

SAND DOLLARS AS SUSPENSION FEEDERS: A NEW DESCRIPTION  
OF FEEDING IN *DENDRASTER EXCENTRICUS*

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This paper describes the feeding behavior, diet, and food size preference of the common Pacific sand dollar, *Dendraster excentricus*. *Dendraster excentricus* is abundant along the Pacific coast of North America from Juneau, Alaska, to central Baja California (Wagner, 1974). This study concentrates on *Dendraster* from Southern California, where the sand dollars inhabit subtidal surf-swept beaches, quiet bays, and estuaries (Merrill and Hobson, 1970).

Individuals of *Dendraster* feed in an inclined posture (Fig. 1) with the anterior portion of the test inserted into the sand when a slight to moderately fast current is running (Chia, 1969a; Merrill and Hobson, 1970). Previous descriptions of feeding in *Dendraster* dealt only with the entrapment of small particles in ciliary currents generated by the epithelium of the spines (MacGinitie and MacGinitie, 1949; Chia, 1969a). In the past, sand dollars have generally been regarded as deposit or detrital feeders (Reese, 1966). However, the present work reports methods of capture of large particles (>50  $\mu\text{m}$ ) and small active prey. Specimens of *Dendraster* from Puget Sound have been reported to eat diatoms, algae, and sand grains (Chia, 1969a), but no quantitative analysis of their diet or selectivity has been described to date. This dearth of information is remarkable in view of the great abundance and extensive geographic range of *Dendraster excentricus*.

MATERIALS AND METHODS

Specimens of *Dendraster excentricus* from a sub-tidal, protected outer coast population at Zuma Beach, Los Angeles County, California, were used except as noted. Laboratory specimens were kept in holding tanks connected to a 1500 gallon recirculating seawater system; they consumed detritus in the tanks as well as the *Artemia salina* nauplii provided as food. All experiments with live specimens of *Dendraster* were done at 12 to 14° C (normal temperature range at Zuma Beach).

Feeding behavior in the inclined position was observed with a dissecting microscope mounted on a boom arm (Bausch and Lomb). Food was placed on the test surface with a taper cut catheter tube connected to a syringe barrel. Large food items (*Artemia*, Sephadex beads, sand grains, etc.) were inserted into the food grooves by the same method. Diatom suspensions (*Navicula distans*) were introduced in a #21 syringe needle connected to a catheter.

Sand dollars were force-fed by gently inserting a syringe needle or catheter tube beneath the buccal spines and injecting the food. Great care was necessary to avoid touching the spines or the peristomal membrane, since the sand dollars would reject the food if disturbed in this manner.

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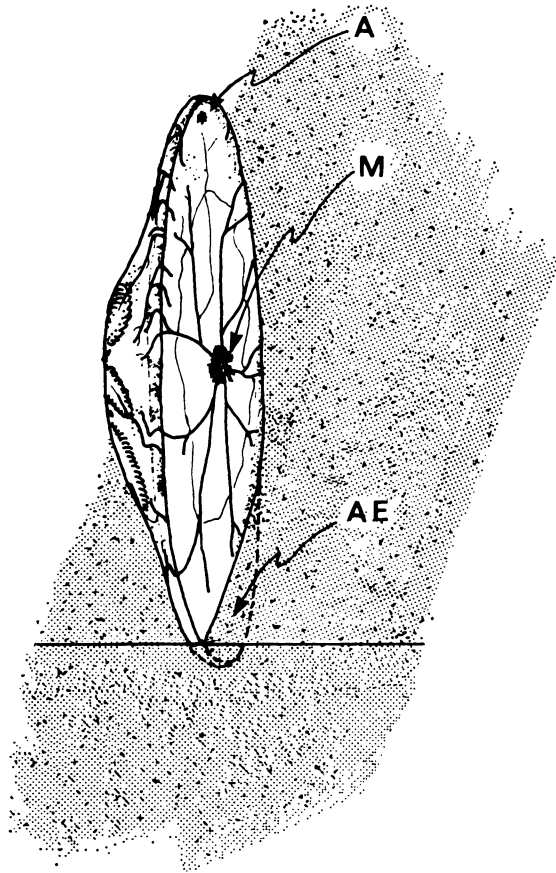


FIGURE 1. Inclined posture of *Dendraster excentricus*. The anterior edge of the test (AE) is inserted into the sand. In this position, sand dollars suspension feed by capturing particles which come in contact with the test. The mouth is indicated by M, the anus by A.

