

Intraspecific density regulates positioning and feeding mode selection of the sand dollar *Dendraster excentricus*

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Abstract

Dendraster excentricus is a common sand dollar of nearshore benthic habitats along the west coast of North America, and has the ability to feed either on deposited or suspended food particles. Field surveys and manipulative experiments demonstrated that intraspecific density and sediment organic matter (SOM) content of sediments are among the factors that regulate the proportion of sand dollars that forage as deposit versus suspension feeders. High local density was associated with a lower proportion of deposit feeding animals in both field surveys and under controlled experimental conditions. Conversely, the proportion of deposit feeders was elevated in treatments in which SOM levels were subsidized, regardless of local density. These data fit Levinton's model of resource limitation in relation to deposit-and suspension-feeding communities, and expand the list of biological processes regulated through density dependence. Analyses of carbon stable isotope ratios ($\delta^{13}\text{C}$) of sand dollars and their potential sources of primary production suggest individuals rely primarily on suspended particulate organic carbon (POC) or drift macroalgae. Sediment organic matter was not a substantial source of carbon for most individuals. There was a significant inverse relationship between size and $\delta^{13}\text{C}$ values; smaller individuals depended to a greater extent on macroalgae. There was no consistent relationship between isotopic ratios, feeding mode and density, which may be due to the high mobility of the species, their ability to respond rapidly to changing environmental conditions and the dynamic nature of their habitat. Our results suggest that biological interactions influence feeding mode of this species. This is a complementary mechanism to those described previously, in which physical factors such as flow and lift/washout have been shown to regulate sand dollar positioning.

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1. Introduction

Benthic invertebrates exhibit a wide diversity of foraging tactics. A subset of these animals demonstrates an ability to alternate between deposit and suspension feeding modes. These facultative suspension/deposit feeders should have a distinct advantage when competition for food resources increases either in the water column or in the sediment (Taghon, 1992). Although

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evidence has been presented suggesting that dense aggregations of suspension feeders can deplete food in the water column (e.g., Buss and Jackson, 1981; Peterson and Black, 1987), there is a general pattern among soft-sediment taxa to switch from deposit to suspension feeding as flow (and particle flux) or local competition for food increases (O'Neill, 1978; Taghon et al., 1980; Olafsson, 1986). This pattern fits Levinton's hypothesis, which proposes that food limitation should be more prevalent in deposit-feeding communities than in suspension-feeding communities because of the relatively high and variable flux of food particles in the water column compared to sediments (Connell, 1961; Levinton, 1972).

As applied to feeding behavior, foraging theory (MacArthur and Pianka, 1966) has progressed far beyond considerations of energetic returns. Feeding mode selection should be based on maximizing fitness, and is influenced by reproduction (Mangel and Clark, 1986), predation (Peterson and Skilleter, 1994) and competition (Peterson, 1982; Skilleter and Peterson, 1994), among other factors. Experiments testing the effects of competition on feeding mode regulation have focused on interspecific interactions (e.g., Levin, 1981; Olafsson, 1986), and the potential effect of intraspecific competition on feeding mode has been largely neglected. Taghon (1992) assessed intraspecific density effects on feeding rate and growth of two polychaete species, but did not examine if intraspecific density could regulate the selection of feeding mode by individuals.

In this paper, we evaluate whether there is intraspecific density-dependent regulation of feeding mode selection by the sand dollar *Dendraster excentricus*. Previously, changes in prey density leading to prey switching by predators have been documented for marine invertebrates (e.g., Lawton et al., 1974; Kuhlmann and Hines, 2005). Here, we propose a system analogous to prey switching, in which a feeding mode switch occurs in response to variations in the density of conspecifics as well as their food supply. Density-dependence is a fundamental property of population dynamics and animal behavior in benthic communities. For instance, it has been documented to regulate growth in clams (Olafsson, 1986), settlement of barnacles along the rocky intertidal (Connell, 1985), migration of scallops (Powers and Peterson, 2000), predation rates on newly settled reef fish (Hixon and Carr, 1997) and recruitment to adult populations (e.g., Beverton, 1995; Chesson, 1998). However, the role of intraspecific density in determining feeding mode selection remains untested in the field.

The sand dollar, *D. excentricus*, is a patchily distributed subtidal species found over sandy bottoms either

along outer coasts or within bays and tidal channels of the west coast of North America (Merrill and Hobson, 1970). Highsmith (1982) reported that sand dollar larvae preferentially settled within beds of adult conspecifics in areas where predation by tanaids was limited, although cannibalism may also be significant (Timko, 1975). Sand dollars can form dense aggregations greater than 650 individuals m^{-2} (Chia, 1969). Within these beds, individual sand dollars can position themselves either flat to the bottom (prone), or with the anterior end of the animal buried in the sand and the rest of the animal jutting above the seafloor (inclined) (Clark, 1901). The unusual vertical posture of *D. excentricus* has been associated with the posterior eccentric position of the apical system and petals of the test (Lawrence et al., 2004). The only other reports of vertical posture exhibited by sand dollars include *D. vizcanoensis* based on its eccentric morphology (Merrill and Hobson, 1970), as well as observations of *Heliophora orbiculus* off the Atlantic coast of Congo and Angola (Darteville, 1935) and the non-eccentric *Encope michelini* along the gulf coast of Florida (Lawrence et al., 2004). Merrill and Hobson (1970) were first to note that *D. excentricus* tended to lay prone during slack tides, and inclined parallel to flow direction under moderate and high tidal flow or wave surge conditions. They argued that the inclined posture reduced lift and washout of sand dollars under heavy flow (for further treatment, see Telford, 1981), and that orientation parallel to flow direction rendered drag insignificant. Later, O'Neill (1978) used hydrodynamic models to demonstrate that inclined sand dollars acted as lifting bodies, resulting in increased feeding efficiency under moderate to high flow.

Our initial observations in a shallow estuarine system, the Estero de Punta Banda in Baja California, Mexico, revealed that inclined sand dollars did not appear to orient parallel to flow direction, but with random direction. Furthermore, over small spatial scales (10 m), density appeared to be positively related to the proportion of inclined animals. While the vast majority of previous studies of sand dollar behavior focused on exposed coast populations, our observations of sand dollar behavior were made within a protected embayment in a habitat subjectively classified by Merrill and Hobson (1970) as "coastal inlet". Therefore, we were interested in determining if mechanisms other than washout might regulate sand dollar positioning in this system.

Timko (1975) conducted a series of laboratory experiments that indicated a number of factors could influence the positioning of individual *D. excentricus*. Among these factors were both water movement and density. Through

feeding experiments using both *Navicula distans* and fluorescent beads, Timko (1975) demonstrated that orientation and feeding mode were tightly linked. However, she concluded that density was not likely to be a major regulating factor on orientation in the field since there was not a correlation between inclination and aggregation. For instance, sand dollars at Scripps Pier, CA, were observed to be inclined but not aggregated, while sand dollars in Puget Sound, WA, were aggregated in high densities but not inclined (from Timko, 1975).

