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**SAND GRAIN ANGULARITY
AS A FACTOR AFFECTING COLONIZATION
BY MARINE MEIOFAUNA**

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ABSTRACT

Plexiglass tubes filled with sterilized sand of different angularities were buried at mean water level in a sandy estuarine beach on Long Island, New York. After 90 days the tubes were recovered and the meiofauna were separated from the colonized sand and enumerated by major groups. Organism variation and total numbers indicate that the meiofauna community more readily colonize tubes filled with sand having the most angularity. The greater angularity provides a greater environmental heterogeneity which would result in an increase in the number of habitats, provide more predator free space, build up greater food supplies, and afford more protection from particle abrasion than the rounder sands. Certain individuals such as copepods seemed to populate environments of intermediate angularity. A combination of factors such as body shape, lower permeability, and sharp edges on angular grains may have prevented population build up of these organisms in environments of greater angularity.

(*) Died, July 1977, Nahant, Mass. during SCUBA field research activities.

INTRODUCTION

Only recently have studies on community function and structure of marine benthos included a vital component of this ecosystem, the omnipresent meiobenthos. Studies of individual species are cited in some of the earliest scientific publications but because of the size of meiofauna (< 1 mm) and difficulties encountered in taxonomy, quantitative work on community ecology is comparatively recent (McINTYRE, 1969).

If the importance of the marine meiobenthos is to be fully understood, knowledge of its ecology must be thoroughly investigated. One factor which may effect meiofauna community ecology is habitat complexity. The interstitial ecology of these organisms is known to be influenced by sediment granulometry (COULL, 1970 ; HEIP and DECRAEMER, 1974 ; RENAUD-MORNANT, 1971 ; TIETJEN, 1969 ; WARWICK and BUCHANAN, 1970 ; WIESER, 1959, 1960). But these studies have considered mostly sand grain size as a factor affecting the community structure and little attention has been paid to the angularity of the sand grains which may play a greater role in spatial heterogeneity.

The present study was carried out in order to determine if the angularity of sand grains can influence the number and kinds of meiofauna living in the sediment. Since interstitial meiofauna can migrate freely in the sediment (BOADEN and PLATT, 1971 ; BUSH, 1966 ; HARRIS, 1972), a colonization experiment was established in a sandy beach. Previous colonization experiments involving interstitial fauna have been carried out with success by RENAUD-DEBYSER (1959, 1963), who demonstrated that interstitial organisms migrate in response to tidal movements of interstitial water and BOADEN (1962) and NAIR and GOVINDANKUTTY (1972) who showed that meiofauna selectively colonize buried, sand-filled tubes according to the size of sand within the tubes.

METHODS AND MATERIALS

THE PRELIMINARY SURVEY.

A private beach with little wave action on Baldwin Bay, Long Island, was used as the experimental site because it was relatively

undisturbed yet readily accessible at any time. A preliminary survey of the littoral zone using three vertical and three horizontal mean tide samples taken with 30 cm by 3.1 cm Lucite core tubes was carried out to determine relative numbers and types of organisms to be expected. In the laboratory the contents of each core was washed into an Erlenmyer flask with 100 ml of isotonic magnesium chloride solution, and allowed to stand undisturbed for one-half hour to anesthetize the organisms. Next, the organisms were stained for two hours with the addition of 10 ml of 0.1 percent rose bengal. Finally 110 ml of a 20 percent buffered formalin solution was added (thus making the contents of the flask a 10 percent solution of formalin) to preserve the animals.

The organisms were elutriated from the sediment as follows. First the contents of the flasks were gently swirled to suspend the meiofauna. Then the suspension was filtered through a 63 μ mesh net which retained the stained organisms with only a small amount of sediment. Five subsequent washings of the sediment followed. Thus, each sample was filtered and washed six times. The sixth washing was used as an arbitrary stopping point because a seventh washing resulted in the extraction of few and, often, no additional organisms. After washing into a counting dish, the fauna was enumerated and sorted to major taxon.

Additional cores were taken on the beach for sediment size analysis. Samples were taken to the laboratory where they were dried in an oven. Three weighed replicates were then sieved through a series of screens (4.76 mm to 0.10 mm) on a vibratory shaker for 5 minutes. The portion remaining on each sieve was weighed to 0.1 milligram to determine the size distribution of sand present on the beach.

