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Larvae in Predator-Free sites: Adult Sand Dollar Beds**

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INDUCED SETTLEMENT AND METAMORPHOSIS OF SAND DOLLAR (*DENDRASTER EXCENTRICUS*) LARVAE IN PREDATOR-FREE SITES: ADULT SAND DOLLAR BEDS¹

RAYMOND C. HIGHSMITH

Friday Harbor Laboratories, University of Washington, Friday Harbor,
Washington 98250 USA and Department of Zoology, University of Washington,
Seattle, Washington 98195 USA

Abstract. *Dendroaster excentricus* larvae capable of metamorphosis presented with various substrates show a significant preference for adult-associated sand. Adult *D. excentricus* produce a chemical cue, possibly a small peptide (molecular mass < 10,000), that is sequestered by some component in the sand and that is stable for at least 7 wk. Thus, larval settlement occurs within or adjacent to existing sand dollar beds which often contain several hundred adults per square metre. Experimental evidence indicates survival of newly metamorphosed *D. excentricus* is significantly reduced by an extremely abundant, tube-building predator, *Leptochelia dubia* (Crustacea: Tanaidacea). Tanaidacean and possibly other micropredators, however, are excluded from sand dollar beds by the reworking activities of adult sand dollars. Thus, preferential settlement of *D. excentricus* larvae near adults of the species should result in increased larval and juvenile survival.

Key words: *Dendroaster*; intertidal; larva; *Leptochelia*; metamorphosis; patchy; predation; Puget Sound; sand dollar; soft bottom; Tanaidacea.

INTRODUCTION

The sand dollar, *Dendroaster excentricus* (Eschscholtz), occurs in dense clumps or aggregations of up to several hundred individuals per square metre in sandy, shallow-water habitats along the west coast of North America (e.g., Chia 1969, Merrill and Hobson 1970, Birkeland and Chia 1971, Parks 1973, Celmer 1975, Niesen 1977). In the Puget Sound region, records indicate that intertidal sand dollar beds persist at the same location for at least several decades (Birkeland and Chia 1971, P. Illg, *personal communication*), much longer than the typical maximum 8–9 yr life span of individuals (Birkeland and Chia 1971, Celmer 1975). Yet there are also many apparently suitable locations that are unoccupied by sand dollars, even large stretches of seemingly identical beach adjacent to existing beds (C. Birkeland and K. E. Mesmer, *personal communication*). This patchy distribution could be due either to differential survival or to larvae settling preferentially in locations occupied by adults. In this paper I report a test of the latter possibility showing that the clumped distribution results from a complex set of interactions between adults and larvae of *D. excentricus* and between adults and a predator on the larvae.

METHODS

This study was conducted at the Friday Harbor Laboratories of the University of Washington, San Juan Island, Washington, USA.

Gametes were obtained by injecting adult sand dollars with 2–3 mL of 0.55 mol/L KCl and placing them aboral surface down on a chilled Syracuse dish. One drop of sperm was suspended in 50 mL of filtered sea water and added to ≈800 mL of filtered sea water containing the eggs of one or occasionally two females. At gastrulation, the cultures were switched to 3.8 L jars and fed daily with *Dunaliella tertiolecta* Butcher, *Phaeodactylum tricornutum* Bohlin, and *Isochrysis galbana* Parke. The sand dollar cultures were stirred continuously and were maintained in a running seawater bath so that temperatures in the culture vessels (≈11–14°C) were similar to those experienced by larvae in nature. The time from fertilization to capability to metamorphose ranged from 3–8 wk with 5–6 wk most common. Initially, competence to metamorphose was determined by inspecting eight-armed larvae with opaque, golden-yellow gut regions for the presence of tubefeet and spines (see Chia and Burke 1978: Fig. 3a). As experience was gained, a direct test of ability to metamorphose was conducted by placing a few larvae in a bowl containing a substrate (see Results) known to stimulate settlement and metamorphosis.

Adult sand dollars and associated sand were collected intertidally at Ship's Bay and Buck Bay, Orcas Island. Tanaid collections and/or density measurements were made at both of these locations plus Shoal Bay, Lopez Island, and at False Bay and Argyll Lagoon, San Juan Island. Procedures employed in the various experiments are given with the results for each.

