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Comparison of Macrofaunal Invertebrates in Sand Dollar (*Dendraster excentricus*) Beds and in Adjacent Areas Free of Sand Dollars

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Abstract

Abundances of macroinfaunal invertebrates in sand dollar (*Dendraster excentricus*) beds and in adjacent areas free of sand dollars were studied at 10 intertidal sites in the Pacific Northwest region of the USA and Canada. Each site was sampled once in late summer of 1977. There were no significant differences in overall diversity of species between the beds and adjacent areas; nor did cluster analysis indicate a "sand dollar bed community." However, a polychaete (*Armandia brevis*) was significantly more abundant inside the beds than just outside them. Conversely, in comparison to the beds, adjacent regions contained significantly more specimens of the following species: a bivalve (*Transennella tantilla*), several tubicolous crustaceans (*Corophium* spp., *Ampelisca agassizi*, and *Leptochelia savignyi*) and two polychaetes (*Glycinde polygnatha* and *Malacoceros arenicola*). Sediment characteristics at each study site were not correlated with the presence or absence of sand dollars; moreover, a comparison among the 10 sites revealed no sediment characteristics typical of sand dollar beds. At most of the sites, significantly fewer tube-building invertebrates occurred inside sand dollar beds than outside. The discussion considers the possibility that mechanical disturbance by the sand dollars tends to exclude some macroinvertebrates (especially tubicolous ones) from sand dollar beds.

Introduction

Recent investigations in marine ecology have emphasized the roles of biological agents in organizing soft-sediment communities. Field experiments have confirmed that competition, predation and disruption of the sediment are important structuring forces (Woodin, 1974, 1978; Orth, 1977; Virnstein, 1977; Brenchley, 1978; Wiltse, 1980).

Sand dollars (*Dendraster excentricus*) occur at high densities intertidally in Puget Sound, USA (Birkeland and Chia, 1971) and may play a dominant role in the organization of intertidal communities of this region. They are large animals, which alter sediment stability by their burrowing activity. Rhoads and Young (1971), Brenchley (1978) and Woodin (1978) have shown that such species have important effects on soft-sediment community structure. Merrill and Hobson (1970) have listed species which are more numerous in subtidal sand dollar beds than in adjacent sediments, and Kellerhals and Murray (1969) have compared a sand dollar bed community with an eel grass bed community in Boundary Bay, British Columbia, Canada.

The foregoing investigations have included only species lists without supporting data and are insufficient for making broad generalities about the fauna associated with beds of *Dendraster excentricus.* Therefore, the purpose of this study is to describe the macrofaunal invertebrates associated with sand dollar beds and with adjacent sand dollar-free areas over a wide geographic region of the Northwest Pacific. Intertidal sand dollar beds were studied at 10 sites from Hornby Island (Canada) in the north to Puget City, Washington State (USA) in the south. Since sand dollars both ingest (Chia, 1969, 1973) and mechanically disturb the sediment (Smith, 1980), sediment characteristics inside and outside the beds were compared in an attempt to relate differences in sediment structure to faunal differences. Although statistical analysis brought to light no "sand dollar bed community", the abundances of several species were significantly different inside sand dollar beds than outside the beds. The discussion section considers possible reasons for these associations.

Materials and Methods

Study Sites

Infaunal macroinvertebrates were collected inside and outside the *Dendraster excentricus* beds at the 10 sites shown in Fig. 1.

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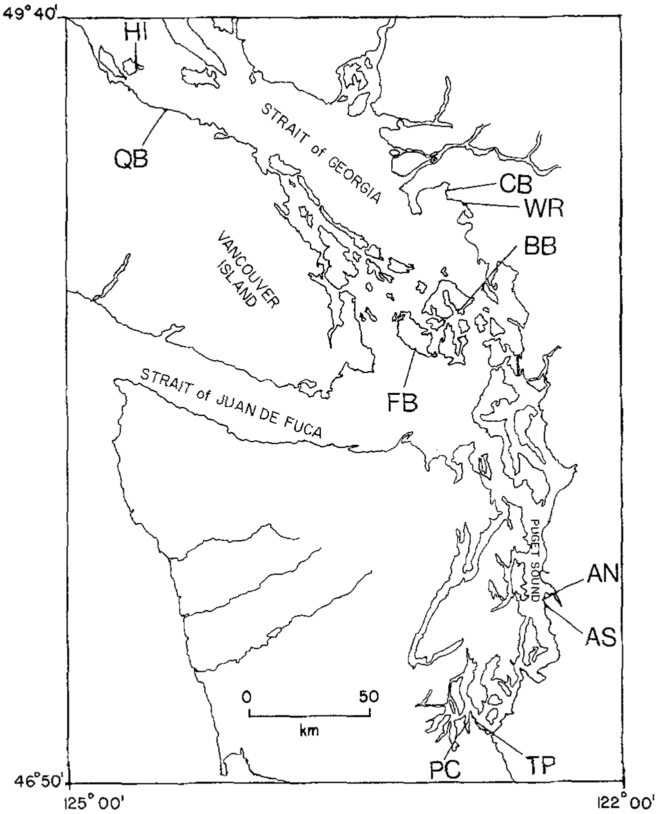