Our goal was to build on Timko's work and test the density mechanism under field conditions in the Estero de Punta Banda. Because intraspecific competition for food resources may increase with density and promote suspension feeding, we also tested whether food subsidies to the sediment could alter the proportion of sand dollars feeding in deposit and suspension modes. Given that a variety of studies have shown that the stable isotopes of carbon can be useful in discerning between water column and benthic sources of organic matter in estuarine systems (Fry and Sherr, 1984; France, 1995), we measured the $\delta^{13}\text{C}$ values of sand dollar tissues, suspended and sediment organic matter and two proxy species for potential food sources. These data were needed to examine the degree of reliance on suspended and/or deposited organic matter over longer time periods than those associated with instantaneous observations of feeding behavior. We also employed $\delta^{13}\text{C}$ measurements to examine the potential relationship between density and feeding mode.

2. Methods

2.1. Study site

The Estero de Punta Banda is located 100 km south of the USA–Mexico border ($31^{\circ}42'–31^{\circ}47' \text{ N}$ and $116^{\circ}37'–116^{\circ}40' \text{ W}$) on the Pacific coast of Baja California, Mexico. The estuary has a main channel 7.6 km long, a median depth of 5 m and is permanently connected to Todos Santos Bay by a 125 m wide mouth (Ortiz et al., 2003). It has 21 km² of both permanently and periodically submerged *Zostera* and *Spartina* beds as well as mud and sand flats (Ibarra-Obando and Poumian-Tapia, 1991, 1992). The system is strongly influenced by semidiurnal tides, and the strongest current speeds are close to the mouth (up to ca. 1 m s^{-1} ; Pritchard et al., 1978). Up to 60% of the estuary's water can be exchanged during one tidal cycle during spring tides (Paz Vela, 1978), and hence the system has a low residence time. The majority of sand dollars can be found patchily distributed near the mouth over relatively

shallow sand flats (<3 m at high tide) covering an area approximately $1000 \times 500 \text{ m}$ (Fig. 1).

2.2. Mensurative surveys

Sand dollar beds were surveyed to determine relationships between density and positioning (as an indicator of feeding mode). Surveys were conducted on February 18, May 8, August 29 and November 9, 2004 during slack or new incoming tides. A linear transect across the sand dollar field was laid out during each census, along which 0.1 m^2 weighted PVC quadrants were deployed at random intervals (1–5 m) to survey the population. Dive teams recorded the number of sand dollars that appeared in inclined or prone positions within each quadrant ($N=100$ on each date). Position was evaluated based on the visibility of the peristome (visible = inclined). Preliminary investigations performed in February suggested two clear size classes of sand dollars (<45 mm and >45 mm), and therefore we recorded the number of specimens from each class within each quadrant during the May, August and

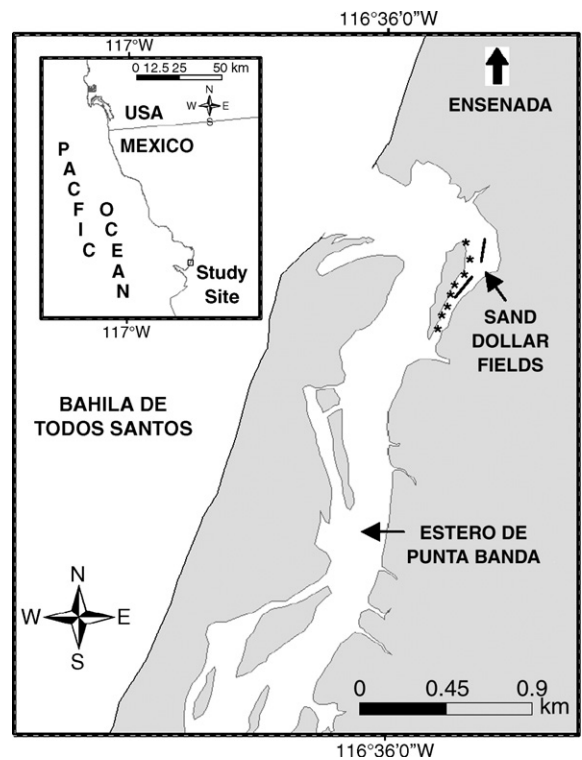


Fig. 1. Location of sand dollar beds within Estero de Punta Banda where seasonal censuses and manipulative experiments were conducted. Survey transects are marked by lines, and locations of experimental blocks are denoted with. The estuary is shown at low tide.

November surveys, and measured the sizes of individuals from the final 10, 15 and 20 quadrants, respectively. Sizes were measured as the largest diameter of the test along the same axis that Timko (1975) referred to as length.

In May and November, two survey transects were also conducted at sites with obvious density gradients over small (<10 m) spatial scales. During these non-random surveys, four 0.1 m² point measures of density were collected from high-, medium- and low-density zones along each transect. High-, medium- and low-density zones were identified visually based on previous abundance surveys. To test the hypothesis that the $\delta^{13}\text{C}$ of individuals varied as a function of density and feeding mode, we collected three inclined and three prone sand dollars from each density zone for stable isotope ratio analyses. In addition, small cores (1.13-cm² × 5-mm depth) were collected from each density zone for sediment organic matter (SOM) measures and $\delta^{13}\text{C}$ analysis of sediment organic matter. Two replicates were collected at each density level and transect ($N=24$ total). Particulate organic matter (POM) in the water column was concentrated by filtering water immediately above the sediment-water interface during the incoming tide with a 30 cm wide, 33- μm mesh plankton net fixed in place for 10 min ($N=6$ separate plankton tows in April and $N=3$ in November). The net was tied to a boat and weighed down and was oriented perpendicular to the current. A subsample of the concentrate was placed on ice and filtered onto pre-combusted GF/F filters in the laboratory in preparation for isotopic analyses. Unfortunately, we neglected to collect filamentous algae during the study. Instead, proxy species for water column POM and filamentous algae were collected. These proxy species reflect the isotopic composition of POM and filamentous algae integrated over time. An abundant bubble snail (*Bulla gouldiana*, a herbivorous opisthobranch that feeds on green algae; $N=6$ individuals), and a clam (*Macoma* sp.; $N=2$ pooled samples) were collected for isotopic analyses only during May because they were absent from the study area in November. Samples destined for SOM and $\delta^{13}\text{C}$ analyses were kept on ice in the field and frozen at $-20\text{ }^{\circ}\text{C}$ upon arrival at the laboratory.

2.3. Manipulative experiments

In May and November we also conducted field manipulations to tease apart the effects of local density and food availability on sand dollar feeding mode. If local density controls sand dollar feeding mode by reducing deposited food resources ahead of suspended food

resources, we would expect a smaller percentage of animals in the prone position at higher densities. Alternatively, if SOM content shifts the balance of feeding-mode benefit by increasing the amount of food available to deposit feeders, we would expect a larger percentage of animals in the prone position in enriched sediments, regardless of density. Finally, if lift/washout is the lone regulating mechanism for sand dollar positioning, density and SOM enrichment should have no effect on the orientation of experimental animals.