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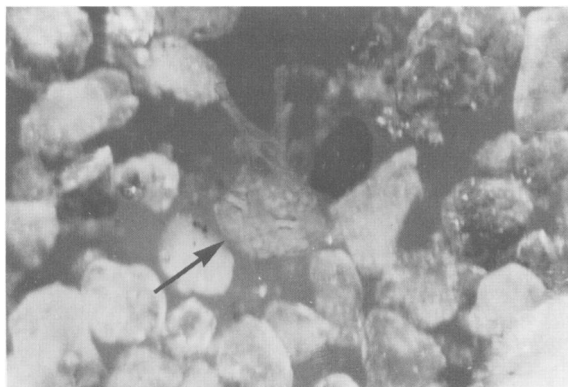


FIG. 1. Pluteus larva of *Dendraster excentricus* just prior to metamorphosis among sand grains. Total length of larva $\approx 750 \mu\text{m}$. Note adult rudiment in gut region.

LARVAL SETTLEMENT AND METAMORPHOSIS

Substrate preference

To test for differential settlement, larvae competent to metamorphose (Fig. 1) were placed in glass bowls containing different substrates (10 larvae per bowl, three bowls per treatment) ranging from filtered seawater only to an adult sand dollar with sand (Table 1). Significantly more metamorphosis occurred in bowls with substrates associated with adult sand dollars (treatments C, D, E, and F) than in either of the controls (treatments A and B; $P < .001$, χ^2 tests). In addition, there was significantly more metamorphosis in bowls with sand collected from a dense aggregation of adults (treatment D) than in bowls containing a portion of the same sand that had been baked in an oven prior to the experiment (treatment G; $P < .001$, χ^2 test). The combination of treatments F and G indicates that the cue for larval settlement and metamorphosis is a heat-labile substance produced by adults and that substrate texture is not a factor in the response. The experiment was allowed to run for 25 d, except for F where results were immediately obvious, to see how long metamorphosis would be delayed in the absence

of an appropriate cue. During this period the bowls were not disturbed in order to search for new juveniles, but I examined the water in the bowls and found that most (21–30) of the larvae in treatments C, D, and E were no longer visible in the water column within 12 h, whereas only a few (0–7) larvae had disappeared in treatments A, B, and G. The data in Table 1 represent individuals actually recovered at the end of the experiment. This experiment clearly demonstrates that larvae settle preferentially on substrates associated with adults due to some factor produced by the adults and that the larvae will delay metamorphosis for 25 d or more in some cases if such substrates are not present. The settlement cue is destroyed by heating.

Sequestering agent on sand

Treatments B and D were repeated (Table 2) and, as before, there was significantly greater metamorphosis in sand collected within a sand dollar bed (treatment H) than in sand collected where there were no sand dollars (treatment I; $P < .001$, χ^2 test). In addition, I rinsed an adult sand dollar with filtered seawater and placed it in a bowl of nonadult sand (from the same lot as used in treatment I) for 20 h, drained the bowl, and distributed portions of the sand among three bowls with filtered seawater and added 10 larvae per bowl (treatment J). Nearly all of the larvae metamorphosed within 20 h (Table 2), providing further evidence that the factor inducing settlement is produced by adults. However, if the sand is baked first (as in treatment G) and then placed with an adult for 20 h followed by 30 min of rinsing in gently flowing seawater, it does not induce settlement (Table 2, treatment K; $P < .001$, χ^2 test). The control sand (H) was also rinsed but did not lose the adult factor. Thus, it appears that an organic entity, possibly living, on or among the sand grains sequesters or concentrates the adult factor.

Dialysis experiment

The substance that induces settlement in larvae of the regular urchins *Arbacia punctulata* and *Lytechinus*

TABLE 1. Number of *Dendraster excentricus* larvae metamorphosing or remaining as plutei out of 30 larvae per treatment. Sand was collected from beach areas where there were no adult sand dollars (B), only 10–15 adults/m² (C), or >300 adults/m² (D).

| Treatment | No. larvae | | | Time (d) |
|--------------------------------------|----------------|--------|---------|----------|
| | Meta-morphosed | Plutei | Missing | |
| A. Filtered seawater | 11 | 15 | 4 | 25 |
| B. Sand—no adults | 1 | 11 | 18 | 25 |
| C. Sand—low-density adults | 17 | 0 | 13 | 25 |
| D. Sand—high-density adults | 22 | 0 | 8 | 25 |
| E. Adult plus sand from D* | 18 | 0 | 12 | 25 |
| F. Adult only | 25 | 1 | 4 | 1 |
| G. Sand from D baked at 150°C (12 h) | 4 | 20 | 6 | 25 |

* Adult removed after 2.5 d.

