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Analysis of Sediment and Gut Contents of the Sand Dollars *Mellita tenuis, Encope michelini*, and *Encope aberrans* off the Central Florida Gulf Coast

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Sand dollars are conspicuous macroinvertebrates on particulate substrates in intertidal and shallow water environments. Their locomotion and feeding can have major effects on the sediment and infauna. We investigated the sediment and gut contents of three species of sand dollars off the central Florida gulf coast. Sediment comprised quartz particles at two sites and mixed quartz particles and carbonate shell hash at the third site. At all sites, gut particles were smaller than those of the sediment. This could have been the result of the teeth of the Aristotle's lantern crushing the particles. However, particles in the food grooves of two species (*Mellita tenuis* and *Encope michelini*) were similar to those in the gut contents, smaller than in the sediment. This indicates that selection for small particles from the sediment occurred and that crushing of particles was not necessary to account for the small size of particles in the gut for those collections. The concentration of organic matter in the gut contents was much greater than that of the sediment, indicating that selection of organic matter not associated with the inorganic sediment particles occurred. It is possible that the contribution of organic matter not associated with the inorganic sediment particles is of considerable importance to the nutrient requirements of the sand dollars.

Introduction

Sand dollars can occur in high densities on intertidal and subtidal particulate substrate (Salsman and Tolbert, 1965; Weihe and Gray, 1968; Stanley and James, 1971; Ebert and Dexter, 1975; Lane and Lawrence, 1980; Penchaszadeh and Molinet, 1994; Cabanac and Himmelman, 1996; Borzone et al., 1998; Sissons et al., 2002; Swigart and Lawrence, 2008). They ingest sediment particles and a variety of small microorganisms, organic particles, or detritus (Lane and Lawrence, 1982; Mooi and Telford, 1982; Ellers and Telford, 1984; Telford et al., 1987; Telford, 1990). Their locomotion and feeding can have considerable impact on the sediment and infauna (Salsman and Tolbert, 1965; Bell and Frey, 1969; White et al., 1980; Findlay and White, 1983; Creed and Coull, 1984; Reidenauer, 1989; Sissons et al., 2002).

The capture and ingestion of sediment particles by sand dollars have been described by Ellers and Telford (1984), Telford et al. (1985, 1987), Telford and Mooi (1986), and Telford (1990). Particles are captured by specialized tube feet and passed from one tube foot to another until they reach a food groove where they are consolidated into a mucus strand. Short tube feet in the food groove move the mucus strand to the mouth, where it is ingested. Telford et al. (1987) concluded that the size of the tip of accessory tube feet determines the size of particles ingested and that the nature of the relation between sediment particles and feeding may affect the distribution of sand dollar species. Telford and Mooi (1986) and Telford et al. (1987) suggested that partitioning of particle sizes was the basis for the co-occurrence of *Leodia sexiesperforata* and *Encope michelini.*

A major question regarding particle feeders has always involved the relationship between the characteristics of the particles of the sediment and those that are ingested. This is important, because particle selection in feeding would have consequences for the sediment. Initial studies by Goodbody (1960), using *Mellita* (=*Leodia*) *sexiesperforata*, and Bell and Frey (1969), using *Mellita quinquiesperforata* (=*tenuis*), simply detected that the size of sediment particles was essentially the same as that of gut particles; this determination was made without the provision of data. Similar sediment and gut particle sizes have been reported for *Echinarachnius parma* by Ellers and Telford (1984). Telford et al. (1985) found no difference in particle size in the sediment and food grooves for *M. quinquiesperforata* (=*isometra*) but distinctly smaller sizes of particles in the gut, and they suggested that this resulted from fracture of the siliceous particles during ingestion. Similar sediment and food groove particle sizes have been reported by Telford and Mooi (1986) for *M. quinquiesperforata* (=*tenuis*) and *M. quinquiesperforata* (=*isometra*). They found that the sand grains in the gut were pulverized. Fracturing sediment particles could account for the observation of Lane and Lawrence (1982)

TABLE 1. Location [coordinates and global positioning satellite (GPS) units in parentheses], depth, dates of collections, and mean [± standard deviation (SD)] width (mm) of *Encope michelini*, *Encope aberrans*, and *Mellita tenuis*.