For diet analysis, animals collected in the field were immediately fixed in 80% ethanol after being brought from the water. The sand dollars were dissected and the bolus of food nearest the mouth was removed. Each bolus was divided into 3 or 4 equal parts and each part was smeared on a glass slide, dried, and stained with 1% Nile Blue Sulfate or Lugol's Iodine. Chitin was detected by fluorescence microscopy (Leitz fluorescence microscope). Five fields of view at 100 $\times$  magnification (which covered about 30% of each smear) were selected at random on each slide; each item therein was identified and its surface area was measured with an eyepiece micrometer.

For quantitative measurements of gut contents, the tissues were allowed to harden in 80% ethanol for one week, after which the gut was excised intact. The gut was slit open and the contents were removed, washed with distilled water, dried, and weighed. The gut contents were then hydrolyzed in hot concentrated

chromic acid for 48 hr, washed three times in distilled water, dried, and reweighed. The amount of organic matter in the gut contents was approximated as the loss in dry weight following acid hydrolysis.

Captured material held in the spines and tube feet was collected by injecting the sand dollars intraperistomially with 0.5 ml 0.54 M KCl solution immediately after the animals were brought from the water. After about 30 sec, the sand dollars would release anything that the spines and tube feet held, and the material was collected in a dish.

For the experimental determination of size selectivity, a sand dollar was positioned in the inclined posture by inserting the anterior end into a block of agar; the animal was placed in a 15 liter tank in which a unidirectional water flow was maintained at 11 cm/sec (a normal current speed for Zuma Beach; Timko, 1975). Equal numbers of fluorescent plastic beads (Duke Standards, Palo Alto, California) of 30, 40, 50, 80, and 100  $\mu\text{m}$  diameters were added to the water, giving a total of 0.1 g beads in the tank. After one hr in the tank, the sand dollar was removed, fixed in 80% ethanol, and the beads it had captured on its oral surface were scraped off. The beads were counted and their sizes measured on a Leitz fluorescence microscope.

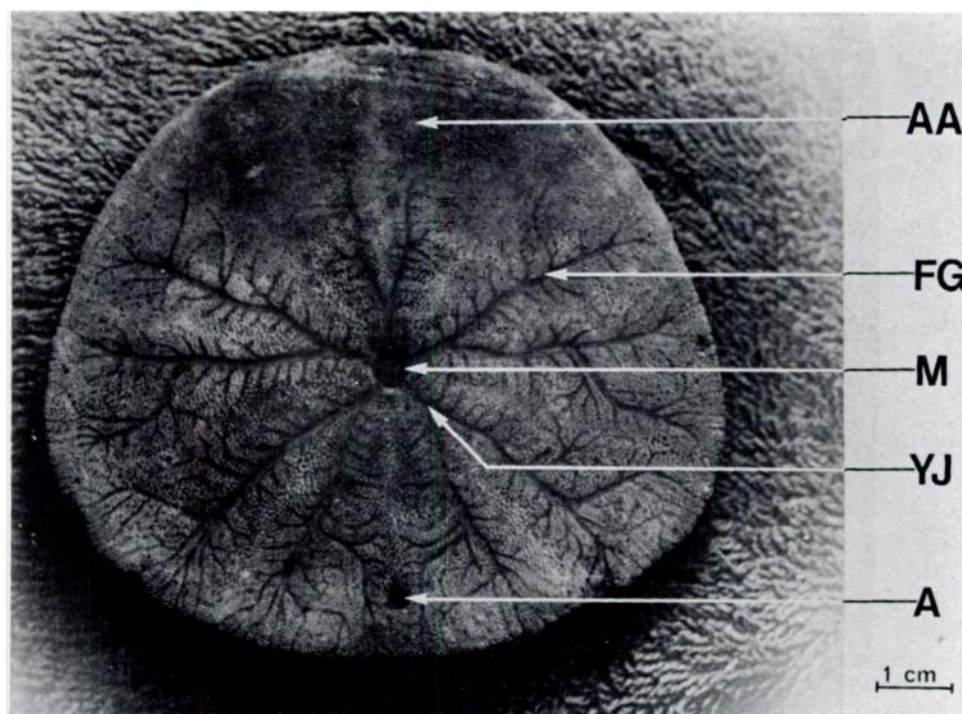


FIGURE 2. Oral surface of a *Dendraster* test that has been denuded of spines. The anterior portion of the test which is inserted into the sand is marked AA. One of the Y junctions, the major intersections of the food grooves (FG) near the mouth (M), is marked by YJ. The anus is indicated by A. The maximum diameter of the sand dollar in the photo is 84 mm.