Salinity of the overlaying water was measured using a refractometer.

THE FIELD EXPERIMENT.

Numerous sand samples were obtained from a number of locations throughout the New York and New England areas and analyzed for specific roundness according to POWERS (1953). This method involved assigning fifty grains to one of six classes by comparison with photographs. Average roundness of the sample was determined by multiplying the number of grains in each class by the geometric mean for each class (0.14 for very angular, 0.21 for angular, etc.) and dividing the sum of the products by the total number of grains analyzed for each sample. Three replicates for each type of sand were taken. The three sand samples most approximating each of the following classes were used in the experiment: (1) very angular to angular, (2) subangular to subrounded, and (3) rounded to well rounded.

The very angular to angular sand was obtained from a newly dug pit of glacial sand in West Boylston, Massachusetts. Subangu-

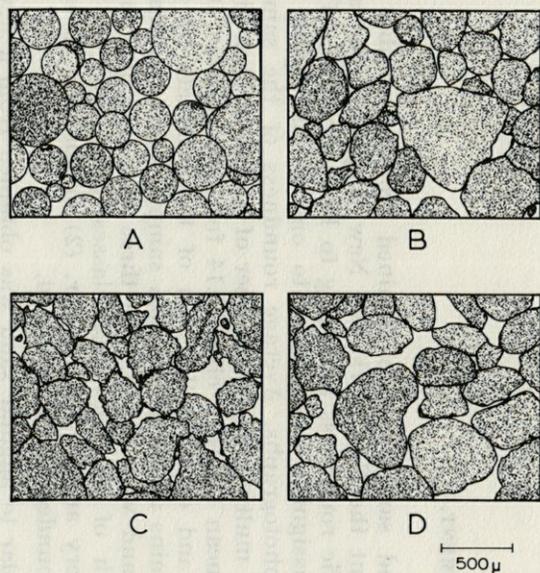
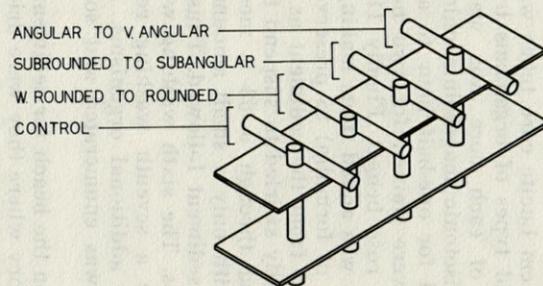


FIG. 1. — Line drawings taken from actual photomicrographs representing two dimensional views of the different roundness categories used in the experiment. Note especially the varying complexities of the interstitial space. A : glass beads; B : subrounded to subangular sand; C : angular sand; D : control sand from Baldwin Bay.

FIG. 2. — Design of the apparatus used to compare the attractiveness of the various sand roundness categories. Labels indicate the type of sand contained in each set of tubes on the frame. All tube diameters are 3.1 cm with lengths of 30.0 cm.



lar to subrounded sand was found on a beach in Glen Cove, New York. Glass beads, purchased from VWR Scientific, New York, were used to simulate the rounded environment.

Each of the roundness categories of sand was sorted for size by passing the sediment through a series of sieves and was later mixed in proportion to simulate the sizes of the sand found at the experimental site. Roundness values were again calculated. The very angular to angular sand had a roundness value of 0.215, that of the subangular to subrounded category was 0.380, and the glass beads came very close to the geometric mean of well rounded sands with a value of 0.85. Figure 1 depicts the three, experimentally defined, sand environments. Also included is the Baldwin Bay sand which had a calculated roundness of 0.370.

In order to remove any living matter and organic material on or adsorbed to the sand grains, all sediments were acid treated. This process involved soaking the sand in 30 percent hydrogen peroxide for five hours and then cleaning it in hot 4 N sulfuric acid for 24 hours.

WILSON (1955) found that in order to impart a greater attractiveness to acid-cleaned sand the sediment should be soaked in seawater before experimentation. Therefore, before beginning the experiment, seawater from Baldwin Bay was filtered through a 63 μ mesh net, and all sands were soaked in the filtrate for one week. Sand collected from Baldwin Bay was also prepared in the same manner and used as a control.

