Acknowledgments

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… I would answer you: Ocean will say it – the arc of its lifetime is vast as the sea-sand, flawless and numberless. Between cluster and cluster, the blood and the vintage, time brightens the flint in the petal, the beam in the jellyfish; the branches are threshed in the skein of coral from the infinite pearl of the horn.

-Pablo Neruda from *The Engimas,*
*Canto General* (1950)
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Spatial and Temporal Patterns of Feeding and Food in Three Species of Mellitid Sand Dollars

Susan Elizabeth Hilber

Abstract

Sand dollars are abundant and conspicuous macroinvertebrates in sandy habitats in the Gulf of Mexico. They ingest sediment and associated organisms. Given their high abundances, size, and deposit feeding, they likely are the most important consumer coupling primary productivity with the rest of the food chain in these habitats. Moreover, sand dollars bioturbate sediments and affect species diversity and community structure.

Three species of sand dollars in the family Mellitidae, *Mellita tenuis*, *Encope michelini* and *Encope aberrans*, were studied off the West Coast of Florida. Food and feeding of these sand dollar species were studied to understand their relationship to spatial and temporal patterns.

Particle size and organic content gut contents, collected from inshore and offshore sites, were analyzed and compared with sediment collected concomitantly. Offshore sediment is coarser and has a higher organic content than inshore sediment. The gut particle sizes are similar for *E. michelini* and *M. tenuis*. The gut contents of *E. aberrans* have larger particles. All three species have gut particles smaller than the ambient sediment. The gut contents and sediment have higher organic content in the fall than the spring. Additionally, the gut organic content varies diel, with peaks shifting by date. The gut organic content of the three species was higher than the sediment. The gut organic content of *E. aberrans* was significantly less than that of co-occurring *M. tenuis*. 
The particle sizes and organic content of the gut contents of *Mellita tenuis* and *Encope michelini* are similar. However food type ingested may differ. *Encope aberrans* may coexist with *E. michelini* and *M. tenuis* because it occupies a different niche. Inconsistent peak feeding times could reflect differences in food availability and predation pressure. Inverse relationships between particle size and organic content exist for sediment and gut contents. High densities of *M. tenuis* inshore may deplete the organic content of the sediment and reverse the negative relationship between particle size and organic content.
**Introduction**

In the shallow, warm waters of the Gulf of Mexico, sand dollars in the family Mellitidae can be found in sandy bottoms from a depth of 0.5-90 m (Hendler 1995). Sand dollars are deposit-feeding herbivores (and incidentally detritivores) that consume benthic microalgae (Lane 1982) and are consumed by piscine predators, such as triggerfish and elasmobranches (Frazer et al. 1991; Kurz 1995). Therefore, sand dollars couple primary productivity to the higher trophic levels. Given their high densities in sandy bottoms, they are arguably the most important consumer of primary producers and microfauna in their habitat. Sand dollars exhibit behavioral patterns seasonally (Lane and Lawrence 1982), on a diel scale (Salsman and Tolbert), and in regard to substrate preference (Serafy 1979). Knowledge of the spatial and temporal aspects of food and feeding would clarify their role in the ecosystem. For this reason, *Mellita tenuis*, *Encope michelini*, and *Encope aberrans* were investigated to better understand their feeding ecology.

Four species regularly occur in the Gulf of Mexico, but differ in habitat preferences. *Mellita tenuis* is commonly found inshore along the eastern Gulf of Mexico in fine sediments (Hendler et al. 1995). *Leodia sexiesperforata* occurs occasionally in the Gulf, in low abundances (Hendler et al. 1995), and for this reason was not included in this study. The offshore species, *Encope aberrans* and *Encope michelini*, occur on sand
plains with crushed shell and quartz particles. In some areas, *Mellita tenuis* densities can reach 74 individuals·30cm$^{-2}$ (Salsman and Tolbert 1965). Densities of *Encope aberrans* and *E. michelini* are generally much less than *Mellita tenuis*, 2.00±1.53 - 1.03±1.00 *Encope michelini*·m$^{-2}$ and from 2.00±1.41 - 0.17 ± 0.46 *E. aberrans* ·m$^{-2}$ off Egmont Key (Lawrence et al. 2005).

In order to appreciate the ecological role of sand dollar feeding, an understanding of the physical mechanics of the feeding system is essential. According to Smith (1984), clypeasteroids (irregular, bilaterally symmetrical echinoids) evolved from regular echinoids (sea urchins) in the Paleocene to occupy a new habitat, sand bottoms. One group, the sea biscuits, has a relatively thick body. The others, the sand dollars, have a thin, disc-like body. The evolution of tube feet on both the oral and aboral sides allowed sand dollars to feed on particles, a new food source for echinoids (Smith 1984). Instead of macroscopic food (algae and animals), sand dollars feed on sand particles and microscopic organisms.

Sand dollars are covered with short spines, which aid in movement and feeding (Telford et al. 1985). Food grooves on the oral side work in conjunction with the spines and tube feet to carry food to the mouth. Internally, the lantern, the chewing apparatus of echinoids, has five broadly flattened pyramids and teeth, which grind the food (Hyman 1955). The flattened test of sand dollars has greatly influenced the structure and functioning of the internal anatomy. Although the basic echinoid form remains, the gut is modified (Hyman 1955). The esophagus exits the lantern into the capacious stomach, which is nearly concentric to the test margin. The next region, the intestine is narrow and doubles back to meet the anus.
Sand dollars have evolved an interesting way for ingestion of food. Mucus traps particles and the spines work in conjunction with the tube feet to transport food to the mouth. There are two opposing models for sand dollar feeding: the sieve hypothesis, originally proposed by MacGinitie and MacGinitie (1949) and later supported by Goodbody (1960) and others, and a challenging view proposed by Telford et al. (1985). According to the sieve hypothesis, diatoms, other microalgae, detritus, and sand are filtered through the spines of the sand dollar according to size. Only small grain sizes, generally less than 100 μm, fit in the interstices between the spines. In turn, the podia grasp onto the small particles and transport them via ciliary currents. Once in the food grooves, food is moved to the mouth. Buried sand dollars utilize sediment on both the aboral and oral sides of their bodies. At one point, it was believed that the chief function of lunules was to present a short cut for food being transported from the aboral side to the mouth (Telford 1981). However, that appears to be only a minor aspect of lunule function. In fact, lunules generally serve to deflect lift from wave action and currents (Telford 1981). There are some problems with this feeding model. Mainly, sand dollar guts contain particles greater than 100 μm, and the velocity and direction of ciliary currents oppose transport vectors (Telford 1985). Telford (1985) did not believe observations supported this theory.

Telford et al. (1985) observed feeding of *Mellita tenuis* and came to some new conclusions. First, they found sand dollar feeding is intermittent instead of continuous. Second, instead of ciliary currents creating a smooth flow to the mouth, most currents are weak, in opposing or perpendicular directions, or centrifugal. According to Telford et al. (1985), feeding begins with barrel-tipped tube feet grasping particles from the sediment.
These particles are coated with mucus secreted from the tips of the tube feet. Eventually mucus cords form in the food grooves. The cords are then moved into the mouth. They found no evidence of particle rejection. In addition, the authors found sand dollars selected diatoms in greater proportion to their occurrence in the benthos; between 90-100% of particles in the food grooves were diatoms. Within the gut, 97% of particles were less than 100 μm, which was significantly different from the ambient sediment.

Telford et al. (1985) argued that the lantern is responsible for breaking up larger particles into the fine particles observed in the gut and that the ciliary currents primarily serve to ventilate and cleanse the sand dollar surface. This new model does explain the role of the lantern, which the sieve hypothesis ignored. It seems that the Telford et al. (1985) model does take into account some details that were ignored or missed in the formulation of the sieve hypothesis. Telford’s theory for the feeding mechanism followed direct observation and thus seems convincing.

