

BRYOZOA: ORDOVICIAN TO RECENT
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INTERSTITIAL BRYOZOANS: UNEXPECTED LIFE FORMS IN A HIGH ENERGY ENVIRONMENT

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ABSTRACT

Single grains of sand and fine gravel (<2.8 mm) function as substrata for some 30 species of cheilostome, cyclostome and ctenostome bryozoans on a near shore, shallow shoal on the Atlantic coast of southern Florida. Only two species are typical free-living cupuladriids. The remaining members of the fauna settle, grow, and reproduce within the limits of a single grain. The high energy environment prevailing on the shoal causes constant shifting of sediment grains even in average weather conditions. Since most species possess no means to reorient their sand grain, they are forced to perform most or all of their functions in the interstitial space. Members of the fauna are characterized by small zooids, and many reach sexual maturity with well below 10 zooids in the colony.

Warm water shelf areas throughout the world have long been known to be inhabited by characteristic faunas of free-living and rooted cheilostome bryozoans. By the same token the fine grained nature and relative instability of this extensive type of sedimentary environment have been assumed to prevent colonization by other bryozoan growth forms. Our finding of an interstitial bryozoan fauna from an environment with constantly shifting sediment grains indicates that such sandy shelves may indeed support additional diverse thriving bryozoan communities.

INTRODUCTION

Certain bryozoans having specialized colony forms (rooted and free-living) are adapted to life in soft bottom habitats (Harmelin 1977, Cook & Chimonides 1979). Otherwise, bryozoans are limited to solid substrata of one type or another. In most sandy shelf areas, populations of encrusting forms should be restricted to the scattered occurrences of rock, shell, coral and other substrata, which give them sufficient space and time to grow to reproductive maturity. To most bryozoologists (including the authors!), a shallow high-energy sand shoal environment would have seemed the least likely place to encounter a diverse encrusting fauna. However, in this paper we report that, in fact, not only does such a fauna exist, but the species involved show a variety of specializations for exactly this habitat.

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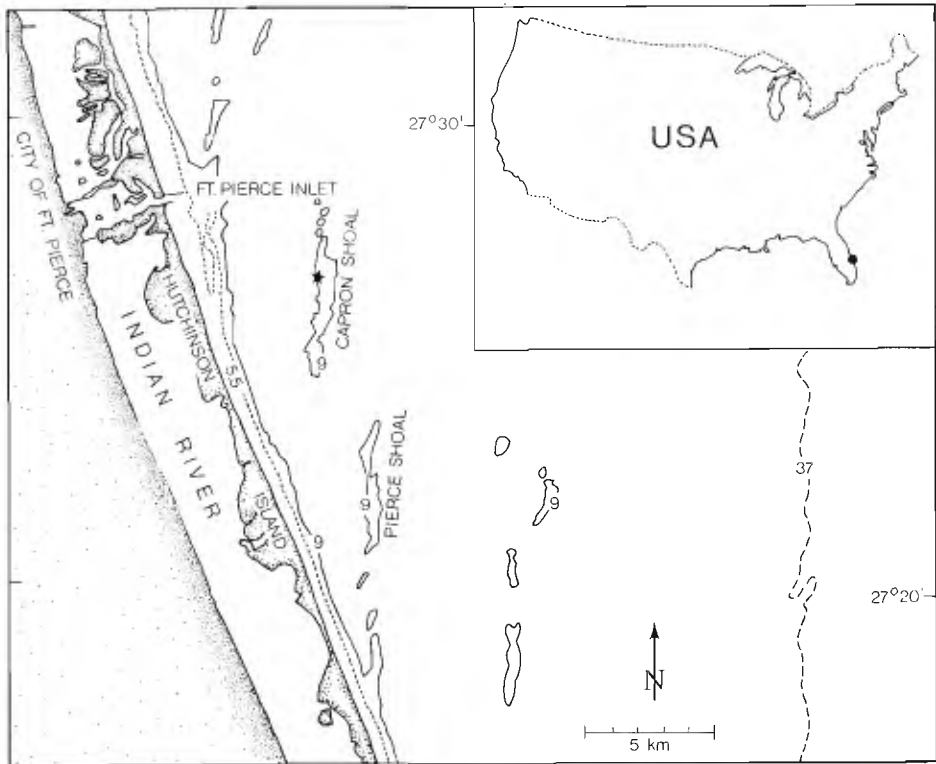


Fig. 1. Bathymetry of the inner Fort Pierce shelf (depth in metres). Sample location on Capron Shoal indicated by asterisk.