The experimental design consisted of three density treatments and two sediment SOM enrichment treatments (plus additional controls described below). During each experiment, we constructed 8 replicate blocks along a transect located within the sand dollar field. In each block, two sets of three 0.1-m² enclosures were deployed. Each set of three enclosures was oriented in an equilateral triangle with 1-m vertices. Enclosures consisted of four 10-mm wire mesh walls erected in a square. The top of each wall rose 3 cm above the sediment surface, while the wall foundations extended 7 cm into the sediments. During deployment, sand dollars were removed from inside the enclosures. We randomly assigned one of the sets of enclosures in each block as SOM-enriched and the other as SOM-unenriched. To enrich enclosures, we excavated surface sediments adjacent to a nearby marsh and transported these sediments to the experimental plots. One liter of excavated sediment was added to each set of enclosures designated as SOM-enriched. Sediments were mixed by hand in both the enriched and unenriched treatments following subsidy additions. Among each set of three cages that comprised an enriched or unenriched unit, we randomly assigned three density treatments: 80 indiv m⁻², 160 indiv m⁻² and 400 indiv m⁻². Once constructed, we allowed the blocks to remain undisturbed for 24 h in order to settle.

The process of caging animals and manipulating sediments is invasive. The proper controls for these experimental manipulations are measures from completely unmanipulated, 0.1-m² sites. Therefore, we used our natural abundance surveys of the corresponding month as controls. In order to match densities, we only used survey plots of 70–80 indiv m⁻², 140–160 indiv m⁻² and ≥ 300 indiv m⁻² for the low, medium and high density controls, respectively.

Sand dollars used in the experiments were collected >50 m away from experimental blocks. Because surveys indicated a bimodal size distribution during May and August, we selected individuals from within a narrow size range (~50–65 mm; $N=1024$ each month). Sand dollars that appeared damaged or strongly

discolored were excluded from the experiments. Although we could not ensure all animals were in equal condition, we attempted to minimize this factor by collecting sand dollars from as small an area as possible and by placing all experimental specimens in a 4 × 4-m natural depression the day before the experiment began.

No sand dollars had gained access to within the enclosures in the 24 h before the experiment began, suggesting they were effective in separating non-experimental from experimental sand dollars. Enclosures in both the enriched and unenriched units of each block received 8, 16 and 40 specimens corresponding to the 80 indiv m⁻², 160 indiv m⁻² and 400 indiv m⁻² treatments, respectively. In each enclosure, we haphazardly placed 50% of the sand dollars in the inclined position and the remaining 50% in the prone position. Sand dollars were observed moving about the enclosures and changing position almost immediately following placement. Two hours after introduction of the sand dollars we checked each enclosure and recorded the number of inclined and prone sand dollars. From each enclosure, small cores (1.13 cm² × 5 cm depth) were collected for sediment (SOM) measures. During the November trial, small cores (1.13 cm² × 5 cm depth) were also collected from three enriched and three unenriched enclosures for sediment grain size analysis. All sediment cores were stored on ice for transport to the laboratory. Once there, samples were frozen at -80 °C until analysis.

In both May and November, the experiments were allowed to continue for 24 h, at which time the orientation of sand dollars was registered again. During the May trial, we sized all sand dollars from one treatment enclosure within each block. In each block a different treatment enclosure was selected for sizing specimens (in two of the blocks no sand dollars were sized). During the November experiments, we lost 2

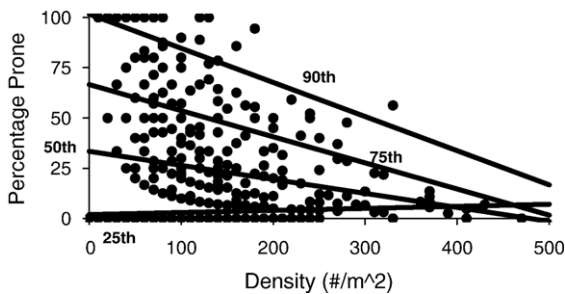


Fig. 2. Relationship between *D. excentricus* positioning and intraspecific density. Data are from four hundred and one 0.1-m² quadrants pooled from field surveys in February, May, August and November. Also plotted are four lines representing selected 100th regression quantiles: 90th ($p < 0.001$), 75th ($p < 0.001$), 50th ($p < 0.001$) and 25th ($p = 0.08$).

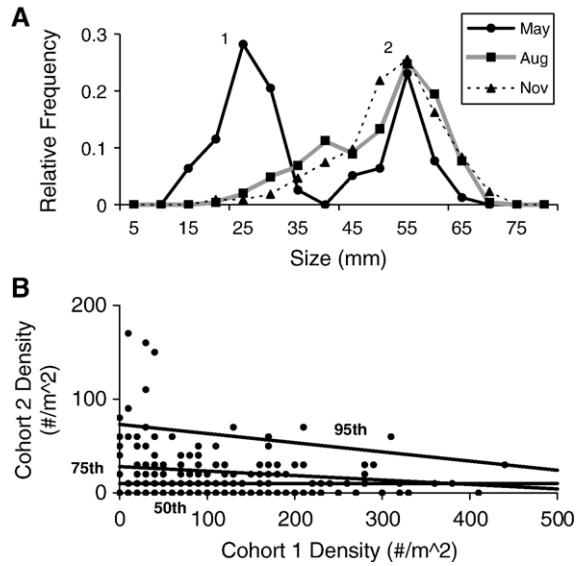


Fig. 3. (A) Size-relative frequency distributions for *D. excentricus* taken from 0.1 m²-survey plots in May (10 plots), August (15 plots) and November (20 plots). Letters indicate separate size classes (cohorts) during the May surveys. (B) Scatterplot of the relationship between densities of a (1) smaller- and (2) larger-sized cohort(s) during the May surveys. Data are from one hundred and four 0.1-m² plots. Also plotted are four lines representing selected 100th regression quantiles: 95th ($p = 0.123$), 75th ($p = 0.152$), and 50th ($p = 0.999$).

blocks prior to the introduction of the sand dollars due to large sediment drifts. The remaining six blocks were lost before the 24-h measures could be made, and before specimen sizes were recorded.

2.4. Stable isotope analyses and laboratory measures

In preparation for $\delta^{13}\text{C}$ measurements, the diameter of each sand dollar was measured, its perimeter removed with scissors to gain access to interior organs and the intestines carefully dissected. The presence or absence of sand grains and other particulates within each intestine was noted. The intestines were rinsed with distilled water, dried at 60 °C for 48 h and ground for stable isotope ratio analyses. Muscle samples of the California bubble snail and clams were similarly processed. Except for the clams, for which two individuals were pooled in each sample for isotopic analyses, all animals were processed individually. SOM samples were treated with 1 N HCl to remove carbonates. Carbon isotopic ratios were analyzed on a Europa Hydra 20/20 Mass Spectrometer at the Stable Isotope Laboratory of the University of California, Davis. Precision (1 SD) of external standards analyzed during the sample run was $\pm 0.15\text{‰}$ ($N = 31$). $\delta^{13}\text{C}$ values are reported relative to PeeDee belemnite using

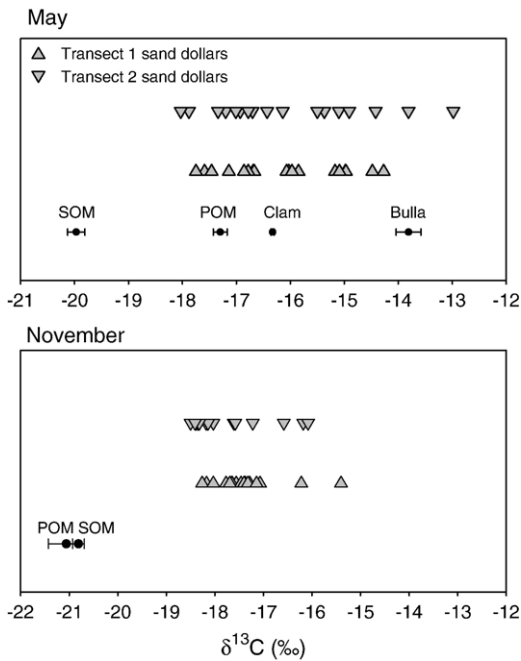


Fig. 4. Carbon stable isotope ratios of individual sand dollars, particulate organic matter (POM), sediment organic matter (SOM) and other food web components. Each triangle represents a single sand dollar.

standard notation: $\delta (\%) = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$, where R is the ratio of the heavy to light element. Although $\delta^{15}\text{N}$ values were measured simultaneous to $\delta^{13}\text{C}$ determinations, we did not find differences in nitrogen isotopic ratios among potential food sources. Those data are therefore not presented.

