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The significance of grain size and pore water content for the interstitial fauna of sandy beaches

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Abstract

The grain size distribution of four sandy beaches, three in the Baltic Sea and one at the Swedish West Coast, is described. A core sampler of new construction and giving successive subsamples of 10 or 20 cm³ is used to establish the horisontal, vertical and lateral distribution of grain size and grade of sorting for the four types of beaches. In a core with the total mean diameter of the grains of 500 μ the corresponding values of the subsamples may vary from 100 to 800 μ. The lateral distribution in the beach is less heterogenous. Layers of quite different grain size may have the same grade of sorting just as well as a stratum of homogenous sand may contain adjacent subsamples of quite different sorting. The significance of these differences for the interstitial fauna is shown in choice experiments with the turbellarian *Coelogynopora schulzii* and the tubificid *Aktedrilus monospermatecus*. Representing two different modes of locomotion – creeping by means of cilia and burrowing by means of peristaltic movements of the whole body – they show no significant preference for graded sand fractions in the range 1000 to 74 μ. Contrary to this animals with a sliding type of locomotion e.g. the enchytraeid *Marionina subterranea* and the harpacticid *Parastenocaris vicesima* have shown definite grain size preferences in earlier experiments by the author. The amount of pore water was determined by a rapid and accurate carbide method and examples from two of the beaches, one heterogenous and the other very homogenous, clearly show the effect of grain size and sorting upon the distribution of pore water. The different intensities of water content, water circulation and oxygen availability caused by the grain size distribution is maintained to be of greater importance for the interstitial fauna than the mere space-restricting property.

Резюме

Описано распределеление частиц песка разных размеров на отмелях в четырех участках, три из которых находятся у берегов Балтийского моря и один – на западном побережье Швеции. Средние размеры песчинок в этих участках – 300, 400, 500 и 1200 μ. При работе использовали бур новой конструкции, с помощью которого можно вынимать пробы песка из разных слоев объемом 10 и 20 см³. Отмечается гетерогенность песка в горизонтальном и вертикальном направлениях: в пробах песка, где средний размер частиц 500 μ, величина песчинок варьирует от 100 до 800 μ. Распределение слоев песка с разными размерами частиц часто беспорядочное. Выясняется значение размеров песчинок для животных, обитающих в скважинах грунта. Проводилось изучение избирательности у турбеллярий *Coelogynopora schulzii* и тубифицид *Aktedrilus monospermatecus*. Данные животные не обнаруживают заметной избирательности в песках с частицами разного размера в пределах от 1000 до 74 μ. В противополо жность этому у животных со скользящим типом движения (*Marionina subterranea* и *Parastenocaris vicesima*) в более ранних опытах автора установлено различное отношение к песку с частицами разных размеров.

Количество воды устанавливали с помощью быстрого и точного карбидного метода. Сравнение проб песка из участков с гетерогенными и гомогенными частицами ясно показывает влияние размеров песчинок и их распределение на содержание воды в промежутках между частицами грунта. Особенности среды, обусловленные размерами и распределением частиц грунта, имеют большее значение для животных, обитающих в скважинах, чем другие факторы среды.

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1. Introduction

In the interstitial environment of the sand-living microfauna grain size has by far been the most studied factor. The primary cause of this somewhat prejudiced focus is certainly the manifold adaptions of the fauna to a life in the pores between the sand grains. Though often presented as the only measured component of the environment it is not the grain size proper that limits the distribution of the fauna but the fraction of the pore system which is filled with water. A vast literature exists on the geological properties of sandy sediments, and as this is rather scattered a short summary of the more important works is given. Prenant in numerous works (1932, 1955, 1958, 1960, 1962, 1963) refined the methods for measuring the grain size and the work of 1960 comprises an exhaustive bibliography on granulometric literature. In the following only works not represented there will be commented. Morgans (1956) pointed out the necessity of uniformity in methods and presentation of results in the ecological work and the methods suggested by him are recommended for ordinary ecological studies. Porosity, probably a more adequate measure of the interstitial spaces, has been admirably studied by Fraser (1935), who presented two important formulas: 'critical ratio of entrance' and 'critical ratio of occupation'. The credit of drawing these useful formulas into the ecological discussion has Renaud-Debyser (1963: 16) though she erroneously refers to Graton & Fraser (1935) and gives the diameter of the voids at rhomboedral packing II as 0.414 D instead of 0.414 D^8. Real field measurements of the diameter and area of pores in soil was made by Haarløv & Weis-Fogh (1953) and this technique enabled the interesting results of Haarløv (1959) showing how spaciously the microarthropods are living in the soil. Measurements of the actual amount of pore water in a beach are relatively scarce, most previous works dealing with capillarity and saturation grade of sand of different grain sizes: Bruce (1928), Wiszniewski (1934, 1947), Pennak (1940, 1942, 1951), Neel (1948), Davant & Salvat (1961), Ganapati & Rao (1962) and Ruttner-Kolisko (1962). Callame (1963) discussed the effect of beach morphology on the dynamics of interstitial water. Rullier (1957) showed how superficial layers of fine sand at low tide contained more water than underlying coarser strata. In addition to these more principal works on the physical properties of the substrate a lot of information is published as descriptions of the habitat at ecological investigations of interstitial animals. Delamare-Deboutteville (1960) and Swedmark (1964) has summarized several of these works. Other studies are: foraminiferans: Blanc-Vernet (1958); cnidarians: Salwini-Plawen (1966); turbellarians: Sterrer (1965); gastrotrichs: Schrom (1966); polychaetes: Soika-Giordano (1955), Sourie (1957), Amoureux (1966); tardigrades: De Zio (1964), De Zio & Grimaldi (1964, 1966) who also stressed the significance of the interstitial water as limiting factor; crustaceans: Wells & Clark (1965); total fauna: Renaud-Debyser & Salvat (1963). On the basis of the state of interstitial water Salvat (1964) divided the tidal beach into four zones. Pure experimental approach to the relation between fauna and granulometry is scarce. A list of the most important works is found in Gray (1966). To this can be added the thorough studies of Wallace (1958, 1959) who experimentally showed the influence of pore size and water content on the migration of soil nematodes. Grain sizes preference of an interstitial oligochaete and a harpacticid was presented by Jansson (1966 a, 1967 a).

