

MARINE BENTHOS, SUBSTRATE AND PALAEOECOLOGY

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ABSTRACT. The distribution of marine benthos in the Irish Sea is influenced by the nature of the substrate. The majority of epifaunal species are suspension feeders or carnivores and are associated with rocks or coarse-grained sediments. The majority of infaunal species are deposit feeders and are associated with fine-grained sediments. The relationships of the organic content of the sediment and the physical nature of the substrate to the benthos are discussed. It is argued that epifauna, and benthos living in well-sorted sands, are more likely to be transported after death than most infauna. Fossil epifauna are most likely to be found *in situ* at unconformities, disconformities, and bioherms. Over half of the species of epifauna but only one-third of the species of infauna have hard parts and are preservable as fossils.

GEOLOGISTS are accustomed to the association of a rock facies and its contained fauna, and such terms as black-shale facies, sandy facies, and reef facies usually evoke a picture of well-known depositional environments and their faunas, relatable to the experience of the individual concerned. Yet in spite of the geologist's dependence on, and indeed intimate knowledge of sediments, he rarely pursues so far as he might the relationship between sediment and fauna. We believe that a discussion of certain aspects of the relationships between living organisms and their sediments may provide a useful contribution to a subject which is perhaps more appreciated by ecologists than by palaeoecologists. (A recent article by Purdie (1964) which appeared after this paper was submitted shows that geological appreciation of this problem is indeed growing.)

An important aspect of the relationship between marine faunas and sediments was demonstrated by Petersen (1913), who divided the benthos of the Danish seas into epifaunas and infaunas. He recognized as epifauna those animals living upon, or associated with extraneous matter or vegetation resting on, the substratum forming the bottom, and as infauna, animals living in the sediments forming the level sea bottom. Various other terms, such as epibionts and endobionts (Schafer 1956) have been introduced to overcome etymological objections and to include plants as well as animals. Epibenthos and endobenthos are perhaps more satisfactory, but the original terms are entrenched in the literature and will be used here. The epifauna may be divided into sessile forms, occurring on rock, shells, weeds, and other objects on the sea floor but rarely on sediments, and active forms which can move freely over the substratum (Buchanan 1958).

Influence of sediment on benthos. Grain size, the most obvious feature of a sediment, affects the organism both directly and indirectly. Feeding methods are related to grain size; mode of attachment or movement depends on plasticity or the availability of hard surfaces; organic content and grain size are frequently a reflection of the strength of bottom currents; and the aerobic or anaerobic nature of the sediment is generally a function of grain size, although it is basically dependent on the rate of water circulation.

Grain size and feeding methods. The distribution of the faunas of the central part of the northern Irish Sea is well known (Jones 1940, 1951, 1952, 1956). From published and

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unpublished data it is possible to calculate the numbers of species of invertebrates on the various grounds off Port Erin, Isle of Man, in relation to the method of feeding. For this purpose they can most conveniently be classified as:

1. Suspension feeders (sestonophages)
2. Deposit feeders (detritus collectors and soil swallowers)
3. Carnivores
4. Uncertain feeding habit

There is no sharp distinction between epifauna and infauna, apart from ecological position, but infaunas are made up largely of species dependent for their food on detritus or plankton; that is, they are deposit or suspension feeders, together with a proportion of carnivores. Epifaunas, on the other hand, contain few or no deposit feeders but usually a number of specialized feeders such as browsers and sponge eaters (Thorson 1957), although these can in a broad sense be classed respectively as deposit feeders and carnivores. Epifaunal animals are naturally not adapted to burrowing as are many members of the infauna. They tend to be better protected than infaunal animals, with thicker shells, tests or carapaces.

Table 1 is an analysis of the feeding methods of 79 of the more abundant species of infauna. For each feeding method the species are classified by the grade of sediment

TABLE 1

Feeding method	% on each type of deposit				
	Mud	Muddy sand	Fine sand	Gravel/Shell	Widely distributed
Suspension	0	20.5	36.5	29	8.5
Deposit	62.5	61.5	54.5	33.5	58.5
Carnivores	37.5	9	9	29	16.5
Uncertain	0	9	0	8.5	16.5
Total number of species	8	24	11	24	12

to which they are confined or centred upon. Where they occur more or less equally on two or more kinds of sediment they are classified as 'widely distributed'.

In Table 2 the feeding habits of 56 species of epifauna are analysed.