STUDY AREA

Capron Shoal is located off the northern end of South Hutchinson Island about 7 km south of Fort Pierce Inlet, on the Atlantic coast of Florida (Fig. 1). The crest of the shoal trends roughly north-south at an acute angle to the coast for about 6 km, with a minimum depth along the crest of 6 m, falling off to more than 17 m toward the coast, and eventually to 40 m offshore. Mean annual wave heights average 2.1 ft. and winds are principally from the E & NE (Duane *et al.* 1972). During all but summer months, wind and current conditions are often severe, and even in fair weather some sediment shifting has been observed on the shoal crest.

In general, the shoal sediment is a well-sorted biogenic sand of medium to coarse grain size containing 15-30% quartz. The biogenic fraction is composed mostly of barnacle plates and mollusk fragments (Duane *et al.* 1972, Wilcox & Gamble 1974). A tendency to downslope coarsening in the shoal sediments has been noted (D. Mook pers. comm. 1983).

METHODS

Sand samples were taken in September 1982 and April 1983. Samples were taken using a small sled type dredge and returned in seawater to the lab. for sorting and analysis. Both samples were taken at the top of the slope on the shoreward side of the shoal near buoy 10A, as this was one of the few positions that could be reliably located by a combination of sonar and sightings, but the two sample locations were not identical.

1/32 (= 69 g) of the fall sample and 1/64 (= 255.5 g) of the spring sample were sorted under a dissecting microscope at a magnification of 12 \times for analysis of species present, colony size, reproductive condition, habitat size, and topographic preference. Grain size composition was determined by gentle dry sifting to avoid breakage of the very irregular and fragile grains dominating the shoal sediments. In addition, pore space was evaluated from linear measurements made on epoxy embedded grains from the spring '83 sample (cf. Williams 1969).

RESULTS

Both fall '82 (Fig. 2A) and spring '83 (Fig. 2B) samples consist of medium to coarse grained well sorted sands. The slight but significant difference between the two samples may be due to slightly different positions of the slope or to seasonal hydrological changes.

Thus far, at least 37 taxa are represented on grains smaller than 4.75 mm: 16 anascan cheilostomes, 19 ascophoran cheilostomes, one cyclostome and one boring ttenostome.

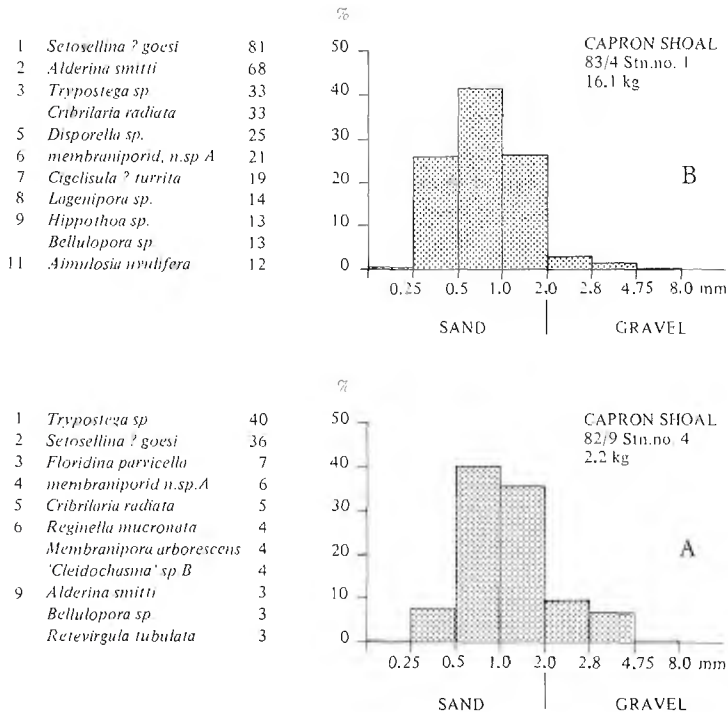


Fig. 2. Grain size composition and list of dominant bryozoan species (excl. Cupuladriids) of the two Capron Shoal samples analysed (A collected Sept. 1982; B collected April 1983). The grain size compositions of the two samples are significantly different in a statistical test ($P < 0.1$, $\chi^2 = 47.54$).