Reports differ on food types ingested by sand dollars. Culver (1961) reported only diatoms and other microalgae in the gut of *Mellita quinquiesperforata (=isoforma)*. She did not report inorganic matter in the gut, but Bell and Frey (1969) reported “terrigenous detritus” in the gut of *M. quinquiesperforata*. Other reports indicate *Mellita tenuis* ingests diatoms, foraminifera, dinoflagellates, organic detritus and sand grains smaller than 500μm (Lane 1977; Lane and Lawrence 1982; Ghiold 1984). The sizes of sand particles in gut contents of *Mellita quinquiesperforata* are smaller than that of the substratum (Borzone et al. 1997). As Findlay and White (1983) found that *M. tenuis* also ingests bacteria and non-photosynthetic microeukaryotes; the diet of sand dollars is not
strictly herbivorous. *Mellita tenuis* ingests diatoms, but Lane (1977) found diatoms can pass through the gut undigested.

Evidence exists to support the idea that several species of sand dollars can coexist in the same habitat due to resource partitioning of sediment particle sizes (Phelan 1972 and Telford et al. 1987). Sister species *Encope aberrans* and *Encope michelini* are found together in the Gulf of Mexico; however *E. aberrans* is larger than *E. michelini* (Hendler et al. 1995) and have distinctly different food grooves (Mooi 1989). In addition, mixed populations of *E. michelini* with *Clypeaster subdepressus* and *Leodia sexiesperforata*, as well as *E. aberrans* co-occurring with *Mellita tenuis*, can be found in the Gulf of Mexico (pers. observation; Telford et al. 1987). Based on analysis of particles in the food grooves, Telford et al. (1987) concluded sand dollars feed on different fractions of the sediment as a result of difference in size of food collecting tube feet. Although of interest, size of particles in the food grooves and gut may not indicate feeding preference. Telford et al. (1985) suggested the accumulation of fine particles less than 50 μm in the gut of *Mellita quinquiesperforata* resulted from crushing diatoms and fracturing sand grains by the teeth. Their analysis showed no selection of fine particles in the food grooves as they are virtually identical to those in the sediment. In contrast, Telford and Mooi (1986) found *Encope michelini* has particles greater than 200 μm but not less than 100μm in their food grooves.

Sand dollars have specific requirements for substratum. Sediments either too fine (<60μm) or too coarse (>1mm) do not support populations of the sand dollar *Mellita tenuis* (Pomory et al. 1995). Ghiold (1979) found *Mellita quinquiesperforata* (= *isometra*) burrowed most efficiently in 3 Φ sand grains, confirming the observation of

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Bell and Frey (1969) that individuals could not move on coarse gravel. Generally, fine sediments can suffocate the sand dollars by clogging the intermeshes between their spines and podia whereas coarse sediments are an impediment to movement and feeding because the tube feet cannot grasp the grains (Pomory et al. 1995). The quality of sediments not only is important in determining distribution of sand dollars, it may play a role in determining if a sand dollar is capable of movement, and even righting (Kenk 1944; Weihe and Gray 1968), important to an individual’s ability to survive and avoid predation when prone. Populations of *E. aberrans* and *E. michelini* have been found to be almost always distinct off the coast of North Carolina (Phelan 1972). These observations suggest the three species have preferred habitats that are related to depth and substratum type.

Sand dollars exhibit diel patterns in activity. Salsman and Tolbert (1965) documented nocturnal behavior of *Mellita tenuis*. The sand dollars began moving through the substratum around early evening and eventually reached a maximum speed approximately one hour after activity began. Activity declined in the hours just before dawn. Diel rhythms can result from rhythms of physical conditions, such as light, predators or food. As sand dollars do not have vision, it is unlikely light affects diel activity other than as a cue. *Mellita tenuis* may intensify feeding in the hours just before or after sunset associated with the nocturnal rhythm noted by Salsman and Tolbert (1965). Lane and Lawrence (1982) reported significantly more food in the gut in the night than in the day.

Predation could be one possible reason for a diel activity pattern. Crozier (1919) suggested fish were predators of the sand dollar *Leodia sexiesperforata* and MacGinitie
and MacGinitie (1968) suggested the spiny lobster, *Panulirus interruptus*, prey on *Dendraster excentricus*. Merrill and Hobson (1970) saw the crabs *Loxorhynchus grandis* and *Cancer* sp. feeding on the test ambitus of *D. excentricus*. The gray triggerfish, *Balistes capriscus*, feeds on the test ambitus of *Mellita tenuis* (Frazer et al. 1991, Kurz 1995). As fish are primarily diurnal and crabs nocturnal, fish predation may be the cause of nocturnal behavior in sand dollars.

Seasonally, feeding behavior may change due to food availability, light or temperature. Cool winter temperatures and light may alter plankton and benthic biomass (Findlay and Watling 1998, Mitbarkar and Anil 2002), and reproduction, i.e. allocating resources to gonad growth versus somatic growth (Lane and Lawrence 1979). The caloric content from lipid of the silt-clay fraction of the substratum at Mullet Key with a population of *Mellita tenuis* is highest in the summer (Lane and Lawrence 1982). Lipid is a major component of diatoms (Dawes 1998). Lane and Lawrence (1982) reported feeding rate by *M. tenuis* is higher in summer than winter.

The microbial community of sand habitats exhibits patterns in behavior, also. Pennate diatoms migrate between the sediment and water surface level to optimize light conditions and avoid predation by surface predators (Mitbarkar and Anil 2002). Centric diatoms rely on tidal currents and wave action for resuspension. Furthermore, pennate and centric diatoms enter resting stages and lie dormant in the substrate while retaining their photosynthetic capacity until either resuspended or more optimal environmental conditions return (Mitbarkar and Anil 2002). Though phytoplankton biomass may be small, they can contribute 30-70% of the total primary productivity at the sediment-water interface in shallow waters (Findlay and Watling 1998). In addition, diatoms are a
valuable source of proteins and lipids for grazers (Romer and MacLachlan 1986). Therefore, migration and resuspension could have cascading effects on the benthic food web. The copepods *Acartia grani* and *Centropages typicus* emerge from the substrate at dusk and migrate to the surface to feed (Calbert 1999). Ostracods exhibit a similar behavior, but some ostracods only migrate between 0 and 50 cm from the substrate to feed, providing a food source for mid-column suspension feeders (Macquart-Moulin 1999). Findlay and Watling (1998) found seasonal variations in the microbial conditions in shallow water communities depending on turnover and nutrient availability. Possibly, the rhythms of consumers mirror the rhythms of their prey. Consequently the diel rhythms observed in sand dollars might be explained by the diel rhythms of their food.

Sand dollars have a profound effect on their environment (Bell and Frey 1969). *Mellita tenuis* may be packed on a sand plain to the point of overlapping individuals (Weihe and Gray 1968, Hyman 1955, pers. observation). The layer in which sand dollars can live and respire is shallow, yet still can be incredibly productive and made even more so by their presence, due to their bioturbation. Findlay and White (1983) found that the passage of a sand dollar effectively increased the depth of redox discontinuity from 0.2 cm to 0.8 cm, however, the chlorophyll *a* concentration in the sediment was unaffected by *M. tenuis* feeding. Bioturbation, such as that from sand dollars, enhances the oxygen content of the benthos, loosens sediments, and stimulates sediment transport, all important factors in determining species diversity and community structure (Dernie et al. 2003). Lane and Lawrence (1982) suggested in months when *M. tenuis* had negative absorption efficiencies, i.e. excreting more carbohydrates and proteins than taken in, they effectively enrich the sediment. This would especially be true when sand dollars travel
from high to low nutrient substrates. Furthermore, during summer 2005, a severe red tide on the west coast of Florida caused mass mortalities of fish and invertebrates offshore and caused an anoxic zone of approximately 200 km$^2$ (FWRI 2005). In September 2005, a site 8.5 km west of Egmont Key was visited. No living sand dollars were found, only *Mellita tenuis* and *Encope aberrans* tests were found along with a visible detrital layer on top of the substrate. However, inshore off Fort De Soto North Beach, *M. tenuis* appeared closer to the shore than normally, in only a few centimeters of water (pers. observation). Possibly, *M. tenuis* was migrating inshore to avoid the anoxia, thus moving between high and low nutrient areas. Sand dollars, by aerating the sediment and grazing on the benthic community, have a distinct impact on their habitat. A better understanding of sand dollar feeding may further highlight their importance to the ecosystem.