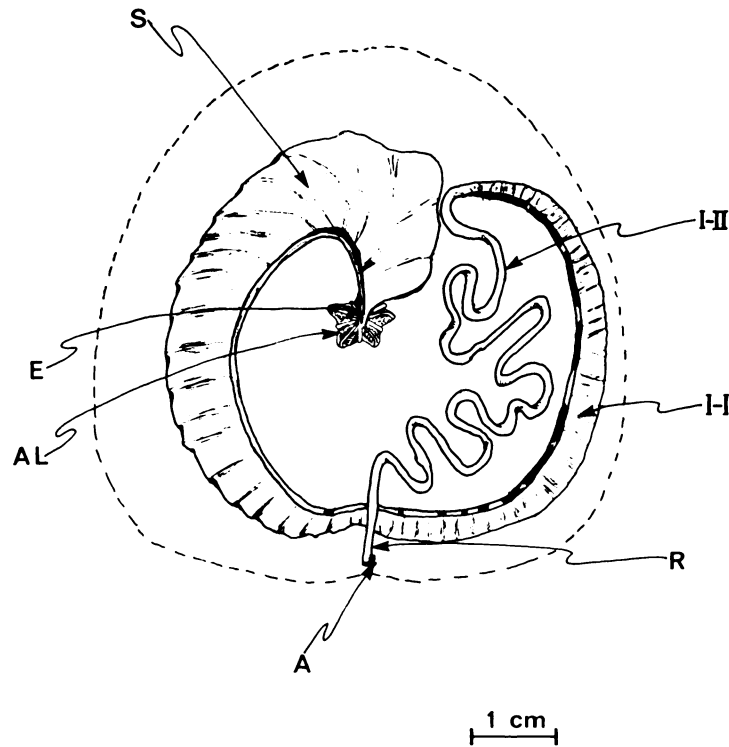


FIGURE 3. Digestive organs of *Dendraster*, viewed from the aboral side. The outline of the test is marked by a dashed line. Aristotle's Lantern (AL) is the masticating apparatus. Esophagus (E), stomach (S), intestine I (I-I), intestine II (I-II), and rectum (R) follow the terminology of Reisman (1965). The anus (A) exits on the oral surface. In an average size sand dollar (maximum length about 60 mm), the length of the different gut sections would be: esophagus, 5 mm; stomach, 70 mm; intestine I, 70 mm; intestine II, 90 mm; rectum, 10 mm.

## RESULTS

### *Brief description of feeding structures and digestive system*

Specimens of *Dendraster* were observed feeding in the inclined posture (Fig. 1) and the prone posture, in which they lay flat upon the substrate or buried in it. Feeding behavior in either position was identical, except as noted below.

The oral surface of *Dendraster* is covered by straight primary spines about 4 mm long, secondary spines about 1 mm long, numerous suckered tube feet, and bidentate pedicellariae. The pedicellariae are of two size classes, the larger averaging 0.6 mm long and the smaller averaging 0.14 mm long (Chia, 1969b). Food grooves (Fig. 2), lined with stubby, non-suckered ambulacral tube feet, extend over the oral surface except for the area which is usually inserted into the sand in the inclined posture. Some food grooves extend over the margins and onto the aboral surface for a short distance.

The mouth is contained within a buccal cavity that is covered by five groups of straight buccal spines which are about 4 mm long. The floor of the buccal cavity

is formed by the peristomal membrane, which overlays Aristotle's lantern. Buccal tube feet, which are similar to ambulacral tube feet but slightly longer, line the area where the five main food grooves enter the buccal cavity.

The digestive tract has five distinct regions (Fig. 3): esophagus, stomach, intestine I, intestine II, and rectum (Reisman, 1965). The digestive organs are suspended by mesenteries within the central cavity of the test.

#### *Food capture*

Three types of food handling behavior were observed which depended upon whether the food was motile prey, nonmotile material, or particles  $<50 \mu\text{m}$  in diameter.

*Dendraster* is capable of capturing actively swimming prey. Laboratory observations showed *Dendraster* easily caught and ingested about 80% of the small crustaceans (nauplii of *Artemia salina*, mysids, calanoid copepods, etc.), that contacted the oral surface. The spines, tube feet, and large bidentate pedicellariae were used in prey capture. Prey capture was observed only on the oral surface of the sand dollar. Initially, when prey contacted the oral surface, the primary spines within about 1 mm of the contact moved their distal ends together, forming a cone-like trap over the prey (trapping response). When a sand dollar was actively capturing prey, as when given a meal of *Artemia*, the numerous cone traps were apparent to the unaided eye. Within a few seconds of the trapping response, the large bidentate pedicellariae extended with open jaws. If prey were nearby, the jaws snapped open and shut vigorously, usually resulting in the rapid capture of the prey. The prey rarely escaped from the pedicellariae; furthermore, the cone traps hampered the prey from swimming away. In flowing water, the cone traps may also keep prey from being swept off the test by the current.