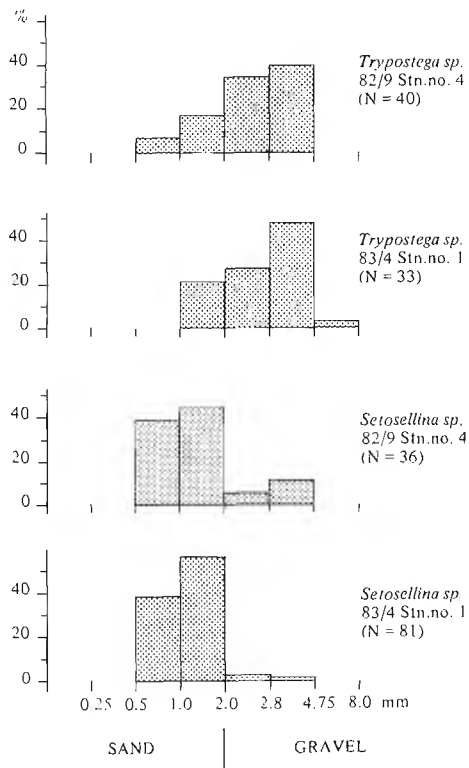
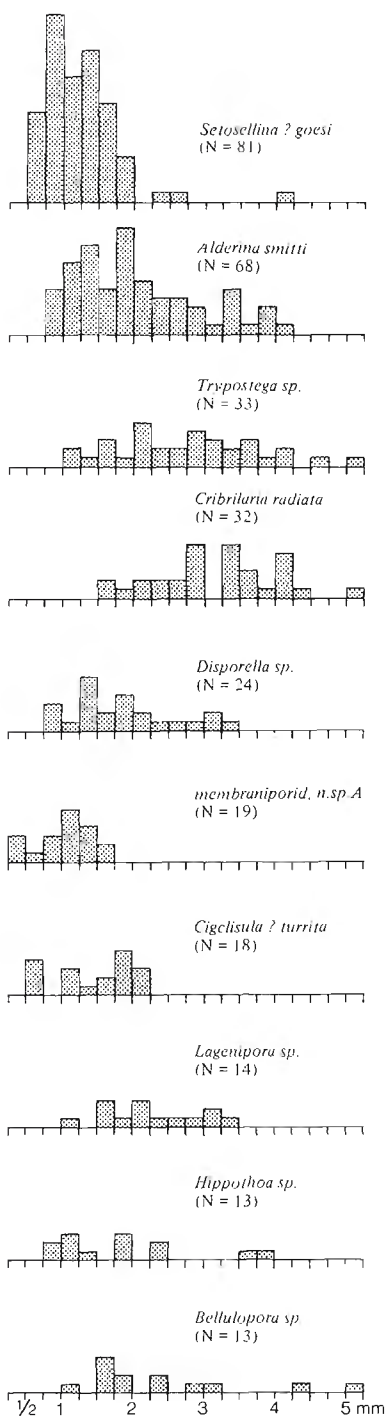


Fig. 4. Substratum size of the two most dominant species in the two samples. The substrate size range exploited in the two populations of *Trypostega* is statistically similar ($P > 50\%$, $\chi^2 = 0.01$), whereas the apparent similarity between the two *Setosellina* populations may not be supported statistically ($2\% < P < 5\%$, $\chi^2 = 4.21$).

Fig. 3. Substratum size for the 10 dominant species of the spring sample (cf. Fig. 2B) as determined by measurements of the second axis of each substrate grain. The substratum size preference is supported statistically for most species by the χ^2 -values shown in Table 1.

