The Effect of Grain Size on the Distribution of Small Invertebrates Inhabiting the Beaches of Puget Sound

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ABSTRACT

The position with respect to the general configuration of the shore-line and the direction and force of the currents of five localities in Puget Sound is such that they represent a series of decreasing exposure, Richmond Beach being the most exposed, Bainbridge Island the most sheltered locality. This is reflected in the composition of the substrate, the former locality having the coarsest, the latter the finest substrate. Perpendicular to this horizontal gradient there runs a vertical gradient due to the tide, the coarse grades being deposited in the upper, the fine grades in the lower intertidal.

The intertidal distribution of at least some of the more common species of invertebrates on the beaches is not so much determined by levels of tidal water as by the pattern of distribution of certain grades of substrate. For example, species of this sort will penetrate into the upper intertidal if the preferred substrate occurs there, but they will remain in the lower intertidal if the substrate is confined to this zone.

On the beaches there exist mixtures of sand which constitute barriers separating major faunal components from each other. It is assumed that substrates with a median diameter of approximately 200μ constitute such a barrier separating the bulk of interstitial sliders from a great number of burrowing animals. The former can move only in sand coarse enough to maintain an interstitial system; the latter, for mechanical reasons, will find fine sand more favorable than coarse. This distinction, however, does not apply to nematodes which are able to move even in the interstices of fine sand. There are various ways in which grain size and shape can influence the distribution of the fauna. These types of relationship are discussed.

INTRODUCTION

The small invertebrates living on marine beaches have only within the last 25 years become the subject of thorough studies. Although a number of excellent papers dealing with particular groups have recently appeared, stimulated to a large extent by the work of Remane (1933), *e.g.* Ax (1951), Gerlach (1953), more general papers treating the whole fauna from a predominantly ecological point of view are still scarce, the greatest bulk of information on that subject being found in Remane (1940), Pearse *et al.* (1942), several of the papers by Delamare Deboutteville and his associates (*e.g.* 1955), and in the review by Pennak (1950). It is particularly the effect of single environmental factors on the composition and peculiarities of the sand fauna which has yet to be analyzed in more detail. Since the most important factor in this connection is the substrate itself, more information on the relationship between the latter and the fauna in general would be desirable.

The present paper is a contribution to this topic. The work on which it is based was undertaken between October 1955 and August 1956 when the author held a research fellowship of the International Cooperation Administration at the Department of Zoology, University of Washington, Seattle.

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I am most grateful to the specialists without whose help I could not have finished my work. The following persons undertook to identify my material:

Mrs. G. C. Carl (J. F. L. Hart), Victoria (cumaceans); Dr. P. A. Chappuis, Toulouse (copepods); Dr. Olga Hartman, Los Angeles (polychaetes); Mr. Clarence R. Shoemaker, Washington, D. C. (amphipods); Dr. Willis L. Tressler, Washington, D. C. (ostracods). Dr. Melville Hatch, Seattle, helped with the other peracarids.

The following groups were studied by

myself: nematodes, gastrotrichs, archiannelids, and the single hydrozoan (Wieser 1957a, b, 1958, 1959).

My ambition was to cover all the small invertebrates occurring on the beaches, but unfortunately for one of the most important groups, the turbellarians, no specialist could be found. Otherwise all numerically important groups are included in my investigation. Of the less abundant taxa the small lamellibranchs had to be excluded.

A general account of the oceanographic features of the area under investigation can be found in University of Washington (1953), Wang (1955), and in my paper on the Puget Sound nematodes (Wieser 1959).

All the indications of tidal height in the following pages are referred to mean lower low and are given in feet.