Location	Coordinates (GPS)	Depth (m)	Date	Species, mean (± SD) width (mm)
22.4 km west of Charlotte Harbor (CH)	26°32.43′N, 82°29.16′W (26.54528 N, 82.487778 W)	18	20 March 2004 28 Sep. 2004 20 March 2005	*E. michelini*, 85.2 ± 4.87
8.5 km west of Egmont Key (EK)	27°35.00′N, 82°50.00′W (27.583333 N, 82.833333 W)	7	21 March 2004	*E. aberrans*, 106.0 ± 6.90 *M. tenuis*, 63.8 ± 7.28
Anna Maria Island (AMI)	27°32.09′N, 82°44.49′W (27.535833 N, 82.746944 W)	2–3	20 June 2004 25 Sep. 2004 30 Oct. 2005	*M. tenuis*, 74.2 ± 8.60

that small particles in the gut of *M. quinquiesperforta* (=*tenuis*) were more frequent than in the sediment. Different sediment and food groove particle sizes indicating selection have been reported by Telford and Mooi (1986) for *L. sexiesperforta* and *E. michelini*. Chia (1969) reported that the particles in the gut of *Dendraster excentricus* were small, but this probably resulted from suspension feeding in the water column. Small, heavy particles that occur in the gut diverticula of small sand dollars (Chia, 1973; Borzone et al., 1997) could result from differential movement of heavy and light particles within the gut.

Systematic, comparative studies of feeding by sand dollar species and of the relationship between the gut contents and the sediment are essential. These studies provide information that indicates the type of sediment on which the sand dollars are found, the effect of feeding on the sediment, and the trophic role of sand dollars. In this study we characterized the sediment and gut contents of *Mellita tenuis*, *E. michelini*, and *Encope aberrans*.

MATERIALS AND METHODS

Collections to compare particles of the sediment and gut contents were made at three sites that differed in depth and distance from the coast from 20 March 2004 through 30 Oct. 2005 (Table 1). The deepest and farthest site was approximately 20 km off Charlotte Harbor (CH), with mixed quartz sand and shell-hash sediment (Fig. 1). Only *E. michelini* were found there. The site approximately 7 km off Egmont Key (EK) was shallower and nearer the shore, with quartz sand sediment. Both *E. aberrans* and *M. tenuis* were found there. The site off Anna Maria Island (AMI) was immediately offshore in shallow water, with quartz sand sediment. Only *M. tenuis* was found there. Test diameter was measured as the width between the anterior notches for *E. aberrans* and *E. michelini* and at the position of the anterior lunules for *M. tenuis*.

Specimens were preserved using the method of Telford et al. (1987). Immediately after collection, 20% buffered formalin in seawater was injected into the coelomic cavity and the specimens were immersed in formalin. Intact guts were dissected from 20 specimens of each species per collection. Guts and their contents were stored in vials with 20% buffered formalin. The sizes of 150 sediment particles from each gut were measured using a calibrated micrometer (Telford and Mooi, 1986). A wet smear of gut contents was placed on a slide and examined under a light microscope. Several different locations on the slides were examined for particle size measurements. Resolution decreased at magnifications $> \times 400$, such that accurate measurement of very small particles was difficult. The smallest particles measured were 0.005 mm, although the actual size may have been smaller. Because the mean sizes of 150, 200, and 250 particles did not vary significantly (2.4 ± 3.12, 2.3 ± 2.92, and 2.2 ± 2.69, respectively; Kruskal–Wallis, $P = 0.956$), 150 particles were measured for each sample.

The remaining gut sample contents were dried for at least 24 h at 60°C. The dried gut contents were weighed and ashed in a muffle furnace at 500°C for 4 hr to calculate the percent organic concentration (Paine, 1971).