Table 1. χ^2 -values in comparing substratum size of the seven most dominant species from the spring sample (cf. Fig. 3). Apart from *Alderina smitti* compared to *Disporella* sp. (bold figure) all comparisons are significantly different. Figures in italics represent minimum χ^2 -values in cases where not all size-classes can be included.

	2	3	4	5	6	7
1 <i>Setosellina ? goesi</i>	170.7	170.7	95.4	182.3	42.0	234.6
2 <i>Alderina smitti</i>		59.7	280.9	13.3	101.1	64.8
3 <i>Trypostega</i> sp.			45.8	91.7	288.0	136.8
4 <i>Cribrilaria radiata</i>				73.4	90.9	172.1
5 <i>Disporella</i> sp.					66.6	39.2
6 membraniporid n. sp. A						110.3
7 <i>Cigclisula ? turrita</i>						

Twenty-seven of these occurred in the sand fraction (0.06-2.0 mm). The most abundant species in the two samples are listed in Fig. 2, but as long as the cause of the sediment variation has not been established, the reason for the obvious difference between the two samples must remain obscure.

Twenty of the species found on grains smaller than 4.75 mm were ovicelled. Fifteen of these species had ovicelled specimens on grains in the sand fraction.

Grain size (substratum) preference is illustrated in Figs 3-4. Fig. 3 shows that the grain sizes utilized by the most common species in a population differed clearly both in terms of range and actual grain size (cf. Table 1). The fact that for two of the most abundant species, *Trypostega* sp. and *Setosellina ? goesi*, the specific grain size preference is maintained even with the shift in grain size composition between the fall and spring samples (Fig. 4), suggests that this pattern is the result of active selection. Although the visual within-species similarity can only be supported statistically for the two *Trypostega* populations, it is quite obvious that both species maintain a characteristic grain size preference — coarse sand in *Setosellina* and fine gravel in *Trypostega*.

Furthermore, for most species there was an apparent preference shown by settling larvae for crevices, concave surfaces, and holes (Figs 5, 6).

DISCUSSION

Ways of life

We have tried to group the ways of life of these organisms into categories based on our present observations.

Free living. Maturo (1968) found the cupuladriids *Cupuladria doma* and *Discoporella umbellata depressa* to be the most common free-living species on the continental shelf off the southeast Atlantic coast of the U.S. between Cape Hatteras and the Straits of Florida. These two species were also the most abundant bryozoans at Capron Shoal. The third most abundant species was *Setosellina ? goesi* which we refer to the same group. Unlike *Discoporella* and *Cupuladria*, *Setosellina* does not have the capacity of secondarily thickening its basal wall. It cannot, at least in this environment, grow free of its sand grain — instead it completely covers the surface of the grain with a single layer of zooids. By vibracular action *Setosellina* colonies were able to change their orientation relative to adjacent grains, thus increasing or maintaining sufficient pore space for feeding.