TABLE 2. Number of *Dendraster excentricus* larvae metamorphosing or remaining as plutei out of 30 larvae per treatment. Sand was collected from beach areas where there were >300 adults/m² (H) or no adult sand dollars (I).

| Treatment | Meta- morphosed | Plutei | Time (h) |
|---|--------------------|--------|-------------|
| H. Sand—high-density adults | 26 | 4 | 20 |
| I. Sand—no adults | 9 | 21 | 20 |
| J. Sand from I placed with adult for 20 h | 26 | 4 | 20 |
| K. Sand from H, baked, then placed with adult for 20 h, then rinsed | 2* | 34 | 3.5 |

* Out of 36 (12 per bowl).

nus pictus, probably has a molecular mass of 5000 or less (Cameron and Hinegardner 1974). To see if the factor inducing sand dollar settlement was also of low molecular mass, an experiment was conducted using dialysis tubing (average pore size = 2.7 nm) through which only molecules of molecular mass <10 000 can diffuse.

The tubing, 1 cm wide when flat, was placed in filtered seawater and brought to a boil twice to eliminate contaminants. Sections of tubing were packed for a length of \approx 5 cm with sand from a sand dollar bed. The sections were securely tied at the ends, rinsed thoroughly with filtered seawater, and placed in each of three bowls containing filtered seawater. For controls, an equal mass of loose sand from the same lot was placed in each of three bowls. In addition, equal lengths of similarly prepared dialysis tubing were placed in each of three bowls with filtered seawater. Ten larvae were added to each bowl. The number of larvae metamorphosing in bowls with sand-filled dialysis tubes was not different from that in bowls with loose sand (Table 3); none metamorphosed in bowls with tubing only. The more rapid response to the sand-filled tubes may have been due to a concentration gradient resulting from diffusion of the adult factor through the tubing. The behavior of the larvae suggests they can detect this gradient because they tend to move toward the tube and to spend a large proportion of their time near it. All but three of the larvae that metamorphosed settled within 1 cm of the tube (often under it) and none settled $>\approx$ 2 cm away; no larvae settled directly on the tube. I have subsequently used the dialysis tube method many times to obtain juveniles and the settlement pattern is invariably the same. Some individuals even initiate metamorphosis within 10–20 min of their addition to the bowl. Clearly, the substance that induces larval settlement and metamorphosis has a low molecular mass. Larval settlement in these clean bowls within a few minutes after introduction further indicates that surface textures or films are not directly involved in the settlement response.

TABLE 3. Cumulative number of *Dendraster excentricus* larvae metamorphosed out of 30 larvae per treatment. Sand is from a high-density aggregation of adult sand dollars; 10 larvae per bowl, three bowls per treatment. See text.

| Treatment | Cumulative time (d) | | |
|-----------------------|---------------------|----|----|
| | 1 | 3 | 7 |
| Sand in dialysis tube | 13 | 16 | 17 |
| Loose sand | 5 | 7 | 20 |
| Dialysis tube only | 0 | 0 | 0 |

Enzyme experiment

An interesting benefit resulting from diffusion of the settlement cue through dialysis tubing is that sand can be treated with various enzymes, which are too large to pass through the tubing, without risk of direct effects on the larvae. A preliminary experiment using this method was conducted to see if the substance inducing larval settlement is a peptide. A sand slurry was collected from around adult sand dollars and divided into three 10-mL portions. I added 1 mg trypsin, which cleaves only those linkages whose carbonyl group is contributed by either arginine or lysine (Lehninger 1970) to one portion and 0.5 mg pronase, which cleaves all peptide linkages, to a second portion. The third portion served as a control. All three were stirred every 10–15 min for 2 h, while remaining at room temperature. An equal amount of each slurry was placed in dialysis tubing. After rinsing, each tube was added to a bowl of filtered seawater and 20 larvae introduced. A bowl of filtered seawater only was used as an additional control. There was significantly less metamorphosis in the bowl with pronase-treated sand ($P < .025$) than in either the control sand or trypsin treatment bowls (Table 4). Still, significantly more larvae metamorphosed in the pronase treatment bowl than in the filtered seawater bowl ($P < .005$; χ^2 tests). Supplemental experiments with various enzyme concentrations, other enzymes, and antibiotics (see section on sequestering agent) will be necessary but the results indicate that this method is workable and suggest the tentative hypothesis that the settlement cue may be a small peptide lacking bonds in which arginine or lysine donate the carbonyl function.