2. Localities

The localities studied are four: Askö in the vicinity of the Askö Laboratory, the Swedish marine station in the Baltic situated about 60 km to the south of Stockholm; Tofta 20 km to the south of Visby, Gothland; Simris-

Tab. 1. The main features of the localities.

	Askö	Tofta	Simrishamn	Tylösand
Beach slope	7°	5°	8°	2°
Ground-water pressure	great	low	great	low
Grain size, mean, μ	550	400	1200	300
Grade of exposure	great	great	great	great
S ‰ of the sea	6.5	7	8	22
Annual precipitation mm (mean 1931–1960).	451	529	575	735

hamn on the east coast of Scania; Tylösand on the west coast of Sweden, 10 km to the north of Halmstad. The main features of the localities are shown in Tab. 1 (Jansson 1967b).

3. Grain size

a) Methods. – The distribution of various grain size in the beaches was established by means of samples taken in transections at right angels to the water-line and at various distances from the sea with a core sampler, modified from Nääs & Odentun (1957) and of the following construction (Fig. 1). A steel pipe about 40 cm long and wide enough to contain a tube of brass of 10 cm² cross-section is at one end furnished with a mouthpiece of hardened steel and in the other one with a removable, heavy ironhandle. The opening of the mouthpiece is somewhat restricted to decrease the friction between the sand and the walls of the brass tube, and so the shortening of the core seldom exceeds 1–2 cm. The inner tube is cut up into tight-fitting rings of 1 cm height, pressed together between an inner edge of the mouthpiece and the iron handle. Rings holding both 10 cm³ and 20 cm³ were used. If a core longer than 40 cm was desired a hole was dug at the side of the sampler, a tin plate forced horisontally into the sand at the same level as the first ring and the sampler removed. The tin plate was then cleared from sand and taken away and the second core sampled with the mouthpiece inserted at the now exposed area. To get the subsamples the core sampler is put horisontally and the mouthpiece screwn off. The inner tube is then pushed out ring by ring and its content neatly cut off by sliding each ring towards the edge of the outer tube. Each subsample is then transferred to a small glass vial with a tightfitting lid, all the sand being removed from the ring by washing with filtered seawater. The material for this procedure is shown in Fig. 1. The samples are then brought to the laboratory and treated according to Morgans (1956). The sieving time was 10 minutes and the mesh sizes of the Tyler screens used were: 4000, 2000, 1000, 500, 250, 125, and 74μ. For each sample a cumulative curve was drawn in a semilogarithmic diagram but here only the mean values are presented as a whole. In this way the horisontal and vertical distribution of the grain size in the beach is obtained and by taking corresponding samples in parallel sections also the lateral distribution can be established.

1. Equipment for obtaining quantitative samples, core sampler with mouthpiece removed.

b) Microdistribution in the field. – Figs. 2–5 show typical grain size distribution of the

four localities. The subsamples had a volume of 10 cm^3 except for Askö stations A, C and D and Simrishamn all samples, where the volumes were 20 cm^3.

Askö. – The sand of this beach is very heterogenous (Fig. 2). Though the mean grain size for the whole cores are of the same magnitude – 500–600 μ – the separate stations show a diversity of sizes from 200 to 1200 μ. The Phi quartile deviation (QDØ) is as individual. In station A the upper fine sand layers (200–300 μ) have very diverging grades of sorting, 0.81–0.37, while the underlying coarser layers are uniform with values around 1.0. At station B the top 4 cm have a homogenous sorting with values around 0.5 but downwards the irregularities in grain sizes are also reflected in the grade of sorting resulting in a range of 0.96–0.57. Down to the 600 μ-layer in station C the sand has QDØ-values from 0.77 to 0.63, and this uniformity also imprints the rest of the core though the corresponding values here lie around 1.0. The abrupt change of sorting grade between 12 and 14 cm depth is very striking (0.77–1.11). Station D has at the top a good sorted substratum with a medium diameter of 300 μ but downwards the sorting grows worse with values around 1.0 in the deeper coarser layers.

Tofta. – The medium grain sizes of the three stations successively decrease landwards (Fig. 3). Station A has medium grain diameters from 100 to 800 μ and also the sorting is varying (0.27–1.18). Station B is dominated by a coarse surface layer, QDØ = 1 and also the rest of the core has high deviation values. In station C the sorting is good at the top and in the bottom of the core but worst in the uppermost 300 μ-layer with values around 0.9.

Simrishamn. – This beach greatly differs from the other localities through the large size of the grains – medium diameters below 100 μ are rather scarce though they increase in frequency landwards (Fig. 4). Station A has a coarse layer at the top with a QDØ of 0.58. All the underlying strata have nearly the same sorting, 0.4. In station B all the subsamples lie between 0.29 and 0.50. Corresponding values in station C are 0.35 and 0.58, and in station D 0.36 and 0.50. Besides for the large grains this beach is therefore also characterized by a good and uniform sorting.

Tylösand. – The medium grain sizes for the whole cores decrease landwards and especially in the two middle stations subsamples of clearly different coarseness strikingly overlie one another as the bottoms in a cake. In station B two layers of 300 μ-class with a heterogenous sorting – 0.75–0.45 – surround coarser and more homogenous strata with values around 0.6. The different layers of station C has a not quite so patchy deviation as the medium grain sizes may suggest. Except the lower 400 μ-layer which is badly sorted the values of the other strata are distributed within the range 0.65–0.34. In station D the sorting within the whole core is very uniform – QDØ 0.57–0.50 – except for a few layers. A part of the 300 μ-stratum, situated between 13 and 15 cm depth shows the best sorting of the whole investigation. The sand at station E is the finest and best sorted of all the localities. About 50% of the subsamples has a medium diameter within 190–200 μ and the sorting shows values – except for the 200–300 μ-strata at the extreme bottom – of 0.41–0.27.