Sediment cores for SOM and grain size analyses were thawed and washed through a 2-mm mesh to remove any large debris. Sediment SOM content (as a

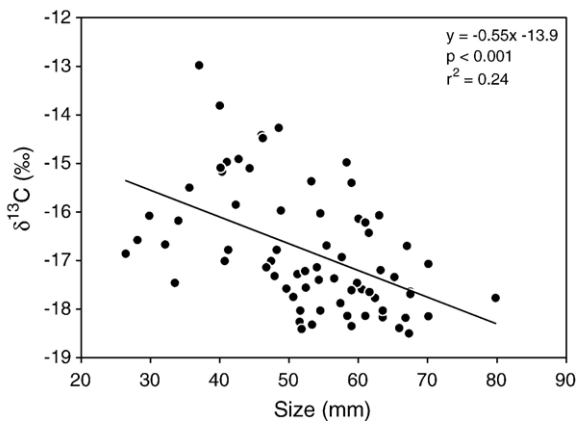


Fig. 5. Relationship between sand dollar size and carbon isotopic composition.

percentage) was determined as the weight loss of dried sediment after combustion at 500 °C for 12 h. Sediments intended for grain size determination were digested with hydrogen peroxide and wet-sieved through a 63- μm mesh. Both fractions from each core (≥ 63 and $< 63 \mu\text{m}$) were dried at 60 °C for 24 h and weighed to determine percent sand.

2.5. Statistical analyses

We analyzed the relationship between the percentage of prone sand dollars and density using regression quantiles. Data were pooled from all four surveys periods since results were not qualitatively different among months. Regression quantiles were employed because we observed a “wedge-shaped” distribution in our data (Cade et al., 1999), and because they provide a more comprehensive description of biological patterns that may be influenced by multiple limiting factors. This form of regression allows analyses of changes near the maxima in a response variable (positioning), as opposed to the center of the response variable’s distribution. Therefore, it provides a better estimate of the impacts of a measured variable (density) when it is the “active

Table 1

Summary of two-way ANCOVAs of the carbon isotopic composition of inclined and prone sand dollars collected along high to low density transects in May and November 2004

Transect	Factor	SS	df	MS	F-value	p-value
May # 1	Density	2.522	2	1.261	0.978	0.406
	Feeding mode	0.864	1	0.864	0.67	0.43
	Density × feeding mode	0.864	2	0.432	0.335	0.722
	Size	0.25	1	0.25	0.194	0.668
	Error	14.18	11	1.289		
May # 2	Density	0.171	2	0.085	0.099	0.906
	Feeding mode	8.756	1	8.756	10.19	0.009
	Density × feeding mode	2.475	2	1.238	1.44	0.278
	Size	3.788	1	3.788	4.409	0.06
	Error	9.452	11	0.859		
Nov # 1	Density	0.527	2	0.263	0.633	0.549
	Feeding mode	1.812	1	1.812	4.351	0.061
	Density × feeding mode	0.473	2	0.236	0.567	0.583
	Size	0.252	1	0.252	0.604	0.453
	Error	4.581	11	0.416		
Nov # 2	Density	1.135	2	0.567	14.708	0.001
	Feeding mode	0.392	1	0.392	10.153	0.011
	Density × feeding mode	0.943	2	0.471	12.221	0.003
	Size	0.005	1	0.005	0.14	0.717
	Error	0.347	11	0.039		

Size was used as covariate.

limiting constraint” (Cade et al., 1999). Each quantile was generated using the least absolute deviation method in Blossom version W2005.05.26 software (© USGS). Regression quantiles were also used to investigate the relationship between the densities of successive size classes from the May survey period (when classes were most easily distinguished) to determine if successive cohorts partitioned habitat use spatially. A one-factor ANOVA on untransformed data was used to test for differences in sediment SOM among density zones from our targeted surveys. In all cases in which parametric tests were employed, *F*-tests revealed no significant heteroscedasticity among data groups.

The carbon stable isotope values for sand dollars collected from the mensurative transects were analyzed using two-factor ANCOVAs with density (high, medium, low) and feeding mode (inclined or prone) as factors and size as a covariate. Because it was likely that there were differences among transects in the actual density of sand dollars within each category, the data from each transect were analyzed separately. Analysis of

SOM isotopic values indicated there were no differences among samples collected within or among transects in a given month. Hence, these data were pooled for the purpose of elucidating the source of organic matter supporting sand dollar feeding.

We analyzed the results from each experimental trial (May and November) and time point (2 and 24 h) separately using two-factor ANOVAs. The need to treat trials and time points separately arose after a preliminary three-factor, mixed model ANOVA revealed significant interaction effects with time. Density and sediment enrichment were considered fixed factors, and the response variable was percentage of prone specimens. Grain size measures comparing enriched and unenriched sediments for the November trials were analyzed by *t*-tests. No grain-size cores were taken from control (survey) plots. Kruskal–Wallis tests were used to test for differences in SOM and specimen size among density and enrichment treatments, because *F*-tests indicated significant heteroscedasticity in each response variable for each of the main effect tests and transformations failed to produce