Information about the food and feeding of sand dollars is extremely limited. Except for Timko (1976) and O’Neill (1978) on *Dendraster excentricus* and Lane and Lawrence (1982) on *Mellita tenuis*, information is restricted to general statements about food composition. Even their studies are limited to a single site and laboratory observations. Additional information on population differences of a species and of other species of sand dollars would contribute to understanding better their biology and ecology.

*Mellita tenuis*, *Encope aberrans* and *Encope michelini* of the central Florida Gulf Shelf provide the opportunity to make such comparisons. They are scutellid sand dollars in the family Mellitidae (Mooi 1989). They have interesting differences in their distribution. Serafy (1979) reported the distribution of the three species on the Florida Gulf Shelf. *Mellita tenuis* was most abundant at a station with well sorted, fine quartz
sand with a modal grain size of 0.18 mm at 6 m depth. It was much less abundant at a station with crushed shell and poorly sorted quartz sand with a model grain size of 0.6 mm. A few *Encope michelini* also occurred at this site. *Encope michelini* and *Encope aberrans* occurred in fewer numbers at greater depths of 18 and 37 m on crushed shell and quartz sand. *Encope michelini* was much more common than *E. aberrans*. We have found *E. michelini* and occasional *E. aberrans* at one of Serafy’s 18 m sites and *E. aberrans* along with abundant *M. tenuis* at one of his 6 m sites. Neither species of *Encope* were found at sites less than 4 m depths from Panama City to Naples, Florida where *M. tenuis* was found (Tan and Lawrence 2001). However, Telford and Mooi (1986) and Kurz (1995) found *M. tenuis* and *E. michelini* together near Cedar Key, Florida and in the Florida Keys. *Leodia sexiesperforata* is also found at Cedar Key (J. Herrera, pers. communication).

The question addressed here is whether food and feeding of three species of sand dollars in the family Mellitidae (*Mellita tenuis*, *Encope aberrans* and *Encope aberrans*) vary with respect to species and over space and time. Organic content of the gut contents and sediment are expected to differ on both a diel and seasonal scale. In addition, the organic content of the sediment across sites should be different; thereby supporting different sand dollar species. Particle sizes in the guts should be smaller since smaller particles, due to their surface area to volume ratio, have a higher nutritive value than larger particles and sand dollars possess powerful lanterns to further crush those particles.
Materials and Methods

Collection Sites

For the seasonal study, specimens and sediment were collected from March through September 2004. *Encope michelini* were collected approximately 22.4 km off Sanibel Island, Florida (26° 32.43’ N, 82° 29.163’ W, Hourglass Station J, Serafy 1979) at 18 m depth (Fig. 1). *Encope aberrans* and *Mellita tenuis* were collected approximately 8.5 km off Egmont Key, Florida (27° 35.00’N, 082° 50.00’ W, Hourglass Station A, Serafy 1979) at 7 m depth in March. *Mellita tenuis* were also collected in June and September 2004 off of Bean Point, Anna Maria Island (27° 31.54’ N, 82 ° 45.26’ W) at 1-2 m depth. Additional sediment collections and sand dollar densities measurements were taken from sites in Tampa Bay (27° 49.42’ N, 82 ° 24.10’ W) at 1-2 m depth. Sediment only was collected from sand dollar sites at the North (27° 38.41’ N, 82 ° 45.49’ W) and East (27° 35.48’ N, 82 ° 42.10’ W) beaches of Fort De Soto Park, and Lido Key (27° 9.40’ N, 82 ° 35. 12’ W) in 1-2 m depth (Table 1).

At each site, when weather conditions permitted, a 30 m transect line was run in triplicate. A 1 m² quadrat was placed every 5 m and the number of sand dollars was counted to determine the density. In poor weather conditions, a 1 m² quadrat was thrown randomly (n=3) and sand dollars were counted. The width of each was measured at the
Figure 1. Sand dollar collection sites. *Encope michelini* was collected from the Offshore Charlotte Harbor site. *Encope aberrans* was collected from Offshore Egmont Key. *Mellita tenuis* was collected at all other sites (map: Google Earth v3.0 2005).

widest point (just above the II and IV ambulacra, after Loven 1874) with Vernier calipers to determine a size-frequency distribution.

For the diel study, 20 *Mellita tenuis* were collected every 3-4 hours at Anna Maria Island, June 20, 2004 and September 25, 2004. *Encope michelini* were collected in a similar manner at the offshore Charlotte Harbor site in March 20, 2004 and September 17, 2004.
Table 1. Collection sites.

<table>
<thead>
<tr>
<th>Collection Site</th>
<th>Coordinates</th>
<th>Depth (m)</th>
<th>Date</th>
<th>Species present</th>
</tr>
</thead>
<tbody>
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<td>22.4 km W W</td>
<td>Charlotte Harbor</td>
<td>26°32.43' N, 82°29.163' W</td>
<td>18</td>
<td>9/27/2003 Encope michelini, Encope aberrans</td>
</tr>
<tr>
<td>Egmont Key</td>
<td>8.5 km W</td>
<td>27°35.00' N, 82°50.00' W</td>
<td>7</td>
<td>9/28/2003 Mellita tenuis, Encope aberrans</td>
</tr>
<tr>
<td>Anna Maria Island</td>
<td>27°32.09' N, 82°44.49' W</td>
<td>2-3</td>
<td>6/20/2004</td>
<td>Mellita tenuis</td>
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<td>Tampa Bay, W</td>
<td>Apollo Beach</td>
<td>27°49.07' N, 82°24.23' W</td>
<td>2</td>
<td>9/25/2004 Mellita tenuis</td>
</tr>
<tr>
<td>Lido Key</td>
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<td>2-3</td>
<td>10/28/2004</td>
<td>Mellita tenuis</td>
</tr>
<tr>
<td>Fort De Soto N</td>
<td>North Beach</td>
<td>27°37.11' N, 82°44.24' W</td>
<td>2-3</td>
<td>10/28/2004 Mellita tenuis</td>
</tr>
<tr>
<td>Fort De Soto E</td>
<td>Beach</td>
<td>27°26.51' N, 82°43.36' W</td>
<td>3-4</td>
<td>10/28/2004 Mellita tenuis</td>
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</table>

Preservation of Samples

All specimens collected were preserved by the method of Telford et al. (1987). Immediately after collection, specimens were injected with 20% formalin in seawater into the coelomic cavity. They were then immersed in the formalin solution and stored until analysis. Sediment collected was also preserved with 20% formalin and refrigerated. Sediment from the offshore Gulf site with and without formalin was compared because addition of formalin may slightly increase the organic content of the samples (Crisp 1971). Sediment samples with formalin were, on average, 1.5% higher than the sediment without formalin. However, the necessity of specimen preservation, i.e. eliminating decomposition before samples could be processed, outweighed the small increase in values.
Analysis of Gut Contents and Substratum