Lateral distribution of grain size is exemplified with values from Askö, the most heterogenous beach. Tab. 2 shows the medium diameters for subsamples of two parallel sections situated half a meter apart. The distance between the stations within each section is 0.5 m. Except for the stations B and B′ the volume of the subsamples is 20 cm^3. While the medium size of the sand grains sometimes varies considerably vertically and horisontally the agreement between the parallel samples and subsamples is rather good. Of the 40 pairs of corresponding subsamples 9 show differences of more than 100 μ laterally. The greatest differences are met with in the two seward stations.

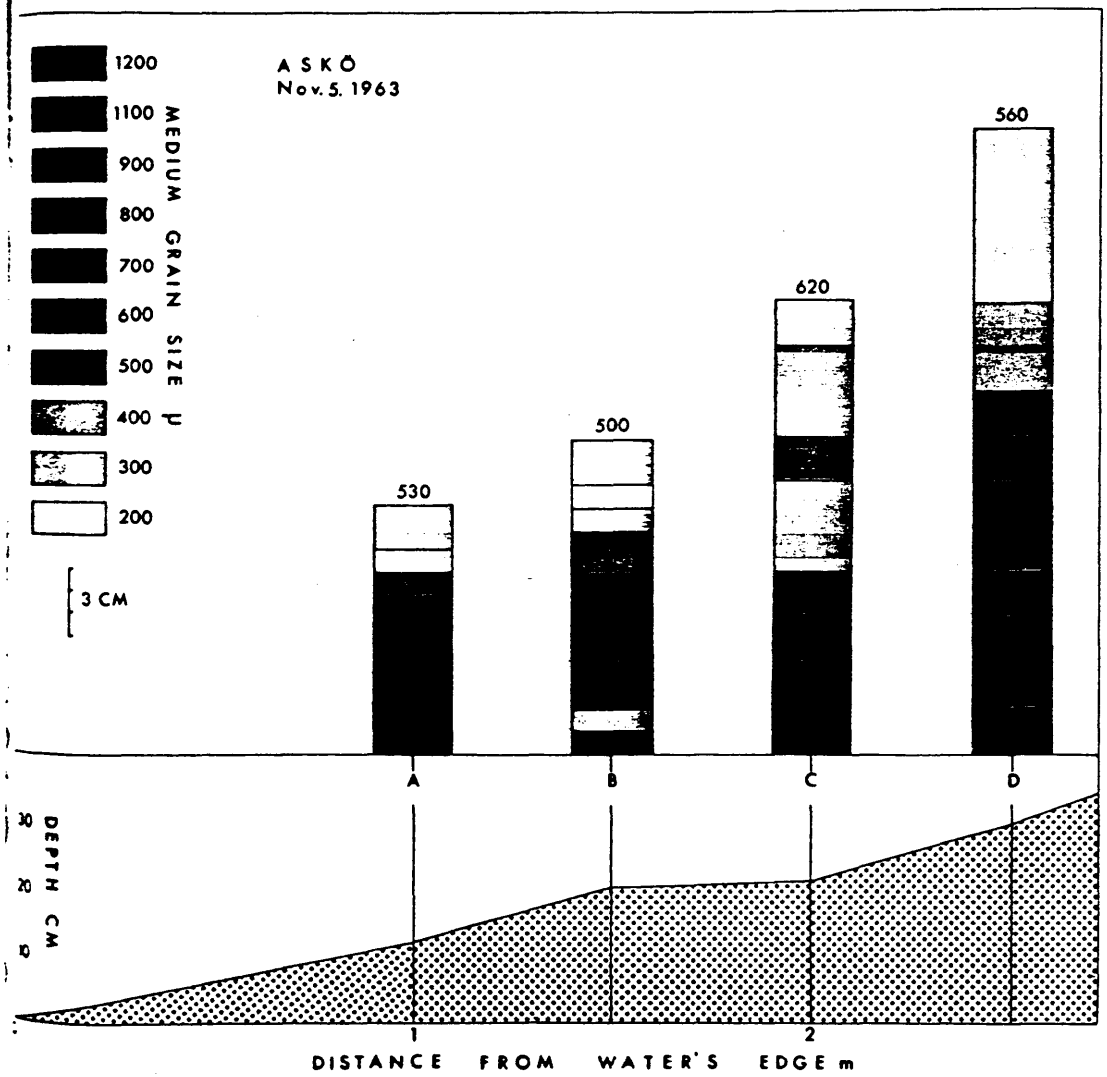


Fig. 2. The grain size distribution of Askö beach. Lower part of the diagram: section through the beach with hydrostatic ground-water level as base line. Upper part: sand cores represented by vertical bars with the surface layer at the top. On the basis of the mean values the bars have been divided into areas of corresponding hundreds. Figure on top of each bar indicates medium grain size for the whole core.