Frames supporting plexiglass core tubes 3.1 cm in diameter and 30.0 cm long were built. Each frame supported four vertical and four horizontal tubes (see Fig. 2). This arrangement was made so that both horizontal and vertical migration of the meiofauna could be measured. The tubes were filled with the acid treated sand grains of the three different roundness categories: on each frame one horizontal tube and its adjoining vertical tube were used for each type of sediment. The extra tubes at the end of the frame were filled with acid treated control sand from the Baldwin Bay beach. The sand filled tubes were stoppered and transported to the beach. Each frame with tubes was then placed in a hole dug in the sediment, the rubber stoppers removed, and the hole filled with sand in such a way that the uppermost part of the tubes was 3 cm below the surface of the beach sand.

After a period of 90 days, the frames were recovered and returned to the laboratory. The fauna in the tubes was then processed and enumerated in the same manner as described previously.

PERMEABILITY.

It has been shown that permeability, the ability of water to flow through the sediment, may affect the reactions of organisms (WEBB, 1958). This property is probably most controlled by the sand grain sizes (WEBB, 1958, 1969), but theoretically, the angularity of the grains may also contribute to this variable. In order to determine how different the three sand categories were, permeability determinations were carried out in a manner similar to that as described by WEBB (1958). A plexiglass tube having an inner diameter of 1.8 cm and a length of 75 cm was filled with sand to a depth of 10 cm. A few layers of plankton netting were fitted over the bottom of the tube and secured by a rubber band. The tube was clamped vertically in place and filled with distilled water. The time required for a head of 65 cm of water to drain to a mark .15 cm from the bottom of the tube (i.e. 50 cm of water to pass through 10 cm of stable sand) was used as the permeability value. The 10 cm of sand was considered stable when the drainage times in three consecutive trials did not differ by more than ± 0.5 percent. In order to achieve this degree of accuracy, the sand had to be uniformly mixed, free from air, and fully settled (i.e. the level of the column did not fall when the tube was tapped). Five determinations were made for each type of sand tested.

RESULTS

The preliminary survey taken during May 1973 revealed a density of 223 organisms per 10 cm³. The average density during January 1974 was 99 organisms per 10 cm³. The density grew greater again during the May 1974 survey in which 212 organisms per 10 cm³ were found. I used cm³ rather than units of cm² because it provided a better comparison to the fauna found in the colonized tubes. Although the density did vary during the year, the types of organisms and their numerical percentages remained fairly constant. The main components of this beach community were : approximately 80 percent nematodes, 11 percent Collembola juveniles, 6 percent copepods and 2 percent turbellarians.

The intertidal zone studied consisted mainly of medium to coarse sand (see Table I for specific sand grain sizes and proportions and Figure 3 for a cumulative percent frequency curve). The

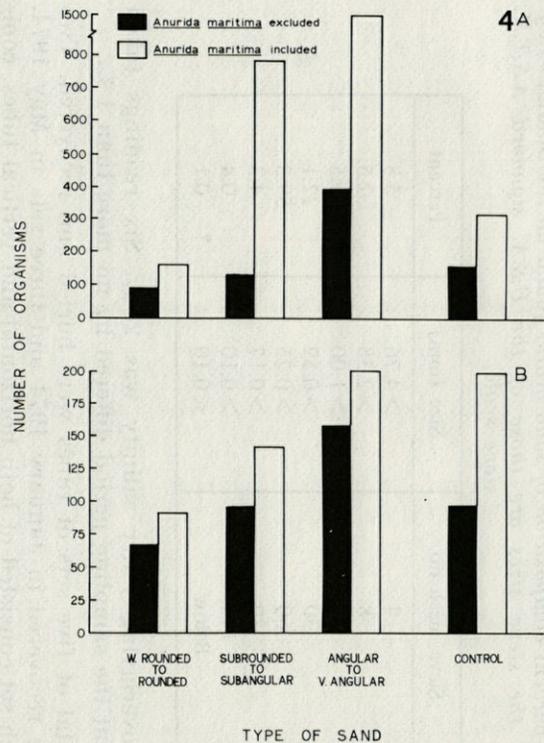
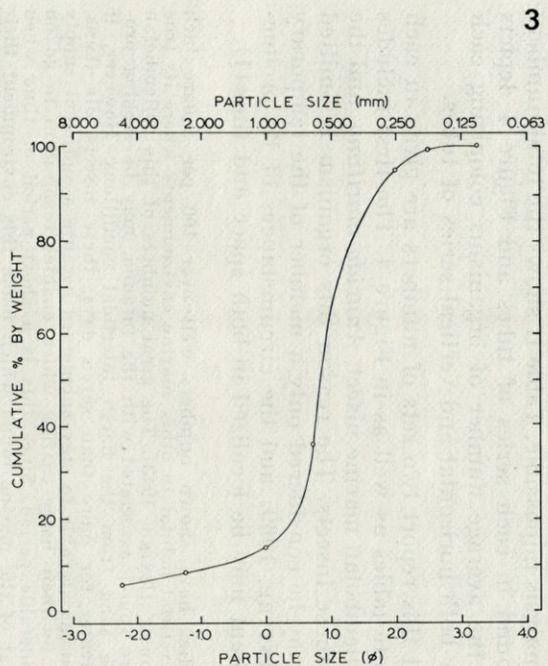