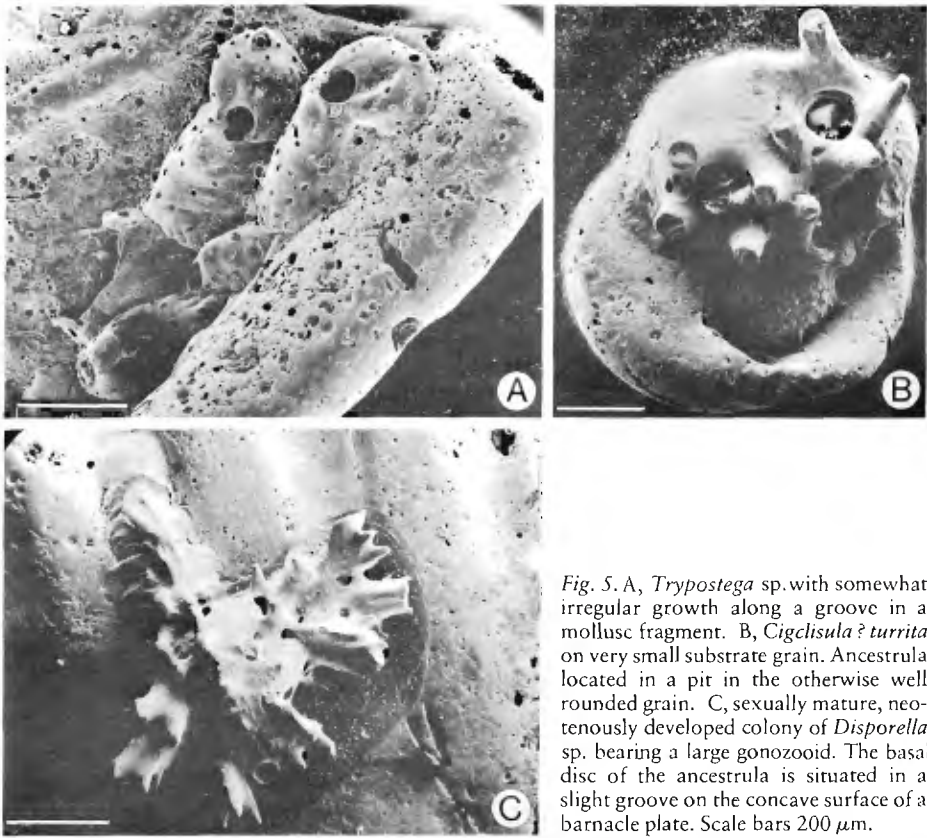


Fig. 5. A, *Trypostega* sp. with somewhat irregular growth along a groove in a mollusc fragment. B, *Cigclisula*? *turrita* on very small substrate grain. Ancestrula located in a pit in the otherwise well rounded grain. C, sexually mature, neotenously developed colony of *Disporella* sp. bearing a large gonozooid. The basal disc of the ancestrula is situated in a slight groove on the concave surface of a barnacle plate. Scale bars 200 μ m.

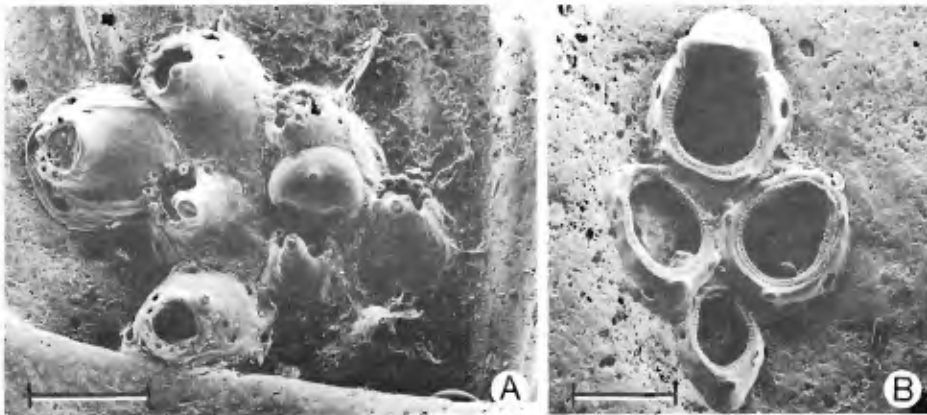


Fig. 6. A, sheet-like growth of *Aimulosia uvulifera* on the concave surface of a bivalve fragment. The ovicell is situated next to the ancestrula (invisible, located in the umbonal cavity). B, characteristic, semiderminate colony shape of *Alderina smitti* growing on the concave surface of a mollusc fragment. Scale bars 200 μ m.

Based on colony form and structure a distinction between setoselliniform and lunulitiform morphotypes has been suggested, most recently by Cook & Hayward (1979). However, when the actual mode of life is considered, a distinction between their rooted lunulitiform colonies on the one side and free-living lunulitiform and setoselliniform colonies on the other appears more useful. In fact, in the Capron Shoal environment at least, the *Cupuladria doma* and the *Setosellina* and possibly the *Discoporella* as well, have very similar modes of life. Large colonies completely surround the grain, have setiform vibracula with which they are capable of orienting themselves, and this vibracular movement in *C. doma* has been observed to include both upwards digging (to the surface) and downwards movement to regain an interstitial position.