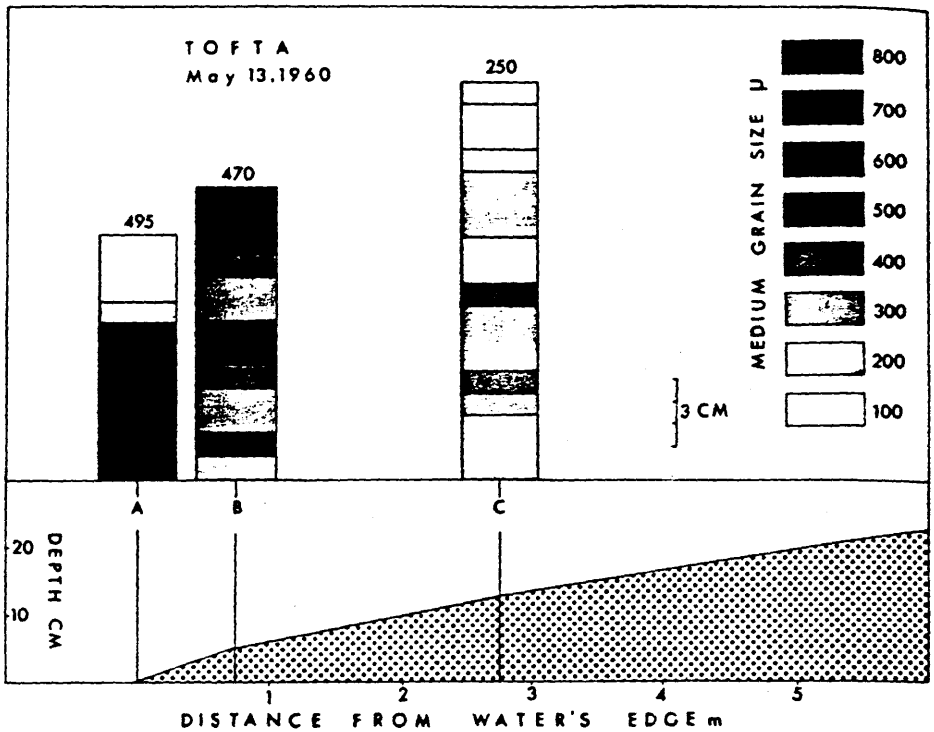


Fig. 3. The grain size distribution of Tofta beach plotted as in Fig. 2.

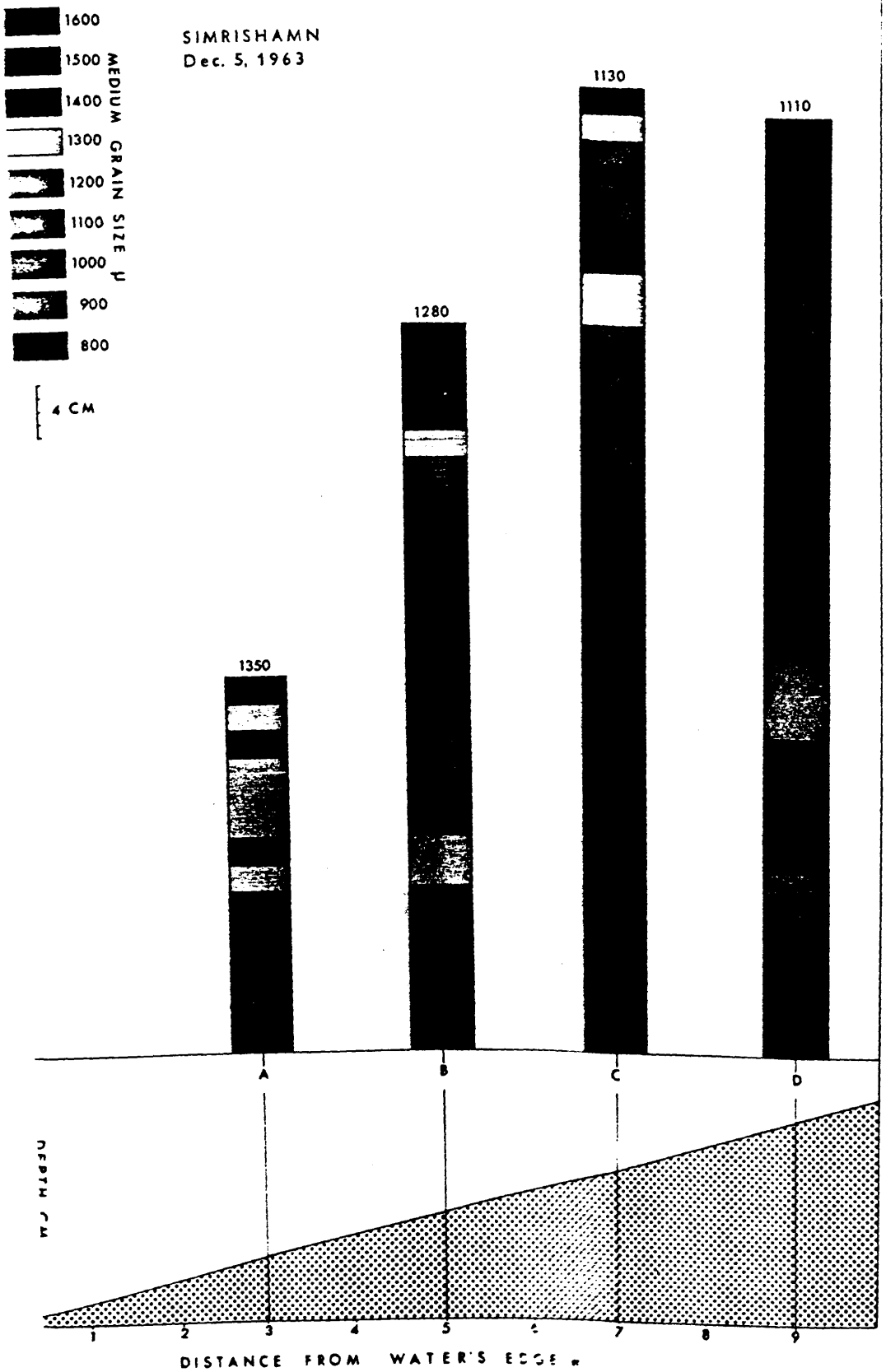


Fig. 4. The grain size distribution of Simrishamn beach plotted as in Fig. 2.