FIG. 3. — Cumulative curve (arithmetic ordinate) for the sand grain size distribution on the Baldwin Bay Beach.

FIG. 4. — Histograms of the average number of organisms colonizing the tubes filled with the different roundness categories of sand. A : vertical tubes; B : horizontal tubes.

TABLE I

Sizes and percent composition of sand grains found on the Baldwin Bay. Values of the sieve sizes are those of the U.S.A. standard A.S.T.M. sieve scale.

Sieve mesh no.	Size (mm)	Percent
4	> 4.76	5.8
8	> 2.38	2.5
18	> 1.00	5.5
30	> 0.59	22.1
60	> 0.25	59.3
80	> 0.17	4.3
140	> 0.10	0.4
Below	< 0.10	0.1

average overlaying water salinity was 28‰. Six readings taken throughout the sampling period differed by no more than 1‰.

A total of five sets of tubes were buried and recovered. Two sets were recovered in January 1974 and three sets in May 1974. Since each set consisted of both horizontal and vertical tubes, comparison between the varying angularities could have been carried out for 10 separate series of tubes. Data are shown, though, for only four of the vertical series because three tubes from series 5 cracked and varying amounts of sediment were lost thus making a quantitative analysis impossible. Table II shows the total numbers of organisms found in each series of tubes and Figure 4 depicts histograms for the average number of organisms colonizing each type of sand for both horizontal and vertical series of tubes.

Throughout this report two sets of numbers are given in each of the appropriate tables as well as in Figure 4. The first includes the juveniles collembolan marine insect, *Anurida maritima*, and the other excludes these insects. The reason this organism is omitted here is that it may be considered only a member of the temporary meiofauna (McINTYRE, 1969) and the circumstances of its production and settlement may be localized in both space and time (1).

(1) Other studies have shown numbers well over 100 per square inch outside of the interstitial habitat in other marine environments where its true habitat may be found (DEXTER, 1943). The great numbers of this collembolan juvenile, which are found associated with the infauna, may be seeking protection within the sand from the harsh intertidal conditions. However, if submerged in seawater for more than seven days, these insects die (IMMS, 1906). These organisms are able to stay submerged because a sufficient supply of air is retained by their hairy coating which enables respiration to go on freely for a considerable period. Since this is a short period of time when compared with that of the marine fauna which make this environment their permanent habitat, a better representation of the meiofaunal community should probably exclude these organisms.