TABLE 2

Feeding method	% on each type of deposit				
	Mud	Muddy sand	Fine sand	Gravel/Shell	Widely distributed
Suspension	0	0	0	31.4	33.3
Deposit	0	20	33.4	17.2	16.7
Carnivores	100	80	66.6	45.7	50
Uncertain	0	0	0	5.7	0
Total number of species	1	5	3	35	12

In Table 3 all species (368 in number) found on each ground during 1947 (including epifauna and infauna) have been analysed. No distinction is made in this case between species confined to one ground and those occurring on several. Where definite information is lacking a species is referred to its most probable feeding method.

TABLE 3

Feeding method	% on each type of deposit			
	Mud	Muddy sand	Fine sand	Gravel/Shell
Suspension Deposit	0	17.5	12.5	24.5
Carnivores	56.5	52	54.5	26
Total number of species	43.5	30.5	33	49.5
	23	127	68	150

There is a marked increase in the proportion of suspension feeders with the increase in grain size, from mud (where none was found) to gravel/shell deposits. Deposit feeders, on the other hand, show a proportionate decrease from the mud and sand environments to the coarser sediments. Carnivores depend on the presence of other organisms and may not be especially affected by grain size.

The grain size of the sediment therefore exhibits considerable control over the type of feeding mechanism acceptable in the different environments and provides an indication of the kinds of mechanism that may have been characteristic of past environments. The relationship is well known (see, for example, Sanders 1956).

Biomass and organic content. Biomass is low in fine-grained muds and well-sorted sands, and reaches maxima in muddy sand and shelly gravel deposits. Fine-grained sand, because of its susceptibility to erosion (see Hjultrom 1935, Inman 1949) and its low organic content, is a relatively unsuitable medium for the support of benthos. But with an increase in organic content (and with it almost certainly an increase in the amount of mud) sand becomes an organically rich medium, ideal for benthonic life. The resistance of the sediment to erosion is increased, moreover, as the organic material and mud bind the sand grains together.

Zenkevitch (1963, pp. 89, 90) stated that as a rule in the Barents Sea the larger the amount of the fine-grained fraction of the sediment, the richer its organic content. In other words, in regions with favourable conditions for deposition of the fine-grained fractions, large amounts of detritus are also deposited, but, on the other hand, these regions are usually unfavourable for the development of bottom life, presumably because of a low oxygen content in the deposit. However, many regions with a sandy bottom and a rich fauna may have a low content of organic matter. Good vertical and horizontal circulation prevent the accumulation of organic matter on the bottom. Hence though one may accept the rule that seas rich in life have more organic matter in their sediment, in some a reverse relationship between the amount of bottom life and organic matter in the sea bed may be created.

Zenkevitch (p. 138) also quoted Idelson (1930) on the quantitative distribution of the fauna on the Spitzbergen bank. On the middle part of the bank, where the bed is

washed clean, the fauna is very scarce. At the edges of the shallow, however, the biomass increases sharply, some 95–99 per cent. of it epifauna. Further on at the slope of the bank the benthos biomass is again reduced and then, on the mud beds surrounding the bank, it rises again. The main factor conditioning this biomass range is the distribution of foodstuffs, mainly organic detritus. The high biomass at the edges of the shallow, consisting mostly of epifauna, is conditioned by the presence of rich detritus washed out from the central parts of the bank and brought by water as a solid suspension. Further on, the reduction of the biomass is due to conditions unfavourable for the development of epifauna and infauna. (This is apparently due, though not stated, to an increase in suspended matter, causing reduction in epifauna, and a lower amount of organic matter in the sediment, which is less favourable to infauna.) The last increase in biomass is due to the infauna, which receives here, in a comparatively calm zone, an abundant amount of sedimentary detritus.

The richest fauna of the Barents Sea grows on sandy silts and silty sand floors. Epifaunal species are numerous on hard floors in the regions of strong currents. Areas rich in infauna are usually poor in epifauna and vice versa. On the one hand, this is explained by the properties of the sea floor since infauna cannot develop in rocky or cliff floors. On the other hand, in some areas the floor could have given refuge to infauna, but the abundant epifauna had taken all the food supplies; the bottom may contain large amounts of sponge spicules and owing to mechanical factors may become unfit for benthos habitation. This occurs on the Kildin bank, where finely cartilaginous and sufficiently silted floors give support to a rich epifauna and are almost devoid of infauna.