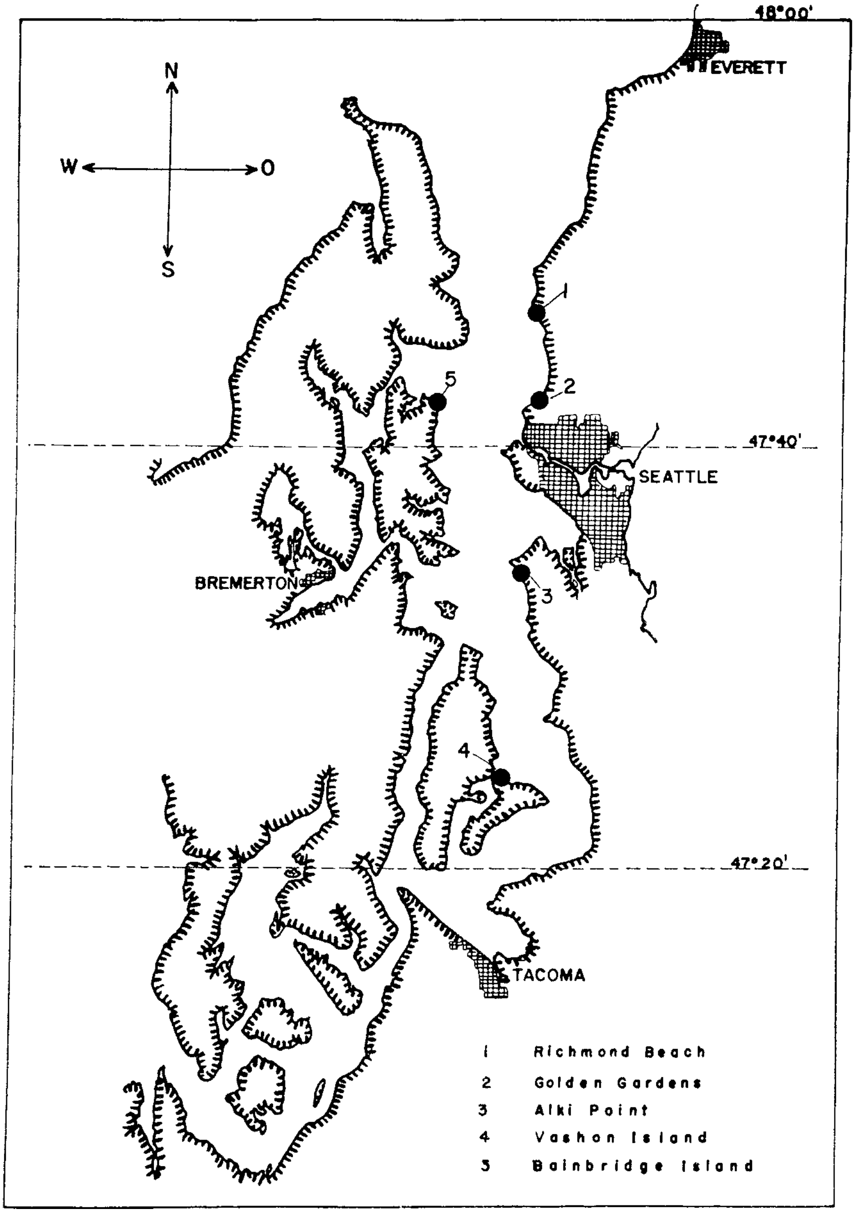
Localities investigated

Five localities were investigated (see Map 1), viz.: 1) *Richmond Beach*, near the railway station: most exposed locality; flat, uninterrupted beach, without boulders; 2) *Golden Gardens*, on the northernmost edge of the public beach: medium fine to coarse sand; between 2 and 4 feet a belt of boulders and rocks, overgrown with *Mytilus* and barnacles; in the lower portion of the intertidal there are patches of *Zostera* in which no samples were taken; above approximately the 3-foot level the beach is steeper than below it; 3) *Alki Point*, between Oregon and Genese Street in West Seattle: medium fine to coarse sand; from 3.5 feet upwards the beach is covered with boulders and rocks, overgrown with seaweeds, barnacles, *Mytilus* etc; in this zone the samples are derived from patches of sand between the boulders; in the lower portion of the beach there occurs the polychaet, *Telepsavus costarum*, apparently an indicator of silty and fine sand; dense algal growth (*Nereocystis*, *Laminaria*, etc.) below low water; 4) *Vashon Island*, in front of the small bridge connecting the two parts of the island: fine to medium fine sand, with boulders in the upper portion of the beach; *Zostera* and *Ulva* in patches in the lower portion; *Telepsavus costarum* reaching up to 5 feet; 5) *Bainbridge Island*, NE point of the island on the beach belonging to the Bainbridge Island State Park: very fine to medium fine sand, very coarse sand around 7-foot level, gravel between 4.5 and 7 feet; *Telepsavus costarum* reaching up to 3–4 feet, patches of *Zostera* reaching up to zero-level.

The position of these five localities with respect to the general configuration of the shore-line and the direction and force of the currents is such that they represent a series of decreasing exposure, Richmond Beach being the most exposed, Bainbridge Island the most sheltered locality. This fact was verified not only by observation in nature (based on the texture of the substrates) but also by the distribution of dyes in the scale-model of Puget Sound which has been built by the Department of Oceanography in Seattle (for this lesson in experimental Oceanography I am indebted to Dr. Clifford A. Barnes).

Sampling

In each locality samples were taken along a transect, roughly between -2 and $+8$ feet. Five to nine samples were taken per locality, in most cases each sample representing a different level of intertidal height. Each sample was taken during ebbing tide when the relevant level of the beach was still damp, sometimes between two waves but most of the time just above the limit touched by waves. No sampling was undertaken in rough weather. The intertidal height of each sample was determined on the basis of the tide chart of Seattle and vicinity. Sampling was carried out in the following way. The substrate was scooped up with a small beaker, and several sub-samples from the same level, a short distance apart, were emptied into a 1000 cc glass cylinder, until the substrate occupied about one-fourth of the cylinder. Filtered sea water was then added and the cylinder shaken vigorously. After allowing the sand to settle for a few seconds the water was decanted and filtered through very fine bolting silk. The material retained by the bolting silk was put into bottles and the bottles stored in a refrigerator until the contents could be examined. Animals were picked out under a dissecting microscope until it was felt a representative number had been collected.



MAP 1. Puget Sound with the five localities investigated.

For each sample the composition of grain sizes was determined by sieving the (dried) sand through a standard set of Tyler screens, using the following mesh widths: 4760μ (no. 4), 2362μ (no. 8), 1190μ (no. 16), 589μ (no. 30), 295μ (no. 50), 149μ (no. 100). Gravel coarser than 4760μ was discarded. Sand and silt finer than 149μ was collected in a pan and considered as one fraction. The fractions were weighed and the results expressed in per cent of the total weight. In order to obtain a characteristic figure for each sample the "median diameter" was computed on the basis of the cumulative distribution curve of the six fractions (see Krumbein and Pettijohn 1938). Since the fraction below 149μ was not differentiated, the "median diameter" of samples in which

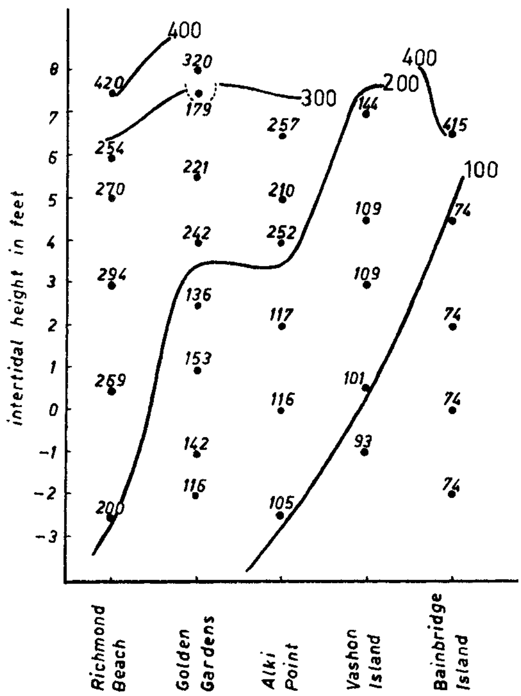


FIG. 1. Position of each sample in the five localities with respect to intertidal height. The five localities are arranged in a series according to their degree of exposure. For each sample the "median diameter" is shown, and the points of approximately equal grain size are connected by curves ("isomegeths").

this fraction made up more than 50% could not be computed. For these samples (of which there were only four) the "median diameter" was arbitrarily fixed at 74μ. Since in this extreme substrate it sufficed to establish the order of magnitude of the mean grain size, its vague determination does not influence any ecological conclusion based on the distribution of the grades of sand.