Three samples of ~ 60 ml of sediment were collected from the sediment surface at each collection. Sediment samples were fixed in 20% buffered formalin immediately after collection. Samples were dried in an oven at 60°C for at least 48 hr, then dry-sieved using the U.S. standard sieve series; sieve segments were weighed [adapted from Mitbarkar and Anil (2002)]. A portion of each sediment sample was taken to measure the percent organic content, as with the gut

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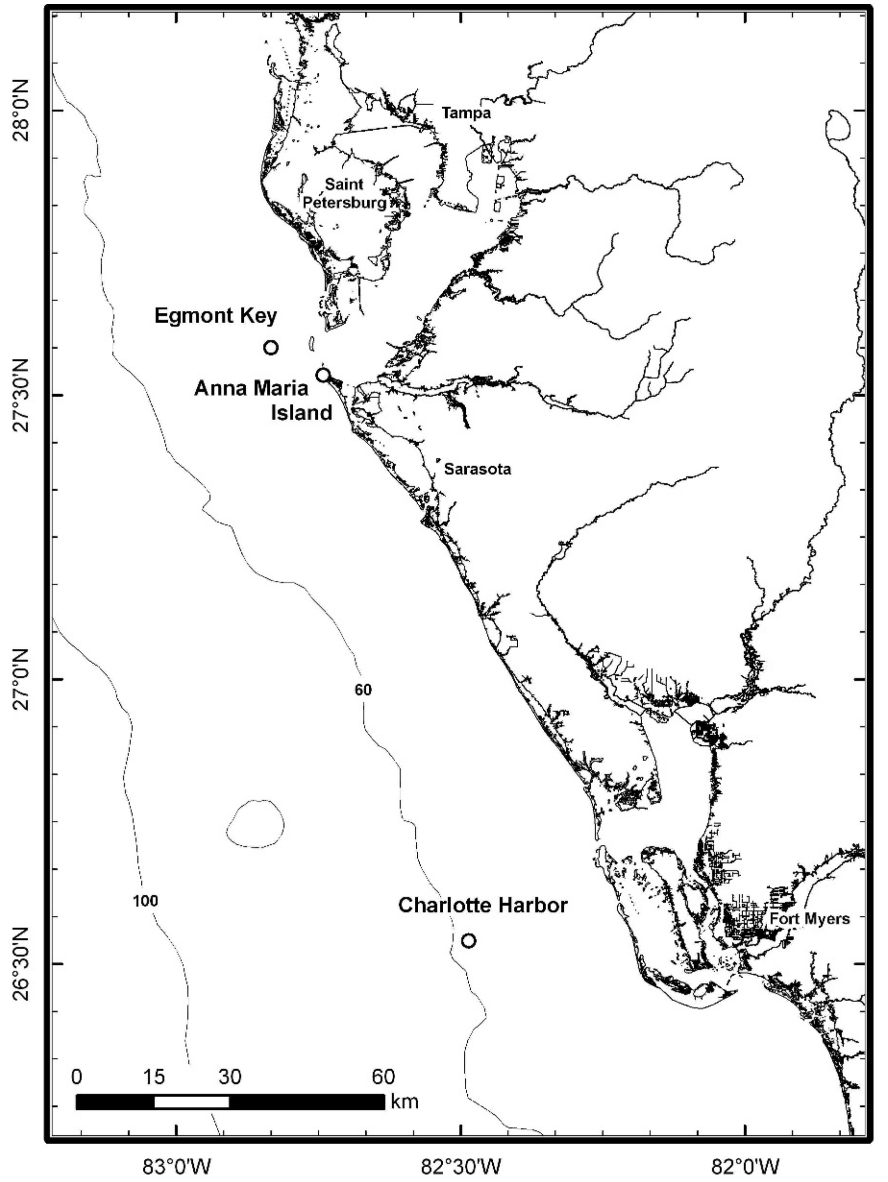

Fig. 1. Map of central Gulf Coast of Florida. Sites are named for nearshore landmarks.

contents. The concentration of organic matter of sediment from the CH site with formalin (4.2 ± 1.3%) was only slightly higher than the concentration of sediment without formalin (2.7 ± 0.52%). Since there was only a small difference, we did not consider it to have a disproportionate effect on percent organic material of sediment and gut content samples.