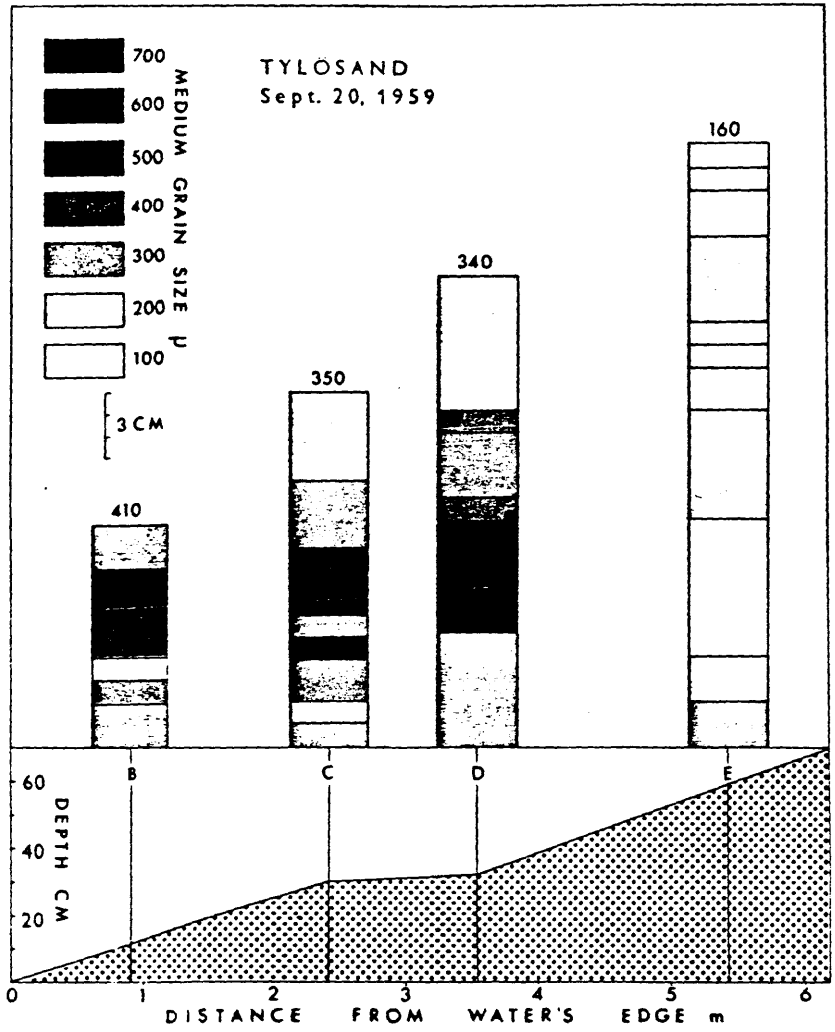


Fig. 5. The grain size distribution of Tylösand beach plotted as in Fig. 2.

Tab. 2. Lateral distribution of grain size in Askö beach, 7.8.1963. Distance from water's edge of A, A′ 2m. Distances within the stations 0.5 m.

Depth cm	Stations B	B′	Depth cm	A	A′	Stations C	C′	D	D′
0–1	350	420	0–2	380	420	380	350	340	300
1–2	340	330	2–4	350	370	460	360	380	330
2–3	390	400	4–6	750	460	420	570	400	350
3–4	490	400	6–8	570	740	420	420	330	350
4–5	400	250	8–10	700	800	370	370	400	370
5–6	900	380	10–12			–	380	280	340
6–7	500	470	12–14			450	360	330	180
7–8	700	450	14–16			550	500	400	300
8–9	690	640	16–18			920	800	350	370
9–10	720	820	18–20			1200	950	350	340
10–11	870	710	20–22					300	340
11–12	870	880	22–24					360	–
12–13	900	960	24–26					580	650
			26–28					720	850
Total mean	625	547		550	558	547	506	417	398

c) *Preference experiments.* – We may ask if this microdistribution and sorting of the sand really have any relevance for the interstitial fauna. Though this question has already been answered by me recently (Jansson 1966 a: 80) further material may be required. Following the technique of Jansson (1967 a) alternative experiments were therefore made. In an alternative chamber the animals were offered two different grain sizes of the same type of sand, packed as firmly as possible and fully saturated with water from the habitat, previously brought to full oxygen saturation. The test animals, all from Tofta beach, were chosen to represent two different types of locomotion: creeping by means of a ciliated ventral surface and burrowing with peristaltic movements of the whole body. For the former type a typical sand-living turbellarian was chosen – *Coelogynopora schulzii* Meixner. As all the specimens were juveniles, lacking genital apparatus, a direct identification to species was not possible. On the sampling locality, Tofta beach, however, only adults of *C. schulzii* has hitherto been found and therefore all the used juveniles most probably belong to this species. The speed of the animals in the substrate was measured to about 6 cm/min and consequently 3 hours in the alternative chamber was regarded as a sufficient time for the animals to seek their preferences. The second type of locomotion was represented by the tubificid *Aktedrilus monospermatecus* Knöllner, a common member of the coastal ground-water fauna in most parts of the world. The animal exhibits a

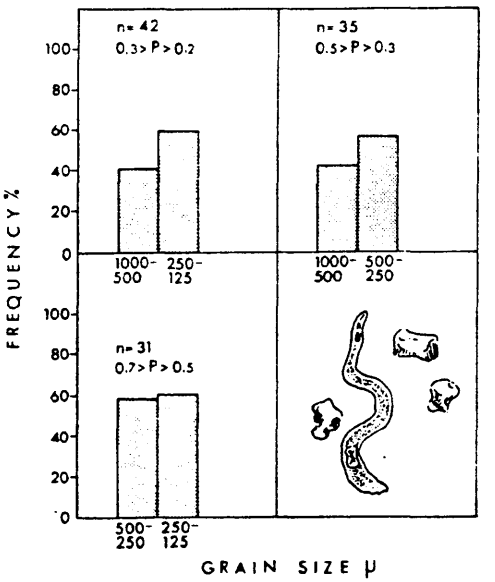


Fig. 6. Grain size preference of *Coelogynopora schulzii* juv. Temperature 21–23°C, salinity 6‰. Tofta October 1960.

decided pattern of locomotion of alternating contractions and extensions of the body, the anterior part being very active as if exploring the immediate surroundings. The evaluated speed of locomotion in sand – 3 cm/min – made a duration of the experiment of 4 hours necessary. At all the experiments the chambers were put in the dark. The number of animals in each experiment is given as n-values in the figures. All specimens of both species were in good condition after the experiment and the locomotory activity in the chambers was good. The results were tested with the chi-square test. The reactions to different grain sizes of *Coelogynopora schulzii* are rather indifferent (Fig. 6). Though medium sand fractions contained a few more specimens the differences are too small to indicate any real preference. *Aktedrilus monospermatecus* shows somewhat stronger reactions with a certain, though insignificant, preference towards the coarser sand (Fig. 7).