TABLE 4. Number of *Dendraster excentricus* larvae metamorphosed 20 h after introduction to treatment bowls. See text.

| Treatment | No. larvae | |
|-------------------|---------------|--------|
| | Metamorphosed | Plutei |
| Sand—control | 15 | 5 |
| Sand + trypsin | 15 | 5 |
| Sand + pronase | 8 | 12 |
| Filtered seawater | 0 | 20 |

TABLE 5. Cumulative number of *Dendraster excentricus* larvae metamorphosed (out of 30) 3 d after introduction to sand isolated for 7 wk and 14 wk. Fresh sand = control. Ten larvae per bowl, three bowls per treatment. See text.

| Treatment | 7 wk | 14 wk |
|---------------|------|-------|
| Fresh sand | 9 | 16 |
| Isolated sand | 9 | 3 |

Isolated sand experiment

To determine approximately how long sand isolated from adult sand dollars will retain the factor that induces larval settlement and metamorphosis, isolated sand was tested after 7 wk and again after 14 wk. For storage, the sand was placed in a beaker and the water poured off. The beaker was covered with parafilm secured with a rubber band and placed in a refrigerator where it was exposed to light only when the door was opened. The isolated sand induced metamorphosis as effectively after 7 wk as fresh sand (Table 5) but after 14 wk the isolated sand was largely ineffective ($P < .025$, χ^2 test). For unknown reasons the larvae used in these tests were less responsive than usual to fresh sand, but there is a clear difference between the 7-wk test and 14-wk test.

PREDATION ON SETTLING LARVAE AND JUVENILES

Introduction and hypotheses

Larvae or newly metamorphosed juveniles of *Dendraster excentricus* disappeared from some of the experimental bowls, especially treatment B (Table 1), so I conducted a few simple tests to see if predators were present in the sand. Gammarid amphipods, the holothurian *Leptosynapta clarkii*, and a small (3–4 mm) crustacean in the order Tanaidacea, *Leptochelia dubia* (Kröyer 1842) (synonymous with *L. savignyi*) were found in treatment B sand. I placed 4–6 individuals of each in separate bowls and added ≈ 20 sand dollar juveniles. After 6 d, all juveniles in the amphipod and holothurian bowls were still present but only 3 of 19 juveniles remained in the bowl with tanaids.

Tanaids are in the superorder Peracarida and brood their young (≈ 32 per clutch for *Leptochelia dubia*) until they are large enough to crawl away. Male *L. dubia* do not have functional mouth parts and do not feed (Richards 1969, Smith and Carlton 1975) but *L. dubia* populations are composed almost entirely ($>90\%$) of females (Smith 1906, Lang 1953, Richards 1969, E. Caine, *personal communication*, R. C. Highsmith, *personal observation*). This skewed sex ratio is apparently maintained by a form of protogyny in which females will not molt into a male unless the ratio of females to males in the immediate vicinity is approximately 10:1 or greater (R. C. Highsmith, *personal observation*).

The preliminary indication that tanaids prey on very

young sand dollars was particularly interesting because tanaids have a hydrophobic (nonwetting) exoskeleton and must secrete mucous tubes, to which they attach sand grains, for stability and to keep from being trapped on the water surface following ebb tide and thus being wafted away. This raised the possibility that tanaids were not able to persist in sand dollar beds because sediment reworking by the adult sand dollars would disrupt their tubes. This would account for the selective pressure making it advantageous for larvae to metamorphose in or near existing *Dendraster* populations, and would also explain why sand dollars evidently are seldom successful in colonizing new locations. The following experiments were conducted to test the hypotheses that (1) the tanaid, *Leptochelia dubia*, preys on settling and recently metamorphosed sand dollars, and that (2) *L. dubia* population densities are reduced in and around sand dollar beds.

Tanaid predation

Sand was placed in an oven at 110°C for 3.5 h to assure that no other predators were present. This sand was placed in each of six bowls with filtered seawater and 12 juvenile sand dollars that had metamorphosed in the previous 1–2 d were added to each. To control for tanaids preying upon sand dollar juveniles because no other live food items were present in the baked sand, freshly collected sand from a location (False Bay) with high tanaid densities was placed in an additional three bowls. From five to seven tanaids, but not less than five females (males do not feed), were placed in each of the fresh sand bowls and in three of the baked sand bowls. This is equivalent to a tanaid density of $2200/\text{m}^2$, considerably lower than densities typically found in the field (see below). Without disturbing the sand and hence the tanaid tubes, I periodically attempted to count the number of live juveniles remaining in each bowl. After 6 d, the sand was thoroughly searched for juveniles. There were significantly more juvenile sand dollars remaining in the bowls without tanaids than in either treatment with tanaids ($P < .001$, χ^2 test; Fig. 2).