The aboral test and gonads were removed from sand dollars with forceps and the guts were extracted from 20 specimens per collection. Guts and their contents were stored in vials and bathed in 20% formalin. The guts were divided into four segments: stomach, upper intestine, mid-intestine, and lower intestine. The location of food in the gut tract was noted (Fig. 2). Extracted guts were cleaned of any test or gonad material. Samples of gut contents were observed under a microscope and the sizes of 150 ingested sediment particles were measured using a calibrated micrometer (following the method of Telford 1986). The optimum sample size was determined by comparing variances for samples sizes of 50, 100, 150, 200 and 250. Similar variances existed between sample sizes of 150, 200 and 250; consequently a sample size of 150 was used. 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 higher than 400X so that accurate measurement of particles was difficult. Thus, the maximum magnification used was 400X. The smallest particles measured were 0.005 mm, though the actual size may have been smaller. Afterwards, the entire gut sample was dried for at least 24 hours in a fume hood under loose cover. The dried gut contents were weighed, ashed in a muffle furnace at 500° C for 4 hours and weighed again to calculate the percent organic material (Paine 1971). Possibly, some organic material from the gut was present in the samples used to measure percent organic material.
Sediment was sampled at the collection sites. Three samples of approximately 60 ml of sediment were collected from the surface layer at each collection. Sediment samples were fixed in 20% buffered formalin immediately after collection. Before analysis, samples were dried in an oven at 60° C for at least 48 hours. Sediment samples were dry-sieved using the US standard sieve series and sieve segments were weighed (adapted from Mitbarker and Anil 2002). A small portion of each sediment sample was taken to measure the percent organic content in the same manner as the gut contents. The
ashing treatment at 500° C does not degrade carbonate sediment, found at the offshore site (Lawrence, pers. communication).

**Food Groove Analysis**

Ten *Encope michelini* collected March 2005, from Offshore Charlotte Harbor, and ten *Mellita tenuis* collected October 2005, from Anna Maria Island were preserved in 20% buffered formalin in individual plastic bags. Sand particles from the food grooves were removed using a spatula and smeared on 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.

**Statistical Analysis**

The size-frequency distribution of test diameters between groups was analyzed using the Kolmogorov-Smirnoff Test (Zar 1999). The particle size distribution in the guts, food grooves and sediment was analyzed using a percent cumulative frequency distribution (Folk 1965). Sediment grain size distribution was also analyzed using the program GRADISTAT version 4.0 (Blott 2000). Particle distributions were compared using the Kolmogorov-Smirnoff Test (Zar 1999) and mean particle sizes were compared using non-parametric tests (Kruskal-Wallace and Mann-Whitney U-test) (SPSS student, version 13.0 2004). The percent organic material of gut samples and sediment was compared using ANOVA techniques and, when necessary, non-parametric tests (Kruskal-Wallace and Mann-Whitney U-test) (SPSS student, version 13.0 2004). The $\Phi$ units, a geological measurement ($\Phi = -\log_2 \text{mm}$), were used when dealing with 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). SI units were used to compare sediment, gut and food groove particles. Descriptive statistics were used to evaluate populations and diel variation in particle sizes and organic content of sediment and gut contents (SPSS student, version 13.0 2004).
Results

Description of Populations

The average size of *E. michelini* off Sanibel Island was 8.12 ± 0.47 cm in Fall 2003, 8.46 ± 0.53 cm in Spring 2004 and 9.03 ± 0.59 cm in Fall 2004 (Fig. 3). The size-frequency distributions increased over time and were all significantly different from each other (Kolmogorov-Smirnoff Test, $D_{0.05,25}=0.26404$). The average size of *M. tenuis* off Egmont Key (Fall 2003) was 6.55 ± 0.50 cm and Anna Maria Island (Summer 2004) 7.15 ± 0.85 cm, (Fall 2004) 7.70 ± 0.77 cm and Tampa Bay (Fall 2004), 10.85 cm ± 0.85 (Fig. 4). The September 2004 Anna Maria Island collection was significantly greater than the June 2004 collection. The size-frequency distributions for the Tampa Bay collections were significantly greater than the other collections of *M. tenuis*, which differed significantly among themselves as well. Densities of sand dollars ranged from 0.43 ± 0.60 *E. michelini*·m$^{-2}$ (September 2004) to 49 ± 21 *M. tenuis*·m$^{-2}$ (Fort De Soto, Apr. 2004). At Anna Maria Island (June 2004), mean density during the day was 21.4 ± 7.9 *M. tenuis*·m$^{-2}$, but after sunset the density was 7.6 ± 3.6 *M. tenuis*·m$^{-2}$.
Figure 3. Size-frequency distribution of *Encope michelini* (test width = diameter taken above anterior notches).

Figure 4. Size-frequency distribution of *Mellita tenuis* (test width = diameter from above anterior lunules).
Particle Analysis

Sediment

The sediment of the eastern Gulf coast is generally quartz sand inshore and quartz mixed with shell hash offshore (FIO 1994). The sediment particle-size distribution varied with site (Fig. 5). The sites with *M. tenuis* had smaller particles and differed among themselves (Table 2). The sediment off Sanibel Island (*E. michelini* site) had a graphic mean particle size of $0.352 \pm 0.937 \Phi$, which corresponds to the coarsest sediment of all the collections. Sediment ranged from very fine gravel to fine sand. The sediment off Anna Maria Island (*M. tenuis* site) had a mean particle size of $1.645 \pm 0.628 \Phi$. The site with the finest sediment was Fort De Soto North Beach ($2.260 \pm 0.461 \Phi$). The inshore sites ranged from course sand to very fine sand. Moreover, sediment grains from offshore and inshore sites are different (Fig. 6). Sediment from the inshore sites is smaller and mostly quartz with very little shell fragments. Offshore, the particles are larger and carbonate particles are more frequent. Both inshore and offshore sediments are composed of smooth, rounded particles.

No significant differences were found among sediment particle distributions (Kolmogorov-Smirnoff Test). However, this seemed doubtful since the particles from inshore and offshore appeared so different in composition and size. Consequently, mean particle sizes from different sites were compared and some differences were observed. Mean particle size of the sand dollar site samples were significantly different (Kruskal-Wallis Test, $\chi^2 = 23.249, p<0.003$) (Fig. 7). The inshore sites in general have smaller mean particle sizes than the two offshore sampling dates. Most pair-wise comparisons
Figure 5. Percent cumulative frequency distributions of sediment particles from habitats with *E. michelini* and *M. tenuis*. Each curve represents a cumulative percent frequency distribution of the mean values in each size category. Note the phi units are on a log scale.

Figure 6. Photographs of offshore and inshore sediment from a light microscope (40X). Left: Sediment from Anna Maria Island. Right: Sediment from Offshore Charlotte Harbor.
Table 2. Mean particle sizes of sediment, food grooves and gut contents.

<table>
<thead>
<tr>
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<tr>
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</table>

were significantly different, except seasonal collections from Anna Maria Island (June and September 2004) and Offshore Charlotte Harbor (March and September 2004) were not significantly different (Mann-Whitney U-test, p<0.05). Sediment from Egmont Key (March 2004) was not significantly different from any other inshore sites, except Anna Maria Island (June 2004).

**Gut Contents**

The gut particle size-frequency distributions among collections (Table 2) were not significantly different between any pairing (Kolmogorov-Smirnov Test). However, this
Figure 7. Box and whiskers plot of mean sediment particle sizes at sites.