TABLE II

The total number of organisms found in each series of tubes recovered. Series 1 and 2 represent tubes recovered in January and series 3, 4 and 5 are tubes recovered in May. Total volume of each tube is 226 cm²

(a) Horizontal Tubes
With *A. maritima* included

Series	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
1	110	148	365	291
2	239	371	292	322
3	47	60	150	193
4	34	40	69	68
5	29	84	135	123
Total	459	703	1 011	997

(b) Vertical Tubes
With *A. maritima* included

Series	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
1	329	966	1 795	433
2	209	1 986	3 962	644
3	65	121	154	125
4	52	59	103	58
5		Broken tubes		
Total	655	3 132	6 014	1 260

Without *A. maritima* included

Series	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
1	78	124	285	102
2	167	186	176	94
3	45	53	131	122
4	22	36	66	52
5	23	83	130	119
Total	482	482	788	489

Without *A. maritima* included

Series	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
1	181	270	775	239
2	58	99	537	254
3	65	100	153	99
4	52	58	101	53
5		Broken tubes		
Total	356	527	1 566	645

TABLE III

The combined number of meiofauna for each taxon found in the various sand grain roundness categories for all tubes recovered.

(a) Horizontal Tubes

Taxon	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
Foraminifera	1	2		
Turbellaria	96	57	124	52
Gnathostomulida	20	22	49	41
Nemerteans	3		1	
Gastrotricha		2	1	
Nematoda	192	306	499	245
Polychaeta		2		1
Oligochaeta	1	17	21	9
Mollusca				1
Halacaridae	4	2	31	51
Ostracoda		1	2	
Copepoda	16	70	58	87
Collembola	124	221	223	508
Tardigrada	2	1	2	2
Total	459	703	1 011	997
Total without Collembola	335	482	788	489

(b) Vertical Tubes

Taxon	W. rounded to rounded sand	Subrounded to sub-angular sand	Angular to v. angular sand	Control sand
Foraminifera		1	3	
Turbellaria	43	82	201	84
Gnathostomulida	30	10	43	30
Gastrotricha		2		
Nematoda	267	391	1 289	458
Polychaeta	2			1
Oligochaeta	7	9	14	23
Halacaridae	4	6	4	8
Ostracoda	1		2	
Copepoda	2	25	8	39
Collembola	299	2 605	4 448	615
Tardigrada		1	2	2
Total	655	3 132	6 014	1 260
Total without Collembola	356	527	1 566	645

In eight out of nine series of tubes retrieved, the tube with the well rounded sand had the lowest number of organisms, the tube with the subrounded to subangular sand had an intermediate number of organisms, and the angular to very angular sand-filled tubes contained the greatest number of organisms. This was the case in enumerations with and without the juvenile Collembola.

Control tubes containing acid cleaned sand collected from the Baldwin Bay beach, were used to study whether or not organisms would preferably colonize sand taken from their own natural environment. This would suggest that meiofauna might recognize the angularity of foreign sands relative to the angularity of sands from their natural surroundings. The calculated roundness value of the Baldwin sand was 0.370, an angularity intermediate between the well rounded to rounded and the angular to very angular categories. If the organisms recognize only sand grain angularity and not selectively colonize sand from their own natural environment, the total number of organisms found in the Baldwin Bay sand should have fallen between the numbers found in the well rounded to rounded and the angular to very angular categories. This indeed was true in all the series of tubes in which *A. maritima* was not enumerated. When the insect was counted, the control tubes contained a number of organisms intermediate between the numbers found in the rounded and angular categories in seven out of nine counts.

TABLE IV
Permeability values and the average for the three types of sand used in the colonization experiment.

Type of sand	Permeability time	Ave. permeability time
W. rounded to rounded	19 min 45 sec 18 min 20 sec 16 min 17 sec 18 min 34 sec 15 min 59 sec	17 min 47 sec
Subrounded to sub- angular	15 min 42 sec 20 min 12 sec 24 min 36 sec 15 min 15 sec 19 min 40 sec	18 min 53 sec
Angular to v. angular	18 min 26 sec 29 min 23 sec 23 min 31 sec 19 min 33 sec 23 min 05 sec	22 min 47 sec

The meiofaunal composition of the combined horizontal series and the combined vertical series is shown in Table III. The most dominant groups found in the tubes were nematodes, collembolan juveniles, copepods, and turbellarians. These were also the major groups found in the core samples taken from the natural environment. In fact, all organisms present in the environment were able to colonize the tubes except rotifers which were also the rarest members of the total community on the beach. Only one was found during the January recovery period or the spring preliminary survey.

Permeability values are shown in Table IV. The well rounded to rounded category had the greatest permeability, the subrounded to subangular sands had an intermediate permeability, while the angular to very angular class had the least.