Fig. 1. Map of Puget Sound and Strait of Georgia, showing sampling sites: TP, Tolmie State Park; PC, Puget City; AS, Alki South; AN, Alki North; BB, Buck Bay; FB, False Bay; WR, White Rock; CB, Crescent Beach; QB, Qualicum Beach; HI, Hornby Island

The sand dollar bed at Tolmie State Park lies largely in the public recreation area. On one side it is bordered by a small stream flowing into the sound; on the other it extends onto private beaches. On the day of the sampling, the bed and adjacent sand flat were covered with a thick mat of drift algae. Many recently-dead sand dollars were present.

At Puget City, the sand dollar bed is limited on one side by rock and terminates on the other side at the boat launching ramp of a marina. The bed is patchy, with dense aggregations of sand dollars and areas of unoccupied sand. On the day of sampling, an oily smell was noticible in the area.

The sand dollar bed at Alki South has been described by Birkeland and Chia (1971). The sand dollars are aggregated in pockets of sand between cobble. The bed terminates on one side where the sediment becomes hard-packed clay, while the opposite edge is apparently a mat of tubicolous crustacean tubes.

The sand dollar population at Alki North is confined to a water-filled channel behind a large sand bar. Its distribution is discontinuous, resembling a series of separate beds, with clusters of sand dollars separated by long stretches of unoccupied sand.

At Buck Bay, the sand dollars occupy the center of a small sand flat. The bed has sharp lateral and seaward margins which do not correspond with any obvious physical features.

The sand dollar population at False Bay is sparse and discontinuously distributed, occupying the channels behind four sand bars at the southern margin of the bay. This site has been described in detail by Pamatmat (1966).

At White Rock, on the sand flat near Semiahmoo Park, there were relatively few sand dollars, all clustered within a few square meters in one of the channels between the series of sand bars which are characteristic of this beach. All were 6 to 7 cm in diameter and possibly represented a single successful recruitment in this area.

The Crescent Beach sand dollars are, similar to False Bay, distributed discontinuously in channels behind a series of sand bars. Eel grass (*Zostera marina*) is present near many of the patches of sand dollars, as are accumulations of empty tests and bivalve shells.

The sand dollar bed at Qualicum Beach extends along most of the public beach, but is divided into patches separated by sand dollar-free regions. The sediment surface is rippled, and, when buried, the sand dollars are invisible under the rippled surface.

On Hornby Island, the sand dollar bed extends the full length of Tribune Bay but includes a few sand dollar-free patches. The sediment is rippled, and, at low tide, the sand dollars are buried deeply.

All of the beaches except Buck Bay and False Bay are subject to heavy recreational use. The tide flat at Buck Bay is privately owned, and the owners occasionally dig clams there. False Bay is owned by the University of Washington, and the tidal flat is used for research and teaching.

Sampling Method

Each site was sampled once at low tide in late summer 1977. The infauna were collected in $10 \times 10 \times 10$ cm cores of sand. Three cores were taken inside and three outside each sand dollar bed. Inside each bed the cores were taken in a 3-m radius within 3 m of an edge. Within the designated area, random positions of the cores were determined by the rapidly rotating investigator technique of Sanders *et al.* (1962), except that in patchy beds cores were not taken in areas unoccupied by sand dollars. In particularly sparse beds (White Rock, Crescent Beach) cores were taken from visible aggregations of sand dollars.

