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Small-Scale Distribution of the Sand Dollars *Mellita tenuis* and *Encope michelini* (Clypeasteroida, Echinodermata) off the Central Florida Gulf Coast

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Small-Scale Distribution of the Sand Dollars *Mellita tenuis* and *Encope michelini* (Clypeasteroida, Echinodermata) off the Central Florida Gulf Coast

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Small-scale distributions of *Encope michelini* were quantified 27 km west of Captiva Island at 20 m depth and of *Mellita tenuis* 7 km west of Egmont Key at 6.5 m depth and at Mullet Key at 1.5 m depth during 2005. *Encope michelini* were aggregated in 33.3% of three plots in March. Off Egmont Key, *M. tenuis* were aggregated in 100% of four plots in March but in none of three plots in Sept. At Mullet Key, *M. tenuis* were aggregated in 37.5% of 16 plots in May, 12.5% of 16 plots in July, and 50.0% of 16 plots Sept. Percentage of organic content was not correlated with sand dollar distribution, except for *M. tenuis* off Egmont Key. The distribution pattern of both species is dynamic. The pattern at Mullet Key changed within 2 to 5 hr after initial observations in two of eight plots in May and July and in five of eight plots in Sept. It is possible that aggregation is influenced by local, short-term concentration of food below the sensitivity of measurement of organic content and that dispersal to random distribution may occur when food concentration is decreased.

Spatial scale is an important factor when looking at distributions of organisms (Underwood and Chapman, 1996). Large-scale studies overlook changes in habitat at smaller scales that have distinct influences on an individual's behavior (Chapman, 2000; Underwood et al., 2004; Siegel, 2005; Commito et al., 2006). Understanding small-scale interactions is important for making predictions about organisms' distributions. Habitat variation, predator–prey relationships, interspecific and intraspecific competition for resources, and reproduction are all strong pressures that drive individual behavior and an organism's distribution pattern and also occur at small scales. An individual is subject to all these pressures in varying degrees. The balance of these pressures is often referred to as determining the ideal free distribution (Kacelnik et al., 1992). The ideal free distribution gives individuals the greatest chance of surviving and reproducing while minimizing costs at a particular moment in time. Understanding the small-scale distribution can give insight into the selective pressures that were influencing the study organism at that moment.

There are three broad categories in spatial distribution: random, regular (or uniform), and aggregated. If individuals have a random distribution, the presence of an individual does not affect the probability that another individual will be found adjacent to it (Pielou, 1960). Random distributions are often the null hypothesis when distribution studies are conducted because random distributions imply that individuals are not influenced by each other or by external stimuli. If individuals have a regular or dispersed (see Underwood et al., 2004) distribution, the presence of an individual decreases the probability that another individual will be found adjacent to it (Pielou, 1960). If individuals have an aggregated distribution, then the presence of an individual increases the probability that another individual will be found adjacent to it (Pielou, 1960).

Patchy or aggregated distributions of benthic organisms on sediment is often observed and attributed at large scales to physical environmental factors such as water depth and movement and sediment type and at small scales to a variety of disturbances and other biotic and abiotic factors (Morrisey et al., 1992). Large-scale distribution of the North American west coast sand dollar is clearly affected by depth, hydrodynamics, and substrata (Merrill and Hobson, 1970). *Mellita quinquiesperforata* were found more abundantly in protected areas of sand flats inside Beaufort Inlet in North Carolina (Weihe and Gray, 1968). Aggregation at an intermediate scale can occur within populations of the sand dollars *D. excentricus* (Merrill and Hobson, 1970), *Encope stokes* (Dexter, 1977), *M. quinquiesperforata* (Lane and Lawrence, 1980), and *Laganum depressum* (Saunders, 1986). Small-scale patchy or aggregated distribution of sand dollars has been reported only for *D. excentricus* (Merrill and Hobson, 1970) and *L. depressum* (Saunders, 1986).

Two obvious factors that could affect small-scale patchiness of sand dollars are sediment particle size and food. Although sediment may appear homogeneous, it is likely to be heterogeneous at a small scale (Tokeshi, 1999). Organic

carbon can be expected to be deposited non-uniformly (Garigue, 1998) and other organic particles will be moved by currents and turbidity (James, 2000). Sand dollars are found primarily in medium- to fine-grain sand sediment (Pomory et al., 1995), but the range of sediment particle sizes in which they are found is great. *Echinarachnius parma* is found in sediment ranging from coarse gravelly sand to almost pure silt (Harold and Telford, 1982). Off the central Florida coast, *Mellita tenuis* is found in fine to coarse sand and *Encope michelini*, in fine sand to fine gravel (Hilber, 2006).

Particle size can also affect feeding. Sand dollars feed by podial particle picking, in which particles adhere to tube feet and are transferred between spines to food grooves (Telford et al., 1985). Telford (1990) suggested that particle size is important in feeding by sand dollars both in the adhesion of particles and their movement through the spine fields. Particles in food grooves of sand dollars are usually < 500 μm and often < 250 μm (Pomory et al., 1995), indicating the prevalence of small particles in their food. Hilber (2006) reported particles in the guts of *E. michelini*, *Encope aberrans*, and *M. tenuis* are small, 65–75 μm. *Mellita quinquiesperforata* feeds selectively on the silt–clay fraction of surface sediments (Lane and Lawrence, 1982). Because *Mellita* and *Encope* use different appendages for feeding (tube feet) and locomotion (locomotory spines) (Telford and Mooi, 1986), it is probable that feeding can occur during movement and involves more precise manipulation of particles (Pomory et al., 1995).