DISCUSSION

Factors which influence the distribution of meiofauna in marine environments are probably too complex and interrelated to allow a general statement of organism distribution to be made on the basis of only a few experiments. However, a study of all environmental variables affecting the distribution of the meiofauna would be an enormous task. Therefore, most studies of the habitat as it affects interstitial biology have been based on usually only one or two parameters (BOADEN, 1963; JANSSON, 1967; RENAUD-DEBYSER, 1963; WIESER, 1959). One such factor which seems to influence the distribution of these organisms on sandy beaches is the degree of sand grain angularity. My experiments suggest that the meiofauna prefer more angular sands.

Although the experiment restricted totally free interstitial migration, populations found in the colonized tubes resembled the populations found in the environment suggesting that the tubes themselves probably had little or no adverse effect on the main components of the natural meiofaunal community. Observations from this experiment may thus reflect what happens in the natural interstitial environment.

Probably the best explanation for the meiofaunal preference for a greater angularity on sand grains is that a greater number of organisms can live in a more geometrically complex environment. A greater complexity may be beneficial to the total community in several ways. One may be that the complexity allows for

a greater number of spatial niches. The presence of more angles on the sand grains would allow for both a greater surface area and greater environmental heretogeneity which would result in an increase in the number of habitats.

Greater complexity within the environment may also induce population growth and stability. HUFFAKER (1958), in his study of predator-prey interactions and their interrelations with parameters of population changes of terrestrial mites showed that a more complex environment can lead to greater stability of animal populations. His studies demonstrated that populations inhabiting less complex environments were more likely to exhibit self-extinction than those in a more complex environment. The probability of a greater variety of crevices in the angular sand grains resulting in a heterogeneous interstitial environment may have afforded protection by providing more hiding spaces from predators for the meiofauna inhabiting it than did the more rounded sands. Thus, stability of the populations may have been enhanced.

Meiofauna may also have been attracted to the more angular sand grains by the availability of food on the sediment surface. MEADOWS and ANDERSON (1966, 1968) have suggested that certain microorganisms such as diatoms, other algae, and bacteria are more likely to be found in hollows and depressions on sand grains than on smooth surfaces because the crevices offer more protection from abrasion by other particles. Since these microorganisms may provide the principle nourishment for a number of different meiofaunal taxa (COULL, 1973), preferential colonization and greater population growth may have taken place because the angular sand — by nature probably having more crevices than the rounded sands — provided more micro-epibiotic food for the community. In the same manner, the crevices may have even been used for protection from abrasion by the small members of the meiofauna itself, especially in the intertidal environment where grains may be subject to shifting by tidal influence.

Studies on the introduction of geometrical complexity to the environment have been carried out in other ecosystems with similar results. For example, there are numerous reports (BULLOCH, 1965 ; BURCHARD, 1972 ; STEPHENS, 1969 ; TZIMOULIS, 1962) of sunken ships becoming virtual sanctuaries for invertebrates and fish in relatively flat areas which previously supported little life. Discoveries such as these have lead to the successful idea of building so-called artificial reefs in which junk automobiles or old tires are dumped off coastlines in order to produce more gamefish (KYLE, 1958; STONE and BUCHANAN, 1970; STROUD, 1971). Again, this is just another way of increasing the environmental complexity of an

ecosystem which in turn produces greater numbers and presumably more species of organisms.

Although the results of this experiment suggest that an angular environment is more populated by the total meiofaunal community, adverse effects may have been operating against certain groups. For example, copepods made up only 4 percent of the entire community colonizing the angular to very angular sand-filled tubes while they comprised 10 percent of the community colonizing the subrounded to subangular sand. The value for the well rounded to rounded sand was 3 percent (2). The copepods therefore may be avoiding the angular environment. Theoretically, the roundness of the grains should affect the size of the interstices (JANSSON, 1971) and the more angular the sand, the less interstitial space is available. A lack of space may have prevented certain meiofauna from colonizing angular sand even though it provides for more spatial niches.