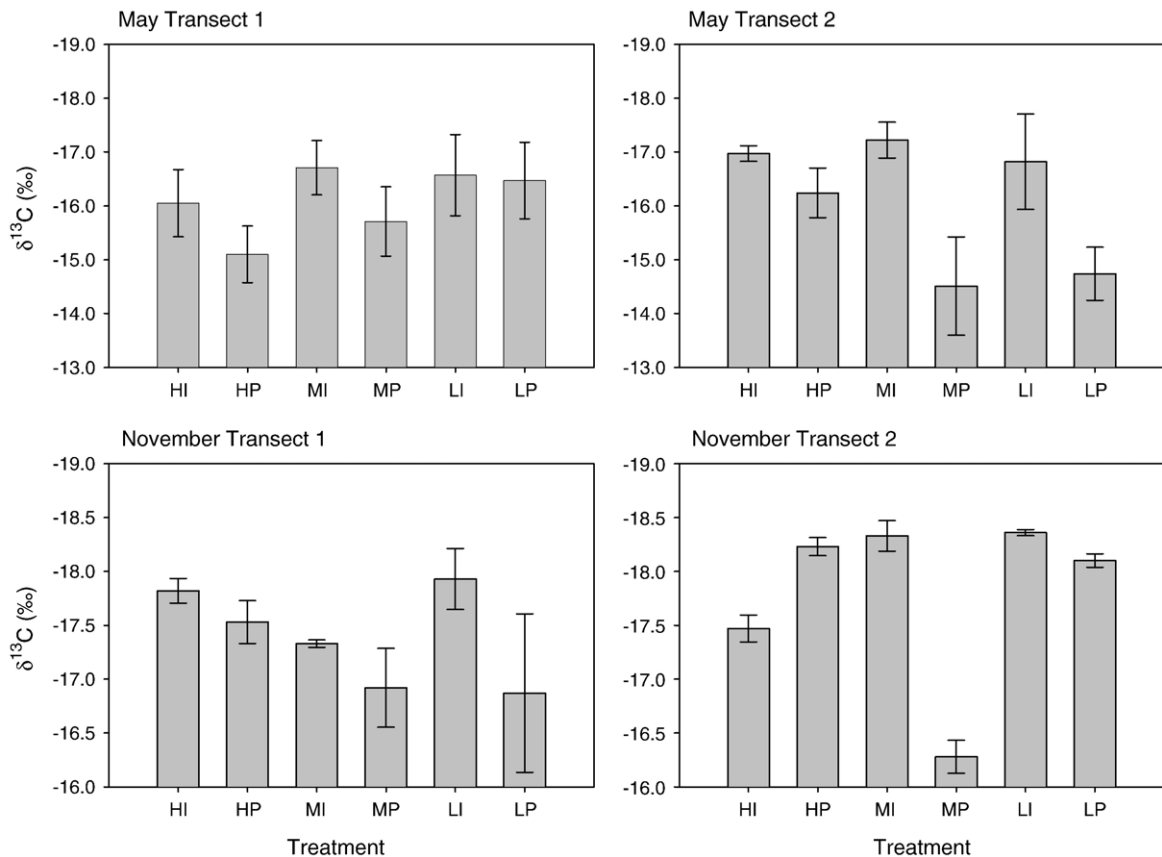


Fig. 6. Carbon stable isotope values of sand dollars collected along a natural density gradient (H: High, M: Medium, L: Low density) in inclined (I) or prone (P) positions (*N*=3, means±1 SE).

Table 2

Sediment organic content (SOM) in *D. excentricus* patches of low (0–80 indiv m⁻²), medium (80–160 indiv m⁻²) and high (200–300 indiv m⁻²) density surveyed twice during 2004

	Means			ANOVA					
	Low	Med	High		SS	df	MS	F-value	p-value
May	0.53±0.13	0.71±0.14	0.49±0.09	Density	0.106	2	0.053	3.581	0.072
				Error	0.134	9	0.015		
Nov	0.39±0.02	0.47±0.08	0.50±0.22	Density	0.014	2	0.007	0.300	0.750
				Error	0.169	7	0.024		

Data are presented as means±1 SE (N=2). One-way ANOVA results if SOM varied significantly in response to changes in density are shown.

homoscedasticity in the data. All univariate significance tests were conducted using StatView 5.0.1 or Systat 11 software (Systat Software Inc.).

3. Results

3.1. Mensurative surveys

The percentage of prone sand dollars decreased with increasing sand dollar density, and the rate of decrease was greater for higher quantiles (Fig. 2). On average, 40% of the sand dollars were prone when densities were <75 indiv m⁻². This percentage dropped to <10% at densities above 325 indiv m⁻². Variation in the per-

centage of prone sand dollars also decreased markedly with increasing density (Fig. 2). These observations support density acting as a regulating mechanism for sand dollar feeding mode selection. The average overall density was 115 indiv m⁻², and decreased slightly from 125 indiv m⁻² in May to 103 indiv m⁻² in November. Size-frequency histograms from the May surveys indicated two size classes; a larger (older) cohort(s) of animals 42–70 mm in test length, and a smaller (younger) cohort of sand dollars with test length of 10–41 mm (Fig. 3A). During the May surveys, the density of the smaller size class decreased as a function of the density of larger sand dollars (Fig. 3B). The rate of change in the density of the smaller sand dollars was

Table 3

Summary of 2-way ANOVA results testing for significance of density, sediment enrichment (C = control, N = not enriched, Y = enriched) and effect interaction on the positioning of *D. excentricus*

	Density			Enrichment			Interaction		
	Among group	Between Group		Among group	Between group		Enrichment* density	Error	
		80–160	80–400	160–400	C, N	C, Y	N, Y		
<i>May 2 h</i>									
SS	0.31				1.765			0.131	4.565
df	2				2			4	66
MS	0.155				0.883			0.033	0.069
F-value	2.242				12.763			0.475	
p-value	0.114	0.195	0.349	0.758	<0.001	0.283	<0.001	0.025	0.754
<i>May 24 h</i>									
SS	0.536				3.891			0.063	2.481
df	2				2			4	66
MS	0.268				1.946			0.016	0.038
F-value	7.130				51.748			0.417	
p-value	0.016	0.065	0.002	0.173	<0.001	<0.001	<0.001	0.365	0.796
<i>Nov 2 h</i>									
SS	0.785				1.283			0.348	2.36
df	2				2			4	52
MS	0.392				0.641			0.087	0.045
F-value	8.646				14.134			1.920	
p-value	0.001	0.023	0.000	0.071	<0.001	0.025	0.003	<0.001	0.121

Positioning observations were recorded after 2 h and 24 h during the May trial, and after 2 h during the November trial. Fisher's post-hoc test results are listed below for between-group comparisons.

strongest at the highest quantiles. August surveys indicated a shift in the mode of the smaller sand dollar's size class toward that of the larger cohort(s). In November, sizes were normally distributed with a single mode at 56 mm. These observations fit the biphasic growth in *D. excentricus* that is characterized by rapid juvenile and slow adult growth (Timko, 1975).

3.2. Stable isotopes

The $\delta^{13}\text{C}$ of individual sand dollars collected in the natural density transects varied from -13.0 to -18.0‰ in May (Fig. 4). There was a ca. 3‰ difference between the $\delta^{13}\text{C}$ values of POM (-17.1‰) and SOM (-20.0‰). Assuming a 0.9‰ enrichment per trophic level (Vander Zanden and Rasmussen, 2001), sand dollars would be predicted to exhibit isotopic values of -16.2‰ and -19.2‰ if they were feeding exclusively on POM and SOM, respectively. Given that sand dollars did not exhibit the more negative isotopic values expected from feeding on SOM (Fig. 4), it appears that both POM and algae may be important components of a given individual's diet, while sand dollars do not appear to be feeding heavily on SOM. Because clams will integrate the isotopic composition of its food sources over time (Tieszen et al., 1983), the consistency between the $\delta^{13}\text{C}$ values of the particulate fraction (-17.1‰) and bivalve tissue (-16.3‰) observed in May suggests the clam was feeding largely on POM for at least some time. As a result, there was considerable overlap in the $\delta^{13}\text{C}$ values recorded in clams and sand dollars. In contrast to the clams and sand dollars, the herbivorous *Bulla* exhibited isotopic values substantially enriched relative to POM and SOM. The average bubble snail value of -13.8‰ is within the range of values typically exhibited by macroalgae in the Punta Banda Estuary (-10.4 to -14.5‰ for *Enteromorpha* sp. and *Ulva* sp.; Rendon-Ibarra and Herzka, in prep). There was a significant inverse relationship between $\delta^{13}\text{C}$ values and the size of the sand dollars collected in May (Fig. 5). Size explained 24% of the observed variability in isotopic values. Smaller individuals (ca. <50 mm) tended to have heavier isotopic values, suggesting that macroalgae were a more important dietary source.