Particle size can covary with the amount of food available for sand dollars. Organic matter in sediment in which *Echinarachnius parma* occurs varies inversely with sediment particle size (Harold and Telford, 1982). This may result from higher nonparticulate organic matter and from microeucaryotes and bacteria adsorbed on the small particles (Findlay and White, 1983).

Small-scale differences in distribution of food in sand dollar habitats are essentially unknown. The high degree of variability in concentration of carbohydrate and protein in the sediment of a population of *M. tenuis* on the central Florida coast (Lane and Lawrence, 1982) suggests the differences can be great. Findlay and White (1983) found great variation in biochemical indicators of eukaryotic microorganisms, considered food for sand dollars, in sediment with a population of *M. quinquiesperforata* on the north Florida coast.

For particle size and food to affect small-scale distribution, it is necessary for the sand dollars to be able to detect differences. This is little documented. A laboratory study by Pomory et al. (1995) showed *M. tenuis* preferentially moved to sediments with small particle sizes (250–499 μm). Various foods and organic compounds stimulate feeding by echinoids in general (Lawrence et al., 2007) and Telford et al. (1985) reported *M. tenuis* sometimes initiates feeding in response to sediment enriched with diatoms. We hypothesized that sand dollars would be more responsive to food than to particle size and that more aggregated distributions of sediment feeding sand dollars might occur in areas of high nutritive quality. This study examines the small-scale distribution of *E. michelini* and *M. tenuis* and its relation to sediment organic concentration.

MATERIALS AND METHODS

Species.—*Encope michelini* L. Agassiz and *E. aberrans* Martens are found off the central Florida Gulf Coast (Serafy, 1979), usually in distinct populations (Hilber, 2006; Swigart, 2006). *Encope michelini* is reported off the Mexican coasts of Tamaulipas and Veracruz and *E. aberrans* off the coasts of Yucatán and Campeche (Durán-González et al., 2005). They are very similar in general morphology (Phelan, 1972). All individuals off Captiva Island were *Encope*. They were not identified to species during diving observations but are assumed to be *E. michelini* because 96% of all individuals found in transects at the site on these dates were this species (Lawrence and Swigart, unpubl.).

Harold and Telford (1990) revised the genus *Mellita*. The publications before this revision that are cited here refer to *Mellita* of the North American western Atlantic and Florida Gulf of Mexico coasts as *M. quinquiesperforata* (Leske). According to Harold and Telford (1990), *M. quinquiesperforata* (combining *Mellita lata*) is distributed from the western Gulf of Mexico (Texas) to Brazil. The species of the west Atlantic coast is *Mellita isometra* Harold et Telford and the species on the Florida Gulf Coast is *M. tenuis* Clark. *Mellita tenuis* is common off the Florida Gulf Coast (Serafy, 1979). Pomory (2003) stated that *M. quinquiesperforata* is the most common echinoderm off the Texas coast. This species is found off the Mexican coasts at Tamaulipas, Veracruz and Tabasco (Durán-Gonzaláz et al., 2005).

Density and distribution.—Densities and distributions were measured at three sites on six dates (Table 1, Fig. 1). Densities of *E. michelini* off Captiva Island (18 March 2005) and of *M. tenuis* off Egmont Key (19 March and 18 Sept. 2005) were measured by counting the number of sand dollars in 30 sequential 1-m^2 quadrats. Because of the high density, densities of *M. tenuis* at

TABLE 1. Description of observation sites and dates with density and percentage of organic content (mean ± SD).

Species	Site	Date	Depth (m)	Size of plot (m²)	n of plots	Density (individuals m⁻²) Mean ± SD	% Organic content Mean ± SD
Encope michelini	~ 20 km west of Captiva Island 26.54°N 82.48°W	18 March 2005	20	30	3	0.9 ± 1.00	4.60 ± 0.75
Mellita tenuis	~ 7 km off Egmont Key 26.58°N 82.83°W	19 March 2005	6	1.75	4	4.13 ± 2.49	1.51 ± 0.37
		18 Sept. 2005			3	no living individuals	1.13 ± 0.06
	50 m off Mullet Key 27.62°N 82.73°W	21 May 2005	1.5	1	16	16.19 ± 4.89	1.33 ± 0.17
		10 July 2005			16	12.0 ± 3.85	1.15 ± 0.13
		10 Sept. 2005			16	18.33 ± 3.21	0.93 ± 0.11

Mullet Key (21 May, 10 July, and 10 Sept. 10 2005) were measured by random 1-m² quadrats.

Dexter (1977) and Lane and Lawrence (1980) used binomial analysis in their studies of distribution of sand dollars. Because it is difficult to determine if distribution varies within the population (Sokal and Rohlf, 1981; Krebs, 1989), the nearest neighbor test is better. The distribution of the sand dollars was measured at three sites (Table 1) using Clark and Evans' (1954) nearest neighbor test ($R = r_A \cdot r_E^{-1}$) as shown in Krebs (1989). When necessary, the Donnely edge correction was used as shown in Krebs (1989). Potential values range from 0 to ~ 2.12. A value of 1 represents a random distribution. Values below 1 suggest aggregation whereas values above 1 suggest uniform or regular distributions.