The substrate

The sorting of sand depends on the strength of water movements. Since the five localities investigated represent a series of decreasing exposure to currents, the mechanical composition of the five beaches can also be arranged in a series, Richmond Beach having on the average the coarsest sand, Bainbridge Island the finest. The sand on Vashon Island and Bainbridge Island consists largely of very fine fractions, but the organic content is low.

Perpendicular to this horizontal gradient, as far as the composition of the substrate is concerned, there runs a vertical gradient due to the tides. Water movements within the tidal zone on most marine shores cause fine sand to be deposited lower downshore than coarse sand since the momentum of the upswell is greater than that of the backwash. There are, however, exceptions to this rule (see also Pennak 1950 for conditions on lake shores).

The mechanical composition of each sample from my five localities is thus determined by two gradients—the horizontal one, represented by the series Richmond Beach-Golden Gardens - Alki Point - Vashon Island - Bainbridge Island, with Richmond Beach being the "coarsest locality," and the vertical one, represented by the series of intertidal levels from high water to low water, with high water being the "coarsest level."

This two-dimensional scheme can be represented by a diagram in which the "median diameter" is taken as an indicator of the composition of the substrate in each sample (Fig. 1). It can be seen that the decrease in mean grain size from high to low water is fairly regular. There is only one major irregularity in Golden Gardens, caused by an accumulation of fine deposits in the upper portion of the beach. The approximate points of equal "median diameter" can be connected, and these "isomegeths"[1] show fairly well the regular distribution of grades of sand in the area investigated. Roughly, coarse material can be found in the upper left, fine material in the lower right of Figure 1. Of great ecological importance is the fact that substrates of similar mechanical composition may be deposited on quite different tidal levels according to the strength of the water movements in the area.

In Tables 1 and 2 the specifications of all the samples are given. The complete list of all the species found in the five localities is given in Wieser (1959).

[1] From ισομεγεθης = of equal size.

TABLE 1. *Intertidal height, median diameter, and date of collection of samples*

Sample no.	Intertidal height (ft)	Median diameter (μ)	Date	Sample no.	Intertidal height (ft)	Median diameter (μ)	Date
Richmond Beach				Alki Point			
1	−2.5	200	5.13.57	16	−2.5	105	5.12.57
2	0.5	269	4.23.57	17	0	116	4.11.57
3	3.0	294	3.17.57	18	2.0	117	2.10.57
4	5.0	270	6.17.57	19	4.0	252	6.13.57
5	6.0	254	4. 7.57	20	5.0	210	12.20.56
6	7.5	384	5. 5.57	21	7.0	207	6.29.57
Golden Gardens				Vashon Island			
7	−2.5	116	10.31.56	22	−1.0	93	2.22.57
8	−1.5	147	6.22.57	23	0.5	101	5.25.57
9	−1.0	142	10.31.56	24	3.0	109	5.25.57
10	1.0	153	1. 9.57	25	4.5	109	2.22.57
11	2.5	136	3.14.57	26	7.0	144	6.29.57
				Bainbridge Island			
12	4.0	242	1.20.57	27	−2.0	74	12.28.56
13	5.5	221	3.14.57	28	0	74	4.26.57
14	7.0	320	10.27.56	29	2.0	74	4.26.57
15	7.5	179	5.17.57	30	4.5	74	12.28.56
				31	7.0	415	6. 2.57

THE INTERTIDAL DISTRIBUTION OF ABUNDANT SPECIES IN RELATION TO THE SUBSTRATE

The distribution of the animals on the beaches is governed partly by the factor of tidal exposure and submersion, partly by the composition of the substrate. In my area of investigation the former factor is constant for all localities, the latter is variable.

In order to understand better the factors which determine the range of distribution of intertidal animals it seems necessary to study the variation of distribution limits under the influence of local factors, the predominant of which is the substrate.

As far as my area of investigation is concerned the hypothesis suggests itself that the upper distribution limit of a species depending on fine sand will be higher up the shore in fine than in coarse sand and, conversely, that the lower distribution limit of a species depending on coarse sand will be lower down the shore in coarse than in fine sand. The following diagrams are designed to test this hypothesis by keeping apart the five localities investigated and by plotting the intertidal distribution of a species in relation to the median grain diameter of the samples in which it was found. All these diagrams are based on Figure 1. Only the most characteristic species are represented in this manner.

Since a general account of the intertidal distribution of *all* species would take up too much space, it will not be given here but can be found as an appendix to my paper on the nematodes of Puget Sound (Wieser 1959).

Hydrozoa

Protohydra leuckarti occurred at practically all tidal levels, but it showed preference for substrates with a median diameter finer than 200μ, so that it occurred higher upshore at Vashon Island than at Golden Gardens (Fig. 2). It might be significant that the species was absent in samples with the finest substrate.

Nematoda

Most of the species can be referred to certain groups as far as their extreme limits of distribution are concerned (Wieser 1959). A great number of species occur throughout the intertidal, amongst them some of the most abundant species of Puget Sound,