After snapping on the prey a few times, the pedicellariae released it and the spines and tube feet moved it toward a food groove. The tube feet generally pushed the prey, whereas the spines would strike or bat it. Along the route to the food groove, several other pedicellariae often snapped on the prey. This process of "pre-oral mastication" resulted in a food particle that was already somewhat macerated when it reached the food groove. Upon reaching the margin of a food groove, the prey mass was transported into the groove by the tube feet which are densely distributed along the margin. Several tube feet pushed the mass into the groove or a single tube foot grasped the mass and placed it into the groove.

Nonmotile food items  $>50 \mu\text{m}$  in diameter (sand grains, algal fragments, etc.) were grasped by the tube feet and pushed toward a food groove. The pedicellariae did not assist in handling nonmotile foods, unless the food was quite large. Ciliary currents were too weak to move large food items effectively.

Ciliary currents were used in the transport of particles  $<50 \mu\text{m}$  in size. The small particles traveled very closely to the test surface and were swept into the food grooves by the ciliary currents. These currents were generated by the cilia along the base of the spines (Chia, 1969a).

#### *Transport in the food groove*

Small particles were enveloped in the mucus secreted in the food groove. The stubby ambulacral tube feet passed the mucus strings toward the mouth. Larger

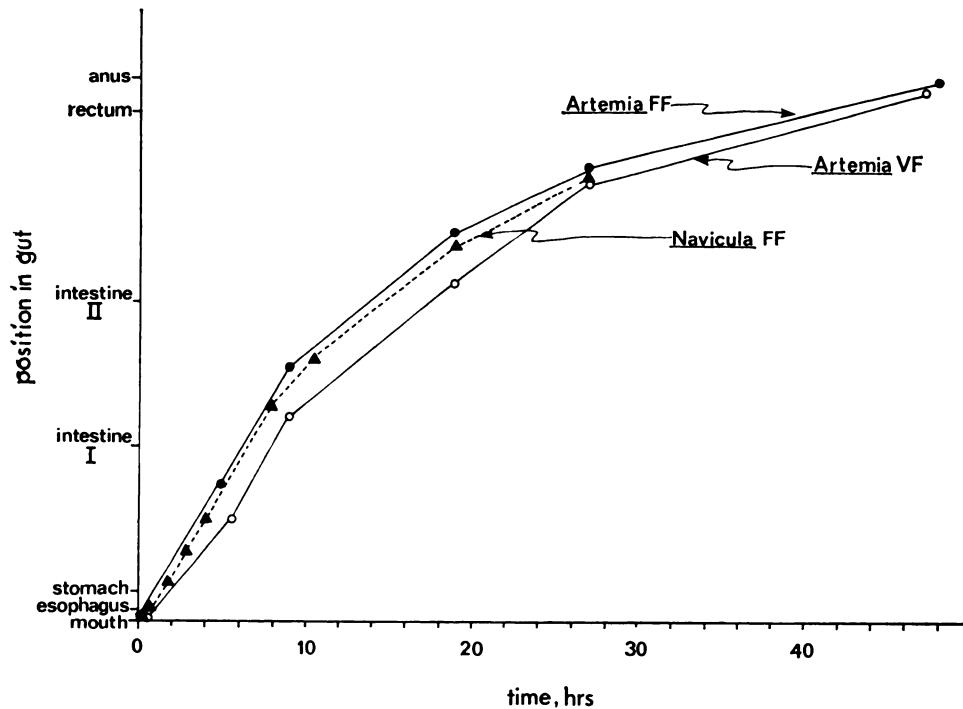


FIGURE 4. Clearance rate of food through the *Dendraster* gut. The ordinate shows the position of the food in the gut and represents linear distance (actual distance varied with the size of the animal; see Fig. 3). Solid circles represent the rate of passage for a meal of *Artemia* force fed to the sand dollars, open circles represent the rate for a meal of *Artemia* fed free choice to the sand dollars, and the solid triangles represent the rate for a meal of *Navicula* force fed to the sand dollars.

items, such as algal filaments and single crustacean prey, were moved without visible evidence of a mucus string. If the food item was several mm long (*e.g.*, pieces of *Phyllospadix* (surf grass) or small polychaetes), it was moved by a coordinated rowing motion of the ambulacral tube feet in contact with the food. The period of a stroke and retraction was about two sec.

When food reached the buccal cavity, it was drawn in by the buccal tube feet. Small items could be taken in by ciliary currents. In the case of foods several millimeters long, the buccal spines (which normally lay flat over the buccal cavity) were raised to admit the large item. Food was drawn past the peristomal membrane by the teeth, which thoroughly ground the food prior to swallowing.