In November, the range of values exhibited by sand dollars was more limited and generally more negative than in May (from -15.4 to -18.5‰). The isotopic composition of both POM and SOM also exhibited depleted values of $\delta^{13}\text{C}$ (ca. 21‰). The lack of a difference between the isotopic composition of POM and SOM and the absence of the proxy species *Bulla*

precluded the use of $\delta^{13}\text{C}$ values as food source tracer during November.

The results of the ANCOVA's used to evaluate whether there were significant effects of density and feeding mode on sand dollar isotopic ratios were not consistent among transects. Feeding mode was significant in May's Transect #2, and there was a significant

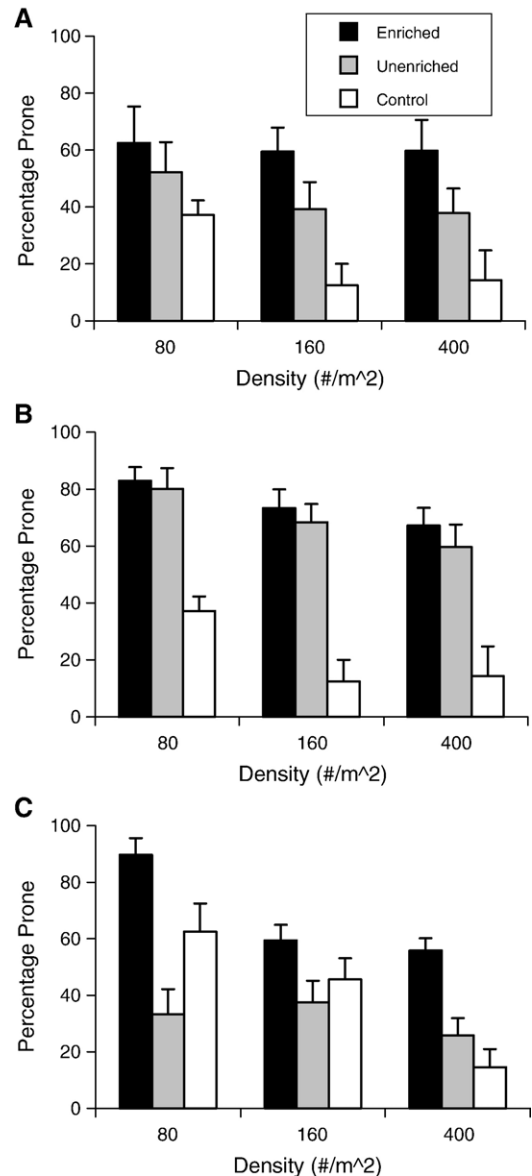


Fig. 7. Mean percentage of *D. excentricus* observed in prone position (+1 SE) in field experiments in which intraspecific density and sediment organic content were manipulated. Experiments were conducted twice in 2004. Positioning observations were recorded at: (A) 2 h during the May trial ($N=8$), (B) 24 h during the May trial ($N=8$), and (C) 2 h during the November trial ($N=6$). Table 3 provides significance results.

interaction between density and feeding mode in November's Transect #2 (Table 1, Fig. 6). None of the factors were significant in May and November's Transect # 1. Lastly, SOM measures from the target surveys did not reveal any significant patterns among sand dollar density zones during either May or November (Table 2).

3.3. Field experiments

The percentage of prone sand dollars demonstrated significant responses to both density (during two of three trials) and TOC enrichment (all three trials) (Table 3; Fig. 7). Density had no effect on sand dollar positioning during the May trial after 2 h ($p=0.114$), but demonstrated significant effects in both the May 24 h ($p=0.002$) and November 2 h ($p=0.001$) measures. Fisher's post-hoc test indicated that in both the May trial after 24 h and the November trial after 2 h, the 80 indiv m^{-2} treatments had a significantly higher percentage of sand dollars in the prone position relative to the higher density treatments (Table 3). For the May 24 h measures, over 60% of the sand dollars in the low-density treatments were in the prone position, while 53% and 49% of the sand dollars were prone in the medium- and high-density treatments, respectively. During the November trial, 62% of animals in the low-density enclosures were observed as prone, while only 34% of the sand dollars in the high-density enclosures were prone. At the same time, an intermediate percentage (42%) of sand dollars in the medium-density treatments were prone.

Each time the experiment was evaluated, the effect of sediment enrichment on the percentage of prone individuals was greater than that of density ($p<0.001$ at all three time points). All between-treatment comparisons for sediment enrichment were significant according to Fisher's post-hoc test, except for the control-unenriched (May 2 h) and unenriched–enriched (May 24 h) comparisons (Table 3). Overall, 69% of the sand dollars in the enriched enclosures were observed in the prone position, while only 33% of the control sand dollars were prone. An enclosure effect was observed, as 48% of the sand dollars in the unenriched treatments were prone, which was significantly higher than observed in the control treatments but significantly lower than the enriched treatments in 2 of the 3 analyses (Fig. 7). There were no significant interactions between main effects during any of the trials.

A posteriori checks of the experimental manipulations indicated that attempts to minimize sources of artifacts were successful (Table 4). We observed no difference in the size of sand dollars among treatment types (mean test length: 58 ± 3 mm; density, $p=0.094$; enrichment, $p=0.294$). Although we lost all enclosures before size measures were completed in November, similar protocols from the May trials for selecting sand dollars were employed. There was also no significant difference in SOM among density treatments during May ($p=0.847$) or November ($p=0.306$). We were successful in artificially elevating SOM in enriched enclosures during both trials (May, $p=0.025$; November, $p=0.008$). During the May

Table 4
Summary and checks of treatment manipulations

	Grain size (% sand)		Organic matter (%)		Test size (mm)	
	May	November	May	November	May	November
<i>Density</i>						
80	–	–	0.68 ± 0.08	0.76 ± 0.12	59.6 ± 0.7	–
160	–	–	0.81 ± 0.14	0.66 ± 0.10	61.1 ± 1.1	–
400	–	–	1.08 ± 0.21	0.73 ± 0.11	57.7 ± 0.8	–
<i>df</i>	–	–	2	2	2	–
<i>t</i> -value or <i>H</i>	–	–	2.367	0.332	4.736	–
<i>p</i> -value	–	–	0.306	0.847	0.094	–
<i>Enrichment</i>						
C	–	–	0.58 ± 0.04	0.46 ± 0.05	57.3 ± 0.8	55.2 ± 0.6
N	–	99.6 ± 0.1	0.67 ± 0.06	0.66 ± 0.07	59.2 ± 0.7	–
Y	–	96.0 ± 0.1	1.18 ± 0.19	0.90 ± 0.13	58.4 ± 1.0	–
<i>df</i>	–	4	2	2	2	–
<i>t</i> -value or <i>H</i>	–	16.18	9.615	7.384	2.448	–
<i>p</i> -value	–	<0.001	0.008	0.025	0.294	–

Means (± 1 SE) of sediment grain size, sediment organic matter and *D. excentricus* size are grouped both by density and sediment enrichment treatments (C = control, N = not enriched, Y = enriched). T-test (grain size) and Kruskal–Wallis (organic matter and test animal size) results on untransformed data for significance of main effects observed during May and November are included. $N=2$ for grain size, $N=6$ for organic matter, and $N=8-40$ (treatment dependent) for test size means.

experiments, enriched enclosures had SOM levels (0.90%) roughly 1.5 times greater than control and unenriched plots. In November, SOM from enriched enclosures (1.2%) was approximately double the levels found in the other treatment. While grain size was statistically different between enriched and unenriched plots ($p < 0.001$), the actual difference in sand content was only 3.5%. Laboratory experiments by Timko (1975) indicated *D. excentricus* do not favor coarse or fine fractions of beach sand, and therefore we expect the differences between treatments had minimal impacts on our results.