Figure 8. Size-frequency distribution of particles in the guts of Encope aberrans, Encope michelini and Mellita tenuis. (A.M.I. = Anna Maria Island, E.K. = Egmont Key.)
may be suspect because approximately 75% of the gut particles for *Encope michelini* and *Mellita tenuis* were less than 9.9 \( \mu \text{m} \), which may unduly skew the results of the distribution test. Moreover, the shapes of the size-frequency distributions indicate differences (Fig. 8). *Encope aberrans* has larger gut particles. Approximately 75% are between 10-99.9 \( \mu \text{m} \). Larger-sized particles were also present. The cumulative frequency distributions for *E. michelini* and *M. tenuis* were similar, but, the shape of the cumulative frequency for *E. aberrans* is appears different from the other two species (Fig. 9). The gut contents of *E. michelini* have smaller particles than *M. tenuis* (Figs. 10 and 11). The guts are characterized by some large particles (10-200 \( \mu \text{m} \)) and many very small particles (< 9.9 \( \mu \text{m} \)). The guts of *M. tenuis* have more loose organic material, probably filamentous algae or detritus. The guts of *Encope aberrans* had the largest average particle size, 0.0757 ± 0.1153 mm, as well as the largest maximum size (1.6925 mm). In addition, the distribution was different from the other two sand dollar species (Fig. 8).

The mean sizes of gut particles were compared across seasons for *M. tenuis* and *E. michelini* and species co-occurring at Egmont Key, *M. tenuis* and *E. aberrans* (Fig. 12). Nonparametric statistics were employed to compare the means as variances were not homogeneous. Gut particles from *M. tenuis* collected June 2004 were significantly larger than September 2004 (Mann-Whitney U-test, p<0.000). The gut particles of *E. michelini*, collected in March 2004 were significantly greater than the September 2004 collection (p<0.000). Gut particles from *E. aberrans* were significantly greater than *M. tenuis*, both collected March 2004 from Egmont Key (p<0.000). Notably, *E. aberrans* had the largest range of values, whilst the ranges of the other two species were much less. Centric and
Pennate diatoms, filamentous green algae, flat worms (possibly parasites), and foraminifera were observed in the gut contents of all species.

**Comparison of Sediment, Food Grooves and Gut Particles**

The sediment particle, food grooves, and gut particle distributions were compared. The average particle size in the food grooves was 0.0147 ± 0.0383 mm for *E. michelini* and 0.0659 ± 0.136 mm for *M. tenuis*. This is not significantly different from all their gut contents. However, the particle distribution of the food grooves is larger than the gut contents (Fig. 13). The average gut particle sizes ranged from 0.0086 ± 0.013 for *Mellita tenuis* to 0.076 ± 0.12 mm for *Encope aberrans* (Table 2). The average sediment particle sizes ranged from 0.7834 ± 0.001915 mm (offshore September 2004) to 0.2088 ±...
Figure 10. Photographs of gut contents of *E. michelini* from a light microscope (100x). Left: (A) a foraminiferan test is left center. Right: (B) long pennate forms.

Figure 11. Photographs of gut contents of *M. tenuis* from a light microscope (100X). Left: (A) several large sediment particles with jagged edges and (B) some gut tissue. Right: (C) tufts and filamentous strands of green algae.
Figure 12. Box and whiskers plot of mean particle sizes of gut contents of *Encope aberrans*, *Encope michelini*, and *Mellita tenuis*.

Figure 13. Comparison of particle size distribution in food grooves and gut contents. Left: *Encope michelini* collections. Right: *Mellita tenuis* collections.
0.00138 mm (Fort De Soto North Beach April 2004). The mean particle size for the sediment is larger than the gut particles by one order of magnitude. It is important to note that the sample sizes of sand dollars and sediment were disparate ($n_{\text{gut particle}} = 20, n_{\text{sediment}} = 3$); which prevents valid statistical comparison. Sediment particles are large and rounded (Fig. 6), while the gut particles are much smaller and often have jagged edges (Figs. 10 and 11). 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.

**Organic Content Analysis**

**Sediment**

The percent organic content of the sediment was examined. Across *Mellita tenuis* sites, the percent organic content was significantly different (Kruskal-Wallis Test $\chi^2 = 29.163, p=0.001$). In addition, sites were compared pair-wise (Mann-Whitney U-test, $p<0.05$) to analyze specific differences. Sediment from Fort De Soto East Beach (October 2004) had significantly greater organic content than other inshore sites (Fig. 14). Sediment from Anna Maria Island 9:30 am, September 2004 was not significantly different from any other sites. Yet, other than the collections from the same day, the $p$-values were very close to being significantly different (Table 3). The Tampa Bay sites, although not significantly different from each other, had significantly lower organic content compared to all other sites, except Anna Maria Island 9:30 am, September 2004. Lido Key shared the most with the other sites and was only significantly different from four other sites (Anna Maria Island, September 2004 1:30 pm, 5:00 pm, and 8:00 pm collections and Ft. De Soto E. Beach October 2004). Seasonally, the sediment from
Figure 14. Box and whiskers plot of percent organic content of sediment from sites. Percent organic content is calculated by dividing the weight (g) of the sample post-ashing by weight (g) pre-ashing.

Table 3. Pair wise comparisons of percent organic content of sediment from sites with Mellita tenuis. The nonparametric Mann-Whitney U-test was utilized because variances were not homogeneous. The upper right triangle gives information on significant differences (sig. = significantly different at p<0.05, n.s. = not significantly different); the lower left triangle gives the p-values for the pair wise test.

<table>
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<th>Collection</th>
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<th>AMI 9/04</th>
<th>AMI 9/04</th>
<th>AMI 9/04</th>
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<th>Ft. De Soto N</th>
<th>Lido Key</th>
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<th>Tampa Bay 2</th>
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<td>n.s</td>
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<td>0.513</td>
<td>0.487</td>
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Anna Maria Island had significantly lower organic content in June 2004 than September 2004 (Kruskal-Wallis $\chi^2 = 8.265, p=0.004$). Geographically, the sites vary across space (Fig. 1). The sediment organic content did not vary over a diel period (Anna Maria Island, September 2004, Table 3). Inshore, the average organic content ranged from $0.355 \pm 0.046\%$ (Tampa Bay 2 October 2004) to $1.759 \pm 0.294\%$ (Ft. De Soto E October 2004). At the offshore *Encope michelini* site, sediment organic content was $4.24 \pm 1.26\%$ (September 2004), which is on average 2-4 times higher than the inshore sediment.

The mean particle size and mean organic content of sites were compared. Smaller particles have slightly lower organic content, however, there was some variation (Fig. 15). The sediment from Fort De Soto East Beach, at the mouth of Tampa Bay, has a greater organic content than any other inshore sites although its mean particle size is quite small. In contrast, the offshore site has larger particles and greater organic content. Larger particles correlated with higher organic content ($R^2_{\text{linear}} = 0.699$).

**Gut Contents**

The organic content of the gut samples varied over time, both seasonally and hourly. Gut mean percent organic content for *Mellita tenuis* ranged from $26.96 \pm 6.28\%$ (3 pm June 2004) to $44.48 \pm 4.93\%$ (1:30 pm September 2004). The sediment organic content at Anna Maria Island is, on average, $0.579 \pm 0.185\%$; this corresponds to a 47-77 fold difference in organic content between the gut contents and the ambient sediment. The gut contents from *Mellita tenuis* collected in September 2004 had a significantly greater overall organic content than the June 2004 collection (ANOVA, $F = 68.510$,
p<0.000) (Fig. 16). Furthermore, the sampling times were significantly different from each other (ANOVA, F= 18.292, p<0.000). In June 2004, the 11 am collection was significantly higher than the 3 pm collection, and the 3 pm collection was significantly lower than the 9 pm collection (Tukey HSD, p<0.05). For September 2004, the diel collections were not significantly different from each other. Most September 2004 collections were significantly greater than the June 2004 collections, except 11 am June 2004 and 9:30 am September 2004 (Table 4). For the June 20, 2004 collections, the 11 am collection had the greatest organic content and the 3 pm collection had the lowest. In September 25, 2004, the 8 pm collection had the greatest organic content and the 9:30 am collection had the lowest, albeit this was greater than any of the June 2004 collections. The gut contents had 30-55 times more organic content than the sediment.
Table 4. Pair wise comparisons of percent organic content of gut contents of *Mellita tenuis*. Upper right triangle relates significant differences (=sig.) or not significant (n.s.) using Tukey’s HSD; lower right triangle, are pair wise comparisons using the Bonferroni post-hoc test. Two different measures were used to test whether the statistics were equivalent in sensitivity, however there was only 1/28 cases where the two tests disagreed.