Besides affecting the amount of interstitial space, the compact arrangement of the angular sand may also affect sediment permeability. Permeability may be an important factor in organism reaction (BOADEN, 1968; WEBB, 1958) because the more permeable the sediment, the greater the penetration of oxygen and other nutrients. The angular to very angular sand exhibited less permeability when tested than the subrounded to subangular sand and these were both less permeable than the well rounded to rounded category. If less permeability also occurred in the experimental tubes containing the more angular sand, there may have been a lower amount of nutrients and oxygen percolating through this sediment than in the more permeable rounded sands. This may also have discouraged certain meiofauna from entering these tubes.

A large error, though, may be associated with the permeability values and caution must be exercised when correlating them with an experiment such as this one. Each permeability value appears to be due to a specific sand grain orientation. Reorientation of the grains, which most likely took place during the onset and retreat of the tides, occurs suddenly and may have given rise to a new lattice with a different geometry four times a day for the 90-day colonization period. Therefore, the values of permeability, even if taken from the tubes actually used in the experiment, may be somewhat variable because sand grain orientation on a beach may be only ephemeral.

Another possible disadvantage of an angular sand environment is that the grains may be too jagged for certain organisms. WEBB

(2) Numbers are calculated from the meiofauna without including the collembolan juveniles.

(1969) describes a reaction of avoidance by the tropical lancelet, *Branchiostoma nigeriense* to certain sand grains. He suggests that the grains were sharp.

Perhaps the few taxa, such as copepods, which were not able to colonize the angular sand in great numbers, are not able to bend their bodies as well as the truly vermiform taxa and are thus not able to make use of the habitat heterogeneity. For these members of the meiofauna it seems that a compromise must be made between inhabiting sand of greater angularity for protection and food and living in a less angular environment for more interstitial space, greater permeability, and the absence of sharp grains. The subrounded to subangular environment would seem to offer the best habitat for these taxa. But these organisms seem to comprise only a fraction of the entire community. The preference of the community as a whole may be for a more angular environment — at least this is suggested by the results from Baldwin Bay.

CONCLUSIONS

1. Meiofauna more readily colonize tubes filled with very angular sand grains rather than tubes filled with more rounded sands and population densities may be limited directly or indirectly by the spatial heterogeneity of their environment.

2. Greater angularity on sand grains provides a geometrically more complex environment. This complexity may provide a greater number of habitats, more predator-free space, and greater protection from particle abrasion thus leading to larger population densities in more angular environments.

3. The greater food source potential within the crevices of more angular sand may also attract meiofauna.

4. A few groups of meiofauna may avoid a more angular environment because they are discouraged by conditions such as less interstitial space, lower permeability, the sharp edges of the sand grains, and by the nature of their body structure and movements.

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SUMMARY

A colonization experiment involving meiobenthic fauna was carried out at the mean tide area on a low energy beach. Tubes filled with sterilized sands of varying angularities were used to test meiofaunal preference. Organism variation and total numbers indicate that the community prefers a more angular sand. The greater habitat heterogeneity provided by angular sand grains may attract these organisms because it offers a greater number of spatial niches, more predator free space, more abundant food sources, and greater protection from sediment abrasion than the rounder sand. A few taxa were not attracted by a greater angularity. A combination of factors may be limiting these individuals including the nature of their body shape, adverse effects of sharp sand grains, and the lower amount of nutrient exchange in the angular sand.

RÉSUMÉ

Une expérience sur une faune méiobenthique dans l'aire de la mi-marée sur une plage de faible énergie a été entreprise. Des tubes à essai remplis de sables stérilisés de diverses angularités ont été employés pour tester la préférence de la méiofaune. La diversité des organismes et les résultats obtenus indiquent que la communauté préfère un sable plus angulaire. Une plus grande hétérogénéité d'habitat provenant des sables angulaires pourrait attirer la méiofaune parce qu'elle fournit un plus grand nombre de niches spatiales, plus d'espaces exempts de prédateurs, une plus grande abondance de nourriture et plus de protection de l'abrasion par les sédiments que dans les sables plus ronds. Certains organismes n'étaient pas attirés par la plus grande angularité. Il se peut qu'une combinaison de facteurs les limite, y compris la forme de leurs corps, les effets contraires des grains aigus, et le peu d'échange de nourriture dans le sable angulaire.

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