4. Discussion

4.1. Feeding-mode selection

Our field surveys and experimental manipulations unambiguously demonstrate that both local intraspecific density and sediment TOC have significant impacts on the behavior of the facultative suspension/deposit feeder, *D. excentricus*. High local density was associated with a lower proportion of deposit feeding animals in both field surveys and under controlled experimental conditions. Conversely, the proportion of deposit feeders was elevated in treatments in which SOM levels were subsidized, regardless of local density. The positioning results we observed were predictable given Levinton's model of resource limitation in benthic communities (Levinton, 1972), which states that food resources in the sediment should become depleted more rapidly than in the water column.

These data comprise the first field test for intraspecific density regulation of feeding mode selection by benthic fauna. Our results are site- and species-specific, but can lead us to speculate about the broad applicability of intraspecific density regulation of feeding mode selection. There are a number of organisms that demonstrate an ability to switch feeding modes. For instance, shallow-water clams (*Macoma* sp.) and polychaetes (*Boccardia* sp.), as well as several species of deep-sea polychaetes are facultative deposit/suspension feeders (Skilleter and Peterson, 1994; Taghon, 1992). Species belonging to the macrobenthos of deep-sea seeps demonstrate significant contributions from both chemosynthetically-fixed and heterotrophically-obtained methane-derived carbon (Levin and Michener, 2002). In the plankton, some bacteria are mixotrophic and possess an ability to maximize nutrient acquisition by feeding both auto- and heterotrophically (Rothhaupt, 1997). Crowding could impact feeding or growth rates for all of these organisms (e.g. Miller and Jumars, 1986),

and an ability to change foraging modes or nutritional pathways may provide a release from intraspecific competition and allow for higher densities or greater fluctuations in local biomass.

In all of our manipulative trials on feeding mode selection, sand dollars exhibited a greater response to sediment enrichment than to density manipulations (Table 3, Fig. 7). This implies that sand dollars were not responding to adult-specific social cues to position themselves, but rather to resource availability within the water column and sediments. Therefore, density is indirectly responsible for positioning via resource availability and not through direct social behavior. Using flume experiments, Timko (1975) examined the responses of individual sand dollars to groups of 20 other sand dollars. Because these experiments indicated no response either in terms of aggregation or feeding behavior, she concluded that *D. excentricus* probably does not secrete a social pheromone. This is congruent with other echinoderms, in which pheromones are rare (Reese, 1966). Our results appear to add additional support for Timko's conclusion. We also observed no interaction between density and enrichment treatments in any of our trials (Table 3), but this may be because we dramatically increased SOM in enriched plots (>1.5 times more than in unenriched plots) and overwhelmed the impact dense aggregations could have on sediment-bound resources, at least over the 24 h that we allowed the sand dollars to respond. Had we used smaller SOM subsidies an interaction might have been observed as high-density plots were effectively depleted of SOM more quickly than low-density plots.

Not only were feeding mode results statistically significant among manipulated treatments, but differences among groups were large and ecologically relevant (Anderson et al., 2000). Even in enriched plots, high-density treatments had as many as 30% more inclined sand dollars than in low-density treatments. These large differences are important because we did observe a notable caging effect associated with collecting and holding sand dollars in 0.1 m² enclosures. We noted that our unenriched treatments had a significantly higher percentage of prone sand dollars than our control treatments; ideally there would have been no difference between these groups (see Table 3). The large difference between unenriched and control and treatment groups is potentially confounding, even if the caging effect is strictly additive (Peterson and Black, 1994). However, the fact that our manipulative and mensurative approaches led us toward similar conclusions regarding the relationship between density and feeding mode makes us confident our results are robust.

Although we conducted both the survey and manipulative components of our study during low and incoming tides, the differences in unenriched and control treatments could be the result of collecting data on different days and, potentially, under different environmental conditions. Alternatively, enclosures may have changed flow, and as a result, the efficiency of suspension feeding for individual sand dollars. Baffling or compressing of streamlines by cages may increase the efficiency of suspension feeding (Peterson and Beal, 1989; Timko, 1975). If so, we would expect a greater proportion of inclined sand dollars within cages relative to controls. Since we observed a lower percentage of suspension feeders within enclosures, we do not think this was a major factor. Alternatively, increased deposition due to the cages and increased surface SOM due to our hand mixing of sediments within enclosures could promote increased deposit feeding. These remain possible causal mechanisms, as SOM levels were slightly elevated in unenriched plots over controls (Table 4). Because drift algae did not appear to collect in experimental units during our tests its potential impact on feeding mode observations can be largely neglected.

4.2. Habitat partitioning between size classes

Survey results indicate that there was habitat partitioning between a younger and older cohort(s) patches over the scale of several meters during May of 2004 (Fig. 3). Because we did not monitor the distribution of newly settled sand dollars there are two alternative explanations for our observation: (1) Sand dollars preferentially settle or survive in sandy habitats suitable for, but not occupied by, older sand dollars in order to avoid cannibalism (Timko, 1975) or competition (e.g. Taghon, 1992). This hypothesis is at odds with the results of Highsmith (1982) who found that *D. excentricus* larvae preferentially settled in adult-associated sand as a means of reducing larval and juvenile mortality that could result from tanaid predation. Highsmith's experiments from Puget Sound populations could be repeated for settling sand dollars from Punta Banda to evaluate the coherence of recruitment processes across this species' range. (2) Sand dollars settle within adult beds, but subsequently migrate to unoccupied patches once predation pressure decreases and competition increases. Competition avoidance is especially interesting in the context of our broader results because all sand dollars <25 mm in length were in the prone position. If these smaller individuals are not able to feed from the water column, they may be forced away from adult competitors in order to find suitable food resources from the sediment.

Unfortunately, neither Timko (1975) nor O'Neill (1978) considered, or at least distinguished, the hydrodynamics of very small sand dollars to elucidate feeding rates and determine their ability to suspension feed.