The positioning of cores outside each sand dollar bed was determined by the configuration of the bed. Where the bed had a clear edge (Tolmie State Park, Alki South, Alki North, Buck Bay), the cores were taken within a 3-m radius just beyond the edge and at the same tide level as the bed, but areas clearly uninhabitable by sand dollars (e.g. the fresh water inflow at Tolmie State Park) were avoided. Where the bed was sparsely populated and patchy (False Bay, White Rock, Crescent Beach), the samples were taken approximately 50 m down the beach at the same tide level as the bed, in areas without sand dollars. At the remaining sites, where sand dollars extended through all of the habitable area, the samples were collected from patches of sand surrounded by the beds.

The sand dollar density in each bed was calculated by counting all adults found to a depth of 10 cm in five 0.25 m^2 patches. These patches were selected by placing a wooden frame near the three sites from which the infauna had been collected. Two random positionings of the frame within the 3-m collection radius were also counted.

The infaunal samples were fixed in 10% formalin for at least 24 h. They were then washed through a 500 μm sieve. Material retained on the screen was transferred to 70% alcohol.

The animals were sorted and enumerated using a dissecting microscope. Only whole animals and fragments with heads were counted. Nematodes, copepods, and ostracods were considered to be large representatives of the meiofauna and were ignored.

The sediments were analyzed to determine whether there were any characteristics peculiar to sand dollar beds. A single additional sample was collected inside and outside each bed. This collection was made by scooping out sand to a depth of 10 cm with a garden trowel. The samples were placed on ice and frozen upon return to the laboratory. The sediments were dried at 100 °C for 24 h and divided into portions for organic carbon and grain size analyses. The organic carbon content was calculated as ash-free dry weight after ignition of the sediment at 500 °C for 1 h. While not as accurate as a carbon analyzer, this method is generally adequate for determination of organic carbon in marine sediments (Byers *et al.,* 1978). Grain size was determined by mechanically shaking the sediment for 10 min through a Wentworth series of sieves. The mean grain size and sorting coefficient were determined graphically as suggested by Hulings and Gray (1971). The silt-clay content was also recorded.

Statistical Analysis

Several statistical techniques were employed in the attempt to detect a sand dollar bed community and to determine the effect of sand dollars on community structure. Cluster analysis was used to detect any pattern in the distributions of species which might represent communities. All species, except nematodes, copepods and ostracods, which were found at three or more sites, plus species of which 10 or more individuals occurred at one site, were included in the analysis. Counts of the three faunal samples inside each sand dollar bed were pooled, as were the three outside samples, and the resulting 20 stations were clustered, using information content as the index of similarity. This measure, described by Williams *et al.* (1966), calculates the similarity between two sites as information gain based on the information content. The stations were also clustered according to their sediment characteristics (listed in Table 1), using the Euclidean distance measure, which is appropriate for continuous data. The computer program for the latter clustering method was BMDP:2M (revised December, 1977) from the BMDP statistical package (Dixon and Brown, 1977).

The Shannon-Wiener diversity index, H' (Shannon and Weaver, 1963), and equitability (the ratio of the measured diversity to the maximum diversity possible in a collection containing N individuals) were calculated for each station using the pooled samples. The computer program for these functions was obtained from Orr *et al.* (1973). The differences in diversity, equitability and the number of species present inside and outside sand dollar beds were compared using paired t-tests.

The numbers of individual species whose abundances equalled at least 1% of all organisms collected, as well as the total numbers of tube-building animals and motile crustaceans (amphipods, except tubicolous species, cumaceans and crabs), inside and outside the sand dollar beds were compared with two-way factorial analyses of variance of the replicated data. The counts in each of the three cores were transformed using ln $(x+1)$ prior to these analyses in order to normalize the distributions.

Results

Each of the *Dendraster excentricus* beaches sampled shares at least three species with any other beach. Four species,

Table 1. Characteristics of sediments inside (+) and outside (−) sand dollar (*Dendraster excentricus*) beds at 10 sites in the Northwest Pacific in late summer, 1977. Mean grain size and sorting coefficient are in phi units