d) Grain size as environmental factor. – The results indicate that the variation of grain size in a beach is often great within small volumes. Even relatively small samples may include well limited layers of different grain sizes. Tofta, station A e.g. consists of 11 successive subsamples of 10 cm^3 volume and of medium sizes from 100 to 800 μ while the total 110 cm^3 has a medium grain size of 495 μ. The distribution of the Phi quartile deviation is often as irregular. Sometimes separate layers of corresponding medium diameters have the same QDØ, other times layers of the same MdØ can hold strata with very divergent sorting. Areas with quite different coarseness may show the same grade of sorting e.g. Askö, station C, where the layers with grain diameters of 600 to 1200 μ all have a QDØ of 1. At Tylösand, station D the 300 μ-layer has an upper third with a sorting of 0.18 while the underlying two thirds are less sorted: 0.53. A coarser sand may therefore be said to offer more room for an interstitial fauna only if the sorting is known to be about equal. Though the measure of the properties of the substrate has been the grain size even in the experiments, it is actually the significance of the pore spaces that have been tested in the alternative experiments. As graded sand was used and the sorting consequently was good the medium diameter of the sand grains may be an indirect measure of the pore voids. Special care was taken to eliminate possible differences in oxygen availabilities between sand of different porosity and so the only difference between the two halves of the chambers ought to be the sizes of the pore voids. In one thing, however, may the experimental conditions deviate from natural ones. The pore pressure, though comparable within the experiments, is probably less in the small volumes of sand in the chambers than in the beach where the great amounts of sand, often firmly packed by the infinite waves, give conditions impossible to recreate in small scale in the laboratory.

Of the previous experiments on the interstitial fauna and grain size only Gray (1966) in studies on *Protodrilus symbioticus* Giard has isolated the mere space-restricting property of the substrate and has been able to show a preference of this animal for grains of 200 to 300μ size. Boaden (1962) buried sands of

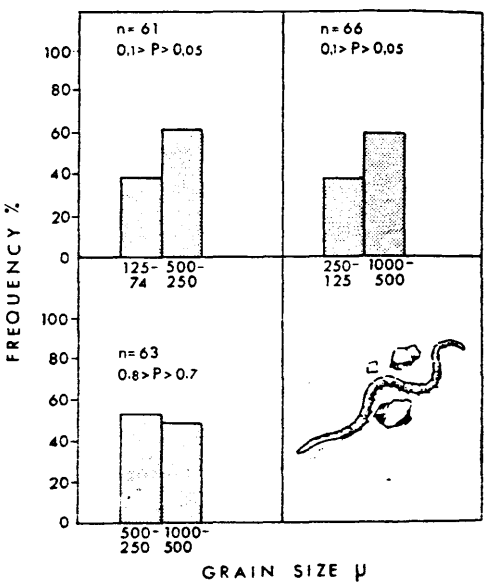


Fig. 7. Grain size preference of *Aktedrilus monospermatecus*. Temperature 16–18°C, salinity 6.5‰. Tofte November 1960.

different grades in a beach and classified the ability of the fauna of colonizing the various grain size classes. As the other environmental factors in this way were allowed to follow a natural variation the result may not show only the grain size dependence but also reactions to e.g. different water content, water circulation and oxygen availability, factors which in my opinion are often of greater significance for the animals than the grain size proper. The same is valid for the work of Wieser (1959) where the intertidal position in five beaches in Puget Sound of several small invertebrates are plotted in relation to medium grain sizes. The concept of "critical grain size", where the 200 μ-diameter constitutes the lower border for the distribution of many animals, certainly works more through its water-holding capacity than through the restrection of space. This is also discussed by Wieser who cites the work of Webb (1958), pointing out the rapid drainage in sands coarser than 200 μ.

The results of the alternative experiments indicate, that the test animal, which creeps on the surfaces of the sand grains by means of a ciliated ventral surface – *Coelogynopora schulzii* – shows no preference for sands of a certain porosity. The animal is very elongate, but this is of little hindrance as the body is extremely flexible and contractile and able to force its way even through very small pore necks. The burrowing mode of locomotion represented by *Aktedrilus monospermatecus*, shows nearly as little dependence upon the grain size. The animal forces its way through the substrate, and a good help is the extraordinary stretchability of the body. Fine plankton gauze has in other experiments been impossible to use as barriers for the animals as they easily crept through. A third type of locomotion within the interstitial fauna is the nematode-like sliding. Animals with this mode of locomotion usually have a very elongate body with no or small appendages and good examples except the nematodes are the typical sand-living harpacticids, though the sliding locomotion here mostly is combined with use of the extremities. Both *Marionina subterranea* Knöllner and the harpacticoidean copepod *Parastenocaris vicesima* Klie are good representatives of this mode of locomotion. Jansson (1966 a: 80) showed how *M. subterranea* distinctly chose between the grain sizes offered in alternative experiments with a preference for the finer sand. Similarly *P. vicesima* was shown to have a strong affinity for sand of 250–125 μ (Jansson 1957 a: 54). The "critical grain size" of 200 μ, however, had no visible influence upon the animals. This might be a further proof that it mostly works through other properties than the grain size proper.