The time for the entire sequence from capture to ingestion varied from 5 to 30 min, with active prey requiring more time than nonmotile items. The average time from prey capture to ingestion was about 15 min, and the teeth usually masticated the prey for another 15 min prior to swallowing.

#### *Rejection response*

Selective rejection of food occurred at two sites: the test surface and the Y junction of food grooves near the mouth (Fig. 2). If an item which *Dendraster*

would not eat (Sephadex beads, bits of agar, acid cleaned sand grains) was placed onto the oral surface, the spines waved vigorously and the material was moved away from the food grooves and toward the nearest test edge, where it was dropped. Often, when the sand dollar was feeding in the prone position, rejected items were pushed only for a short distance, then dropped onto the substrate. The small pedicellariae frequently emerged during the rejection response, but the large pedicellariae did not.

Items which were rejected were also tested for acceptance by injection into a food groove. At times, the injected material was not moved at all. Most often, however, the material was moved toward the mouth, but upon reaching the Y junction, was pushed out of the food groove by the ambulacral tube feet. The Y junction appeared to be the final sorting point for food prior to ingestion, since Sephadex beads that were injected beyond the Y junction at the edge of the buccal cavity were ingested.

Occasionally, a *Dendraster* regurgitated gut contents if the chamber water was not kept cool or sufficiently aerated. During regurgitation, the buccal spines were raised, the gut contents were ejected through the mouth, and the rejection response ensued. In addition, the spines bordering the food grooves interlaced over the food grooves preventing the regurgitated material from entering.

#### *Defecation*

Unlike the sand dollar *Mellita sexiesperforata*, in which the anus is near the mouth, and which ceases feeding during defecation (Goodbody, 1960), individuals of *Dendraster* continued to feed during defecation. Immediately prior to defecation, the periproct was elevated. At times, the periproct would open and water would be taken in and expelled three or four times (anal irrigation) before defecation. Anal irrigation was not a prerequisite for defecation. Feces were ejected in a flocculent jet which extended about 5 mm from the test when the sand dollar was in the inclined posture. If the sand dollar was prone, the feces were expelled while the animal crawled about, leaving a trail of feces behind. During defecation, the marginal spines interlaced over the food groove which lays between the mouth and anus, preventing reingestion of feces. If any fecal material touched the test surface, the rejection response was observed in that area.

#### *Clearance rate and feeding times*

The rate of food passage through different sections of the gut of normally feeding sand dollars was examined by feeding the sand dollars nauplii of *Artemia* vitally stained with 1% Nile Blue Sulfate. Ten sand dollars were placed in a small tank and offered the stained *Artemia* nauplii free choice (voluntarily fed group) for 1 hr, after which the sand dollars were returned to their normal holding tanks. Ten other sand dollars were force-fed by injecting stained *Artemia* nauplii into the buccal cavity. The force-fed animals were kept in small dishes for 1 hr, then returned to their holding tanks. In the holding tanks, both groups of sand dollars resumed their normal ingestion of sand and detritus. At intervals from 6 to 48 hrs following the meal of *Artemia*, two sand dollars from each group were sacrificed, their guts examined, and the position of the stained nauplii marked (Fig. 4).

It took slightly under five hours for the marked food to pass through the stomach and about 10 hours for it to pass through intestine I (Fig. 4). After two days, the labelled food passed the rectum and reached the anus. The rate of progress was similar in voluntarily-fed and force-fed groups, but the absolute position of the food in voluntarily-fed sand dollars lagged about 0.5 hr behind that of force-fed sand dollars. The lag represents the time required for capture and ingestion of the *Artemia* nauplii.

The rate of passage was also measured by using a suspension of *Navicula distans* (a diatom) to account for possible differences in digestive rate for another type of food. Since specimens of *Navicula* were difficult to distinguish from other gut contents, only starved, force-fed sand dollars were used in the experiment. The rate of passage for the meal of *Navicula* corresponded closely to that of the meal of *Artemia* (forced-fed group). Therefore, the rate of passage through the gut was not a function of the type of food ingested.

Determination of the rate of passage of the food allowed estimation of feeding times in the field by extrapolating from the position of the food in the gut. Ten sand dollars were collected from the population at Zuma Beach at 10:00 (twice), 12:00, and 15:40 on different days. The animals were fixed immediately after being brought from the water.