Location	% organics		Mean grain size		Sorting coefficient		% silt and clay	
	+	−	+	−	+	−	+	−
Tolmie State Park	0.49	0.57	2.04	2.13	0.63	0.66	2.2	2.1
Puget City	0.56	0.47	1.48	1.48	0.77	0.83	1.1	1.3
Alki South	0.48	0.29	1.81	1.65	0.72	0.84	2.4	1.2
Alki North	0.51	0.53	2.14	2.19	0.69	0.70	2.1	2.0
Buck Bay	0.50	0.55	2.23	2.52	0.74	0.52	1.6	0.8
False Bay	0.60	0.37	2.48	2.28	0.39	0.62	0.4	0.6
White Rock	0.26	0.27	2.56	2.64	0.37	0.35	0.2	0.2
Crescent Beach	0.50	0.30	1.97	1.83	0.57	0.56	1.1	0.8
Qualicum Beach	0.24	0.22	2.48	2.63	0.64	0.58	0.4	1.9
Hornby Island	0.23	0.26	2.51	2.57	0.31	0.32	0.1	0.2

Table 2. Population densities of species representing at least 1% of all animals collected (excluding False Bay samples) in survey of 10 beaches occupied by sand dollars (*Dendraster excentricus*). Values are pooled counts of three 0.01 m^2 samples. Sample locations are abbreviated as in Fig. 1. Asterisks indicate tube builders

Species	Location									
	TP	PC	AS	AN	BB	FB	WR	CB	QB	HI
				Inside Sand Dollar Beds						
Bivalvia										
Transennella tantilla	0	0	9	2	0	31	0	0	4	0
Mysella tumida	3	3	1	2	303	1	2	0	1	0
Opisthobranch (juvenile)	0	0	2	0	0	0	2	1	0	0
Cumacea										
Cumella vulgaris	15	1	39	1	13	1 588	0	1	0	0
Lamprops quadriplicata	0	0	0	0	0	0	2	34	9	0
Amphipoda										
Paraphoxus spinosus	0	0	17	2	0	3 254	0	0	0	0
Pontogeneia sp.	0	0	1	0	1	35	0	0	0	0
Eogammarus confervicolus	0	0	4	0	0	1 444	0	0	0	0
Anisogammarus pugettensis	1	0	0	1	0	0	0	6	0	0
Synchelidium shoemakeri	0	0	45	16	0	16	1	108	0	1
Euhaustorius washingtonianus	0	0	0	0	0	0	0	75	0	0
Corophium spp.*	0	0	4	0	0	1	0	2	0	0
*Ampelisca agassizi**	0	0	0	0	0	0	0	0	0	0
Tanaidacea										
*Leptochelia savignyi**	0	0	26	0	1	29	0	0	0	0
Polychaeta										
Nephthys caeca	0	0	1	0	1	0	6	3	4	0
Scoloplos armiger	9	10	0	3	10	0	9	75	22	3
Glycinde polygnatha	2	5	23	7	1	0	2	0	0	0
Paraonidae	0	0	0	8	0	0	7	11	2	27
Armandia brevis	2	1	2	8	59	0	0	0	0	0
*Malacoceros fulginosus**	0	0	0	0	0	41	0	0	0	0
*Malacoceros arenicola**	0	0	2	0	0	0	0	0	0	0
Microspio sp.*	0	0	0	0	0	136	0	0	0	0
*Pygospio elegans?**	0	0	0	0	0	0	24	0	0	0
Syllis heterochaeta?	0	0	0	0	0	0	0	162	2	1
Holothuroidea										
Leptosynapta clarki	0	0	1	0	0	360	0	0	0	0
				Outside Sand Dollar Beds						
Bivalvia										
Transennella tantilla	0	0	26	27	5	126	0	0	4	0
Mysella tumida	6	4	3	0	8	7	0	0	4	0
Opisthobranch (juvenile)	2	4	0	2	0	0	0	1	0	0
Cumacea										
Cumella vulgaris	34	5	167	2	8	928	0	42	0	0
Lamprops quadriplicata	0	0	0	0	2	0	2	0	18	10
Amphipoda										
Paraphoxus spinosus	0	0	4	4	0	1 024	0	0	0	0
Pontogeneia sp.	0	0	5	1	0	106	0	0	0	0
Eogammarus confervicolus	0	0	1	0	0	9	0	0	0	0
Anisogammarus pugettensis	3	0	0	0	0	0	0	44	0	0
Synchelidium shoemakeri	1	0	108	10	2	251	1	2	0	0
Euhaustorius washingtonianus	0	0	0	0	0	0	0	6	0	0
Corophium spp.*	10	28	67	0	11	0	0	119	0	0
*Ampelisca agassizi**	0	3	0	0	166	0	0	0	1	0
Tanaidacea										
*Leptochelia savignyi**	0	0	98	0	1	752	0	3	0	0
Polychaeta										
Nephthys caeca	0	0	0	1	6	0	1	4	3	1
Scoloplos armiger	11	5	1	3	11	0	13	67	20	1
Glycinde polygnatha	20	16	38	11	12	0	1	0	0	2
Paraonidae	1	0	0	10	0	0	0	10	7	57
Armandia brevis	0	0	0	6	2	2	0	0	0	0
*Malacoceros fulginosus**	0	0	0	0	0	313	0	0	0	0
*Malacoceros arenicola**	0	0	9	3	24	0	0	10	18	0
Microspio sp.*	0	0	0	0	0	19	0	0	0	0
*Pygospio elegans?**	0	0	0	0	0	0	11	0	0	0
Syllis heterochaeta?	0	0	0	0	0	0	0	18	0	0
Holothuroidea										
Leptosynapta clarki	0	0	0	0	0	84	0	0	0	0