Single grain encrusters. This was the mode of life exploited by most interstitial bryozoans at Capron Shoal. The dominant strategies displayed by most such species included consistent selection by metamorphosing larvae of crevices, concavities and otherwise protected positions on the grains (Figs 5, 6).

As the results showed, sexual reproduction was recorded in colonies of 15 species in the sand fraction. Initiation of sexual reproduction took place at an extremely small colony size. Most often the first ovicells appeared in colonies with between 3 and 6 zooids (Figs 5A, 6). This pattern of sexual reproduction is clearly precocious compared with that found in most encrusting bryozoans. The one cyclostome found at Capron Shoal, a *Discoporella* species, can also be considered 'neotenous', since it never achieved the circular colony form characteristic of the genus, but became sexually mature at a stage comparable to early astogeny of other described species (Fig. 5C). The species of this group thus appear to be able to reproduce very shortly after settlement. Such reproductive patterns resemble patterns described for bryozoan species inhabiting very short lived algal substrata (Winston & Eiseman 1980) or other invertebrates and vertebrates inhabiting ephemeral substrata (such as desert pools), and for certain annual weeds (Harper 1977). Indeed such patterns seem to be characteristic of interstitial organisms in general, along with tendencies toward brooding, hermaphroditism and viviparity (Swedmark 1964). Theoretically, precocity of development is considered to be a major factor of population growth, a few days' decrease in juvenile or pre-reproductive periods leading to an increase in fecundity (Lewontin 1965). Such precocity can be an advantage in increasing populations rapidly in relatively homogeneous environments like subtidal sands where generation can regularly follow generation, i.e. where the habitats (grains) available to offspring are similar to those inhabited by the parents. If such organisms have very short life expectations, precocity may be necessary just to maintain the population in the area over time.

In most species, growth of the colony after settlement continued in the most sheltered or concave portions of grains. But at least one species, *Cigclisula* cf. *turrita*, located the ancestrula in a protected position, but consistently grew toward the edge of the grain forming nodular masses that protruded well away from the grain surface (Fig. 5B).

As true of many other organisms found on small or short-lived substrata 6 species, including a boring ctenostome and 5 uniserial or biserial cheilostomes, had runner-like fugitive strategies, so that the probability of any one zooid being killed (by predation or overgrowth, or in the case of these organisms abrasion) is high, but the probability of some zooids surviving to reproduction is also high (Buss 1979, Jackson 1979).

In addition to these runner-like forms, one species displayed a hit-and-run strategy also observed in other organisms inhabiting short-lived substrata (Winston & Eiseman 1980). *Alderina smitti* colonies were characterized by a semideterminate growth pattern, seldom reaching a size of a more than four or five zooids or producing more than one ovicell (Fig. 6B).

The other cheilostomes included were sheet-like encrusters capable of covering a very large portion of their grains (though in many or most cases also reproductive within a relatively short time of settlement).

Grain-jumpers. One biserial membraniporid (n. sp. A) pursued an extreme variety of fugitive strategy. This species, which had the smallest range and occurred on the smallest grains (Fig. 3), was observed to construct an uncalcified node between two grains, then to continue calcified zooid construction on the second grain. Since the grains are separate, the least physical stress would separate the two parts of the colony, resulting in asexual reproduction by fission. More than half of the colonies of this species showed a reversal of polarity that would indicate repair of a detached colony fragment.

Conditions of life

Grain size and pore space. Grain size is obviously the single most important factor controlling the distributions of the interstitial fauna. Grain size and shape determines the distribution of the water filled pore spaces in which interstitial organisms move and feed. Most interstitial animals are either predators or diatom and detritus feeders. Suspension feeders (such as bryozoans, ascidians and brachiopods) are much less common and are limited to sediments in which there is sufficient water flow to supply them with nutrients (Swedmark 1964).