The size of the plot for measurement varied to meet the density requirements for the nearest neighbor test. The plots off Captiva Island and Egmont Key were circles produced by using a staked cord with a 3.1- and 0.75-m radius, respectively (Fig. 2a). The distance of nearest neighbors was measured for sand dollars present in the plots. Three replicates, contiguous to each other, were made at each date. Because of the higher density, the plots at Mullet Key were 1-m² quadrats divided into 100 equal squares (Fig. 2b). Two plots, each consisting of four sequential 1-m² quadrats, were made parallel to the shore. The location of sand dollars was mapped using the grid and three sediment samples per 1-m² quadrat were taken from randomly chosen squares. A second observation was made 2 hr later in May and Sept.

An experiment was done during observations at Mullet Key on 10 July 2005 to test migration and the potential effect of organically enriched sediment. Two sequential transects of four 1-m² quadrats parallel to the shore were established. Sediment was collected, the number counted, and the location of sand dollars in each quadrat recorded. Two hundred grams of dried fish-food flakes were mixed with 0.1 m³ sand collected at the site and spread evenly over the first and last quadrat of each transect. All sand dollars in the first and third quadrats, one with enriched sediment and one without, were placed in the center of the quadrat. All sand dollars in the second and fourth quadrats, one with enriched sediment and one without, were removed and placed outside the quadrats. After 5 hr, sediment was collected from the quadrats for organic content analysis and the location of sand dollars in the quadrats was recorded again.

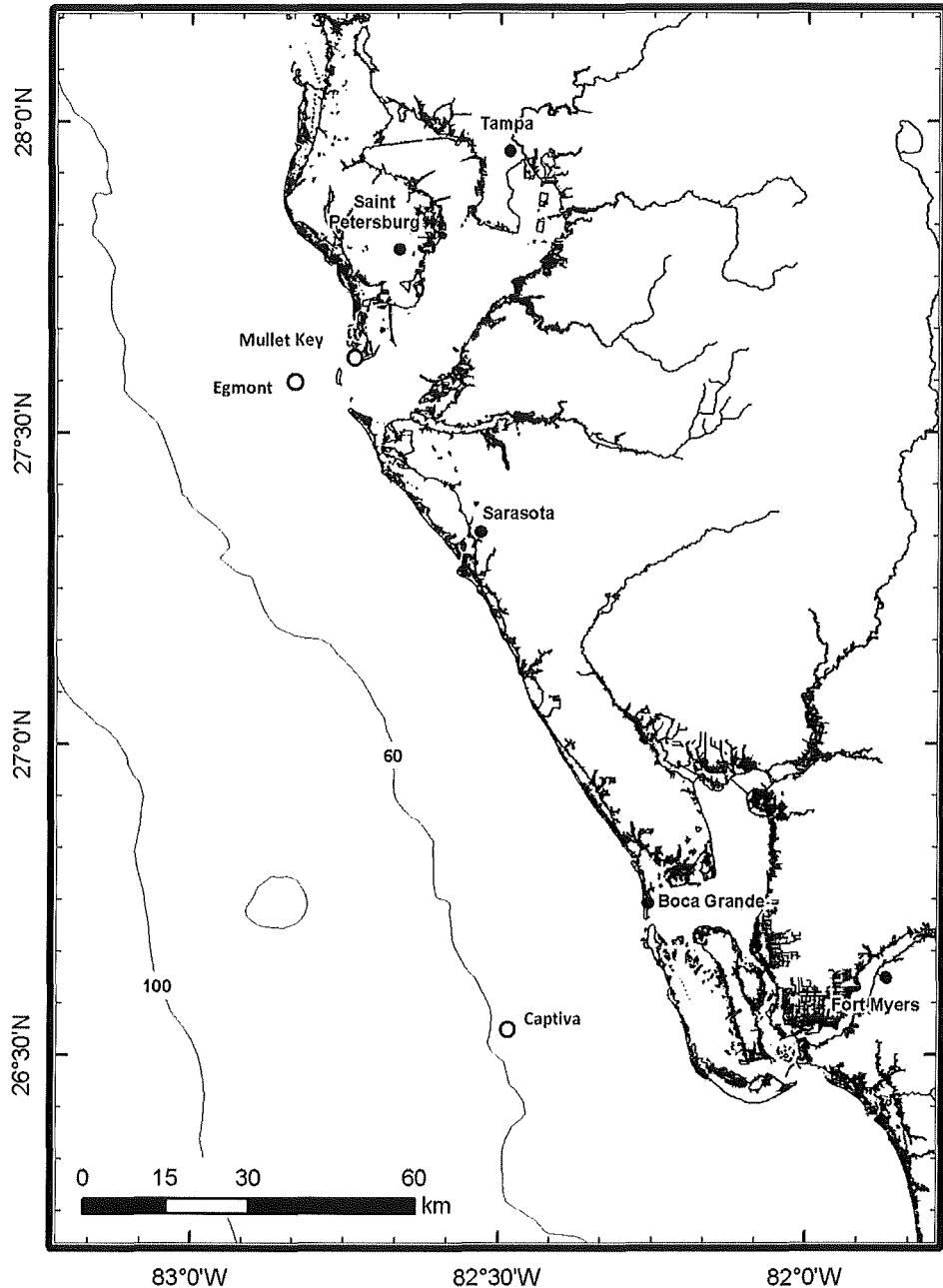*Particle size frequency distribution and organic content.*—Three samples of approximately 100 g

Fig. 1.   Map of the central Gulf Coast of Florida showing all three sites. Sites are named according to nearby islands.

of the upper few centimeters of sediment were collected from within the area for analysis of particle size distribution and organic content. Sediment samples were dried at 60°C for 2 d and sorted by size with the U.S. standard sieve series and weighed. Grains less than 105 μm were ashed at 400°C for 5 hr to measure the percentage of organic content (Scheibling, 1980).