The data indicate that individuals of *Dendraster* fed continuously with occasional pauses. There were few consistent trends in the distribution of food in the guts. In all samples, 80% of the sand dollars were actively feeding (food in the teeth or buccal cavity) at the time of collection. Material in the stomach was in discrete boluses until it reached intestine I, after which it was well packed with few gaps. The gaps between boluses in the stomach indicated that intervals of 15 to 30 min separated the swallowing of each bolus, which is consistent with laboratory observations. Gaps in food distribution in the intestines occurred in 28% of the animals, denoting lapses of 1 or 2 hr duration; the reason for the pauses is unknown.

### Diet

The diet of *Dendraster* from Zuma Beach was determined by microscopic examination of smears of gut contents. Since the food was well masticated before ingestion, it was not possible to identify the numbers of whole prey or other food items that had been eaten. Instead, the surface area of each food fragment was measured, since the gut smears were essentially two dimensional. The food bolus nearest the mouth, divided into 3 to 4 smears, was examined from ten animals on each date.

The seasonal composition of the diet varied considerably (Table I). The gut contents in the summer sample were predominated by dinoflagellates (*Gonyaulax polyedra*, *Ceratium* spp., *Dinophysis homunculus*, *Noctiluca scintillans*), sand grains, organic detritus (stained material not identifiable), chitin fragments (from decapod zoea, cirripede nauplii, amphipods), and algal fragments. The composition of the gut contents was comparable to the material suspended above the sand dollar bed except that the gut contents had a smaller proportion of sand grains. The sediment from a water sample taken above the sand dollar bed in June contained approximately 30% sand grains, 30% dinoflagellates (mostly *G. polyedra*, *Ceratium*



TABLE I  
Seasonal changes in diet.

Category	(Feb. 9, 1975) Winter diet, percentage	(June 10, 1974) Summer diet, percentage	(April 16, 1974) During spring plankton bloom, percentage	(March 30, 1974) Two weeks prior to plankton bloom percentage
Centric diatoms	6.2	5.8	90.3	5.5
Pennate diatoms	1.3	1.4	1.0	3.3
Dinoflagellates	1.0	42.0	1.3	2.3
Small flagellates	0.4	0.5	0.3	0.0
Tintinnids	10.6	3.3	0.0	0.5
Radiolaria	5.4	0.6	0.2	2.9
Foramanifera	4.0	0.6	0.0	0.0
Silicoflagellates	1.4	0.2	0.0	0.1
Chitin fragments	41.6	9.6	2.7	23.2
Algal filaments	8.0	6.1	1.0	19.7
<i>Phyllospadix</i>	2.1	0.0	0.0	2.3
Sand grains	13.2	13.9	2.7	12.9
Wood ash	4.0	0.4	0.3	16.0
Echinoid calcite	0.0	1.9	0.0	0.0
Detritus	0.9	13.7	0.0	0.0
Other	0.1	0.0	0.0	0.0

spp., and *D. homunculus*), 20% chitin containing Crustacea (decapod zoea, cirripede nauplii), 10% centric diatoms (three species of *Chaetoceros* and *Coscinodiscus oculus*), 5% algal fragments, and 5% tintinnids (mostly *Parundella minor*). In contrast to the summer gut sample, the most abundant items in the winter gut sample were chitin fragments (from mysids, amphipods, calanoid copepods), sand grains, tintinnids (predominately *P. minor*), algal fragments, and centric diatoms (*C. oculus*, *C. perforatus*, *Navicula distans*, *Biddulphia (rhombus?)*, *Nitzschia pacifica*, *Pleurosigma* spp.). Comparing the diet before and after a plankton bloom strengthens the contention that *Dendraster* fed on whatever was abundant and available in the plankton (Table I). Prior to the bloom, the sand dollars were feeding primarily on crustaceans and algal fragments. During the bloom, when the diatom *Chaetoceros* composed more than 90% of the suspended material in the water, the sand dollar diet shifted heavily toward *Chaetoceros*.

The diet of the sand dollars from Zuma Beach was compared with that of sand dollars inhabiting two bays (Morro Bay and Newport Harbor, California) for the amount of food in the gut and food quality. Morro Bay sand dollars had been collected in January, 1973, and Newport Harbor sand dollars had been collected in August, 1973. The Zuma Beach sand dollars which were compared to the Morro Bay sample were collected in January, 1973, and the Zuma Beach sand dollars which were compared to the Newport Harbor sample were collected in August, 1973 (N equals 10 for each sample). Due to differences in body weight among individuals, the weight of food was expressed as a percentage of the wet body weight (food index). Differences between food indices and the organic content of the food were tested with one way ANOVA (Sokal and Rohlf, 1969).