To supplement the experimental evidence that tanaids kill juvenile sand dollars, I placed juveniles in bowls with several female *L. dubia* (Fig. 3) and enough sand for the tanaids to make normal tubes (tanaids out of their tubes are awkward, clutch at anything, and usually end up trapped on the water surface) but not enough to shield the animals from view. Typically, a tanaid will take juvenile sand dollars that come close enough to be grasped without the tanaid extending more than approximately two-thirds of its body length out of the tube. The juvenile is picked up with the chelipeds and pulled to the tube entrance or even into the tube. Holding the juvenile by a spine or two in one cheliped, the tanaid pulls off or breaks other spines and eventually breaks open the test and eats

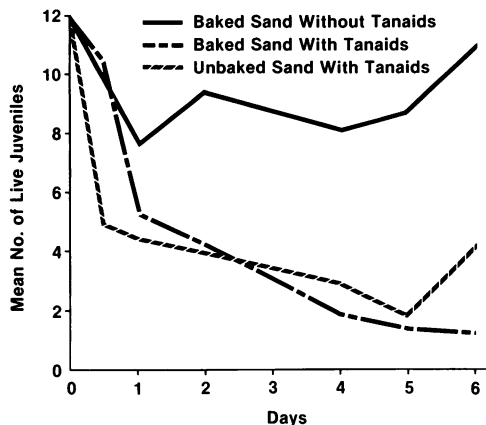


FIG. 2. Mean number of live juvenile *Dendraster excentricus* in bowls with and without the tanaid, *Leptochelia dubia*. See text.

the contents (Fig. 4). Usually, 3–7 min are required to subdue and eat a juvenile.

Eight juveniles ranging in size from 1.5 to 3.0 mm in length including spines (1.0–2.4 mm test length) were placed in a bowl with 12 female tanaids. After 9 d, all of the juvenile sand dollars were still present. Thus, when juveniles reach ≈ 1.5 mm in total length tanaids are no longer able to prey on them successfully. Attacks were observed, resulting in a few (6–10) damaged spines, but the test appeared to be too large to be gripped and fractured in the chelipeds. These larger juveniles were strong enough to pull away eventually and escape.

I conclude from these experiments and direct observations of predation that *Leptochelia dubia* preys on juvenile *D. excentricus* $< \approx 1.5$ mm in length. Thus, if growth in the field is similar to growth in the laboratory, newly settled sand dollars are subject to tanaid

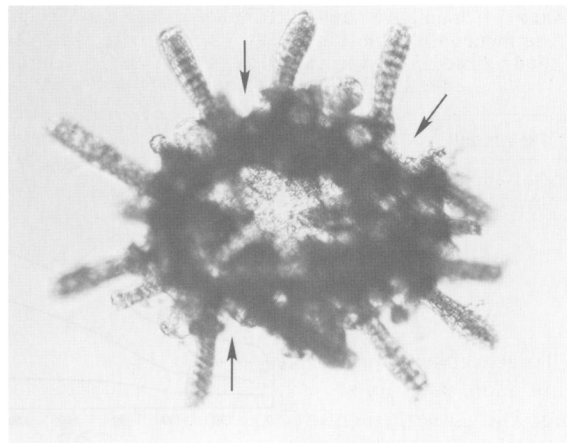


FIG. 4. Back-lighted view of juvenile *Dendraster excentricus* showing damage to test (arrows) resulting from an attack by a female *Leptochelia dubia*.

predation for approximately 3–4 mo (Fig. 5) before reaching an escape in size.

Tanaid distribution relative to sand dollars

Two approaches were used to test the hypothesis that adult *D. excentricus*, in high densities, exclude *Leptochelia dubia* from the same location. First, tanaid population densities within sand dollar beds, near beds (1–10 m away), and far (>10 m) from beds or where there are no beds, were compared. Second, an experiment was conducted to see if sand dollars eliminate tanaids directly. In the first approach, sand was collected from 100-cm² quadrats to a depth of ≈ 2 cm and placed in labeled bottles. In the laboratory, filtered seawater was added and the bottle recapped and shaken vigorously. The contents were then poured into a low, flat dish for sorting. As a result of the shaking a large proportion of the tanaids were trapped on the water surface because of their nonwetting exoskeleton. After these individuals were skimmed off, the sand was agitated vigorously with a probe to bring remaining tanaids to the surface. Counting stopped when no further tanaids were produced during a 2-min period of continuous agitation.

Tanaid densities were, as predicted, much lower in and near sand dollar beds (Table 6), where most quadrat totals were zero, than in locations where sand dollars were absent. Males, as noted earlier, do not feed, but they constitute $<10\%$ of the population.