Grains of less than 105 μm constitute the greatest proportion of the gut contents of *M. tenuis* and *E. michelini* (Lane and Lawrence, 1982, Hilber, 2006) and provide greater sensitivity than ashing the entire sediment (Lane and Lawrence, 1982). The percentage of organic content of these three samples was averaged to obtain a mean for the quadrat.
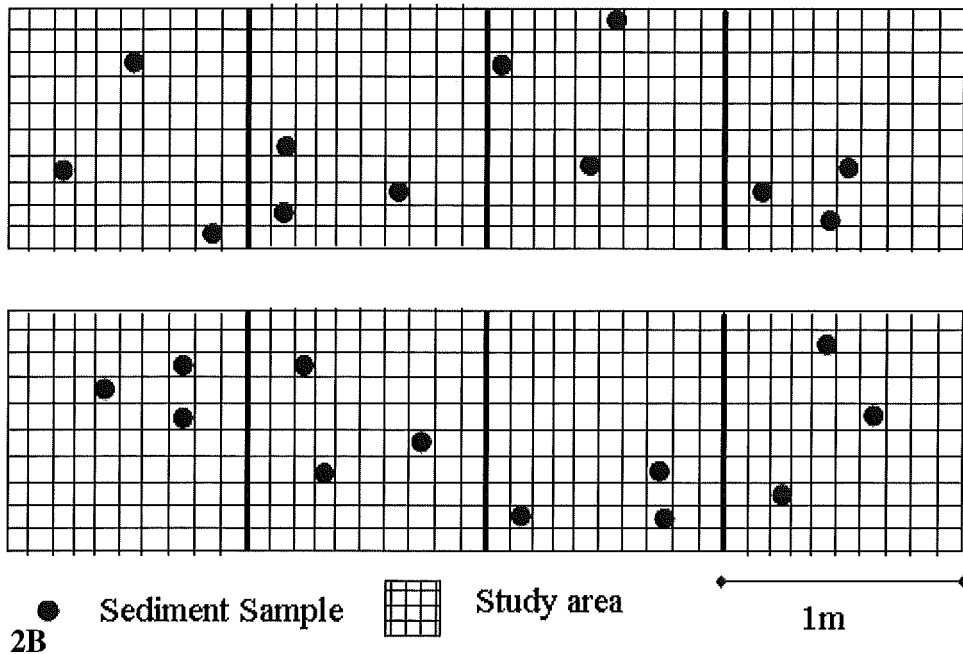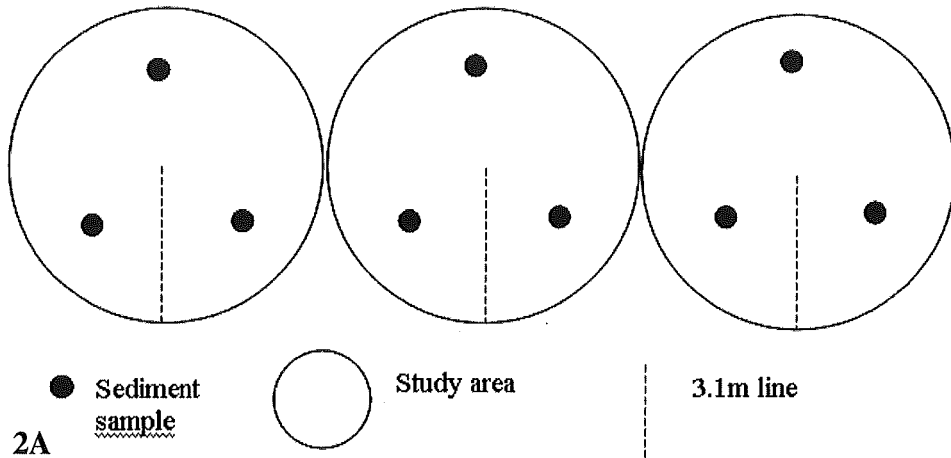
Fig. 2. Study design at the three sites. (A) Sites off Captiva Island and Egmont Key. At Captiva Island 3.1-m line (cord) was used to draw a 30-m^2 circle in the sand. The circle was searched for sand dollars and if found, the distance to the nearest neighbor was measured. Three sediment samples (black circles) were taken equidistant from each other. When completed, another 30-m^2 circle was drawn adjacent to the first and the process repeated. The study design for the Egmont Key site was the same except a 0.75-m line was used to draw a 1.5-m^2 circle. (B) Sites off Mullet Key. A plot was created using a 1-m^2 polyvinyl chloride quadrate divided into 100 squares (Fig. 4). The location of sand dollars was mapped using the grid. Three sediment samples were taken from each plot at randomly determine squares. Eight plots were laid out per dive and there were two dives per month for a total of 16 plots per month. The map of sand dollar locations was used to measure nearest neighbor distance.

Correlations between percentage of organic content and spatial distribution index were calculated for all three sites and for each visit. The Spearman correlation was used because sample sizes were small and the data were not normally distributed.

