median depths between the treatments (one-tailed, paired *t*-test); the mean of the differences in medians between treatments was 0. The probability of detecting a difference between treatments  $\geq 3.0$  mm was 0.8.

We continued the analysis for each of the abundant species, those represented in both treatments in  $\geq 5$  runs (Table 2), separately for adult males and adult females. For adult males, 11 of the 25 species in the data set met this criterion. We did paired, one-tailed *t*-tests on each and found that for four species the mean of the median depths was "significantly" greater in the cores subject to erosion than in the control cores (Table 5). When we corrected the alpha level for multiple testing by the conservative Bonferroni procedure (Snedecor and Cochran, 1980), none of the results remained significant. However, the probability that chance alone produced four or more significant results in 11 trials when alpha = 0.05 is  $< 0.002$ ; therefore, one or more of these "significant" differences is likely to be biologically real. For the four "significant" species, the average increases in median depth were: *Robertgurneya* sp., 1.5 mm; *Coullana canadensis*, 9.6 mm; cf. *Nitocra*, 8.0 mm; *Pholenota* cf. *spatulifera*, 12.2 mm. Unpublished data from an earlier study on energy (neutral lipid) utilization (see Thistle *et al.*, 1995) revealed that males of these species, as a group, had significantly less stored energy (one-tailed *t*-test) after suspension under storm-like conditions than did control individuals (Table 6).

Table 5. Median depth and number of individuals for the adult males of the four species in which the mean of the median depths of adult males was significantly greater in the high-speed-run cores (H) than in the low-speed-run cores (L). When no individuals were present in one of the treatments of a run, the data for that run were omitted from the analysis, and no median depths are indicated. When the median depth occurred between layers, the upper layer is given and marked with an asterisk. A = *Robertgurneya* sp., B = *Coullana canadensis*, C = *Pholenota* cf. *spatulifera*, D = cf. *Nitocra*.

	Run											
	1		2		3		4		5		6	
	L	H	L	H	L	H	L	H	L	H	L	H
A.	0-2	2-4	2-4	6-8	0-2	0-2	0-2*	2-4*	2-4	2-4	0-2*	2-4
	21	32	13	13	10	15	16	7	3	17	6	5
B.	4-6	6-8	6-8	12-14	6-8	30-32	8-10	24-26	—	—	2-4	2-4
	6	11	5	7	5	3	1	6	0	2	1	3
C.	22-24	34-36	18-20	26-28*	16-18	22-24*	16-18	28-30	10-12	6-8	20-22	32-34
	15	15	12	10	7	42	19	28	12	4	7	13
D.	2-4	16-18*	6-8	14-16	2-4*	32-34	28-30	30-32*	—	—	18-20	24-26
	3	2	4	1	4	16	4	2	0	2	5	2

For adult females, 9 of the 25 species in the data set met the abundance criterion (Table 2). In no case was there a significant difference (no correction for multiple testing) in the means of the median depths between eroded and control treatments.

We also tested for a response by pooling within sex among species as in Thistle *et al.* (1995) (Table 7). For adult males (omitting the four species that had been shown to be individually "significant"), the one-tailed, paired *t*-test revealed no significant difference in the means of the median depths between treatments ( $p > 0.50$ ). The test had a probability  $> 0.95$  of detecting a difference greater than or equal to the average difference of the adult males of the four "significant" species (= 7.8 mm). Unpublished data from an earlier energy (neutral lipid)-utilization study showed that males of these species, as a group, also had significantly less stored energy after suspension than did control individuals (one-tailed *t*-test) (Table 8).

Table 6. Relative amounts ( $\log(n + 1)$  transformed) of stored energy (neutral lipid) for adult males of *Robertgurneya* sp., *Coullana canadensis*, cf. *Nitocra*, and *Pholenota* cf. *spatulifera* pooled. "Storm" indicates the simulated-storm treatment; "Control" indicates the control treatment. The simulated storm was run for two or three days.

