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# RESPONSES OF TWO MORPHOLOGICALLY SIMILAR SPECIES OF BENTHIC COPEPOD (HARPACTICOIDA, DIOSACCIDAE) TO AN EROSION RATE THAT OCCURS DURING WINTER STORMS

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HARPACTICOIDA  
EROSION  
SHELF  
STORMS  
VERTICAL DISTRIBUTION

**ABSTRACT.** – Winter storms can put the upper millimeters of the seabed into motion. Small invertebrates in these layers could allow themselves to be suspended or burrow to avoid it, depending on the cost-benefit balance between spending a storm in a deeper layer of the sediment and spending it in the water column. At 18 m depth in the northern Gulf of Mexico (29°40.63'N, 84°22.80'W), both males and females of many harpacticoid copepod species allowed themselves to be suspended, but the males of some species burrowed. Subsequent study revealed that one of the nominal species with burrowing males subsumed two new species. Because storm-induced erosion potentially has large influences on meiobenthic community structure, and information on species' responses to it is so limited, we analyzed the data for the two new species. The females of neither burrowed in response to an erosion rate that would occur in winter storms. The males of *Protopsammotopa tipperi* did, but the results are not clear for the males of *Actopsyllus matthewi*.

## INTRODUCTION

Meiobenthic species were once viewed as obligate residents of the seabed, but it has become clear that some occur in the water column from time to time. Some studies examining the mechanisms by which these species enter the water column have focused on the ability of meiobenthic animals to leave the sediment actively (e.g. Armonies 1988a, Teasdale *et al.* 2004) and the factors that influence that behavior (e.g. Armonies 1988b,c, Walters 1991). Others have examined the passive erosion of meiobenthos by near-bottom flows (Palmer & Molloy 1986, Palmer 1992, Guidi-Guilvard & Buscail 1995).

Benefits that may accrue to meiobenthic individuals in the water column include relief from benthic crowding (Service & Bell 1987), increased dispersal (Chandler & Fleeger 1983, Palmer 1988), greater access to mates (Bell *et al.* 1988, 1989), access to planktonic food (Decho 1986, Pace & Carman 1996, Suderman & Thistle 1998), and codeposition with their food. Possible risks include expatriation (Palmer & Gust 1985), mortality from water-column predators (McCall & Fleeger 1995), and exposure to circumstances under which their energy usage exceeds their ability to acquire energy (Thistle *et al.* 1995b).

The study of passive erosion and particularly the response of meiobenthos to flow (i.e. voluntary entrainment or avoidance of erosion by burrowing)

has been limited and the results contradictory (Palmer 1984, Palmer & Molloy 1986, Foy & Thistle 1991). For meiobenthic animals of temperate coasts and shelves, the matter is of particular interest because they are at risk of being eroded during winter storms.

Temperate winter storms have large spatial scales and can occur several times per month (Sherwood *et al.* 1994). The near-bottom flows they create rework the upper millimeters of sediment, where most of the meiobenthos lives (Huys *et al.* 1986, Sherwood *et al.* 1994, Thistle *et al.* 1995a). Many meiobenthic individuals will be eroded during storms unless they move below the erodible layer. Those that allow themselves to be eroded would enjoy the benefits of entering the water column. Those that burrow below the eroded layer would instead avoid the risks, but moving below the eroded layer brings its own risks, such as reduced access to food (Joint *et al.* 1982) and exposure to low oxygen concentrations. Winter storms could therefore exact costs or provide benefits for individual meiobenthic species and thus affect the relative success of species in this environment.

Thistle *et al.* (1995a) experimentally examined the response of harpacticoid copepods, small crustaceans that are a major component of the coastal and shelf meiobenthos (Hicks & Coull 1983), to a rate of sediment erosion that they would experience during a winter storm. Most of the harpacticoid copepod species they studied did not burrow deeper, but the males of four species did.