4.3. Main sources of carbon for *D. excentricus*

D. excentricus adults have been reported to ingest particles from both the water column and sediments, including small crustaceans, dinoflagellates, tanaids, diatoms, detritus and filamentous algae (Chia, 1969, 1973; Timko, 1976). This species is not size selective in its feeding habits (Timko, 1976). Analysis of the $\delta^{13}\text{C}$ of sand dollars, POM, SOM and two proxy species (a clam and the herbivorous *Bulla*) collected in May 2004 suggests *D. excentricus* relied largely on either suspended POM or drift macroalgae. However, the potential contribution of SOM to the diet of some individuals may not have been entirely negligible. Fifty percent of individuals exhibited isotopic values that were somewhat more depleted than the trophic fractionation-corrected POM value of -16.2‰ , suggesting at least a partial contribution of SOM. Given that there are three potential sources of carbon, and that we only have isotopic data from one element, applying a three-source mixing model is impossible. Nevertheless, we can make the assumption that the consumption of macroalgae is negligible to model the case in which SOM would be most important. Applying a two-source mixing model (e.g. Phillips and Koch, 2002) with a trophic fractionation factor of ca. $+0.9\text{‰}$ (Vander Zanden and Rasmussen, 2001) to those individuals with $\delta^{13}\text{C}$ values $< -16.2\text{‰}$ indicates SOM could account for an average of 31.4% (range 0–63%) of the carbon assimilated if no macroalgae were consumed. However, *D. excentricus* has been documented to feed on green algae in this and other studies (Chia, 1969). In addition, 50% of individuals had $\delta^{13}\text{C}$ values more enriched than POM, suggesting that on average the contribution of SOM is probably lower than 31%. Another scenario suggested by the isotopic data collected from May samples is that sand dollars feed exclusively on SOM and macroalgae; averaging the isotopic ratios of SOM and *Bulla* yields values similar to those measured for POM. In other words, sand dollars with isotopic values of ca. -16‰ could reflect solely the assimilation of organic matter from the sediments and macroalgae, instead of the consumption of POM. This is unlikely, for *D. excentricus* has a well-documented suspension feeding behavior (e.g. Chia, 1969; Timko, 1976). Hence, the primary sources of carbon for the sand dollars in the Punta Banda Estuary are likely to be POM and macroalgae, although some

consumption of organic matter from the sediments may take place. Given that some sand dollar intestines contained filamentous green algae or *Ulva* (10 and 17% of all sand dollars dissected in May and November, respectively), it is likely that the more enriched sand dollars were at least partially feeding on macroalgae.

The carbon isotopic composition of individual sand dollars was size-related; smaller individuals appeared to rely to a greater extent on macroalgae (Fig. 5). Previous studies have suggested the behavior of this species may be size dependent. Chia (1973) described the selective ingestion of heavy sand grains in individuals less than 30 mm long, which presumably act as a weight belt. However, to our knowledge, the feeding habits of this species have not been examined relative to size, although our data suggest ontogenetic differences in food consumption, which may include feeding mode, dietary preferences or variations in the efficiency of suspended particle capture.

The relationship between density, feeding mode and isotopic composition was not consistent among the four high to low density transects examined (Table 1, Fig. 6). Feeding mode was significant in one transect and there was a significant interaction between feeding mode and density in another transect. The lack of a consistent relationship may be due to the high mobility sand dollars can display over short time scales (Chia, 1973) and the dynamic nature of the sandy sediments they inhabit. Since isotopic ratios reflect the foods assimilated over a period of time, $\delta^{13}\text{C}$ values likely reflect different temporal scales than feeding mode and local density. In addition, it is possible that higher replication would have yielded a more consistent relationship between isotopic ratios, feeding mode and density. Future studies should consider that the isotopic composition of *D. excentricus* may be quite variable.

4.4. Multiple interacting factors

Foraging strategies occur in the context of a broad suite of environmental variables such as competition, reproduction, predation and disturbance (Skilleter and Peterson, 1994). Our results demonstrate that density and local sediment resources impact the feeding mode strategies of sand dollars within the Estero de Punta Banda, but this does not preclude flow (tidal; Francisco and Herzka, in prep), disturbance (wave surge, sand drifts) and other causal agents from being important in regulating feeding behaviors. Merrill and Hobson (1970) classified four sand dollar habitats: (1) bay, (2) tidal channel, (3) protected outer coast, and (4) exposed outer coast. Previous studies (e.g., Merrill and Hobson, 1970; Timko, 1975; O'Neill, 1978) of sand dollar positioning focused on coastal (3, 4) populations, and it is possible

that intraspecific density is not important in regulating positioning within these populations. Alternatively, these studies may have suffered by deviating from the method of multiple working hypotheses (Chamberlin, 1965). As a result, their experimental models and subsequent designs may not have allowed them to evaluate density regulation of positioning (Underwood, 1997).

In much the same way, we were able to negate null hypotheses regarding density and SOM effects on feeding mode, but failed to test for the potential impacts of flow and other factors on sand dollar orientation. Quantile regressions indicated that the change in sand dollar positioning was highest at the upper quantiles, and considerably dampened at lower quantiles (Fig. 2). These results suggest that multiple factors regulate the positioning of sand dollars, and potentially include a host of biological and physical interactions. Merrill and Hobson (1970) were the first to note that *D. excentricus* tended to lay prone during slack tides, and inclined parallel to flow direction under moderate to high tidal flow or under wave surge conditions to minimize lift and washout. Later, O'Neill (1978) used hydrodynamic models to demonstrate that inclined sand dollars acted as lifting bodies resulting in increased feeding efficiency under moderate to high flow. Timko (1975) also found that sand dollar aggregations increased suspension-feeding efficiency by compressing the streamlines of flow between adjacent individuals and reducing drag. However, some disagreement remains regarding the relative importance of lift and drag forces. Nakamura (1994) conducted laboratory experiments with *D. excentricus* in a re-circulating flow tank, and found that parallel orientation was more important in reducing drag, as Merrill and Hobson (1970) had suggested, than in maximizing lift, as proposed by O'Neill (1978). An interesting future experiment would be to duplicate our caging experiments, but within field flumes to manipulate flow. Higher flow rates (particle fluxes) have been shown to induce suspension feeding in polychaete worms (Taghon et al., 1980). Flume experiments would be similar to our sediment enrichments, although this time the enrichments could be made both in sediments and the water column to further examine how sand dollars respond to resource availability. Laboratory flume experiments could also be used to delineate the impacts of particle flux and lift/washout that may both increase with higher flow. Timko (1975) found a synergetic effect of density and suspended food availability on orientation. Recently, Francisco and Herzka (in prep) demonstrated that positioning is related to tidal level while orientation of inclined sand dollars is related to current speed and direction under natural conditions. The inclined sand

dollars tend to be orientated to flow direction under high current speed. During neap tides (low current speed) they orient randomly.

Density-independent regulation of feeding mode selection may also occur in the Estero via disturbance (sensu Smith, 1935). Large (mounds ~ 1 m elevation) sand drifts completely buried our field enclosures over 24 h during the November trials. Some drifts moved at least 2 m across the bottom during this time. Qualitative inspection indicated that these drifts did not bury sand dollars, but clearly sand dollars have to (continually?) reposition themselves in response to this disturbance. If so, tradeoffs between mobility and feeding rates may impact the positioning that is observed (sensu Mangel and Clark, 1986; where tradeoffs occurred between reproduction and feeding). Survey transects also revealed that sand dollars were aggregated on the edge of topographic highs along the sandy bottom. It is unclear if sand dollars move to these sites in response to flow and perceived feeding opportunities. Alternatively, sand dollars may impact sediment stability by baffling currents that can approach 1 m s^{-1} and thereby generate local topography.

Sand dollars in this system are extremely easy to manipulate and provide a model system for an experimentalist interested in feeding behavior. Our results clearly indicate that intraspecific density can play a part in regulating feeding mode selection by a facultative deposit/suspension feeder. Ultimately however, we expect that multiple interacting factors regulate feeding by this species.

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