Replicate	Duration			
	2-Day		3-Day	
	Storm	Control	Storm	Control
1	0.39	0.45	0.29	0.26
2	0.14	0.53	0.11	0.32
3	0.17	0.48	0.17	0.57
4	0.16	0.48	0.18	0.40
Mean	0.21	0.48	0.19	0.40
One-tailed Probability	$< 0.025$		$< 0.05$	

Table 7. The 2-mm layer in which the median depth of the adults of each sex occurred in the flume experiment. Animals collected in the 5-min samples were excluded because they were not present during the treatment portion of the runs. Note that for males four species have been omitted: *Coullana canadensis*, cf. *Nitocra*, *Pholenota* cf. *spatulifera*, *Robertgurneya* sp.

Run	Females		Males	
	Low-speed	High-speed	Low-speed	High-speed
1	4-6	4-6	2-4	4-6
2	2-4	6-8	10-12	6-8
3	4-6	16-18	4-6	12-14
4	10-12	6-8	6-8	4-6
5	12-14	6-8	6-8	2-4
6	4-6	6-8	4-6	8-10

For adult females, the one-tailed, paired *t*-test revealed no significant difference in the mean of the median depths between treatments ( $p > 0.50$ ). The test had a probability of  $> 0.8$  of detecting a difference greater than or equal to the average difference in the means of the median depths of the adult males of the four "significant" species.

#### 4. Discussion

The vertical distribution of the adult harpacticoids may have changed before the cores sliced in the field were processed. The logistics of working at 18 m precluded slicing the cores within seconds of removal from the seabed (e.g. Palmer and Molloy, 1986; Fegley, 1987), but the patterns of vertical distribution we observed were comparable to those obtained from sandy sediment when cores were sliced nearer to the time of collection (e.g. Joint *et al.*, 1982; Foy and Thistle, 1991). Further, in the simulation experiment, our inferences were based on differences in vertical distributions between two treatments rather than absolute vertical distributions.

Table 8. Relative amounts ( $\log(n + 1)$  transformed) of stored energy (neutral lipid) for adult males pooled as described in the text. "Storm" indicates the simulated-storm treatment; "Control" indicates the control treatment. The simulated storm was run for two or three days.

Replicate	Duration			
	2-Day		3-Day	
	Storm	Control	Storm	Control
1	0.29	0.63	0.29	0.68
2	0.16	0.88	0.33	0.56
3	0.20	0.57	0.21	0.63
4	0.20	0.55	—	—
Mean	0.25	0.66	0.28	0.62
One-tailed Probability	< 0.025		< 0.025	

Harpacticoids from our site could have avoided erosion during the flume experiment by moving below the eroded layer. Figure 2 and unpublished data on the 4–8 cm layer show that harpacticoids normally occurred below 3 cm, indicating a refuge was available. No measurements of burrowing speed have been made on these species, but Palmer *et al.* (1992) measured burrowing rates for other copepods of 0.0015–0.027 cm s<sup>-1</sup>. The erosion rate we used was 2 mm per 5 min (0.0007 cm s<sup>-1</sup>), so the required burrowing speed seems achievable. Finally, because adult males of four species did move down core in our experiment, some cues of storm onset in the field (e.g. vibration (Boaden, 1968) or increased interstitial flow (Riedl and Machan, 1972; Crenshaw, 1980)) appear to have been present. Consequently, the harpacticoids from our site should have been capable of avoiding erosion during our simulated storm.

In our analysis of the flume-experiment data, we first considered the six species whose adult males had been shown by Thistle *et al.* (1995) to use important amounts of their energy reserves while suspended by storms because suspension for the males of these species had a known cost that they could have avoided by moving into the seabed. When we pooled the adult males of the six species, a test of reasonable statistical power revealed no evidence of a downward movement. They will be suspended during winter storms. The absence of downward movement also suggests that the net cost of being suspended is less than that of weathering the storm at depth in the seabed. This result was not anticipated and raises the possibility that suspension by winter storms confers compensating benefits. Alternatively, weathering storms at depth in the sediment may entail substantial costs.