In the second approach, sand with a mean density of 19 600 tanaids/m² (four quadrats, range = 9400 to 40 500) was collected and placed in each of two aquaria. A central divider was placed in each aquarium and water supplied to both sides (9 \times 20 cm each) from the same outlet by inserting a Y-tube in the hose. Twelve adult sand dollars, equivalent to 300 sand dol-

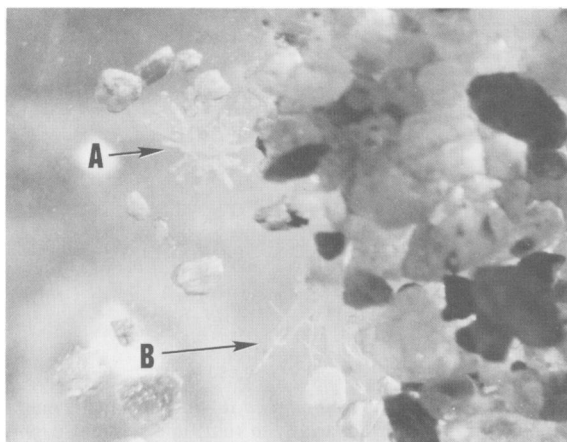


FIG. 3. Newly metamorphosed sand dollar (A) near tube of a female *Leptochelia dubia* (B).

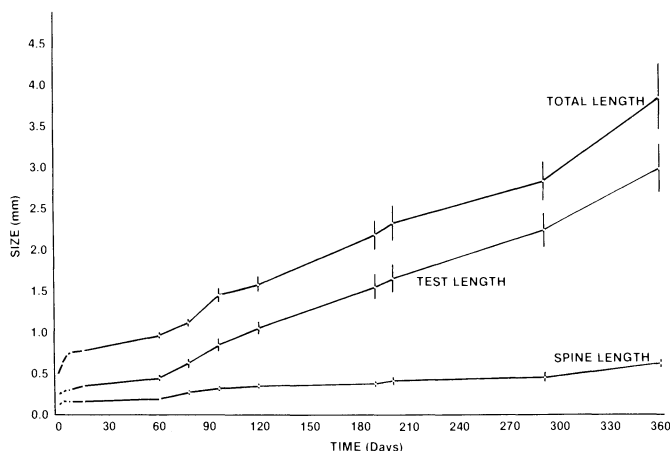


FIG. 5. Mean sizes of eight juvenile *Dendraster excentricus* maintained in the laboratory for 1 yr following metamorphosis in August. Mean spine length was determined by measuring four of the longest spines on each individual. Standard error indicated by vertical bars. The standard error did not exceed line width at points without vertical bars.

lars/m² (Celmer [1975] found mean densities of 350 and 390 sand dollars/m² at Ship's Bay and Buck Bay, respectively), were added to one side of each aquarium. After 16 d, the sand dollars were removed, the sand in each half of the aquaria divided into four samples, and the tanaids counted as previously. Tanaid densities were significantly lower in the portions of the aquaria with sand dollars (Fig. 6). Though not quantified, the reduction in number of small tanaids (<3 mm length) was particularly noticeable in the sand dollar sides.

The sampling data and the experimental results indicate that sand dollars in high densities do reduce or eliminate *Leptochelia dubia* populations. In addition, sand dollars around the edge of beds often move about in the adjacent sand at a rate of 1–2 m/h (Merrill and Hobson 1970, R. C. Highsmith, *personal observation*) stirring up sand in their path (Fig. 7). This type of disturbance, which is sufficient to disrupt tanaid tubes, plus retention of the settlement cue in the sand for several weeks (Table 4) suggests that areas near sand dollar beds may also be both attractive and relatively safe for larval settlement.

Discussion

The results show that *Dendraster excentricus* larvae settle and metamorphose in response to a low molec-

ular mass (<10 000) chemical cue produced by adults of the species. In nature, this response should result in preferential settlement of larvae in and near established sand dollar beds. Birkeland and Chia (1971), working in Puget Sound, found mean densities of 214 sand dollars/m² (range 0 to 629) at South Alki Beach and only 3 individuals/m² (range 0 to 86) at North Alki Beach, although growth rate data indicated that the latter was possibly a more favorable location for adults. Thus, they concluded that juvenile mortality rates must be higher for some reason at North Alki than at South Alki. C. Birkeland (*personal communication*) has since found significantly greater recruitment where adults are present. At North Alki, recruitment occurred in 12 of 13 quadrats (0.125 m²)

TANAIDS PER m² IN EXPERIMENTAL AQUARIA

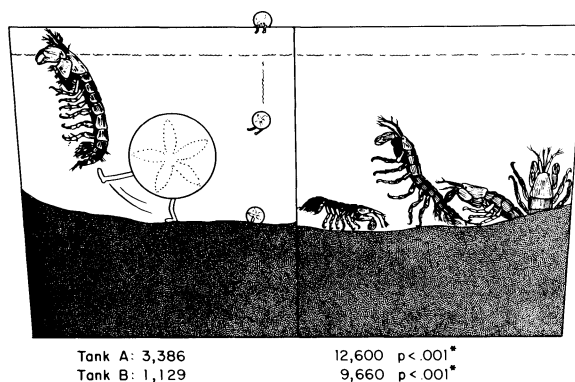


FIG. 6. Number of *Leptochelia dubia* per square metre remaining in sides of aquaria with (left) and without (right) sand dollars. Note that a large female tanaid is ≈ 4 mm in length and an adult sand dollar is ≈ 7 –8 cm across. Probabilities are for a χ^2 test with 1 df.