comprising at least 5% of all individuals observed (excluding False Bay, where faunal densities are an order of magnitude higher than those of any other site), occur at 6 or more of the 10 locations (Table 2). These species are the bivalve *Mysella tumida,* the cumacean *Cumella vulgaris,* the amphipod *Synchelidium shoemakeri,* and the polychaete *Scoloplos armiger.* Two other polychaetes, *Nephthys caeca* and *Glycinde polygnatha,* each total more than 1% of all individuals observed and are present at 7 sites. Tubicolous amphipods (*Corophium* spp.) make up more than 5% of all individuals and were collected on 6 beaches.

The cluster analysis of the species data (Fig. 2) does not suggest a "sand dollar bed community". The two stations at False Bay are in a category by themselves, and the remaining sites are divided into two major groups, the Puget Sound sites and the remaining beaches farther north. Only the sand dollar bed sample at Tolmie State Park appears misplaced by this division. The "inside" and "outside" samples from the same beach are not always most closely related to each other, but samples from adjacent beaches (Alki South and Alki North, White Rock and Crescent Beach) are grouped together.

The cluster of sites based on their sediment characteristics (Fig. 3) follows a pattern similar, but not identical to, that of the faunal data. The division into two major groups separates the Puget Sound beaches from the other areas, with the Buck Bay and Crescent Beach sand dollar beds being included in the former group. The False Bay sediments do not differ notably from those of the other beaches. The clustering does not suggest a sediment composition typical of sand dollar beds, nor do any of the individual sediment characteristics measured (Table 1) show any relation to the presence or absence of sand dollars.

Cluster analysis of the faunal associations (Fig. 2) suggests that the Puget Sound beaches are somewhat different

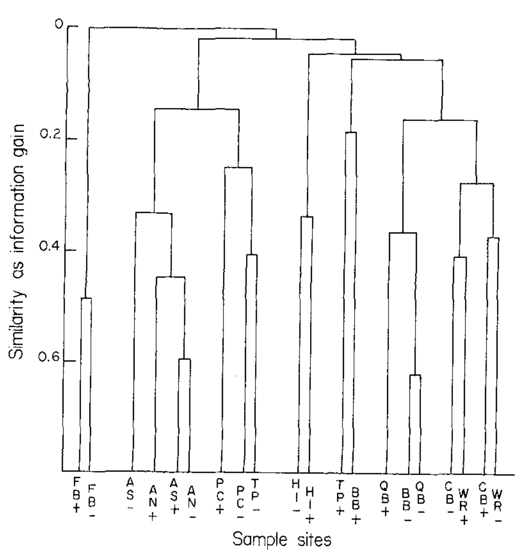

Fig. 2. Clusters of sampling sites in *Dendraster excentricus* beds based on faunal similarity. Similarity is measured as information gain. Site abbreviations as in Fig. 1

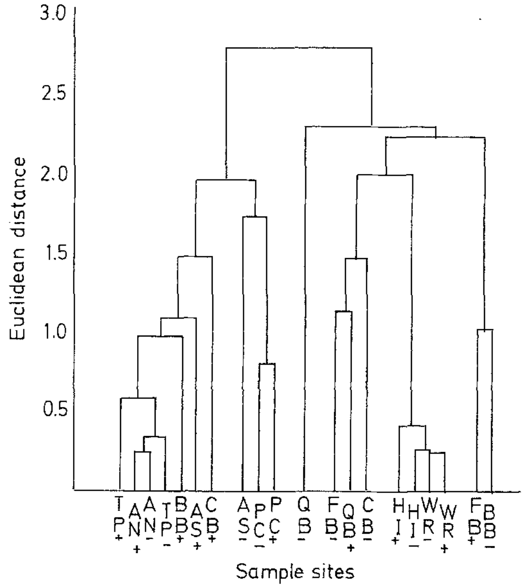

Fig. 3. Clusters of sampling sites in *Dendrater excentricus* beds based on sediment characteristics. Site abbreviations as in Fig. 1