Sand dollars from the protected outer coast population at Zuma Beach had more food of better quality in their guts than sand dollars from the bay populations

TABLE II  
*Amount and quality of food in the guts of sand dollars from different locations.*

Sample	Mean weight of food, gm	Mean food index	Mean relative measure of organic content
Zuma Beach, summer	0.055	0.281	34.7%
Zuma Beach, winter	0.060	0.259	56.6%
Morro Bay, winter	0.023	0.192	45.1%
Newport Harbor, summer	0.021	0.153	20.8%

(Table II). The food index of the Morro Bay sample was lower than that of the January Zuma Beach sample ( $P < 0.05$ ), as was the Morro Bay sample organic content ( $P < 0.05$ ). Similarly, the Newport Harbor sample had a lower food index ( $P < 0.05$ ) and organic content ( $P < 0.10$ ) than the Zuma Beach August sample. The food index did not differ seasonally among the two Zuma Beach samples ( $P > 0.10$ ), but the winter sample contained significantly more organic matter ( $P < 0.01$ ).

#### *Size selectivity*

Analysis of the diet indicated that *Dendraster* was relatively nonselective with respect to types of food; in addition, selectivity concerning food size was examined. The particles which had been held in the spines and tube feet of 25 specimens of *Dendraster* from Zuma Beach were analyzed for size by sieving through a U. S. Bureau of Standards sieve series (Fig. 5). The sand dollars had captured relatively small particles, 60% being  $< 180 \mu\text{m}$ . Comparisons with the material suspended above the sand dollar bed were not made due to the small amount of sediment collected in the water samples.

An Ivlev index (Ivlev, 1961) was computed on the basis of laboratory experiments which used fluorescent plastic beads of five different sizes, from  $30 \mu\text{m}$  to  $100 \mu\text{m}$  in diameter.  $P_1$  was corrected for passive settling of the beads by comparison with controls containing no sand dollars. Five trials were used to calculate an average electivity index (E) for each particle size.

E ranges from +0.67 for absolute preference to -1.00 for total avoidance of any of the particle sizes. The specimens of *Dendraster* did not strongly prefer or avoid any of the particle sizes (Table III). Therefore, the Ivlev index and the size of the captured particles indicate that *Dendraster* was not selective with respect to food particle size within the range of  $1 \mu\text{m}$  to  $180 \mu\text{m}$ .

#### DISCUSSION

The feeding habits of *Dendraster excentricus* differ significantly from those of other sand dollars. Unlike *Mellita sexiesperforata* (Goodbody, 1960), *M. quinquesperforata* (Hyman, 1958), and *Echinarachnius parma* (Sokolova and Kusnetzov, 1960), all of which are microphagous deposit feeders, specimens of *Dendraster* consume large particles, capture active prey, and are capable of both prone deposit feeding and inclined suspension feeding. Feeding in *Dendraster* was previously described by both MacGinitie and MacGinitie (1949) and Chia (1969a). Both

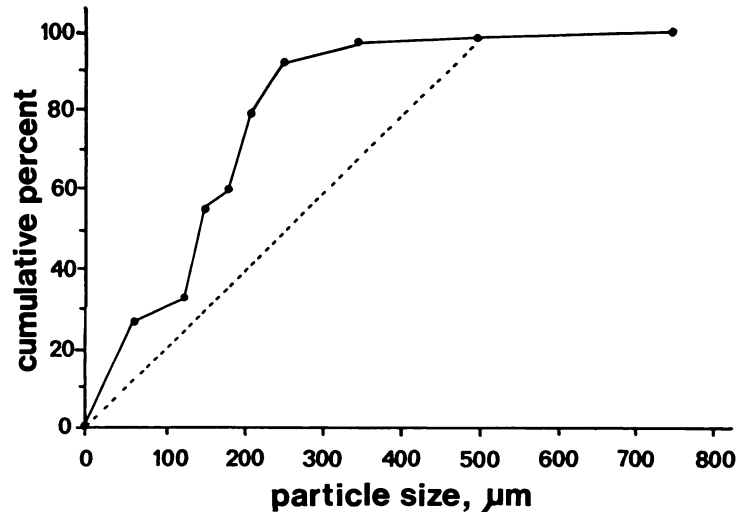


FIGURE 5. Size of captured particles held by the tube feet and spines. If all particle sizes were equally abundant in the sediment collected within the range of 0 to 500  $\mu\text{m}$ , the cumulative percentage of particle sizes would be given by the dashed line. The solid line represents the cumulative percentage for the particle sizes held by the sand dollars. The slope of the solid lines shows that particles of 1 to 225  $\mu\text{m}$  were relatively more abundant ("over-represented") than were particles  $>225 \mu\text{m}$ , but the differences in abundance are not striking.

studies reported ciliary mucus feeding, and Chia's paper was the first to describe the role of the ambulacral tube feet in the transport of mucus strings. However, no previous study included observations of feeding in the inclined posture. The present study indicates that the use of spines and suckered tube feet on the oral surface is probably the dominant method of food gathering, rather than ciliary mucus feeding. Most of the particles in the gut were too large to have been moved by the feeble ciliary currents of the oral surface. Furthermore, most large particles were transported in the food grooves without the secretion of much mucus. Therefore, I suggest that *Dendraster excentricus* be considered as primarily a suspension feeder rather than a deposit feeder or ciliary mucus feeder.