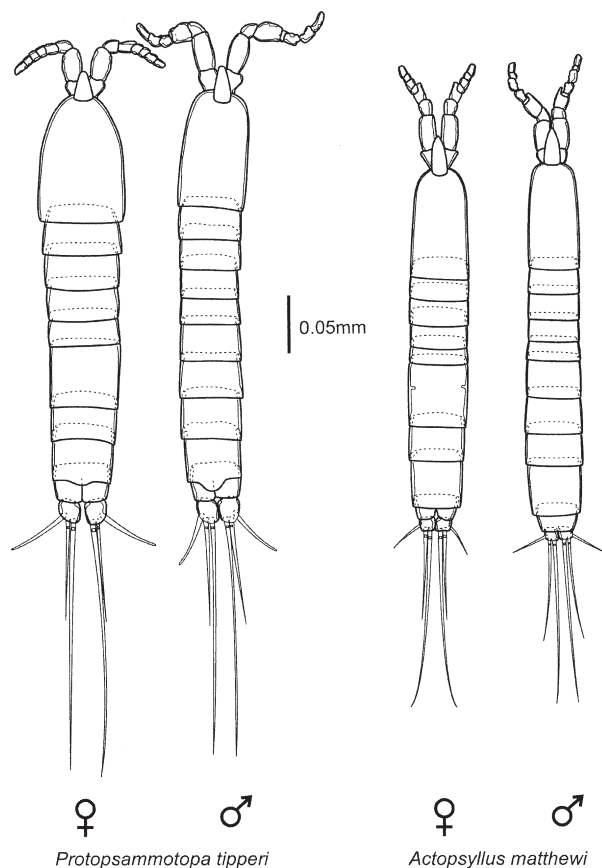


Fig. 1. – Adult *Protopsamotopa tipperi* and *Actopsyllus matthewi* females and males in dorsal view showing the morphological similarity between species and between sexes within species.

Subsequent work revealed that one of these four species was, in fact, two new species, which belong to the same family and are morphologically very similar (Fig. 1, see also Bouck & Thistle 2003). Because the erosion caused by storms is potentially such a large influence on meiobenthic community structure and information on species' responses to it is so limited, we reexamined the specimens of the two new species from Thistle *et al.*'s (1995a) study. In particular, we asked whether either sex of either species moved deeper into the seabed when exposed to an erosion rate that occurs during a winter storm.

## MATERIALS AND METHODS

The seabed at the study site (Fig. 2) in the northern Gulf of Mexico (29°40.63'N, 84°22.80'W, 18 m depth) is an unvegetated, moderately sorted, medium sand (<1% silt-clay by weight, Thistle *et al.* 1995a). The area is exposed to winds strong enough to ripple the sediment several times per month during the winter (December–March). During storms, sediment reworking can occur to depths greater than 3 cm and at rates that can exceed

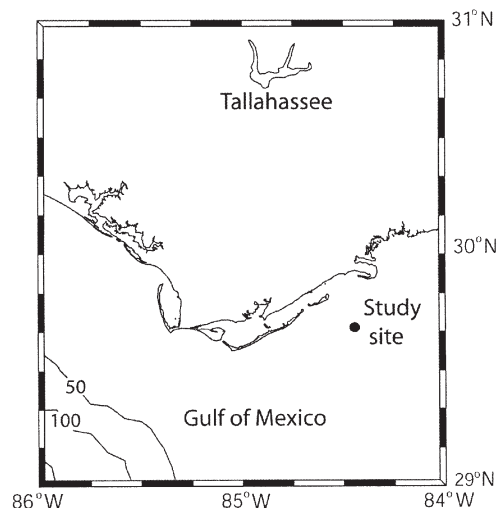


Fig. 2. – Chart of the Gulf of Mexico off northern Florida showing the study site. Contours are in meters.

0.4 mm min<sup>-1</sup> (Thistle *et al.* 1995a). Between storms, most harpacticoids occur in the 0–3-cm layer (that subject to reworking), and the great majority inhabits the top centimeter.

Thistle *et al.*'s (1995a) experiment (Fig. 3) was a treatment-by-block design. On a given day, 15.5-cm<sup>2</sup> cores were taken by divers at randomly selected locations in a 3-m × 10-m plot. For each experimental run, two cores were mounted in a 5-m-long × 0.5-m-wide laboratory flume (described by Foy & Thistle 1991) such that the tops of the core tubes and the contained sediment were flush with the floor of the flume. All water flowing out of the flume during a run passed through a 50- $\mu$ m-mesh sieve, which collected any harpacticoids that left the cores. A low-speed run simulating erosion during nonstorm conditions and a high-speed run simulating those during storms were done on each of 6 days; run order was counterbalanced.