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</table>

Figure 16. Scatter plot of seasonal mean percent organic content of gut contents of *M. tenuis* at Anna Maria Island. (Time of day codes are 1 = 9:30-11:30am, 2 = 1:30-3:30 pm, 3 = 5-6pm, and 4 = 8-9 pm. Percent organic content is calculated by dividing the weight (g) of the sample post-ashing by weight (g) pre-ashing.)
The organic content of gut samples of *Encope michelini* across seasons was significantly different (ANOVA, $F = 110.713, p<0.000$) (Fig. 17). Sampling times were also significantly different from each other (Kruskal-Wallis, $\chi^2 = 79.706, p<0.000$). The 5:55 pm collection for March 20, 2004 had significantly lower organic content, $23.33 \pm 1.91\%$, than collections at 3:10 pm, 8:00 pm, and 10:30 pm (Mann-Whitney U-test, $p<0.05$) (Table 5). The 10:30 pm collection had the highest mean organic content for that day, $27.96 \pm 4.80\%$. The September 17, 2004 collections overall had a significantly greater mean organic content than the March 2004 collections. The collections from that date were not significantly different from each other; but they were all significantly higher than the March 2004 collections (Table 4). The 4:20 pm collection had the greatest mean percent organic content, $36.22 \pm 6.77\%$, of all collections, albeit non-significant. The gut contents had 5.5-8.5 times more organic content than the sediment. The organic content of the sediment and the gut contents could not be compared statistically because of the difference in sample sizes.

The organic content of the gut contents of *Encope aberrans* and *Mellita tenuis* at the same site were compared. *Encope aberrans* collected from 8.5 km west of Egmont Key had a significantly smaller mean organic content than *M. tenuis* (Kruskal-Wallis, $\chi^2 = 29.268, p<0.000$) (Fig. 18).

The mean gut particle size and mean percent organic content for each collection were compared (Fig. 19). The gut contents of *Mellita tenuis* and *Encope michelini* clumped closely to each other across seasons and sites. *Encope aberrans* clumped separately from the other two species. Notably, *M. tenuis*, collected in March 2004 at Egmont Key along with *E. aberrans*, clumped together with other *M. tenuis*, collected at
Figure 17. Scatter plot of seasonal mean percent organic content of gut contents of *E. michelini* at offshore Charlotte Harbor. (Time of day codes are 1 = 8:30-9:30 am, 2 = 1:30-3:30 pm, 3 = 4-6 pm, 4 = 8-9pm, and 5 = 10:30–11:30 pm.)

Table 5. Pair wise comparisons of percent organic content of gut contents of *Encope michelini*. The nonparametric Mann-Whitney U-test was utilized because the variances were not homogeneous (sig. = significantly different, n.s. = not significantly different).

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<tr>
<th>Collections</th>
<th>3/04 9:25am</th>
<th>3/04 3:10pm</th>
<th>3/04 5:55pm</th>
<th>3/04 8pm</th>
<th>3/04 10:30pm</th>
<th>9/04 8:30am</th>
<th>9/04 1:30pm</th>
<th>9/04 4:20pm</th>
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Figure 18. Box and whiskers plot of mean percent organic content from the gut contents of *Encope aberrans* and *Mellita tenuis*, two co-existing species off Egmont Key.

Figure 19. Scatter plot of mean gut particle size and mean percent organic content of gut contents of *Encope aberrans*, *Encope michelini*, and *Mellita tenuis*. 
Anna Maria Island and *E. michelini*, collected offshore. The smallest mean particle size correlated with the greatest organic content ($R^2_{\text{linear}} = 0.617$).
Discussion

Description of Populations

The change in size distributions for *Encope michelini* may indicate a single aging cohort. Recruitment has not occurred at the offshore site (Lawrence, pers. communication). Recruitment of *Mellita tenuis* is higher inshore with typically biannual events (Lawrence, pers. communication). The size-frequency distributions of *M. tenuis* from date to date generally cluster around the same mode, and are probably a single cohort. The similarity in modes among collections may indicate that recruitment is widespread in the Gulf populations of *M. tenuis*. The size-frequency distributions of *M. tenuis* at Anna Maria Island indicate cohort aging as the mean increased from June to September. The Tampa Bay collection of *M. tenuis* is much larger than those from other sites. The difference in their size could indicate a difference in age or growth rate. However, size and age are uncoupled in *M. tenuis* (Tan and Lawrence 2001). Moreover, *M. tenuis* is a stress-tolerant ruderal species, characterized by high fecundity and short life span (Lawrence 1990). Less information on the life-history of *Encope michelini* is available to determine its life-history strategy. However, since *E. michelini* exists in deeper water, it probably experiences fewer disturbances and more stress (due to lower primary productivity) than *M. tenuis*. More research on fecundity and recruitment for this species is needed. The difference in distribution of the two species might indicate
specific habitat requirements, possibly associated with particle size-frequency distribution of the sediment.

**Particle Analysis**

The particle sizes of sediments from the habitats of *E. michelini* and *M. tenuis* are different. The offshore sites have much coarser sediment than the inshore sites. *Encope aberrans*, the largest sand dollar, is found in both inshore and offshore sites intermittently. The range of sediments that *M. tenuis* inhabits is quite wide; from the very fine sand of the East Beach of Fort De Soto and the Tampa Bay sites to the coarser sandy sites west of Egmont Key. The results here, a mixture of quartz and carbonate, are consistent with past studies (Brooks et al. 2003). Quartz particles are predominant inshore and quartz and carbonate particles are mixed offshore. Carbonate sands are porous while quartz is solid (Folk 1965). The types of benthic microalgae could be intrinsically affected by this at the offshore and inshore sites, and may partially explain differences in species distributions.

The gut particles are small. For both *E. michelini* and *M. tenuis*, 60-75% of the particles were less than 10 μm. *Encope aberrans* had larger particles; the mean particle size was 75 μm. However, all species feed on a much smaller subset of the ambient sediment. Lane and Lawrence (1982) found that the majority of the particles in the guts were less than 62 μm. Telford et al. (1985) found that 79% of particles in the gut *M. tenuis* were less than 100 μm. Both of these past studies are close to what was observed in the current study. In addition, mean particle sizes in the food grooves were more similar to those in the guts than the sediment. Sand dollars probably select small particles, and then further crush particles with their lanterns. There is evidence of sand
grain fracture as particles in the guts had sharp edges while those in the sediment were rounded and polished. However, it is unlikely that the calcium carbonate lanterns are able to crush the harder quartz particles. The results here correspond to the findings of Telford et al. (1985): podia select manageable particles and the lantern crushes softer particles to aid digestion.

The difference in gut particle sizes between *Encope aberrans*, *Encope michelini*, and *Mellita tenuis* may explain, in part, why *E. aberrans* can coexist with the two other species. It competes with neither for particles. Whitlach (1980) found advantages to feeding on both large and small particles, while studying the feeding niches of polychaetes. Specializing on small particles provides higher quantities of nitrogen and bacteria, because of the inverse relationship between surface area and volume. Specializing on larger particles, though they are less abundant, greatly increases the probability of encountering a food particle.