TABLE 2. *Relative frequency (percentage) of sand fractions in samples*

Size range microns	Sample 1	2	3	4	5	6	7	8	9
4760–2362	3.0	10.6	8.9	8.8	15.2	10.8	–	–	–
2362–1190	6.4	14.3	16.0	11.3	12.3	22.4	+	–	+
1190– 589	12.2	20.2	23.8	22.6	13.9	26.8	0.1	7.2	0.8
589–295	49.0	44.5	43.1	46.0	41.5	33.8	21.5	42.2	44.9
295–149	28.0	10.1	8.1	11.2	16.4	6.2	76.1	44.4	50.4
<149	1.3	0.2	0.1	+	0.7	+	2.2	6.2	3.9
	10	11	12	13	14	15	16	17	18
4760–2362	0.1	0.1	8.2	2.0	16.3	1.1	–	0.7	–
2362–1190	0.3	0.4	9.2	4.3	13.7	1.8	–	0.2	0.1
1190– 589	5.3	5.0	18.8	16.6	22.2	6.7	0.1	0.5	0.5
589– 295	45.2	38.0	45.3	61.8	37.5	59.9	2.9	20.7	23.1
295– 149	45.7	49.6	17.6	15.1	10.1	30.4	90.2	76.0	73.8
<149	3.4	6.9	0.9	0.3	0.2	0.1	6.8	1.9	2.5
	19	20	21	22	23	24	25	26	27
4760–2362	7.8	3.3	5.4	–	0.1	0.1	0.5	0.3	0.7
2362–1190	9.5	4.0	5.6	0.2	0.2	0.3	1.5	0.8	0.8
1190– 589	18.7	10.2	7.5	1.4	1.0	2.7	7.3	1.2	1.3
589– 295	56.4	62.3	58.5	9.4	12.2	19.1	22.8	45.0	3.5
295– 149	7.3	19.0	22.8	58.0	64.9	61.7	40.2	41.9	16.3
<149	0.3	1.2	0.2	31.0	21.6	16.1	27.7	10.8	77.4
	28	29	30	31					
4760–2362	–	0.1	–	11.5					
2362–1190	0.1	0.2	0.1	26.1					
1190– 589	0.2	0.6	0.2	23.9					
589– 295	1.1	4.6	1.8	12.9					
295– 149	6.0	8.9	41.6	24.3					
<149	92.6	85.6	56.2	1.3					

such as *Neochromadora poecilosoma* and *Hyalacanthion multipapillatum.*

The intertidal distribution of species which in some way are dependent on the pattern of distribution of certain grades of sand is illustrated in Figures 3–6. Figures 3, 4, and 5 show a number of species which reach further upshore in the localities with fine substrate than in those with coarse substrate. In some of these species the upper limit of distribution coincides roughly with the 200μ-line, *e.g.* in *Sabatiera* spp., *Theristus wimmeri*, *Mesacanthoides sinuosus*, *Odontophora peritricha.* In other species the upper limit of distribution lies more around the 100μ-line, as in *Enoplus velatus*, *Longicyatholaimus quadriseta*, *Theristus anticipans.*

Figure 6 represents another group of species which are confined to relatively coarse sand and consequently reach further downshore in localities with coarse substrate than in those with fine substrate. This holds particularly for *Enoploides harpax*, *Nudora armillata*, and *Theristus trecuspidatus.* In these species the lower limit of distribution coincides roughly with the 200μ-line.

Gastrotricha and Archiannelida

The intertidal distribution of all species belonging to these two groups can be inferred from Figure 7. No species of gastrotrich occurred below the 100μ-line and no archiannelid below the 200μ-line. This contradicts the statement by Pennak (1950, p. 460), that "the horizontal distribution of Protozoa, Turbellaria, Nematoda, Gastro-

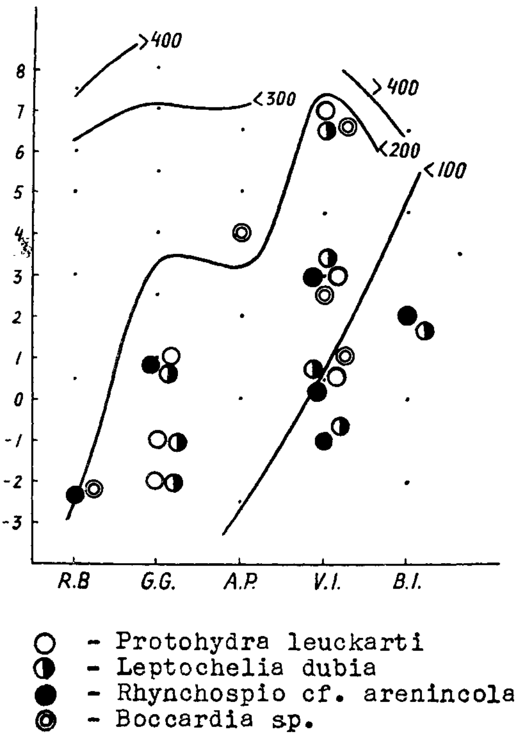


FIG. 2. Distribution of one hydrozoan, one cheliferan and two polychaetes with relation to the "isomegeths." Ordinate: intertidal height in feet.

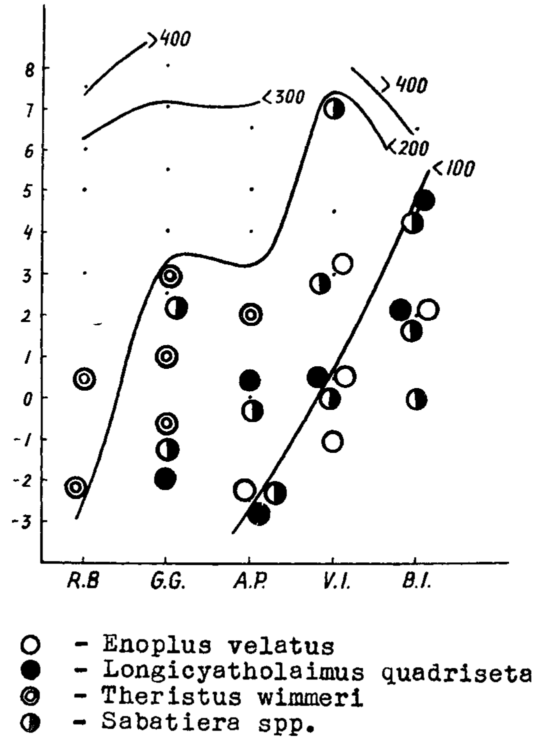


FIG. 3. Distribution of a set of nematodes with relation to the "isomegeths." Ordinate: intertidal height in feet.

tricha, and Oligochaeta shows no particular pattern" and that "most of these organisms are scattered at random throughout beaches . . ."

Polychaeta

Amongst polychaetes the most abundant species was *Rhynchospio* cf. *arenincola*, the distribution of which resembles that of *Protohydra leuckarti* (Fig. 2). No individuals were found above the 200μ-line. The same holds for the less abundant but equally common *Boccardia* sp. (Fig. 2) and, less characteristically, for *Eteone* sp. The distribution of the other species was more or less patchy (Wieser 1959).