Ten *E. michelini* were collected in March 2005 from CH, and 10 *M. tenuis* were collected in Oct. 2005 from AMI for analysis of particle size in the food grooves. After collection they were immediately preserved in 20% buffered formalin in individual plastic bags. Particles from the food grooves of the preserved specimens were removed using a spatula and smeared onto a slide, along with a small amount of deionized water. Particle sizes were measured following the same method for particle analysis of the gut contents.

Mean sediment grain size was analyzed using GRADISTAT software (version 5.0; Blott, 2000). Mean particle sizes and percent organic material of gut samples and sediment were compared using analysis of variance (ANOVA) and, when necessary, nonparametric tests (Kruskal–Wallis and Mann–Whitney U-test) (SPSS, 1989–2004;

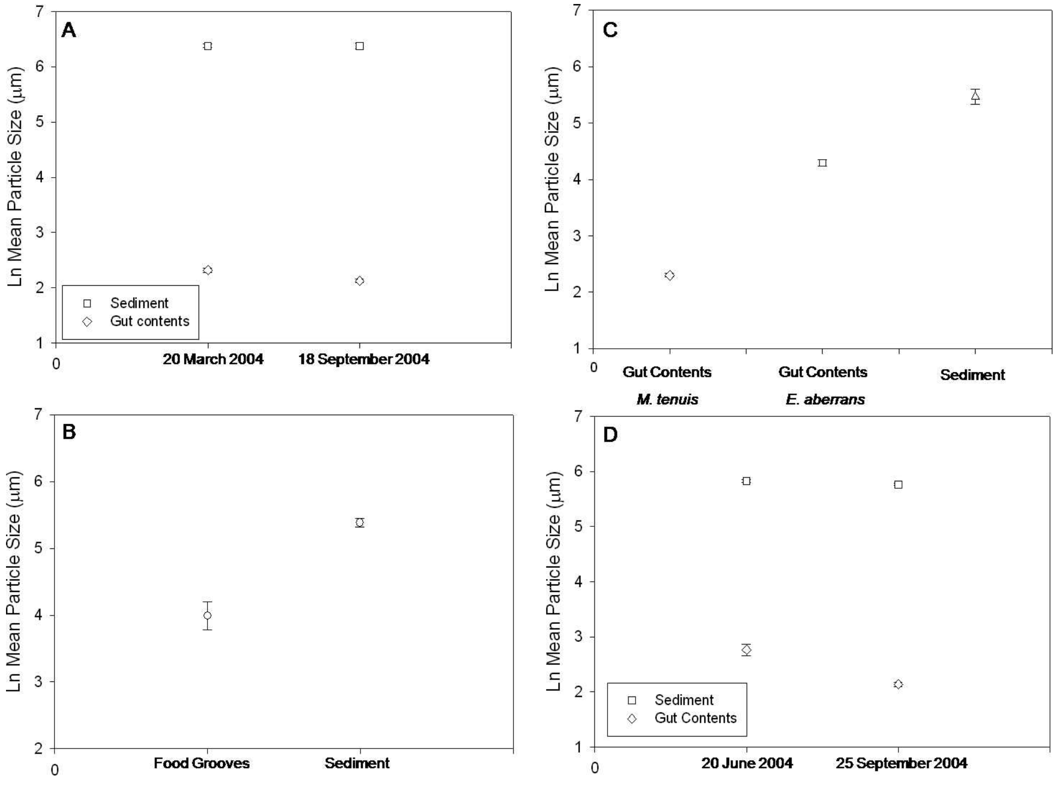

Fig. 2. Particle sizes of gut contents, food groove contents, and sediment. (A) Gut contents and sediment of *Encope michelini* off Charlotte Harbor on 20 March and 18 Sep. 2004. (B) Food groove contents of *E. michelini* and sediment off Charlotte Harbor on 18 March 2005. (C) Gut contents of *Mellita tenuis* and *Encope aberrans* and sediment off Egmont Key on 21 March 2004. (D) Gut contents of *M. tenuis* and sediment off Anna Maria Island on 20 June and 25 Sep. 2004. Ln particle size [mean ± standard error (SE)].