Statistical comparison of sediment and specimen particles proved difficult. When analyzing sediment and gut particles, different techniques were necessarily employed. Mean particle size of sediment samples was determined by sieving and weighing the mass for each size fraction. The volume of gut contents retrieved was so small, using a sieve was impossible. Mean particle size of gut and food groove samples was determined by measuring the first 150 particles encountered. There is an inherent bias between these two analytical techniques. However, the goal for each technique was to estimate the true particle size of the sample and each does so successfully to a degree. Yet, the objective here was to determine whether the guts contained different sized particles from the ambient sediment. Upon visual examination of the different samples, it was evident that
the gut particles are much smaller than the sediment. The measurements provided by the two techniques substantiate this; there was very little overlap in particle sizes for gut and sediment particles. This alone may be evidence of differences in particle size between gut contents and sediment. Moreover, the resolution of the very small particle sizes at high magnification decreased making precise measurement difficult. However, the purpose of measuring gut particles was for comparison to the sediment. In general, particles that were measured as 0.005 mm could be that size or smaller. Particles smaller than 0.005 mm would only further validate the conclusion there are extreme differences between the gut and sediment particle sizes.

Organic Content Analysis

The organic content of the sediment at both Encope and Mellita sites varied across seasons. This, of course, is expected, given the annual increase of algae during the summer and decrease with the cooler temperatures and reduced daylight of winter in the subtropics (Dawes 1998). The sediment organic content did not change significantly over the course of the day. The Mellita Gulf sites are fairly similar in terms of organic content, however elsewhere where Mellita exist the range of organic content is great. The site located on the mouth of Tampa Bay (Fort De Soto East beach) has the highest organic content, most likely because daily tidal cycles bring in and draw out large amounts of water to the bay through the mouth which would probably yield organically rich sediment. Moreover, the Tampa Bay sites had the lowest organic content of all the sites. These sites are inside an estuary, subject to increased fluctuations in salinity, water temperature and sedimentation rates (Dawes 1998). Given the ecological, hydrographical and geographical differences for The Tampa Bay sites, it is not unexpected those sites are
significantly different from the Gulf sites. Possibly, because of these habitat differences, the biology of the sand dollars in Tampa Bay is quite different from populations in the Gulf waters and deserves further investigation.

Similar to the particle analysis, the difference in the organic content of sediment and the gut contents could not be statistically compared because of the difference in sample sizes. However, the great differences in values, less than 1% sediment organic content and 20-40% gut organic content, are probably different.

The organic content at the *Encope* site was much higher than the inshore sites. One may expect the inshore sites to have a higher organic content, given terrestrial nutrient inputs. However, areas of low and high organic content are patchy in the West Florida Shelf (Brooks et al. 2003). Detrital precipitation, currents carrying allochthonous nutrient sources, lower herbivore densities or *in situ* production all may affect levels of organic content offshore. These factors probably play a role in determining species distributions.

Although, the organic content of the sediment does not fluctuate over a diel period, the organic content of the guts does. Higher organic content in the guts may indicate time periods when the sand dollars are feeding. Differences in behavior over a diel period have been observed for deposit feeding echinoderms. Hammond (1982) found diel patterns of activity for several species of deposit feeding echinoderms (*Holothuria mexicana, Isostichopus badionotus, Meoma ventricosa,* and *Clypeaster rosaceus*) in Jamaica. All four species increased activity in the afternoon leading up to midnight and decreased activity in the early morning, and by midday were virtually immobile. Moreover, the behavior that Salsman and Tolbert (1965) documented for
Mellita quinquiesperforata off Panama City, Florida is similar to Hammond’s study. Lane and Lawrence (1982) found significantly more food in the gut of Mellita quinquiesperforata at night than in the day.

Interestingly, the peak times of organic content of the gut contents were not consistent across collection dates. For Mellita tenuis, the peak organic content was 11 am June 2004 and 8 pm September 2004. Encope michelini had peak organic content at 10:30 pm March 2004 and 4:20 pm September 2004. An animal may have a preferred feeding time, for example, around dusk or dawn. A change in peak feeding time could be due to conditions changing with season. Daylight hours, fish activity and predation, and abundance of microalgae all change throughout the year. For example, Buglossidium luteum experiences increased predation seasonally (Nottage and Perkins 1983). Bay scallops in North Carolina experience greater predation when blue crab populations are highest in the summer (Bishop et al. 2005). Reiss and Kroncke (2005) found predation is a factor in seasonal variability of mean abundances of infaunal organisms in the North Sea. During summertime in the subtropics, the abundance of diatoms, dinoflagellates and foraminiferans is highest (Dawes 1998). Deposit feeding polychaetes increase their ingestion rates when high quality food is available and decrease when low quality food is available (Taghon 1982). An optimal feeding time in the summer may not be the same as in the winter. Sand dollars may take advantage of the higher benthic algae populations and conduct their feeding during the shorter summer nighttime periods, when the risk of piscine predation is lower. In addition, during the summer, they can allocate more time to other activities, such as gonad growth (Lane and Lawrence 1979). Conversely, in the winter, when food abundances are lower, sand dollars may allocate more time to foraging
in order to meet minimum nutrient requirements. Sand dollars store lipids in their gonads in the limited space between the aboral surface and the guts (Moss and Lawrence 1972). Thus, sand dollars cannot tolerate long periods of low food supply, i.e. the winter (Moss and Lawrence 1972). Lane and Lawrence (1982) found negative absorption efficiencies of food during the winter months. They also noted constant feeding. However, their observations were made in the laboratory. Many marine species are sensitive to chemical cues from predators and may alter behavior in response (Brown 2003; Lawrence 1991; Rosenberg and Selander 2000; and Solan and Battle 2003). Additionally, differences in photoperiod or light intensity in the laboratory may affect behavior. Since food availability does not vary over the course of the day and peak gut organic content does, the periodicity of feeding in sand dollars most likely is driven by the risk of predation.

The organic content of the gut contents of the three species, by and large, were different from each other. The bioenergetic requirements probably vary with species. In general, metabolic rate scales with ¾ power of biomass; thus larger organisms have a lower metabolic rate (Banavar et al. 2002; West et al. 1997). *Mellita tenuis*, the smallest, would most likely have the highest energy requirements. Yet, the inshore sediment inhabited by *M. tenuis* has low organic content. Indeed, the gut organic content for *Mellita tenuis* is the highest of the three species. *Encope michelini* is larger and would have smaller energy requirements and the organic content of its gut contents is lower than *M. tenuis*. *Encope aberrans* is the largest sand dollar and has the lowest organic content of its gut contents. Ironically, the organic content of the sediment does not correspond with their presumed metabolic rates. Possibly, the high abundance of *Mellita tenuis* inshore locally depletes the microalgae population, which otherwise would be quite high.
However, populations of *M. tenuis* persist despite low organic content. Possibly, incoming tides and currents regularly replenish microalgae at the inshore sites. *Encope aberrans* appears to have an adaptive strategy quite different from the other two species and may further explain why it can coexist with other species of sand dollar. It ingests larger particles and inhabits both inshore and offshore habitats. Where *E. aberrans* and *Mellita tenuis* were found together, the organic content of their gut contents and the particle sizes were significantly different. Thus their niches may not overlap enough for species displacement to occur. *Encope michelini* and *M. tenuis* appear to have distinct habitat preferences; *E. aberrans* appears more flexible. Whitlach (1980) found that deposit-feeding polychaetes living in soft bottom habitats were either habitat generalists- resource specialists or habitat specialists- resource generalists. Possibly, *E. michelini* and *M. tenuis* fall into the latter category while *E. aberrans* is in the former. Though much work has been done on deposit feeders generally, and polychaetes specifically, it remains to be tested whether these rules hold true across taxa. Arguably, sand dollars and polychaetes are subject to similar ecological and evolutionary pressures of deposit feeding in soft bottom habitats, and may follow similar rules for niche occupation.