For the low-speed runs, the cores were subjected to an average friction velocity ( $U_*$ ) of 0.6 cm s<sup>-1</sup>, which was well below the erosion threshold of the sediment. Five minutes after establishing the flow regime, investigators brushed the portion of the flume downstream of the cores to move any harpacticoids on the flume bed into the sieve, which was then replaced with a fresh sieve. After an additional 75 minutes (see below for an explanation of the duration), the flume was brushed as above, and the sieve removed. This sieve contained harpacticoids that either had eroded or had moved out of the sediment, deliberately or accidentally, during the experimental run. After the flume was drained, the cores were removed and sectioned in 2-mm increments to 4 cm.

In the high-speed runs, Thistle *et al.* (1995a) exposed the cores to a flow in which  $U_*$  was 1.9 cm s<sup>-1</sup>, a value chosen to correspond to that at their site during a moderate storm. During a high-speed run, the cores were first exposed to the low speed for 5 minutes, after which the flume was brushed, the sieve was removed, and a fresh sieve was emplaced. The high flow speed was then established and maintained for 75 minutes. Every 5 minutes, the area downstream of the cores was brushed, the sieve was replaced, and 2 mm of sediment were extruded from

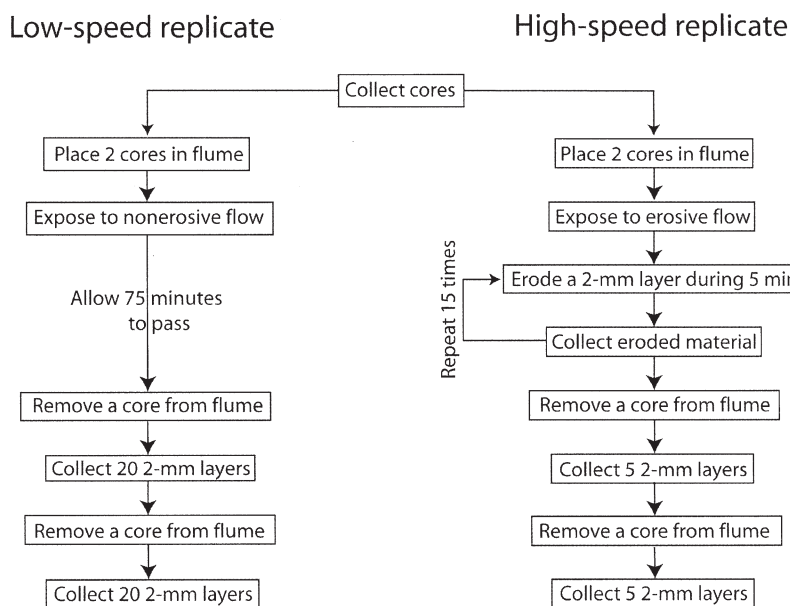


Fig. 3. – A flow diagram showing the steps in the experiment. Cores were assigned to high- or low-speed runs at random. High- and low-speed runs were alternated.

each core (erosion rate =  $0.4 \text{ mm min}^{-1}$ ). At the end of a run, 15 2-mm increments of sediment had been eroded, which corresponded to the depth of sediment that is reworked at the site (Thistle *et al.* 1995a). After each run, five additional 2-mm increments were sliced from each core. The corresponding increments from the two cores were combined.

The samples were preserved in a sodium-borate-buffered solution of 50- $\mu\text{m}$ -filtered seawater and formaldehyde (9:1, v:v). We used a Barnett (1968) trough to concentrate the harpacticoids, which were sorted from the concentrate under a dissection microscope after rose bengal staining. Adults were identified to working species with the aid of a compound microscope and archived in glycerin drops on microscope slides. For the present paper, we separated the specimens previously identified as *Pholenota* cf. *spatulifera* into *Actopsyllus matthewi* Bouck et Thistle, 2003 and *Protopsammotopa tipperi* Bouck et Thistle, 2003.

If a target population's response to a storm were to burrow deeper into the sediment, we anticipated that it would do so in the high-speed runs and therefore display a median depth greater than that it displayed in low-speed runs. For the high-speed treatment, we counted the individuals of the target population in each eroded layer and each sliced layer. These data allowed us to create a vertical profile of the target population from which we calculated its median depth. For the low-speed treatment, we used the sliced layers to create the profile (Table I). As in Thistle *et al.* (1995a), we used parametric *t*-tests to compare the average median depths of a population in the high- and low-speed runs.