SYSTAT, 2007). The Φ units ($= -\log_2$ mm) were used to calculate the mean particle size of sediment, because the sediment was sieved, giving a mass for each size class. However, SI units were used for analyzing the gut particles, since the interest there was in the frequency and sizes of the sand grains (after Telford and Mooi, 1986). Descriptive statistics were used to evaluate populations and variation in particle sizes and organic content of sediment and gut contents (SPSS, 1989–2004).

Results

Body size.—Specimens of the three species differed in size (Table 1). Specimens of *E. aberrans* were the largest, and specimens of *M. tenuis* were the smallest.

Particle size.—Sediment from the EK and AMI sites consisted of small, mostly quartz particles with very few shell fragments, while sediment from the CH site consisted of large and primarily carbonate particles. Sediment from all sites ranged from very fine gravel to fine sand (Blott, 2000). Both inshore and offshore sediments were composed of smooth, rounded particles. The mean particle size from offshore CH particles was twice that of those from offshore EK and AMI (Fig. 2A,C,D). The sediment from CH had a mean particle size of 594 ± 2.014 µm, which corresponds to the coarsest sediment of all the collections. The sediment of all collections off AMI had a mean particle size of 330 ± 1.56 µm.

The mean sediment particle size differed significantly with site (ANOVA, $F = 62.962$, $P < 0.001$). Mean particle size was smallest at EK and largest at CH. Most pair-wise comparisons of particle size are significantly different. All sites were different from each other, except that EK was not significantly different from both AMI collections. Within-site collections were not significantly different (Holm–Sidak, $P > 0.05$).

The mean sizes of gut particles were compared across collections for *M. tenuis* and *E. michelini* and for species co-occurring at EK, *M. tenuis* and *E. aberrans* (Fig. 2C). Gut particles from *M. tenuis* collected 20 June 2004 were significantly larger than those collected on 25 Sep. 2004 (Mann–Whitney U-test, $P < 0.000$). The gut particles of *E. michelini*, collected on 20 March 2004, were significantly greater than those of the 18 Sep. 2004 collection ($P < 0.000$). Gut particles from *E. aberrans* were significantly greater than those from *M. tenuis*, both of which were collected on 21 March 2004 from EK ($P < 0.000$). Notably, *E. aberrans* had the largest range of values, while the ranges of values for the other two species were much smaller. Gut contents of all species also contained centric and pinnate diatoms, foraminiferans, filamentous green algae, and organic debris.

The particle size of the food grooves of *M. tenuis* and *E. michelini* was closer in size to the gut contents than to the sediment (Fig. 2A,B,D). The average particle size in the food grooves was 14.7 ± 38.3 μm for *E. michelini* and 65.9 ± 136 μm for *M. tenuis*, neither of which was significantly different from their gut contents (Kruskal–Wallis, $P > 0.05$). Mean food groove particle sizes were smaller than the mean sediment particle sizes (Fig. 2A,B,D). The mean sediment particle size is larger than the gut particles by one order of magnitude. Notably, the sample sizes of sand dollars and sediment were disparate ($n_{gutparticle} = 20$, $n_{sediment} = 3$), which prevented valid statistical comparison. Comparison of sediment and gut particles proved difficult, because the size fractions of the gut particles were so small, and there was very little overlap between them and sediment particles. However, the great difference in sizes indicates that they are distinctly different from each other.