It seems therefore very reasonable, though the material is small, that of the various types of locomotion creeping and burrowing are less influenced by the grain size while sliding is clearly dependent on the sizes of the grains and pore-spaces. Not only can the pores of the very fine sand be too small for the animals but the coarse sand may have interstices too large for offering support for a sliding body. This was seen in an unpublished experiment with *M. subterranea* where the animals were uncapable of moving in a sand of 2000–1000 μ and lay wriggling in the large pores where they were initially deposited. The same difficulty had *P. vicesima* in sand of 1000–500 μ (Jansson 1967 a: 55). In the Simrishamn beach which is remarkable for the very coarse sand, well sorted, Brinck *et al.* (1955: 12) noted an extraordinary scarcity of nematodes. This was further confirmed during my investigation of the locality in December 1963 when practically no nematodes were found. Maybe the reason is the too coarse substrate unsuitable for a sliding locomotion. This is in good agreement with the results of Wallace (1958) who made beautiful studies of the nematode *Heterodera schachtii* Schmidt in soil of different pore sizes and water films and showed their great importance for the speed and type of locomotion.

4. Pore water

a) Methods. – The water content of the sand was determined in the field by means of a "Speedy Moisture Tester" (manufact. Thos. Ashworth and Co. Ltd., Burnley). This consists

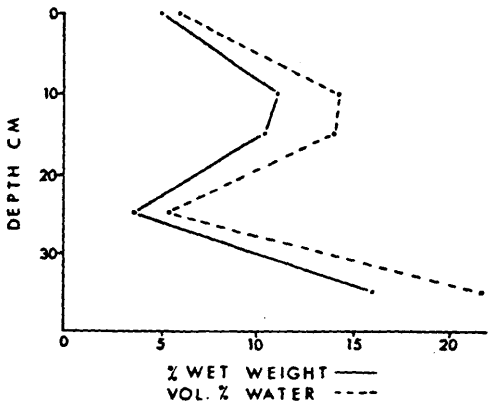


Fig. 8. Relation between pore water content expressed as % wet weight and as volume %. Values from Askö 7.8.1963 station C.

of a sealed chamber where a sample of 26 g is mixed with finely-ground calcium carbide. The resulting gas-pressure is measured on a pressure-gauge, calibrated in % wet weight, accuracy range ± 2% wet weight. The sample was taken with a piece of polyvinyl-chloride tubing, diameter 16 mm, which was inserted with the center at the depths desired. A complete test took about 10 minutes, and was made immediately in the field so errors due to transport were avoided. Mostly a quantitative analysis of several other environmental factors was made in connection to the moisture determinations. Sometimes, e.g. at the interpretation of field distribution of animals, it may be more convenient to measure the amount of water on a volume basis. As at the measurements with the carbide method only the weight of the samples were determined the corresponding volumes had to be calculated of the basis of the connecting grain size measurements. Here the sampled volume – 20 cm^3 for example – was put equal to the volume of the sand only disregarding the eventual expanding effect of the water, which is probably small in a well packed sand. It was then easy to calculate the part of the total volume made up by water. The relation between this mode of expression is given in Fig. 8. The agreement is striking. This means that at the measurement of the pore water in the beach the terms of percent wet weight give a good picture of the first qualification for an interstitial life – waterfilled pore spaces.

b) Distribution in the field. – To show the variability of pore water in the beach, examples of two type beaches are given: one heterogenous – Askö beach –, and one homogenous – Simrishamn beach. Fig. 9 shows the distribution of pore water in Askö beach, August 1963. Data on the medium grain sizes for the corresponding subsamples are contained in Tab. 1 though the cores were sometimes not long enough to cover all points of moisture measurements. The distribution is very irregular. Not even horisontally does the amount of water decrease gradually at corresponding depths as has often been stressed by earlier authors. Vertically, overlying layers may often have a greater content of water than underlying ones, e.g. station A at 0 cm, station C at 10–15 cm depth. The highest value of the section was attained at station A, 15 cm depth (ground-water surface): 16.4% wet weight which in vol.% of total sample corresponds to roughly 21%. Simrishamn beach (Fig. 10) is quite different. Immediately above the ground-water surface the pore water content decreases rapidly for 13 to 15 cm when values of only a few % wet weight are recorded. These low values then dominate up to the sand surface, giving the

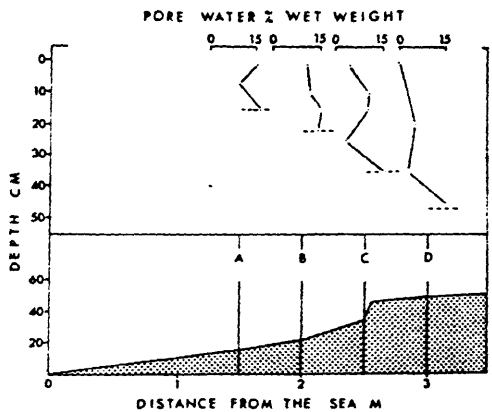


Fig. 9. Distribution of pore water in Askö beach 7.8.1963. Dashed lines indicate ground-water level.

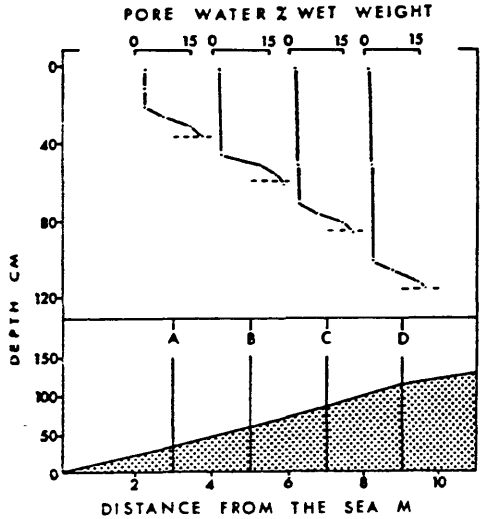
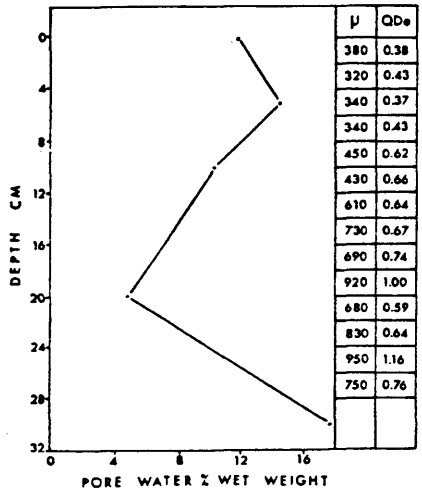


Fig. 10. Distribution of pore water in Simrishamn beach 5.12.1963. Dashed lines indicate ground-water level.