We compared the median depths in the high-speed runs to those in the low-speed runs for each species and sex. To correct for multiple testing, we used the very conservative Bonferroni procedure (Snedecor & Cochran 1980). Thistle *et al.* (1995a) did 18 tests, and we did 4, so we used an alpha of 0.002 for individual tests to ensure an overall significance level of 5%.

## RESULTS

The average median depth of *Protopsammotopa tipperi* males was significantly greater (average = 11 mm) in high-speed runs than in low-speed runs (paired, 1-tailed *t*-test,  $p = 0.001$ ; Fig. 4). The average median depth of *P. tipperi* females in high-speed runs did not differ significantly from that in low-speed runs (paired, 1-tailed *t*-test,  $p = 0.191$ ; Fig. 4).

We found the average median depth of *Actopsyllus matthewi* males was not significantly greater in the high-speed treatment (paired, 1-tailed *t*-test,  $p = 0.141$ ; Fig. 4), but this result may be misleading. On 5 of 6 days, the median depth in the high-speed run was between 6 and 20 mm greater than that in the paired low-speed run. In contrast, on day 5, it was 18 mm less. If the result for day 5 is considered to be an outlier and is omitted, the average median depth in the high-speed runs was significantly greater than that in the low-speed runs ( $p = 0.005$ ) when tested at the usual, single-test significance level (but not when tested at the Bonferroni-corrected significance level). The average median depth of *A. matthewi* females in high-speed runs did not differ significantly from that in low-speed runs (paired, 1-tailed *t*-test,  $p = 0.202$ ; Fig. 4).

In addition, in low-speed runs, the average median depth of the *A. matthewi* population was 9 mm greater than that of *P. tipperi* (Fig. 4). This result was confirmed by that from four previously unexamined monthly samples taken from the site during the winter. In them, the average median depth of *A. matthewi* was significantly greater (paired, 1-tailed *t*-test,  $p = 0.036$ ) than that of *P. tipperi* (Fig. 5).

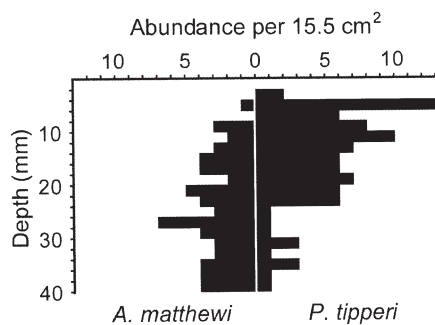
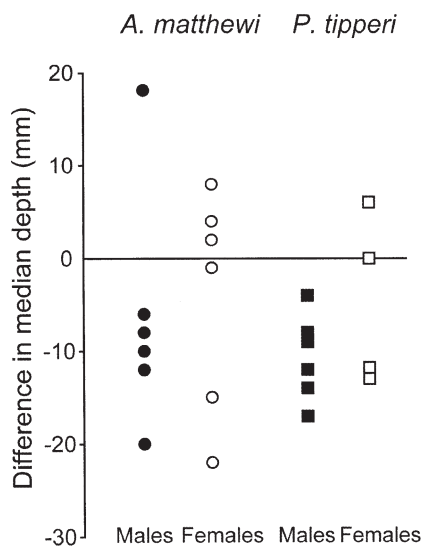


Fig. 4. – Top, Difference in median depth between paired high-speed and low-speed runs by species and sex showing that males of *Protosammotopa tipperi* tend to burrow in response to storm-like conditions. Bottom, Abundances of *Actopsyllus matthewi* and *Protosammotopa tipperi* by 2-mm depth interval, showing the tendency of the former to occur deeper in the sediment than the latter. Data from six low-speed runs were pooled.

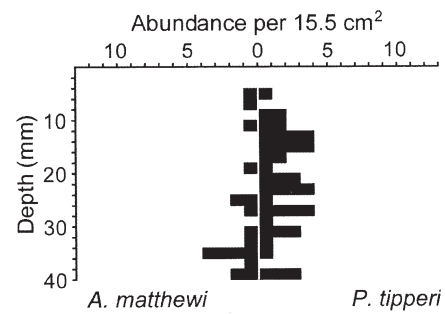


Fig. 5. – Abundances of *Actopsyllus matthewi* and *Protosammotopa tipperi* by 2-mm depth interval, showing that the former occurs deeper in the seabed on average. Data from field samples from four winter months (November, January, February, and March) were pooled.