Copepoda

Huntemannia jadensis (the most abundant species on the beaches of Puget Sound) and *Leptastacus* n.sp. occurred throughout the intertidal. A few other species were found in more than one zone, but the occurrence of most of the species was rather sporadic (Wieser 1959).

Two species, *Dactylopodia glacialis* and *Heterolaophonte strömi*, showed a fairly well established preference for substrates with a median diameter finer than 200μ (Fig. 8); they occurred therefore higher upshore at Vashon Island and Bainbridge Island than at Richmond Beach. A third species, *Heterolaophonte discophora*, perhaps displayed a similar mode of distribution, but was found too infrequently.

Ostracoda

Ostracods occurred predominantly below the 3-foot level, that is, in comparatively fine substrate. Of 12 samples in which ostracods were present 10 possessed a median diameter finer than 150μ. Only *Cytheridea papillosa, Leptocythere tenera* and *Cytherura gibba* occurred in sand with a

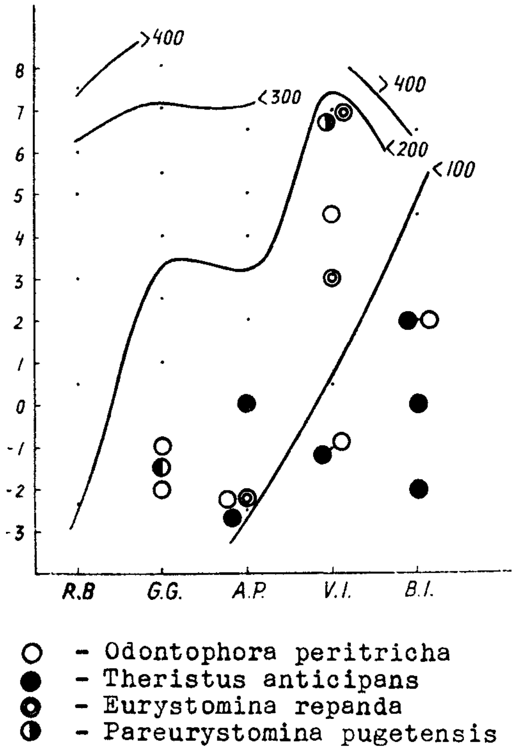


FIG. 4. Distribution of a set of nematodes with relation to the "isomegeths." Ordinate: intertidal height in feet.

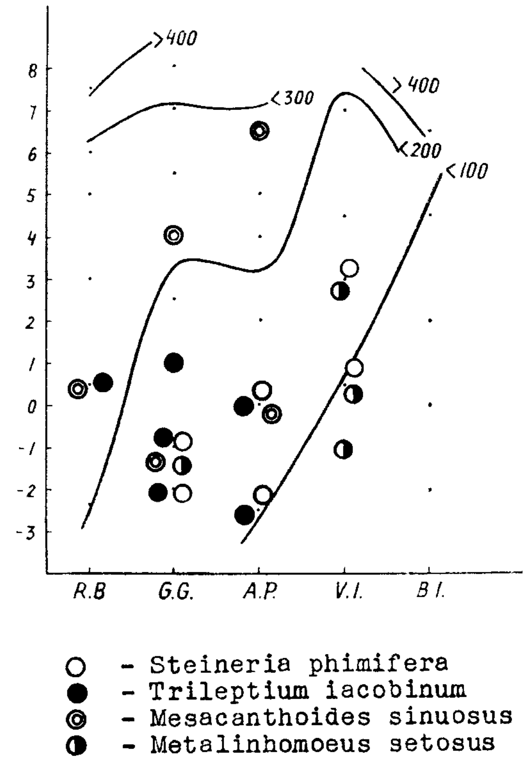


FIG. 5. Distribution of a set of nematodes with relation to the "isomegeths." Ordinate: intertidal height in feet.

median diameter coarser than 180μ. No ostracods occurred above 260μ.

Cumacea

The intertidal distribution of the species of cumaceans can be inferred from Figure 9. It is quite obvious that all three species exhibit a preference for fine substrate. No species surpassed the 200μ-line, except the males of *Cumella vulgaris* which are very active swimmers, while the females and juveniles are not. As far as their intertidal distribution is concerned all three species roughly follow the same pattern.

Other Peracarida

The upper distribution limit of *Leptochelia dubia* roughly coincides with the 200μ-line (Fig. 2).

Exosphaeroma oregonensis occurred in substrates with a median diameter from about 100 to 220μ, and at an intertidal height of 2 to 8 ft.

Amongst the amphipods the most abundant species, *Synchelidium* n.sp., was confined to the lower intertidal (−2.5 to +3 ft). *Corophium salmonis* occurred in the upper intertidal (2 to 8 ft), but only at Vashon Island which is a fine substrate locality.

DISCUSSION

Figures 2 to 9 suggest that the intertidal distribution of at least some of the more common species on the beaches is not so much determined by levels of tidal water as by the pattern of distribution of certain grades of substrate. Species of this sort will, for example, penetrate into the upper intertidal if the preferred substrate occurs there, but they will remain in the lower intertidal if the substrate is confined to this zone.

However, the distribution of such a species cannot always be explained entirely in terms

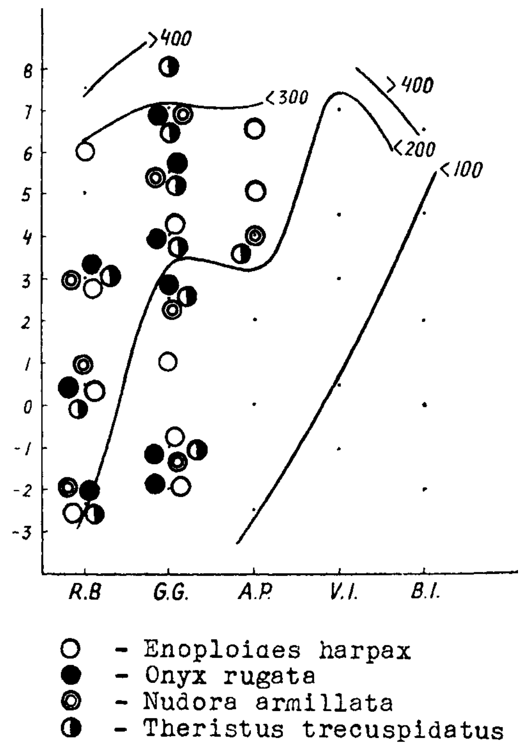


FIG. 6. Distribution of a set of nematodes with relation to the "isomegeths." Ordinate: intertidal height in feet.