Furthermore, differences in the organic content of the gut contents in all three species could be related to the types of food each ingests. *Mellita tenuis* had visibly more loose organic material present in the guts than *Encope michelini*. Even though particle sizes were approximately the same for the two species, *E. michelini* may feed more on epipelic algae and *M. tenuis* may feed more on interstitial free microalgae, as evidenced by gut contents. This was not tested for in this study, however, it deserves investigation.
The porous carbonate particles offshore may provide more sites of attachment for epipelic algae as opposed to the quartz particles inshore, which are more solid and would resist algae attachment. The quartz particles examined were mostly translucent or pure white. The opaque carbonate particles are often stained green. Although particle sizes were similar for the two species, the food material may be quite different.

An interesting relationship between organic content and particle size for sediment and the gut contents was found. Generally, a negative relationship between particle size and organic content exists (Levinton 1989, Whitlach 1981). For the gut contents, *Mellita tenuis* and *Encope michelini* had small particles and high organic content and *E. aberrans* had larger particles and low organic content. However, for the sediment, the exact opposite was found. The inshore sediment particles are smaller, but have a lower organic content and vice versa for the offshore sediments. Inshore sediments should have higher primary productivity given the shallow depth and less light attenuation than in offshore deeper water. Moreover, *M. tenuis*, with its small size and high organic content of the gut contents, would presumably require an abundant food source. The sediments it inhabits have low organic content (<2%). There are several explanations for this trend. Though the organic content of the sediment offshore was higher, not all of that may be edible or palatable to sand dollars, which may preclude *M. tenuis* from inhabiting offshore sites. Secondly, it is possible that *M. tenuis* do not feed at the place they were collected from. During the June 2004 collections at Anna Maria Island, the density of sand dollars decreased after dusk. A lower density at night may indicate a periodic migration, deep burrowing, or increased difficulty in finding sand dollars at night. However, we typically searched 5-10 cm into the substrate, thus making burrowing behavior unlikely. In June
2004, the gut organic content was significantly higher in the morning and night than midday. Thus, at least in the summer, *M. tenuis* appears to increase its feeding during the night. Alternatively, the low organic content of the sediment could be the result of sand dollar feeding decreasing the overall organic content in the sediment at least where they occur. The density of *M. tenuis* inshore is high relative to the offshore *E. michelini* populations. The guts of *M. tenuis* had relatively more strands of filamentous algae than *E. michelini* and *E. aberrans*, indicating that inshore sand dollars can sequester food despite low availability. One way to test if sand dollars alter the sediment organic content would be to compare sediment from adjacent sand dollar and non-sand dollar sites, and to exclude sand dollars from known habitats and test for increased sediment organic content.

In addition to differences in substrate, food types and energetic requirements of *Mellita tenuis* and *Encope michelini*, differential predation pressure may also be a component in the species distribution of sand dollars. In artificial reefs off Cedar Key, Fl, *M. tenuis* experiences almost twice the amount of predation by triggerfish than *E. michelini* (Kurz 1995). *Mellita tenuis* has a thinner test with relatively looser internal calcareous pillar structures (Seilacher 1979) that is easier to break open (pers. observation). This would make it more vulnerable to predation than *E. michelini*. *Mellita tenuis* may not be able to inhabit offshore sand bottoms where fish predation may be higher than in the subtidal beach zone. *Encope aberrans*, occurring both inshore and offshore, has the largest and thickest test of the three species (Hendler 1995; pers. observation), and may even reach a refuge in size, where few adults are preyed upon because of the thick test. Predation pressure may be important in determining the species
distribution. However, more research needs to be done on predation of sand dollars in order to test this.

Deposit feeders differ from other herbivores in that they ingest large quantities of substrate, liberate and digest organic material, and egest the “clean” substrate. The substrate itself presents very little nutrition other than possible minerals. Rather, the organic material on and amongst the substrate is sought by the feeder. Polychaetes, bivalves, sea cucumbers and sand dollars all obtain food this way in the marine benthos. Levinton (1989) states “Deposit feeders satisfy their nutritional requirements from the organic fraction of ingested sediment. This noncommittal statement masks a number of problems and controversies that have occupied the efforts of nutritional biologists, biological oceanographers, and sedimentologists.” At the heart of these problems and controversies are the mechanisms of processing sediment that can have a profound impact on the community. Specifically, where densities of sand dollars are high, such as inshore sand beds with populations of *Mellita tenuis*, the animals may indeed alter the conditions of their habitat. Sediment is constantly disturbed, particles abraded, epipelic and interstitial growth removed, and cleaned substrate made available for colonization (Findlay and White 1983; Reidenauer 1989). Moreover, wave action makes the environment constantly unstable, carrying away and bringing in nutrients. Even at the offshore site, in 18 m depth, deep troughs were observed, probably formed by waves and currents. Sand dollars must contend with this to survive and reproduce. The sand dollar ekes out an existence in the thin veneer of oxygenated substrate, while being subject to fish predation. Sand dollars plow through the substrate daily and thus allow other organisms to exist in their wake.
Conclusions

Sediment particles are larger offshore and have a higher organic content than inshore sediment. The offshore and inshore sediment have distinct cumulative frequency curves. Despite geographic differences, inshore Gulf sediments are similar. Particle sizes in the sand dollar guts are a smaller subset of the ambient sediment. *Encope aberrans* has larger particles in their guts than *Mellita tenuis* at offshore Egmont Key were they co-occur. Based on data from food grooves, sand dollars select small particles that are most likely crushed by the lantern.

The organic content of the sediment differed from inshore sites 0.05-1.8% to 4.2% offshore. Though particle sizes and organic content of the gut contents for *Mellita tenuis* and *Encope michelini* are similar, the types of food they ingest may be different. Food types available may differ between inshore and offshore sites, and thus may affect food type ingested. The guts of *M. tenuis* had visibly more filamentous algae than *E. michelini*. *Encope aberrans* had significantly lower organic content in the gut contents than *M. tenuis*, both from Egmont Key. *Encope aberrans* may select different particles, allowing it to co-exist with both *E. michelini* and *M. tenuis* at different sites. Differences in peak feeding times change over the course of the year and are not consistent across species.

Inverse relationships between particle size and organic content exist for sediment and sand dollar gut contents. Sand dollar densities offshore are low and may not affect
the overall organic content of that habitat. *Mellita tenuis* may deplete the sediment organic content, due to their much higher density inshore. Thus, *M. tenuis* may reverse the negative relationship between particle size and organic content.

In general, more research on deposit-feeding echinoderms needs to be done. Basic information on spawning, recruitment, and adaptive strategies for stress and disturbance is needed for *Encope aberrans* and *Encope michelini*. Future studies of sand dollar feeding should include exclusion experiments, long-term monitoring, and further sediment studies. To determine whether sand dollars deplete resources in their habitats, exclusion experiments could be conducted to test for increased sediment organic content. Sand dollars appear to ingest particles smaller than the average particle size available. Study of the size fraction ingested may provide further insight to their dietary preferences. Moreover, to further establish a periodicity of feeding, sampling over 24 hour periods and over the course of several years would be necessary to document full patterns of their behavior. In addition, it appears that predation may be the driving force in determining peak feeding times for sand dollars. Further investigation of predator-prey relationships may illuminate more on the feeding ecology of sand dollars. Finally, echinoids are generally regarded as being stenohaline, however, *Mellita tenuis* is found in Tampa Bay and grows to a large size. More research on bay sand dollars needs to be conducted in order to understand their adaptive strategy to an estuarine habitat.
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