μ	QDø
380	0.38
320	0.43
340	0.37
340	0.43
450	0.62
430	0.66
610	0.64
730	0.67
690	0.74
920	1.00
680	0.59
830	0.64
950	1.16
750	0.76

Fig. 11. Vertical distribution of pore water in relation to grain size and sorting. Askö 5.11.1963 station D. Ground-water level at 30 cm.

curves an almost theoretical shape. Station B, 60 cm depth, had the highest value – 18.8% wet weight which for the actual type of sand corresponds to 26.5 vol.% water.

5. Grain size affecting the properties of pore water

Ruttner-Kolisko (1962: 448) has beautifully shown how porosity has but little dependence on the mean diameter of the grains but rapidly decreases when sand of different grades are mixed with natural beach sand. Fraser (1935: 917) summarizes the factors governing porosity and states that material deposited by waves appear to have only minor, local variation in porosity, especially in directions parallel to the water-line where it is nearly uniform. Of the factors mentioned as responsible for various grades of porosity the proportions of various sizes of grains are surely governing the distribution of water in Askö and Simrishamn beaches. The Askö value for fully saturated sand, 21% vol., is rather low but is explained by the bad sorting – QDØ = 0.9. In Fig. 11 the vertical gradient of pore water at station D, Askö 5.11.1963 is shown with the medium grain sizes and QDØ-values for each 20 cm³ sample plotted as well. The steep gradient from the fully saturated layer at 30 cm depth to the minimum value at 20 cm can be directly related to the coarse and badly sorted sand dominating the lower layers up to about 18 cm depth. When the medium diameter then decreases to less than half of the previous values and the sorting grows better, the amount of water rises threefold up to 5 cm depth due to higher porosity and capillarity. It then falls again, however, when the distance from ground-water level increases and evaporation starts.

Detritus is another factor sometimes giving irregularities in the water distribution as pointed out by Jansson (1966 a: 81). Fig. 12 shows the amount of pore water at different depths in Simrishamn beach in a parallel to station D. In a section of the sand at 50 cm depth a dark stripe with a sharp upper limit indicated a layer of well decomposed detritus, successively vanishing downwards. Measurements on either side of the clear limit gave the striking bulge of the curve which certainly indicates partly a higher capillarity causing a higher water content of the sand, partly

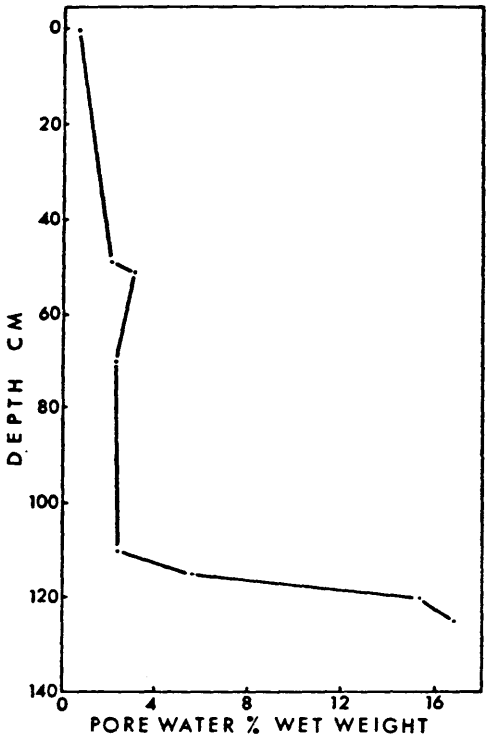


Fig. 12. Vertical distribution of pore water at Simrishamn station D′ 6.12.1963. Detritus layer at 50 cm depth.

the water holding capacity of the detritus itself.

The aeration of the interstitial water is greatly governed by the permeability which in its turn is effected by the size and shape of the sand grains (Fraser 1935: 959). Ruttner-Kolisko (1961: 366) states fine sand (250 μ) as a border area for the circulation of the interstitial water. More than 30% of this grade in a substrate brings the oxygen content to near zero. Brafield (1964: 109) showed the close relationship between the oxygen level of the interstitial water and the drainage time and presented further data in a later work (1965) where the oxygen content could be directly correlated with the percentage of 250–125 μ-sand. High oxygen availabilities in a beach with well sorted sand, medium diameter 200 to 300 μ, was reported by Jansson 1966 b: 166) who suggested a connection between the high availability and "critical grain size". In a later work he discusses the importance of water flow for the oxygen availability of the interstitial water (1967 b), and Simrishamn beach is taken as an example of a beach with high permeability and resulting good oxygen climate. So grain size stands out as a central feature of the sandy habitats though the influence upon the fauna is mostly exerted through other factors.

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7. Addendum

After this work was sent to the printer Salvat (1967) published an excellent work on the environment and macrofauna of some tidal beaches in France around Arcachon. Though a direct comparison with my work is rather difficult according to the quite different types of beaches his study must be mentioned here as the hitherto best study of the environmental conditions of tidal beaches. Among factors relevant in this context grain size, porosity, permeability, dilatancy, content of air and water and circulation of interstitial water were studied. As only one depth at each station was sampled – for the granulometric studies two but apparently treated together – the results refer to the horisontal distribution on the beach. The careful granulometric determination showed a small increase of MdØ landwards but the fractions < 100 μ and > 500 μ were more frequent in the fore shore. Consequently porosity, permeability and dilatancy were better in the back shore. On the basis of the circulation of interstitial water the moderately exposed tidal beach is divided into four zones. The distribution of the animals was mostly correlated with the state of oxygen saturation of the sediment and so these results give further support to my opinion that the influence of grain size upon the animals is exerted mainly through other factors such as circulation of pore water and oxygen availability.

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