TABLE 6. *Leptochelia dubia* densities per square metre: in, near, and far from sand dollar beds. *N* = number of quadrats.

| Location | \bar{x} | Range | <i>N</i> |
|------------------------------------|-----------|--------------|----------|
| In bed | 56 | 0–500 | 18 |
| Near (≈ 1 –10 m from bed) | 272 | 0–2100 | 18 |
| Far (>10 m or bed not present) | 56 500 | 5400–213 000 | 16 |

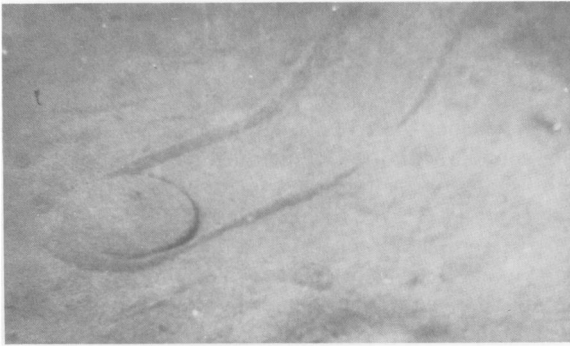


FIG. 7. Adult *Dendraster excentricus* moving through sand near a sand dollar bed.

containing adults but only in 10 of 18 quadrats without adults ($P < .05$, χ^2 test). In another bed at Dye's Inlet (Bremerton), similar measurements revealed recruitment in 7 of 8 quadrats with adults and in only 1 of 6 quadrats without adults ($P < .025$, Fisher Exact Probability test). Further, C. Birkeland and K. E. Mesmer (*personal communication*) transplanted ≈ 5000 adult sand dollars to a beach without sand dollars, and both 11 and 23 mo later, significantly greater recruitment had occurred among the transplanted adults than at nearby locations on the beach. Thus, field data presently available on sand dollar recruitment support the experimental data.

The discrete boundaries of beds (e.g., Merrill and Hobson 1970) suggest that adult sand dollars have some means of remaining aggregated. In addition, Birkeland and Chia (1971) placed 50 adults, scattered more or less uniformly, in a 4-m² enclosure, and the sand dollars eventually aggregated into a clump covering only about 35 cm². Celmer (1975) also found that adults spaced uniformly in a sand-bottomed sea table would form an aggregation within 12 h. To test the possibility that sand dollars produce and respond to a concentration gradient of some chemical released into the water, Celmer (1975) conducted a Y-maze choice experiment, but the sand dollars exhibited no preference for the arm carrying water that had just passed through a tank containing 100 adults. However, when one-half of a sea table was lined with sand from a bed and the other half covered with sand collected just 0.5 m away from the same bed (Buck Bay), 57 of 60 adults, uniformly distributed at the start, moved to the side with sand from the bed (Celmer 1975). This experiment was replicated with a similar result. Celmer's work suggests that *Dendraster* responds chemotactically to a substance released into and retained in the sand. This would be a far more reliable and stable (judging by the isolated sand experiment, Table 4) means of communication than releasing a pheromone into the water column. Possibly the substance to which adults respond is the same one that induces larval settlement and metamorphosis.

There are many predators in soft-bottom habitats and further work will surely show that tanaids are not the only predators on sand dollar recruits. Similarly, sand dollars are not the primary food of female tanaids. Identifiable material in several fecal samples and one gut sample consisted almost entirely of diatom frustules, perhaps gleaned from the sand grains used by the tanaids to extend their tubes. I have also observed diatom grazing by young tanaids that had not yet constructed tubes large enough to conceal their activities. It also seems likely that tanaids will prey on a variety of other larval forms encountered. G. Gallagher and P. Jumars (*personal communication*) have found immunological evidence that *Tanais* sp. preys on larvae of the phyllodocid polychaete *Eteone*. Where they occur in high densities, tanaids must have an extremely important effect on recruitment of other species.