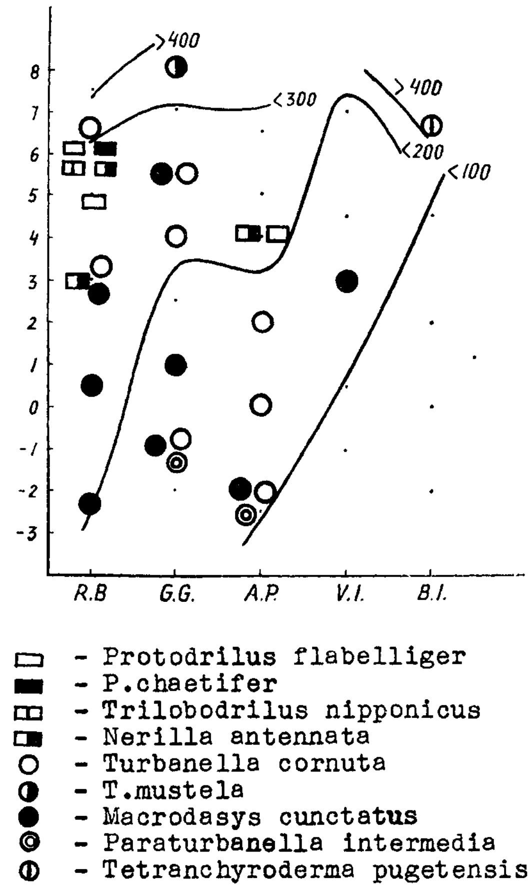


FIG. 7. Distribution of archiannelids (oblongs) and gastrotrichs (circles) with relation to the "isomegeths." Ordinate: intertidal height in feet.

of the presence or absence of certain grades of substrate; very often the availability of the latter is equally important. If, for example, a species does not occur at Richmond Beach this might be due to its preferring grades of sand with a median diameter smaller than 200μ. Consequently the species ought to be restricted *in its whole range of distribution* to samples with a median diameter smaller than 200μ. This certainly is not always the case. The nematode *Anticoma acuminata* is a frequent species in all localities except Richmond Beach, but at Golden Gardens and Alki Point it occurs in samples with a median diameter of 221 and 252μ. The same holds for *Oncholaimium vesicarium* and other species (Wieser 1959).

Such a pattern of distribution might be explained by the fact that at Golden Gardens and Alki Point the lower intertidal consists of relatively fine, the upper intertidal of relatively coarse material (cf. Fig. 1). It will therefore happen quite frequently that waves and rising tide carry animals from the lower into the upper reaches of the beach. In this way species which generally prefer fine sand might occasionally be found—or even become established—in coarse sand. At Richmond Beach on the other hand, the whole intertidal consists of coarse sand. Species preferring fine sand will therefore find less opportunity of being carried in from elsewhere.

A similar explanation might hold for the opposite case. Species which generally prefer coarse sand might be carried into fine sand wherever the intertidal comprises levels of both coarse and fine material, as at Golden Gardens and Alki Point. These

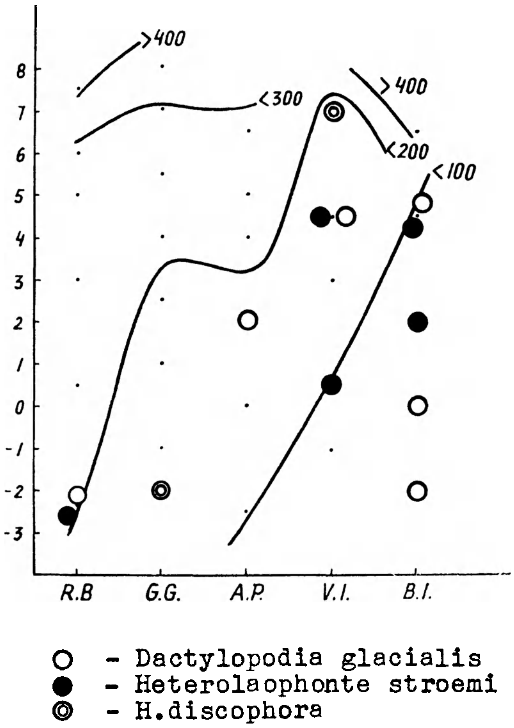


FIG. 8. Distribution of three copepods with relation to the "isomegeths." Ordinate: intertidal height in feet.

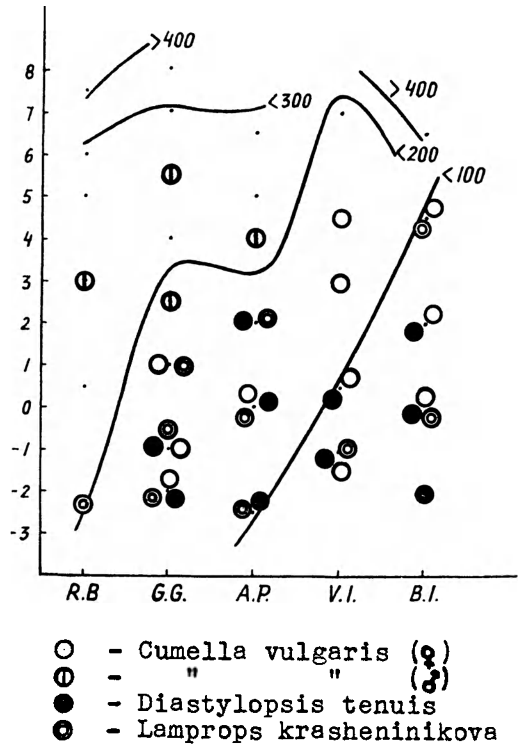


FIG. 9. Distribution of the cumaceans with relation to the "isomegeths." Ordinate: intertidal height in feet.

species will, however, be absent in localities like Vashon Island, in which the intertidal consists entirely of fine material. This assumption would explain the penetration of a number of species, such as *Enoploides harpax*, *Nudora armillata*, *Theristus trecuspidatus*, otherwise confined to coarse material, into the lower reaches of Golden Gardens (Fig. 6).