RESULTS

Particle size and percentage of organic content.— The particle size frequency distribution and percentage of organic content of the sediments are given in Figure 3 and Table 1, respectively.
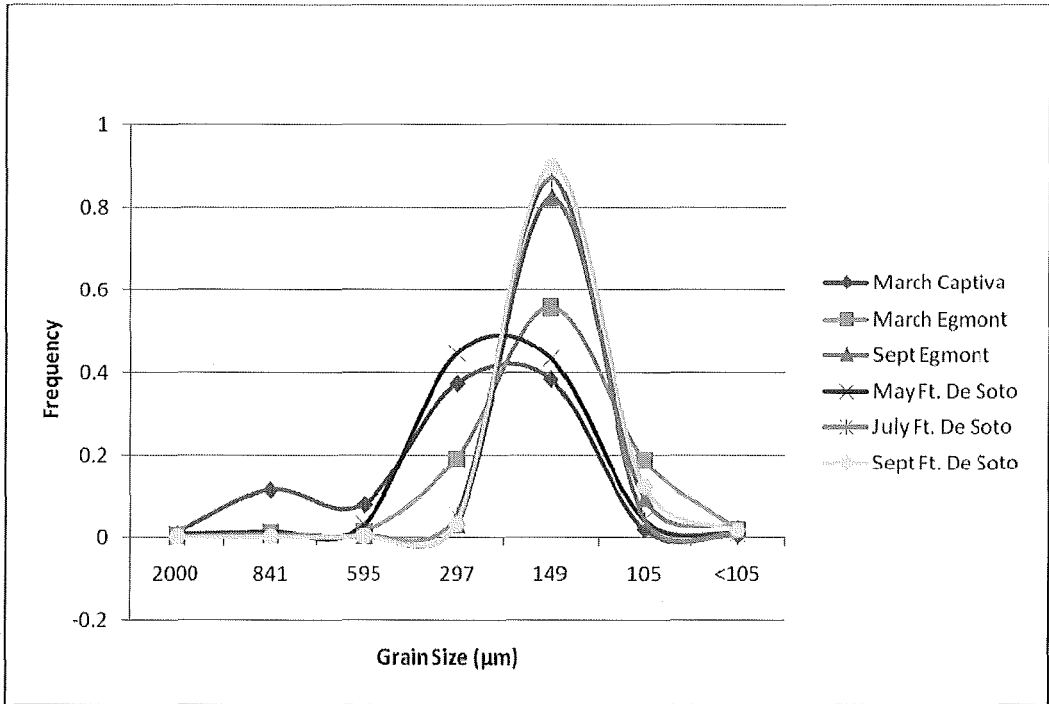
Fig. 3.   Average grain size frequency (×100%) distribution for all sites and dates in 2005.

The variability in particle size frequency distribution and organic content of the sediments was low. The particle size frequency distribution for all three sites was within the preferred range of the sand dollars. The percentage of organic content of sediment of the plots off Captiva Island did not differ significantly ($X^2 = 1.8$, df = 2, $P = 0.4$). Off Egmont Key, the percentage of organic content in March was significantly greater than that in Sept. ($X^2 = 4.5$, df = 1, $P = 0.034$). The organic content of the sediments at Mullet Key varied little at any sampling but varied significantly among months (May vs July: $X^2 = 8.0984$, $P = 0.0044$; May vs Sept.: $X^2 = 21.1420$, $P < 0.0001$; July vs Sept.: $X^2 = 15.3636$, $P < 0.0001$). The mean percentage of organic content for May, July, and Sept. at Mullet Key was 1.33 (±0.17 SD), 1.15 (±0.13 SD), and 0.93 (±0.11 SD) respectively. In July, the second measurement of organic content of the plots that had fish-food flakes added did not show a significant difference (T = 3, df = 3, $P > 0.30$) from the second measurement of plots that did not have fish food added on that date. The fish-food flakes did not increase the measurable percentage of organic content of the sediment.

Density and distribution.—Densities are given in Table 1. Density of *E. michelini* off Captiva Island

was ~ 1 individual m^{-2}, less than that of *M. tenuis* off Egmont Key, ~ 4 individuals m^{-2} and much less than that of *M. tenuis* at Mullet Key, ~ 15 individuals m^{-2}.

Nearest neighbor indices are shown in Figure 4. One of the three plots for *Encope michelini* off Captiva Island showed significant aggregation. All plots for *M. tenuis* at Egmont Key in March showed significant aggregation whereas all in Sept. showed random distribution. The distributions for March were significantly different from those of Sept. ($X^2 = 4.5$, df=1, $P = 0.03$). In Sept., all *M. tenuis* off Egmont Key were dead, possibly as the result of a red tide event in the area (Lawrence et al., 2006). Lawrence et al. (2006) interpreted this as a recent mortality as the tests were intact and gray instead of bleached. Although there was a bottom current on this date, the dead individuals were not moved by it during the period of observation (approximately 1 hr).