from those of the other areas in this respect. The cluster of beaches by their sediment characteristics (Fig. 3) follows a similar pattern, but sediment alone does not explain faunal distributions. Adjacent beaches (Alki South/Alki North and White Rock/Crescent Beach) have most similar fauna, but their sediments may have different characteristics. For example, the sediment of White Rock is most similar to that of Hornby Island. Water circulation inside and outside of Puget Sound, which must control the distribution of planktonic larvae and perhaps the dispersal of adults, is probably an important influence on community composition.

The False Bay community differs substantially from the other associations sampled, having both a greater density of infauna and species not encountered elsewhere. Nothing which I measured can adequately explain this difference. Higher organic content of the sediment might account for greater faunal density, but although the percent organic carbon inside the sand dollar bed is higher at False Bay than at any other site, the organic content outside the bed is lower than that observed at many other locations (Table 1).

Although cluster analysis does not suggest a "sand dollar bed community", analyses of variance show that several species are significantly ($P < 0.01$) more abundant outside the sand dollar beds, while one species is more numerous inside the beds. Species more abundant outside the beds include the bivalve *Transennella tantilla,* the tubicolous crustaceans *Corophium* spp., *Ampelisca agassizi,* and *Leptochelia savignyi,* and the polychaetes *Glycinde polygnatha* and *Malacoceros arenicola,* while the polychaete *Armandia brevis* is more numerous among the sand dollars.

The Shannon-Wiener diversity, equitability and the number of species encountered are not significantly different inside and outside sand dollar beds. However, the

Table 3. Species diversity (H') characteristics inside (+) and outside (−) 10 sand dollar (*Dendraster excentricus*) beds. Eq. Equitability; indiv.: individuals

Location		H'	Eq.	No. of spp.	No. of indiv.
Tolmie State Park	+	2.6595	0.7689	11	50
	−	3.1151	0.8183	14	151
Puget City	+	2.4352	0.8119	8	24
	−	3.0943	0.7737	16	81
Alki South	+	3.4328	0.7142	28	194
	−	2.8962	0.6595	21	556
Alki North	+	3.3072	0.8467	15	59
	−	3.7469	0.8404	22	106
Buck Bay	+	1.3403	0.3215	18	401
	−	2.9166	0.6362	24	331
False Bay	+	2.1087	0.4663	23	7 053
	−	2.7567	0.5799	27	3 702
White Rock	+	3.4021	0.8010	19	70
	−	1.9679	0.7011	7	30
Crescent Beach	+	2.8180	0.6417	21	515
	−	2.9316	0.6482	23	342
Qualicum Beach	+	3.0593	0.8037	14	63
	−	3.2555	0.8334	15	93
Hornby Island	+	1.2680	0.4906	6	35
	−	1.5816	0.4990	9	80

Table 4. Comparison of tube builder and motile crustacean population densities inside (+) and outside (−) sand dollar (*Dendraster excentricus*) beds of varying densities. Sand dollar counts are means ± standard errors of adults per 0.25 m^2. Tube builder and crustacean densities are means ± standard errors of animals per 0.01 m^2

Location		Sand dollars	Tube builders	Motile crustaceans
Tolmie State Park	+	32.8± 5.9	0	6.0± 2.5
	−	0	4.7± 3.3	12.7± 3.8
Puget City	+	123.6±29.2	0	0.7± 0.3
	−	0	11.0± 6.4	3.0± 1.0
Alki South	+	93.2± 9.4	13.0± 7.5	36.0± 7.1
	−	0	63.0± 14.8	97.3± 17.8
Alki North	+	36.2± 5.5	1.0± 1.0	6.0± 2.3
	−	0	6.3± 2.3	6.0± 2.6
Buck Bay	+	59.4±10.9	1.3± 0.7	5.3± 0.7
	−	0	87.0± 53.6	5.0± 1.2
False Bay	+	2.7± 0.4	76.3± 31.0	2 121.7±642.3
	−	0	394.7±149.0	782.0±353.1
White Rock	+	1.0± 0.4	11.0± 2.6	1.0± 0.6
	−	0	3.7± 2.2	1.3± 0.3
Crescent Beach	+	4.8± 1.4	5.3± 0.9	81.0± 13.2
	−	0	45.3± 14.2	32.0± 6.1
Qualicum Beach	+	21.4± 6.0	1.0± 0.6	3.3± 0.7
	−	0	8.0± 3.5	6.0± 1.0
Hornby Island	+	41.0±10.8	0	1.3± 0.6
	−	0	1.0± 1.0	4.3± 0.3