## DISCUSSION

Thistle *et al.* (1995a) were aware that adult male harpacticoids have biological imperatives different from those of adult females, e.g. the males are seeking mates, but the females are mated. In addition, although the bodies of adult males and adult females are similar in shape, females tend to be larger than males (Fig. 1), but males tend to have larger antennules, smaller fifth pereopods, and a smaller endopod on the third pereopod. Therefore, Thistle *et al.* (1995a) followed the practice of analyzing adult males and adult females separately in their study of the specimens that they considered to be *Pholenota cf. spatulifera* and found that adult males moved into the seabed in response to simulated storms but that adult females did not.

After separating their specimens into the previously unrecognized *P. tipperi* and *A. matthewi*, we found that the males of *P. tipperi* moved deeper into the sediment in response to increased flow

Table I. – Median depth in millimeters and number of adults in low-speed and high-speed runs on each day. When a median depth occurred between two layers, we give the number of the boundary between them, e.g. “12” indicates the median depth was between the 10-12-mm and the 12-14-mm layers.

Day	<i>Actopsyllus matthewi</i>								<i>Protosammotopa tipperi</i>							
	Male				Female				Male				Female			
	Low	n	High	n	Low	n	High	n	Low	n	High	n	Low	n	High	n
1	26-28	5	34-36	4	32-34	3	32-34	7	20-22	7	34-36	10	18-20	4	18-20	2
2	26-28	5	32-34	3	34-36	1	30-32	7	14-16	8	26-28	6	—	0	14-16	2
3	22-24	3	32-34	3	12-14	1	34-36	5	14-16	4	22-24	37	12	4	24	6
4	10-12	3	30-32	17	30-32	5	32	14	16-18	15	20-22	9	20-22	9	14-16	4
5	20-22	5	2-4	2	22-24	9	14-16	9	6-8	7	16	2	10	8	22-24	5
6	20-22	5	32-34	7	12-14	5	28	6	8-10	1	26	6	—	0	12-14	3

speed but that the females did not, implying that the cost-benefit ratio of being suspended differed for males and females of this species. Thistle *et al.* (1995b) found that male harpacticoids used much of their energy reserves when suspended but that females did not. Such an asymmetry in energy use during suspension could underlie the results for *P. tipperi*.

The results for *A. matthewi* are less clear. Taken at face value, for neither males nor females was the average median depth significantly greater in high-speed runs than in low-speed runs, implying that *A. matthewi* was similar to many other harpacticoid species (Thistle *et al.* 1995a) in that it did not move down in response to storms. This interpretation may be incorrect because it depends on the inclusion of what appears to be an anomalous data point (Fig. 4). When the outlier was excluded (and multiple testing ignored), the average median depth of adult males of *A. matthewi* in high-speed runs was significantly greater than that in low-speed runs. *Actopsyllus matthewi* males may respond to storms by burrowing, but more research will be required to be sure.

The results for *P. tipperi* and *A. matthewi* raise some questions about assumptions often made by ecologists. When information about the ecology of a species or group of species is unavailable, those that are morphologically similar (either in general or because they share particular suites of characters) or that are closely related are often assumed to be ecologically similar for the purpose of analysis (see for example Jumars & Fauchald 1977). *Protopsammotopa tipperi* and *A. matthewi* are morphologically very similar. They have the same body form (Fig. 1). They are similar in size both absolutely (adult female body length from the anterior margin of the rostrum to the posterior margin of the caudal rami is ~365 µm for the former and ~335 µm for the latter) and in terms of the range of sizes of harpacticoid species also present at this site. Their appendages are largely similar in form and setation, although they do differ in taxonomically important features such as the presence in *A. matthewi* of a seta on the inner margin of the second segment of the exopods of pereopods 2-4 that is absent in *P. tipperi* (Bouck & Thistle 2003). An understanding of the precise degree of their relatedness must await a formal phylogeny of this section of the Diosaccidae, but Bouck & Thistle (2003) placed them in closely related genera. Therefore, if these species had been encountered in the course of, for example, a deep-sea ecological study, they would have been assumed to be ecologically similar. In our work, however, we had information about their responses to two important variables of their sandy, shelf habitat. They react similarly to a rate of sediment erosion that occurs during winter storms (setting aside the anomalous data point), but they respond differently to the gra-

dients (e.g. risk of mortality from surface-feeding predators, oxygen concentration) that are correlated with depth in the sediment. Although relatedness and morphological similarity often predict ecological similarity among species (Remane 1952), our results suggest that such species also can differ in ecologically important parameters.

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