Organic matter concentration.—The concentration of organic matter of the quartz sand sediment of EK and AMI sites was less than that of the quartz sand and carbonate shell hash at the CH site (Fig. 3A–C). AMI sediment mean percent organic matter concentration (SOM) ranged from 0.73 ± 0.11% (20 June 2004) to 0.58 ± 0.18% (25 Sep. 2004). Seasonally, AMI had significantly lower SOM on 20 June 2004 than on 25 Sep. 2004 (Kruskal–Wallis $\chi^2 = 8.265$, $P = 0.004$). At CH, SOM was 4.2 ± 1.3% (18 Sep. 2004), which is, on average, five to seven times higher than the SOM at AMI. The organic matter concentration of the gut samples varied over time. Gut mean percent organic matter concentration (GOM) for *M. tenuis* ranged from 27.0 ± 6.3% (20 June 2004) to 44.5 ± 4.9% (25 Sep. 2004). The gut contents from *M. tenuis* collected on 25 Sep. 2004 had a significantly greater overall organic matter concentration than the 20 June 2004 collection (ANOVA, F = 68.510, $P < 0.000$) (Fig. 3C). Across seasons, the GOM of *E. michelini* was significantly different (ANOVA, F = 110.713, $P < 0.000$) (Fig. 3A); the GOM of the 18 Sep. 2004 collection was significantly greater (33.9 ± 4.7%) than that of the 20 March 2004 collection (25.8 ± 4.4%). At EK, *E. aberrans* had a significantly smaller GOM than *M. tenuis* (Kruskal–Wallis, $\chi^2 = 29.268$, $P < 0.000$) (Fig. 3B). The organic matter concentration of the gut contents greatly exceeded that of the sediment

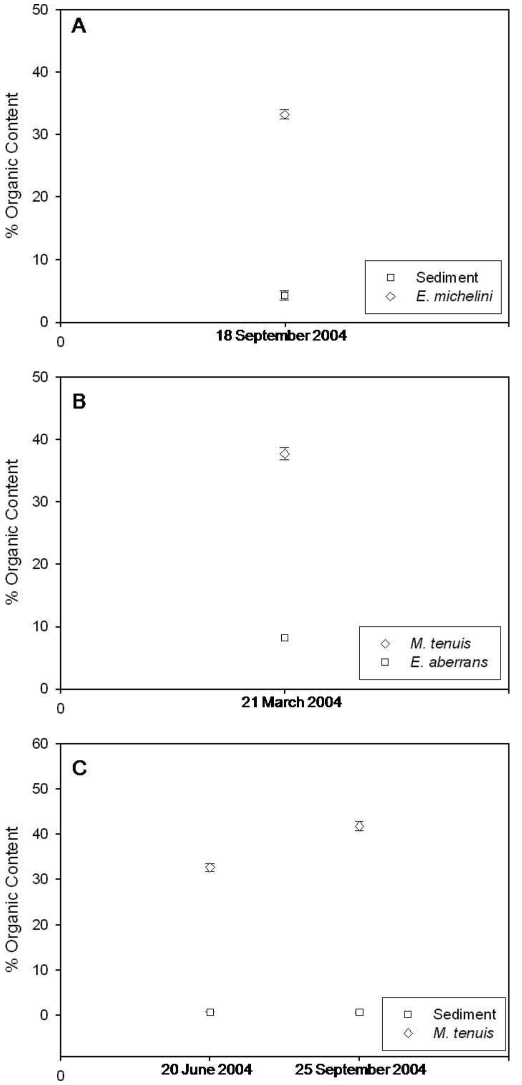

Fig. 3. Percent organic content [mean ± standard error (SE)] of gut contents and sediment. (A) Gut contents of *Encope michelini* and sediment off Charlotte Harbor on 18 Sep. 2004. (B) Gut contents of *Mellita tenuis* and *Encope aberrans* off Egmont Key on 21 March 2004. (C) Gut contents of *M. tenuis* and sediment off Anna Maria Island on 20 June and 25 Sep. 2004.

(Fig. 3A–C). At AMI, with *M. tenuis*, there was a 37–77-fold difference in organic matter concentration between the gut contents and the sediment. At CH, with *E. michelini*, there was a six- to eightfold difference.

Discussion

Sediment particles at the offshore CH site were larger than those at the offshore EK site and the inshore AMI site. This is consistent with the patterns described by Brooks et al. (2003): small quartz particles are predominant inshore in the collection areas, and large carbonate shell-hash particles and quartz particles are found in the area offshore.