When we analyzed the adult males of the abundant species individually, we found four species that moved down, but they moved only about a centimeter (Table 5), and there was no accumulation of individuals in the layer that was not eroded (30–40-mm). The adult males of these species appear to have some ability to avoid being eroded, but they do not escape being suspended by even a moderate storm. Therefore, they will be suspended frequently during winter because storms at least as strong as the one we mimicked occur often at the study site. The results imply that, for the adult males of these four species, the net cost of being suspended by low-speed flows (when reworking rates are low) was greater than that of burrowing below the shallow reworking depths and that the cost balance shifted when it was necessary to move deep into the deposit to avoid being suspended. Despite the cost of suspension to their energy reserves, these adult males only avoid suspension when reworking rates are low, so either costs increase as the depth of shelter increases or some benefit accompanies suspension by high-speed flows that is not present for low-speed flows. For example, Thistle *et al.* (1995) hypothesized that adult males invest energy while suspended to remain poised to clasp mates that turbulence brings to them. Because the frequency of such encounters depends on turbulence intensity,

Table 9. Summary of the results.

Group tested	How tested	
	By species	Pooled over species
Adult males that Thistle <i>et al.</i> (1995) showed to use significant amounts of their energy reserves while suspended		6 spp. pooled; no significant movement down core
Abundant adult males	4 of 11 showed significant but limited movement down core	
Abundant adult females	0 of 9 showed significant movement down core	
Adult males and adult females separately		No evidence of significant movement down core

it increases as flow speed increases (until the simultaneously increasing encounter speeds decrease encounter success).

For the adult males of the remaining species taken as a group, a test of reasonable statistical power revealed no evidence that they moved down core to avoid suspension. That we detected such motion for the adult males of four species suggests that this absence of a response is not an experimental artifact (but see caveats above about early-warning cues). If we accept the results at face value, then the adult males of these species do not move into the seabed to avoid being suspended. Also, because adult males of these species utilized significant amounts of their stored energy reserves while suspended, either some consequence of being suspended must compensate for the energy used or the cost of living at depth during a storm must be enough to tip the balance.

For adult females as a group, a test of reasonable statistical power revealed no evidence that they moved down core to avoid suspension. There was no indication that their vertical distributions were artifactually altered during the experiment, but the lack of response could have arisen from the absence of an early-warning cue (but see above). If we take the results at face value, adult females will be suspended by winter storms. As for adult males, the behavior of the adult females suggests that the balance of costs and benefits is such that it is advantageous to be suspended during a storm rather than to spend the storm below the reworked layer. In contrast with adult males, adult females from this site show no evidence of an energetic cost of suspension Thistle *et al.* (1995), so any benefit accrued while suspended or any cost avoided by not spending the storm below the reworked layer could be smaller than that for adult males.

In summary (Table 9), our results suggest that, although the adult males of a few species attempt to avoid suspension and may succeed in doing so when reworking

rates are low, all the adult harpacticoids that we studied will be suspended during even moderate winter storms. The data suggest that the cost-benefit relationship for harpacticoids during winter storms favors being suspended over escaping from storms below the reworked layer. A corollary of this view is that storm-related processes in the water column are likely to be important in the ecology of these species. In particular, our results suggest that the bulk of the adult harpacticoids risk suspension during many storms, implying that several times each winter adult harpacticoids will have to re-enter the seabed. Little is known of this process (Bell *et al.*, 1989; Walters and Bell, 1994), but the work on the settlement of macrofaunal larvae suggests that both hydrodynamic factors (harpacticoids are similar in size and settling velocity to macrofaunal larvae) and species biology will be involved (Butman and Grassle, 1992; Snelgrove *et al.*, 1993) and that understanding re-entry will be critical to understanding harpacticoid species' distributions.

Finally, the idea that meiofauna could seek shelter by moving into the seabed parallels a hypothesis in stream ecology (the hyporheic-refuge hypothesis). That is, like shelf sands, stream beds contain animals that inhabit the layer of sediment eroded during floods and that risk suspension when the sediment around them is reworked (Palmer *et al.*, 1992). The hyporheic-refuge hypothesis states that these animals move into the sediment below the erodible layer to escape suspension. Palmer *et al.* (1992) tested this hypothesis in a stream and found that copepods moved down in response to increasing flow but still suffered substantial population decreases during floods. It appears that in both stream and shelf environments erosive flows will suspend the bulk of the copepod population.

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