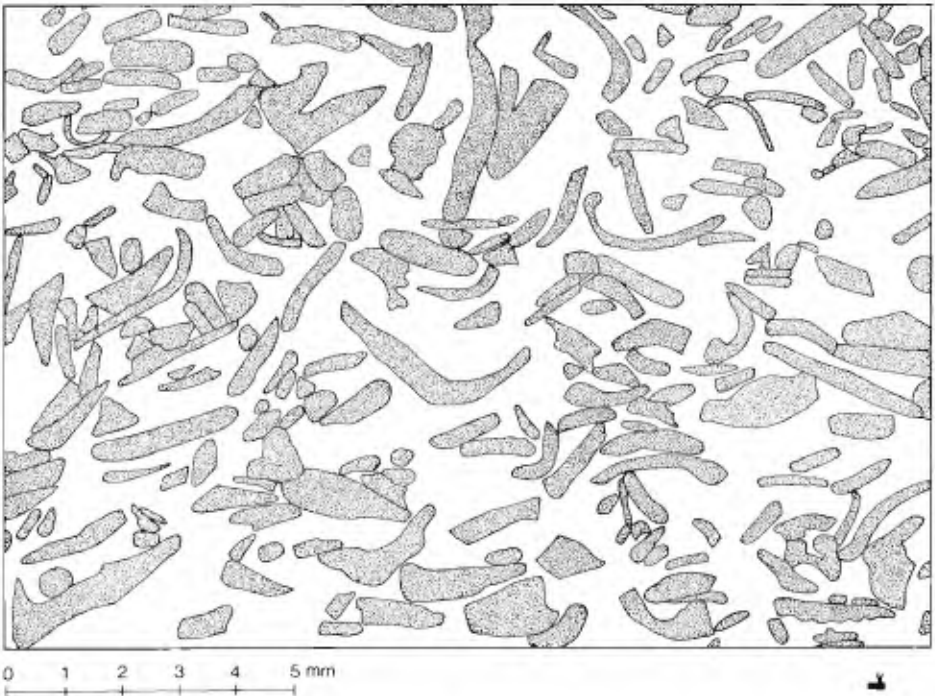


Fig. 7. Grain shape and distribution in a vertical section cut in an artificially embedded split fraction of the spring sample from Capron Shoal. (Pore-space white, grains shaded). Small zooidal silhouette inserted for comparison; size based on the largest non-ovicelled zooid of the *Alderina smitti* colony, Fig. 6B.

Meiofaunal ecologists (Riedl *et al.* 1972) have demonstrated that in sandy subtidal environments at similar depths there is a constant replacement of food and oxygen-bearing water. We have found that sufficient pore space is available in the interstices of this particular sediment for bryozoans to expand their lophophores for feeding (Fig. 7). The preference of most species for concave surfaces adds to the probability that most colonies have space to feed at any time. Very little is known yet about the physical factors acting on these organisms due to water flow through the pore spaces. According to Vogel (1981) rates of flow are about 1 mm per second and Reynolds numbers fairly low, so that viscous forces predominate. The bryozoans must extend their lophophores into what are effectively narrow channels filled with viscous fluid.

There is some experimental evidence suggesting that motile organisms choose areas having a certain shear stress rather than a particular grain size (Crenshaw 1980). Our results indicate that grain size is important to the bryozoans; we have no knowledge of the mechanism by which the larvae choose their grains, or the consequences of such preferences for colony feeding and survival.

Stability of grains. In the title of the paper we called Capron Shoal a high energy environment; in terms of sedimentology and hydrology this is certainly true. However, to the interstitial bryozoans the energy level actually experienced is dependent on their depth beneath the sediment-water interface. The deeper they are located the less the likelihood of wave-generated disturbance. Most colonies could inhabit a very sheltered situation; thus before we know anything about the actual depth limits of colonies in the sediment, questions about environmental energy levels cannot be answered.

However, the precocious sexual development and runner-like growth forms of many of the species support the assumption that sand substrata are ephemeral in some respect. If the short life-span is an adaptation for example to yearly seasonal changes, then the much larger-scale or sporadic occurrence of hurricanes would be unlikely to affect their populations significantly, particularly as the existence of similar habitats (other shoals of similar grains) is predictable in pattern. A continuation of this study will clarify the effect of seasonal differences.

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