To me it seems unquestionable that the texture of the substrate exerts a profound influence on the distribution of the fauna, and I cannot agree with the generalized statement by Pennak (1950) that, amongst other factors, the size of sand grains has "no constant relationship to either number or distribution of organisms." The existence of such a relationship is suggested by the work of Davis (1925), Prenant (1932), and Jones (1950), although these authors did not distinguish between the actual effects of grain size and those of the physiographic environment in general of which the grain size is merely an indicator. However, more detailed ecological research within the last ten years indicates that the effect of grain size itself on "either number or distribution of organisms" is quite real and can be of the following types:

1) Sands of different grain size and shape are of different hardness. Bruce (1928) showed that ungraded sand (from Port Erin, Isle of Manx) can be so firmly packed as to have a porosity of only 20% while graded fractions of the same sand had porosities up to 44.7%. These different degrees of packing might influence the distribution of certain animals, or determine the depth to which certain other animals are able to burrow. A possible relationship of this kind is suggested by the work of Ekman (1947) and by that of Chapman (1949) on the thixotropy and dilatancy of marine soil, but the exact nature of the response of animals to different degrees of

hardness of the substrate is not yet established.

2) The horizontal and vertical transport of sand particles depends partly on their size. Some types of sand will be more stable than others, and this might lead to the establishment of characteristic faunas. Sanders (1958) has pointed out that particles with a diameter of 0.18 mm are most easily moved since for them roughness velocity, settling velocity, and threshold velocity are the same, and that sands of that grain size support a fauna characterized by large populations of infaunal filter feeders.

3) Invertebrates that obtain their food by scraping it off sand grains are dependent to a certain degree on the size of the grains. This holds most characteristically for crustaceans some of which alter their mode of feeding if the particles become too small to be handled by means of maxillipeds and maxillae, while too large particles are abandoned altogether. *Cumella vulgaris*, an epistrate feeder on grains between 500 and 150μ, avoids sand grains larger than 500μ, and switches to deposits feeding in still finer substrates (Wieser 1956). Another cumacean, *Picrocuma poecilota*, seems to feed from sand grains with a diameter of 150 to 350μ (Hale 1943). The larger of two amphipods, *Talitrus saltator*, occurs in coarse sand while the small *Talorchestia deshayesii* is present in fine sand (Dahl 1946). This distribution pattern might also be due to the different relationship between mouthparts and sand grains in these two species.

4) The most important characteristic of sands of different grain size is represented by their systems of interstitial spaces. The relationship between the latter and the sand fauna constitutes the main theme of the present paper. The importance of the interstitial spaces for the fauna is based on two facts: firstly, they provide the actual habitat of a specialized component of the sand fauna, and secondly, some burrowing or semisessile animals depend on the circulation of water maintained through the system of interstitital spaces. This has been shown for *Venus mercenaria* by Pratt and Campbell (1956) and for *Branchiostoma nigeriense* by Webb and Hill (1958).

"Critical grain size"

While studying the distribution of larger animals on rocky shores it was found that certain tidal levels proved to be "critical," that is, at these levels greater changes of fauna took place than at others (Coleman 1933, Evans 1947; for application of the "critical level" concept to the microfauna of seaweeds see Wieser 1952). By analogy the question suggested itself if on beaches there might not be "critical gain sizes" which constitute borders or barriers separating major faunal components.

It is, of course, an abstraction to speak of one grain size as constituting a distribution barrier, since the substrate on a beach consists of a mixture of grades of sand. However, as mentioned in the introduction, in almost all samples investigated the sorting was good, and therefore the "median diameter" can be considered a fair representation of the dominant fractions determining the texture of the whole sample. Consequently, the "median diameter" of a given sample can be used as an indicator of the true mechanical composition of this sample.

Keeping this in mind a survey of Figures 2–9 shows that the 200μ-line is a fairly important distribution barrier. This judgement is based entirely on the observer's first impression of the pattern of distribution of the species. To give it weight a statistical study of far more species ought to be made, but the material is insufficient for this purpose.

The 200μ-line approximately constitutes the lower limit of distribution of *Protodrilus flabelliger* and *Nerilla antennata*, of (with the reservations made on p. 190) *Enoploides harpax*, *Onyx rugata*, *Nudora armillata*, and *Theristus trecuspidatus*; it approximately constitutes the upper limit of distribution of *Sabatiera spp.*, *Theristus wimmeri*, *Pareurystomina pugetensis*, *Eurystomina repanda* *Odontophora peritricha*, *Trileptium jacobinum*, *Dactylopodia glacialis*, *Heterolaophonte strömi*, *H. discophora*, *Protohydra leuckarti*, *Rhynchospio cf. arenincola*, *Boccardia* sp., *Leptochelia dubia*, and of all three cumaceans (except the males of *Cumella vulgaris*).

One of the main reasons why sand with a median diameter of 200μ might be an effective distribution barrier is that around this grain size the interstitial spaces which exist in coarser sand are beginning to fill up with fine material. Thus the 200μ-line might approximately separate species that live in interstitial spaces from those that burrow through the substrate, although I doubt whether this holds for nematodes. Most of them are so slender that I suspect them of being capable of moving even between fine sand grains, which faculty they would have in common with the ciliates studied by Faurè-Fremiet (1950). This author found ciliates in sands with a medium diameter of 120μ, and there is no doubt that the protozoans were true representatives of an interstitial fauna, being characterized by great elongation of the body. In fact, some of them (particularly *Geleia orbis* and *Centrophorella fistulosa*) on the basis of Faurè-Fremiet's outline drawings could easily be mistaken for nematodes. Sands with a median diameter of 120μ might be the finest in which interstitial life is possible for any kind of organism.