diversity and number of species are lower inside than outside the beds at all sites except Alki South and White Rock (Table 3).

Analysis of variance showed that the density of tube builders was significantly ($P < 0.05$) lower inside than outside the sand dollar beds. The overall density of tube builders varied significantly among beaches. The interaction was significant because more tube builders were encountered inside than outside the sand dollars bed at White Rock (Table 4). Density of motile crustaceans inside and outside the beds showed no difference, although the density of crustaceans was significantly different among beaches, and the interaction was significant due to the large numbers of crustaceans in the sand dollar beds at False Bay and Crescent Beach.

Discussion

In the one previous study of the fauna associated with *Dendraster excentricus* beds, Merrill and Hobson (1970) found no animals endemic to the subtidal, outer coast sand dollar beds of southern California, but they listed species which were recurrent in and characteristic of the beds. Most of the species more numerous inside than outside the beds were fish or crustaceans. Merrill and Hobson felt that some organisms occurred in the beds because the sand dollars stabilized the substrate by curtailing the erosion of sand and also provided shelter from predators. The results of the present study differ in some respects from those of Merrill and Hobson. I found no species which seemed characteristic of sand dollar beds, but the polychaete *Armandia brevis* was significantly more numerous in the beds than in adjacent areas (Table 2). The total number of crustaceans (excluding tubicolous forms) was not greater in the beds than in the adjacent substrate at most of the beaches (Table 4).

The chief reason for the difference between the present results and those of Merrill and Hobson (1970) is that I sampled intertidal rather than subtidal sand dollar beds. Since the sampling was done at low tide, fish and possibly motile crustaceans which might take refuge among submerged and inclined sand dollars could not be present. In addition, intertidal sand dollars, which burrow at low tide and position themselves with their tests inclined above the sediment surface at high tide, probably do more to destabilize the sediment than to stabilize it. The repeated burrowing and inclining of intertidal sand dollars must frequently overturn the sediment, and sedentary tube-building organisms should find it difficult to coexist with sand dollars.

At White Rock, more tube builders were collected near the sand dollars than away from them. However, at this location there were only 4 specimens of *Dendraster excentricus* m^{-2}, the lowest density encountered at any site. So few sand dollars apparently has no adverse effect on tube-building organisms.

Diversity, equitability and the number of species present were not significantly different inside and outside the sand dollar beds. Since the total number of animals collected at some of the sites was low, the validity of the *t*-statistic for comparing diversities is questionable (Hutcheson, 1970), and attempts to base any conclusions on the diversity values are risky. However, diversities and numbers of species present were lower inside than outside the beds at all sites except White Rock, where the sand dollar population is probably too low to have any effect on diversity, and at Alki South (Table 3). Thus, there is some suggestion that fewer species are able to coexist with sand dollars, resulting in lower species diversities in sand dollar beds.

Previous studies have considered benthic communities mechanically disturbed by epifaunal burrowers. Fewer species have been encountered in areas disturbed by rays, crabs and moon snails than in undisturbed sites (Orth, 1977; Virnstein, 1977; Woodin, 1978; Wiltse, 1980). Wiltse (1980) attributed the lower diversities in snail enclosures to the loss of small tube-building polychaetes, particularly spionids. Similarly, exclusion of tubicolous organisms (including the spionid *Malacoceros arenicola*) may reduce the diversity of infauna in sand dollar beds.

Tube-building organisms may limit the distribution of sand dollars by ingesting their larvae (Highsmith, 1977). Conversely, epifaunal burrowers, in general, and specifically *Dendraster excentricus*, can restrict the distribution of tube builders by mechanically disrupting the sediment (Brenchley, 1978). Thus, Brenchley has predicted spatial separation of motile burrowers from sedentary tube builders. The foregoing observations provide field evidence that the predicted separation occurs.

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