Mellita tenuis at Mullet Key showed significant aggregation in 37.5% of the plots in May, 12.5% in July, and 50% in Sept. (n = 16, $P < 0.05$ for each). The sand dollars in one plot (6.25% of the plots) of Sept. had a regular distribution ($P < 0.05$). There are no differences in distribution pattern between months ($X^2 = 2.84$, df = 2, $P = 0.24$).
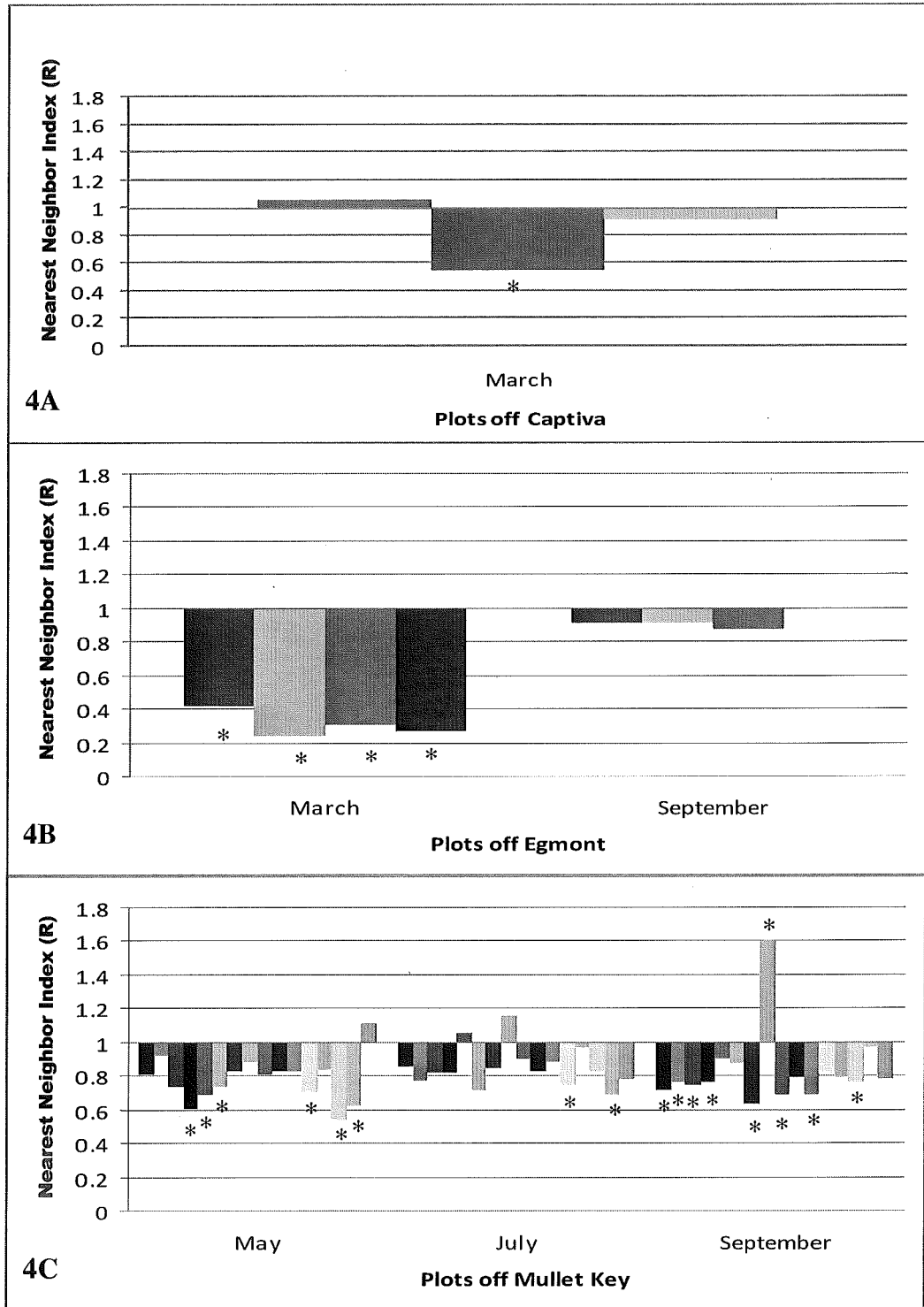
Fig. 4. Nearest neighbor indices for all sites and plots sampled in 2005. *Encope michelini* was sampled at the plots off Captiva Island in March (A). All other plots are *Mellita tenuis*: (B) plots off Egmont Key; (C) plots off Mullet Key). Bars below 1 indicate more-aggregated plots and bars above 1 indicate more-regular or uniform plots. "*" designates plots that are significantly different ($P < 0.05$) from a value of 1 (random distribution). Different shades represent different individual plots. Width of bars varies solely because of space constraints.