Gut particle sizes were smaller than sediment particle sizes. Both *E. michelini* and *M. tenuis* had smaller gut particles than *E. aberrans*. Lane and Lawrence (1982) and Telford et al. (1985) reported that most gut particles of *M. tenuis* were < 100 μm in size. Telford et al. (1985) suggested that ingested particles were crushed by the teeth of the Aristotle's lantern. Ellers and Telford (1991) estimated that the forces generated by the Aristotle's lantern of clypeasteroids have the capacity to crush even quartz grains. We observed some sand particles with sharp edges in the guts of *M. tenuis*, while those in the sediment were rounded and appeared polished. However, the food groove particles of *E. michelini* at CH and of *M. tenuis* at AMI were similar in size to gut contents, indicating selection of particles in those situations. That the size of gut particles of *E. aberrans* at the EK site was much larger than that of co-occurring *M. tenuis* and of the offshore *E. michelini* is interesting. It indicates that *E. aberrans* has less capacity to crush particles, but it is difficult to understand why this should be the case. In addition, mean particle sizes in the food grooves of *M. tenuis* at the AMI site and of *E. michelini* at the CH site were more similar to those in the guts than to those in the sediment. This indicates that selection of particles by the tube feet had occurred.

Telford and Mooi (1986) and Telford et al. (1987) suggested that the mechanics of attachment of particles to the accessory tube feet is the basis for restriction of clypeasteroids to specific sediment types and within a limited particle size range. Telford and Mooi (1986) reported that the mean particle size in the food grooves was 181 μm for *Mellita isometra* and 183 μm for *E. michelini*. In contrast, we found the mean particle size in the food grooves was 66 μm for *M. tenuis* and 15 μm for *E. michelini*. It is unlikely that the tube feet of the very closely related *M. isometra* and *M. tenuis* and *E. michelini* and *E. aberrans* differ substantially. The differences between our observations and those of Telford and Mooi (1986) may be related to differences in the sediment where the populations occurred. Telford and Mooi (1986) gave the mean particle size of the sediment as 186 μm for *M. isometra* and 212 μm for *E. michelini*. In contrast, the mean particle size of the sediment for the populations we studied was 8.6–17.3 μm for *M. tenuis* and 9.0–10.3 μm for *E. michelini*.

Although the three species differed in size, there is no indication that body size itself affects the sizes of particles ingested. None of the studies of the mechanism of feeding by sand dollars cited above indicate that body size is involved, although it may be related to the size of the barrel-tipped feeding tube feet. Telford and Mooi (1986) reported the size of the barrel-tipped feeding tube feet is greater in *E. michelini* than in the smaller *M. tenuis*. The size of these tube feet in *E. aberrans* is not known. Phelan (1972) noted that the peristome is larger and the food grooves are wider in *E. aberrans* than in *E. michelini* and suggested that the two species are adapted to different feeding conditions. These differences in the size of the peristome and food grooves may affect capacity instead of selection.

The mean organic matter concentration was higher in the particles of shell-hash sediment than in the particles of the quartz sediment. This is probably related to the porosity of shell hash (Folk, 1974). Crushing shell hash should have biological importance, while crushing nonporous quartz particles may not. The concentration of organic matter was much higher in the gut contents than in the sediment. Sand dollars ingest a variety of living microorganisms, algae, and organic debris (Goodbody, 1960; Bell and Frey, 1969; Lane and Lawrence, 1982; Ellers and Telford, 1984; Telford et al., 1985). Culver (1961) found only diatoms and other algae and no inorganic particles in the guts of *M. quinquiesperforata* (=*isometra*) off the North Carolina coast. Kang et al. (1999) observed that *Astriclypeus manni* is a deposit feeder on organic debris in sediment. These observations indicate that organic matter in the gut of sand dollars can be considerable and in some circumstances may be more important as food than that associated with inorganic sediment particles.

Considering the importance of sand dollars on particulate substrates, there have been remarkably few attempts to analyze their biology and ecology. Not only is analysis of more species warranted, but comparison of populations of species in different habitats is necessary.

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