GENERAL DISCUSSION

Preferential larval settlement in response to a particular substrate has been demonstrated in a number of marine invertebrates, e.g., barnacles (Crisp 1979), serpulid polychaetes (Knight-Jones et al. 1971), echinoids (Caldwell 1972, Cameron and Hinegardner 1974), asteroids (Birkeland et al. 1971), and preferential settlement near adults of the same species has been reported also, e.g., the brittle star *Ophiothrix fragilis* (Warner 1971), the oyster *Crassostrea virginica* (Crisp 1967), the polychaetes *Sabellaria alveolata* (Wilson 1968) and *Ficopomatus uschakovi* (as *Mercierella enigmatica*; Straughan 1972), but this is the first experimental demonstration of the specific benefit of larval substrate selection in a soft-bottom habitat: avoidance of an extremely abundant predator. Woodin (1976) proposed that the sharp boundaries between various infaunal assemblages were a result of the negative influence of resident adults on settlement of larvae, especially those produced by other assemblages. Although predation on settling larvae and postmetamorphic juveniles is thought to be an important means by which recruitment is prevented (Mileikovsky 1974, Woodin 1976), there are virtually no experimental data available on this point. In addition to the data presented above that tanaid predation may prevent sand dollar settlement in new locations, Woodin's (1976) hypothesis is supported by Wilson's (1980) experimental demonstration that the tube-building terebellid polychaete, *Eupolymnia heterobranchus*, significantly reduces survivorship of *Neresis vexillosa* larvae.

With respect to *Dendraster excentricus* excluding *Leptochelia dubia*, G. Brenchly (*personal communication*), in both laboratory aquaria and field enclosures, also found that sand dollars reduced the densities of various infaunal species including *Leptochelia dubia*. Generally, intertidal *Dendraster excentricus* populations, by reworking the sand while assuming a

vertical position during high tide and burying at low tide, probably exclude suspension feeders or other tube-building organisms, such as tanaids, which either require a stable substrate or stabilize the substrate by their own tube-building activities.

The effect of *Dendraster* suspension feeding (which in the Puget Sound region is limited to some fraction of the two high-water portions of the tidal cycle) on mortality of larvae attempting to settle is unknown. Woodin's (1976) hypothesis predicts that high densities of suspension feeders should, by their feeding activities, prevent virtually all larval settlement including larvae of their own species (see also Mileikovsky 1974). Timko (1979) reported that *D. excentricus*, positioned mouth-up in bowls, would ingest 3-wk-old sand dollar plutei placed on the oral surface. In the settlement experiment (Table 1), 30 larvae were placed in bowls with an adult (aboral surface up) and after 24 h, 26 (25 juveniles and 1 larva) were still present. In addition, I added 6 eight-armed larvae to a bowl containing an adult lying obliquely on its oral surface and followed them individually. In three cases there was no contact between the larvae and adult. In the other cases, where a larva landed on the adult near a food groove, the long tube-feet bordering the groove placed the larva in the groove where it remained for up to several minutes before being ejected by the shorter tube feet lining the groove. In one instance this sequence was repeated when the long tube feet contacted the larva once again. Timko (1979) stated the larvae in her experiment were ready to metamorphose as judged by arm movement, but in my opinion this by itself is not an adequate indication of readiness to metamorphose (see Chia and Burke 1978). As in regular urchins (Cameron and Hinegardner 1974), sand dollar larvae competent to metamorphose are capable of extending tube feet through the vestibule and attaching to the substratum. If metamorphosis ensues, attachment is followed by eversion of the adult rudiment and burial in the sand, even while the larval arms still project aborally (R. C. Highsmith, *personal observation*). These events can occur within a period of only 3–5 min (Chia and Burke 1978) or less (R. C. Highsmith, *personal observation*). Clearly, more work is needed using adults in a normal feeding position on a sand substrate and larvae capable of metamorphosis.

Larvae that are not exposed to sand dollar beds when they are ready to metamorphose eventually become less selective and will settle in other locations (Table 1). The work reported above suggests that, in the Puget Sound region, these larvae and juveniles are likely to be eliminated by *Leptochelia dubia*. New sand dollar beds probably arise when a large number of less selective larvae settle in a location where *L. dubia* densities have been reduced by disturbances such as storms. Tanaids probably recolonize disturbed locations rather slowly because the young are brooded (≈ 32 per clutch) for a period of ≈ 40 d until they are

able (at ≈ 1 mm length) to walk away from the parental tube and initiate their own tube system (R. C. Highsmith, *personal observation*).

Dendraster excentricus beds also occur on outer coast beaches (Merrill and Hobson 1971). These beds are subtidal with the location of their shoreward margin usually occurring just seaward of the breaker line (Merrill and Hobson 1970). Whether or not a system of preferential larval settlement, predation, and predator exclusion, such as described here for intertidal sand dollar beds in protected bays, determines the distribution of outer coast sand dollars remains to be determined.

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