5A   Plots off Mullet Key - May

5B   Plots off Mullet Key - July
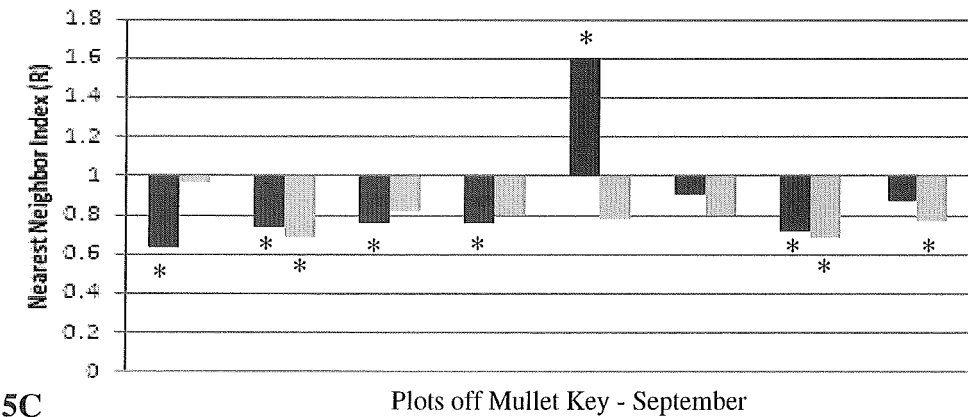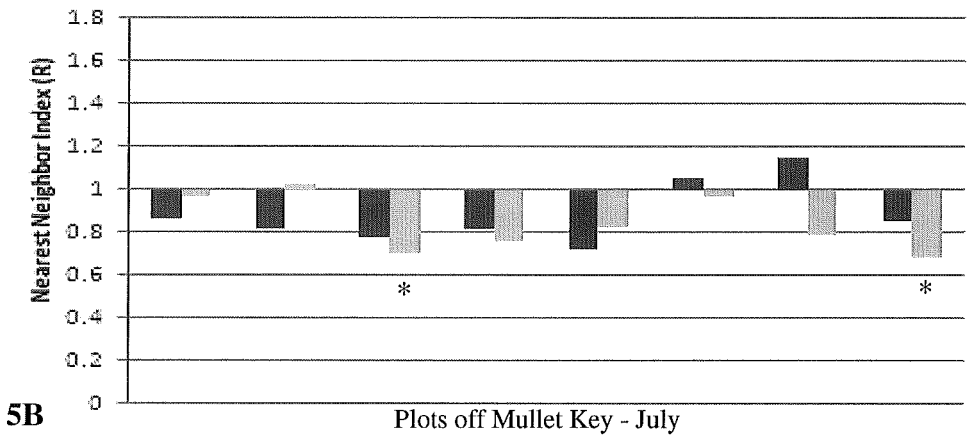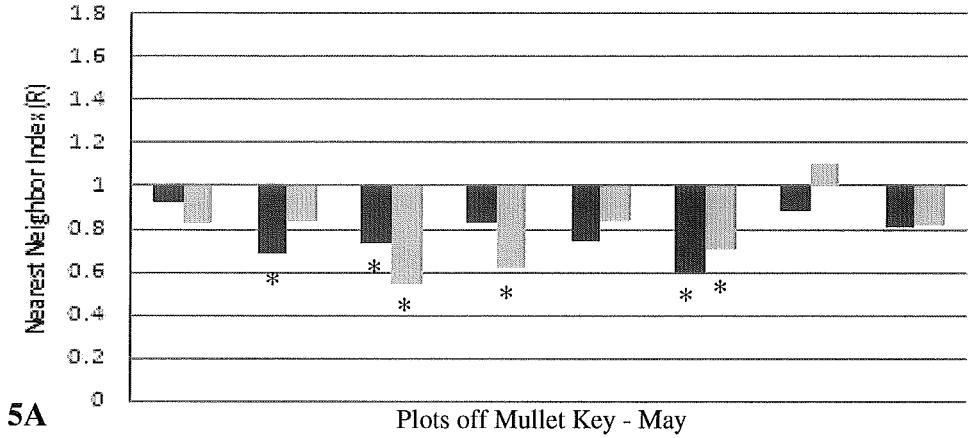
5C   Plots off Mullet Key - September

Fig. 5.   Nearest neighbor indices of *Mellita tenuis* at all plots located off Mullet Key, separated by month in 2005: (A) May, (B) July, (C) Sept.). Bars below 1 indicate more aggregated plots while bars above 1 indicate more regular or uniform plots. "*" designates plots that are significantly different ($P < 0.05$) from a value of 1 or random distribution. Darker bars represent the first observation at that date and lighter bars represent the second. Bars are arranged so that each group represents one quadrat at two different observations.
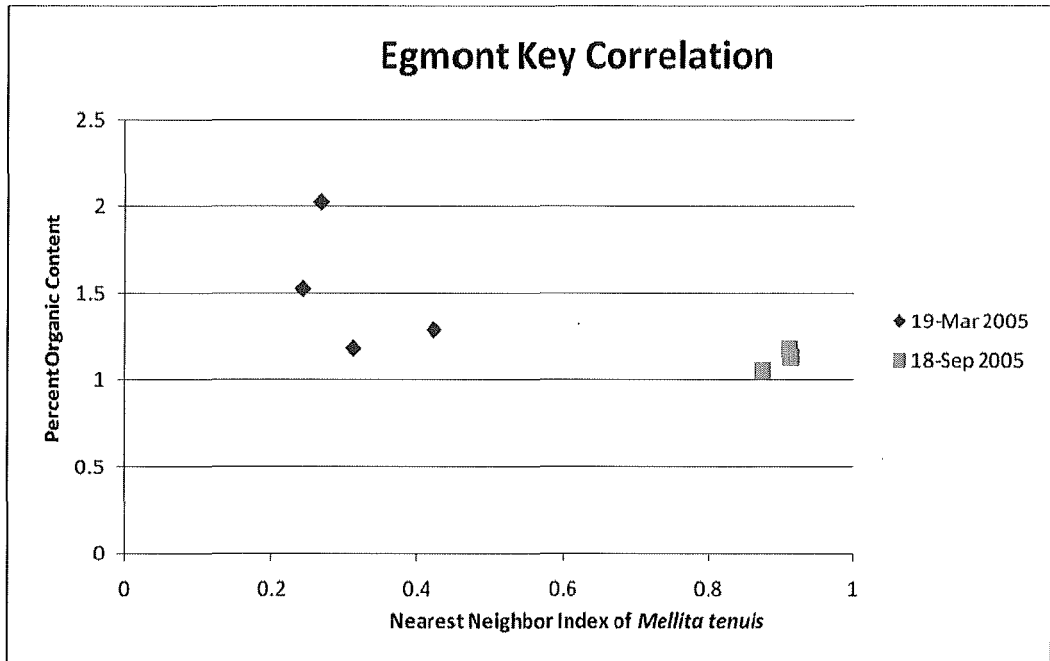
Fig. 6. Correlation of nearest neighbor index (R) for *Mellita tenuis* and percentage of organic content of the sediment off Egmont Key for two dates in 2005. The correlation is significantly negative ($r_s = -0.82$, n = 7, $P < 0.02$).