TABLE III

*Electivity index for different particle sizes. The electivity index for the  $i$ th particle size,  $E_i$ , is calculated as  $E_i = (p_i - P_i) \div (p_i + P_i)$ , where  $P_i$  is the proportion of the  $i$ th particle size in the mixture offered to the animal and  $p_i$  is the proportion of the  $i$ th particle size which the animal captures or ingests relative to the other sized particles ingested.*

Particle size, microns	$E_i$ , mean of 5 trials
30	-0.037
40	+0.167
50	-0.141
80	+0.061
100	-0.195

Inclined individuals of *Dendraster*, especially in dense aggregations which hydrodynamically enhance the efficiency of particle capture (Timko, 1975 and in preparation) are extremely effective suspension feeders. The fact that *Dendraster* captured and ate active prey has consequences when the community structure of sandy bottom areas is considered. In areas where sand dollars form dense beds, such as in Southern California (Merrill and Hobson, 1970), the sand dollars are probably important benthic suspension-feeding predators which consume large numbers of small prey such as mysids, amphipods, copepods, and the larvae of other benthic animals which attempt to settle in the area.

Chia (1969a) reported that specimens of *Dendraster* which he examined from Puget Sound, Washington, invariably had empty stomachs. Specimens of *Dendraster* examined in the present study usually had food in the stomach, but the boluses were spaced since the sand dollars masticated a mouthful of food for about 15 minutes before swallowing it. These food boluses passed out of the stomach fairly rapidly (in 5 hr). Although other echinoids are known to exhibit diurnal periodicity in feeding (Lawrence and Hughes-Games, 1972), *Dendraster* was found to feed continuously in this study. This result is to be expected, since there is no known diurnal variation in food availability nor is there any possibility of evading visually-hunting predators in the daytime.

Reports of diet composition and selectivity in sand dollars are scarce. Hyman (1958) stated that the gut of *M. quinquesperforata* contained nannoplankton but no sand grains. *M. sexiesperforata* specialized on particles  $<20 \mu\text{m}$  in size (Goodbody, 1960). Chia (1969a) recovered diatoms, sand grains, and pieces of algae from the food grooves of Puget Sound *Dendraster* and suggested that the diet was generalized. The data on size selectivity and diet presented here confirm the generalized nature of the diet of *Dendraster*. The instances of selective rejection indicated that a criterion other than size must be the basis for rejection. The role of the tube feet in rejection is especially interesting, since rejection appears to be initiated by the tube feet on the oral surface and those at the Y junction.

Chia (1969a) hypothesized that a generalized diet might contribute to the abundance of *Dendraster*. In addition to a generalized diet, the efficient prey-handling behavior and continuous feeding reported here are undoubtedly important factors which have allowed *Dendraster excentricus* to attain great abundance and widespread distribution.

I would like to thank Dr. James G. Morin and Dr. Jon E. Kastendiek for collecting the subtidal samples of Zuma Beach sand dollars. Dr. Morin assisted throughout the completion of this project. This paper is taken from research done in partial fulfillment of the requirements of the Ph.D. at the University of California, Los Angeles.

#### SUMMARY

1. *Dendraster excentricus* used the spines and tube feet to capture large food items such as algal fragments. In addition, the large bidentate pedicellariae were used to capture active prey.

2. Rejection of food occurred at the test surface or at the Y junction of the food grooves. The rejection response was well defined.

3. Specimens of *Dendraster* from a protected outer coast location ate primarily small crustaceans, diatoms, algal fragments, and sand grains. In a summer sample, diatoms were the most abundant item in the diet; in a winter sample, crustaceans predominated the diet.
4. Sand dollars from a protected outer coast sand dollar bed had more food of higher organic content in their guts than did sand dollars from two bay habitats.
5. Food passed through the stomach in 5 hr and through the entire gut in 2 days. Specimens of *Dendraster* from a protected outer coast habitat fed continuously.
6. Individuals of *Dendraster* were nonselective with respect to particle size in the range of 30  $\mu\text{m}$  to 100  $\mu\text{m}$ . Sixty per cent of the particles captured by specimens of *Dendraster* in the field were < 180  $\mu\text{m}$  in size.

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