The figure of 200μ as a grain size of ecological importance was mentioned also by Krogerus (1932) in a study on the relationship between dune sands of various grain sizes and beetles. Krogerus found that in a curve representing the water-holding capacity of sands of various grain sizes a break would occur around the size of 200μ. That is, if exposed to air, sand coarser than 200μ will give off water at a much quicker rate than sand finer than 200μ, the break being due to the discontinuous transition from more or less closely packed find sand in which the capillary forces are high, to coarse sand in which a system of interstitial spaces is developed and the capillary forces are comparatively low. This is in excellent agreement with the finding of Webb (1958) that in sand consisting of grains larger than 0.2 mm drainage of water is rapid, "not exceeding 11 minutes for a 10 cm column . . . while the drainage time through grains of 0.2 to 0.1 mm in diameter was more than 25 hours." In consequence, the lancelot, *Branchiostoma nigeriense*, which is a ciliar feeder and dependent on strong water circulation, if given choice of various substrates always chose those of high permeability, that is, substrates with grains between 0.2 and 0.3 mm. An addition of 25% of fine sand apparently obstructed the water circulation through the interstitial spaces and rendered the substrate unfavorable to the animals. The mystacocarid *Derocheilocharis remanei* also occurs in sands with a median diameter between 0.2 and 0.3 mm (Delamare Deboutteville 1954).

Distribution of locomotor types

Animals living in sand can move along either by sliding within the interstitial spaces or by pushing and burrowing through the medium. The former mode of locomotion is possible only in sand coarse enough to permit the development of an interstitial system (see Remane 1933, 1940). The latter mode ought to be most common in fine sand. The distinction between the two types is by no means sharp. Animals which in fine sand are burrowers might in coarse sand slide through interstitial spaces. Several copepods, for example, are likely to represent such intermediary types.

It would be interesting to know the distribution of these locomotor types with respect to the texture of the substrate, particularly with respect to the grain size of 200μ just mentioned. An attempt to summarize the pertinent data has been made in Figure 10. The unit in the diagram is the number of species in each sample for all groups investigated except nematodes. Most of the nematodes have to be considered as inhabitants of interstitial spaces, but as already mentioned they are so slender as to represent a group apart from all others. Moreover, Gerlach (1954) has shown that some species are burrowers, and although it is quite easy to recognize characteristic species of this type by their blunt shape it is by no means impossible that a number of species of less extreme shape may also employ this mode of locomotion. The decision as to which species uses which mode of locomotion is particularly difficult to reach in this group.

In Figure 10 the following species were considered as interstitial "sliders": all archiannelids, all gastrotrichs, and amongst copepods *Arenosetella* spp., *Pararenosetella gracilis*, *Leptastacus* n.sp., *Paraleptastacus* n.sp., and *Paraleptocaris* n.sp. (based on verbal information by W. Noodt). All other species apart from the nematodes are burrowers.

It can be seen that above the 200μ-line sliders are represented in all samples and that the number of burrowing species rarely exceeds six per sample. Below the 200μ-line there also occur sliders in a number of samples but most of them at Golden Gardens and Alki Point, where both coarse and fine sands are in close proximity (see p. 189). In most of the samples below the 200μ-line there are more than 10 burrowing species. No sliders were found below the 100μ-line.

These results enable us to see more clearly another way in which grain size might affect the distribution of animals on the beach. As was shown by Webb (1958), when the tide is receding the level of interstitial water will fall more rapidly in coarse than in fine sand. Consequently, in coarse sand there will be a premium on those animals that are able to follow the level of water as rapidly as it falls. This will be easiest for animals adapted to life in interstitial spaces since sliding in these spaces is virtually unimpeded and, theoretically at least, the animals should be able to stay close to the falling water level down to any depth (copepods, according to Pennak 1942, can still be found at a depth of 25 cm). Burrowing animals would find this much more difficult, since even a few centimeters below the surface the resistance of the medium is considerable.

In fine sand, on the other hand, capillary forces are greater, and the water level will fall more slowly when the tide is receding. Burrowing and slowly moving animals will therefore be able to stay close to the falling water either by burrowing downwards into the sand or by following the ebbing tide towards the low water mark.

Thus, put in another way, we may distinguish on the beach between "vertical

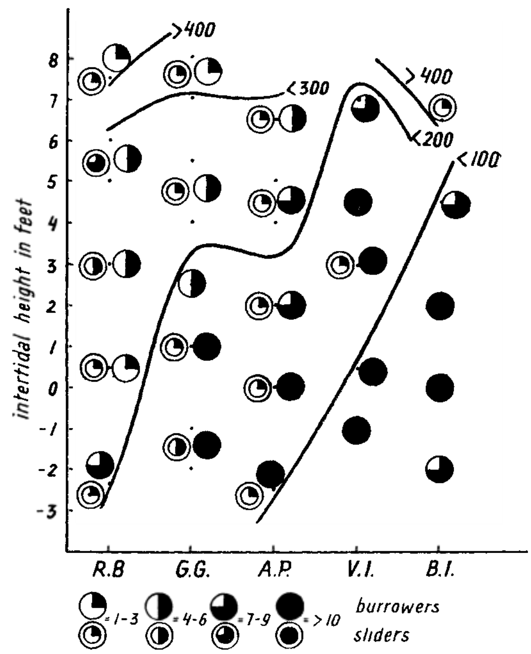


FIG. 10. Distribution of locomotor types with relation to the "isomegeths." Simple circles = burrowers; double circles = interstitial sliders. The number of species belonging to each type is indicated by the varying size of the black segments in the circles.

migrants," animals that move vertically within the sand layers, and "horizontal migrants," animals that move horizontally on the beach between high and low water mark. In the latter case the mode of locomotion may be either by crawling or by swimming. The driving force for each animal is to stay within a sand layer of optimum humidity. A similar distinction between "vertical" and "horizontal" migrants was established by Watkin (1941) and Remane (1940, p. 107). To the former type belong all interstitial forms, to the latter agile and large animals like amphipods and cumaceans, but perhaps also smaller forms like ostracods.

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