The nearest neighbor indices of the first and second observations of a month were compared (Fig. 5). There were no differences of distribution frequency between first and second observations of any month (n for all months = 8, $P > 0.10$). There were more plots with aggregated distributions than expected by chance in May ($X^2 = 6.0$, df = 2, $P = 0.0497$), Sept. ($X^2 = 8.0$, df = 2, $P = 0.0183$), and when all dates at Mullet Key are considered ($X^2 = 6.5$, df = 2, $P = 0.0387$). There not significantly more plots with aggregated distributions than expected by chance in July ($X^2 = 2.0$, df = 2, $P = 0.3678$).

In July, sand dollars in seven of the eight plots changed distributions from their initial placement. Of the four plots that contained experimentally aggregated individuals, only one contained an aggregated distribution 5 hr later. This plot did not have fish food added to the sediment. Of the four plots from which sand dollars had been removed, one had aggregated individuals. That plot had fish food added to the sediment.

Correlation of nearest neighbor index and organic content.—The nearest neighbor index of *E. michelini* and percentage of organic content of the sediment off Captiva Island are not significantly correlated. The nearest neighbor index of *M. tenuis* and percentage of organic content of the sediment off Egmont Key are not significant-

ly correlated for March and Sept. but with an increase in n are significantly negatively correlated for both months combined ($r_s = -0.82$, n = 7, $P < 0.02$; Fig. 6). The nearest neighbor index of *M. tenuis* and percentage of organic content of sediment at Mullet Key are not significantly correlated for any month.

DISCUSSION

Encope michelini and *M. tenuis* showed both aggregated and random distributions. *Encope michelini* were aggregated in one of three plots off Captiva Island at one observation. *Mellita tenuis* were aggregated in three of four plots off Egmont Key at one observation, but in none of three plots at another. At Mullet Key, *M. tenuis* had aggregated distribution in only 16 of 48 plots observed on three dates. We never observed extreme aggregation of piles of sand dollars as reported by Merrill and Hobson (1970) for *D. excentricus* during extended periods of calm seas or layers of individuals as reported by Sokolova and Kunetzov (1960) for *Echinarachnius parma*.

The distribution pattern of *M. tenuis* at Mullet Key changed (aggregated to random or random to aggregated) over a 2-hr period in seven of 16 observations. *Mellita tenuis* in six of the eight quadrants, in which they had been placed in the center or removed, had random distribution

after 5 hr. Merrill and Hobson (1970) similarly noted nearest neighbor analysis showed no consistent pattern in the small-scale distribution pattern of *D. excentricus*.

Sand dollars are mobile. Locomotion up to 25 mm min^{-2} has been reported for *Mellita lata* (Kenk, 1944), 14.6 mm min^{-2} for *M. quinquiesperforata* (Weihe and Gray, 1968), and ~ 2.5 mm min^{-2} for *E. michelini* (Kier and Grant, 1965). Weihe and Gray (1968) reported that *M. quinquiesperforata* stop or reorient direction of movement when they encounter each other. In absence of encountering objects, movement continues. Bell and Frey (1969) reported trails 15–100 cm long occurred behind moving *M. quinquiesperforata*. This behavior would be expected to lead to random distribution. The question, then, is why do aggregations occur?

Aggregation of *E. michelini* and *M. tenuis* occurred despite lack of measurable differences in organic content or particle size frequency distribution of the substratum. However, percentage of organic content may not be the best indicator of food stimuli. Even if quantitative differences did not occur, qualitative differences could have been present. Chemosensitivity to food has not been studied in sand dollars, but Telford et al. (1985) noted feeding is sometimes initiated when *M. quinquiesperforata* are exposed to diatom-rich sediment.

Although we found no measurable difference in organic content within the study areas, *M. tenuis* decreases the concentration of bacteria and microeucaryotes (Findlay and White, 1983) and foraminiferans (Reidenauer, 1989) during feeding. More complete methods of measuring sand dollar food supply and feeding methods need to be conducted. *Encope michelini* shows the inclined feeding posture associated with suspension feeding (Lawrence et al., 2004) and anecdotal reports suggest *M. tenuis* does also on the Florida Gulf Coast (Lawrence, unpublished). However, this posture is not common and the regular (uniform) distribution that facilitates suspension feeding and can on occasion be observed for *D. excentricus* (O'Neill, 1978) is unlikely to occur with *E. michelini* and *M. tenuis*.

The data indicate the small-scale distributions of *E. michelini* and *M. tenuis* is dynamic. Saunders (1986) came to the same conclusion for *L. subdepressum*. Sand dollar behavior could be influenced by factors other than food supply (reproduction, hydrodynamics, and competition). *Mellita tenuis* spawns in March and April (Lane and Lawrence, 1979) and therefore reproduction does not explain the distributional changes at Mullet Key in May, July, and Sept., or the more aggregated population of sand dollars

off Egmont Key in Sept. Although size data are not reported in this study, juvenile sand dollars were not found at the site, suggesting that a spawning event had not occurred in the earlier months of the study. There is nothing to suggest that hydrodynamics changed within the 2-hr break between observations at Mullet Key. There are no known competitors for the sand dollars at these sites.

Variability in food concentration is still a likely factor in sand dollar distribution. The sand dollars essentially function as grazers, moving through an area or staying in a localized area with abundant food until it is depleted and then moving again. For this hypothesis to be successfully tested, however, more knowledge is needed about what, specifically, sand dollars eat and what cues might cause a sand dollar to begin or stop eating. The relation between small-scale food supply and sand dollar distribution could then be tested.

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