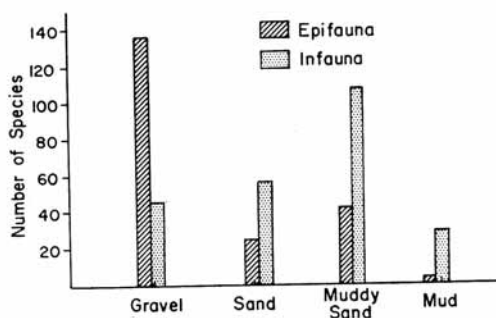
Savilov (1961) reported that in the northern Okhotsk Sea there is a replacement of one ecological zone by another in proportion to distance from the coast and increase in depth. In shallow coastal waters, rocks are occupied predominantly by a sessile epifauna consisting largely of suspension feeders. In the next zone on sandy bottoms mobile suspension feeders, mainly bivalves, predominate. This is followed by a wide zone of muddy sand with an infauna consisting mainly of detritus feeders, bivalves being replaced in the deeper parts by ophiuroids. Bottom feeders (soil swallowers) occupy the central deep part of the sea where there is a pronounced prevalence of sedimentation over erosion. Finally, in the depths from 1,000 to 3,000 m. the predominant group in the fauna is composed of immobile suspension feeders on soft bottoms. Carnivores cannot be allocated to any particular zone.

Nature of surface and plasticity of sediment. Firm surfaces, not necessarily rock outcrops, are suitable for attachment by such means as cementation, byssal or pedicle fixation, adhesion, etc. They also provide certain organisms, such as gastropods, with a suitable surface for locomotion. Many species are able to attach themselves to pebbles or shells exposed on the surface of an unconsolidated sediment.

Soft substrates vary considerably in their fluidity, which is a reflection of grain size and shape, and porosity (see Weller 1959). Relatively firm sediments may preclude the development of burrowers, as Chapman and Newell (1947) have shown with *Arenicola*; unstable sands do not encourage the development of life; and some muds are too soft to permit the survival of benthos. Indeed it is the common experience of geologists to find an absence of endemic life in originally fluid sediments, which have subsequently

revealed their instability by flowage (e.g. bottom structures in mudstones and slump structures in mudstones and sandstones).

Grain size and the distribution of epifauna and infauna. The varying abundance of epifauna and infauna in different sediments of the sea floor of the Irish Sea is shown in text-fig. 1. The proportion of epifaunal species decreases from gravel grounds to mud, whereas the proportion of infaunal species increases. A similar trend would be shown if the number of individual epifaunal and infaunal animals were plotted.



TEXT-FIG. 1. Histograms of the frequency distribution of infaunal and epifaunal species on different sediments in the Irish Sea off Port Erin, Isle of Man.

The factors which have determined these changing proportions are complex and interrelated. Three of them have been discussed—feeding methods, organic content, and physical nature of the sediment; all are related to grain size. A fourth, strength of bottom currents, is also relevant. Different species are influenced by these factors to differing degrees and it is not possible at this stage to categorize the species more closely than epifauna and infauna.

The rock terms used in text-fig. 1 suggest more mature deposits than are actually the case. The sediments are generally poorly sorted, including the two which yield the greatest number of species and individuals—muddy sand and shelly gravel.

Physically at least, the terms muddy sand and shelly gravel, as used in marine ecology, have much more in common than their names might at first imply. An organically rich muddy sand because of its suitability as a medium for benthonic life will, in the right conditions of temperature and salinity, support an abundant benthos. Under a low rate of sedimentation such an environment could develop into a shelly sediment in which the range of particle size (matrix+shells) could be as great as or even greater than that of a gravel/shell bank. The major difference between the two environments is that the shell/gravel sediment is formed in high energy conditions, whereas the shell bed of muddy sand forms in low energy conditions—an obvious difference, but one that has far-reaching implications so far as reworking and faunal type are concerned.

Sessile epifauna can live in either environment but shell/gravel grounds tend to support more epifauna than muddy sand environments where there are generally fewer suitable surfaces for attachment. Because of the different amounts of mud in the two environ-

ments, deposit feeders are more abundant in muddy sand, and suspension feeders more abundant in shell/gravel grounds.

We are now in a position to define in general terms the different ecological classes of animals to be found on, and in, different sea floors. Fine-grained sediments encourage the development of an infauna which consists mostly of deposit feeders; coarse-grained sediments support a community of infauna and epifauna which are mainly suspension feeders; rock surfaces support an epifauna of suspension feeders. Fine-grained sand is a poor medium for benthonic life and what little there is consists largely of infauna. Carnivores may inhabit all four environments.

Transportation. Work on the erosion and transport of sediments by Hjulstrom (1935) and Inman (1949) has demonstrated the comparative resistance of sediments of different grain sizes to erosion (see text-fig. 2). Fine-grained sand (of about 0.18 mm. diameter) marks the transition zone between transport in suspension and transport by surface creep. It is more easily moved than either the finer or the coarser grades of sediment and so tends to be better sorted. Although practically nothing is known of the behaviour of different grades of poorly sorted deposits in currents of different strengths, it is known that turbulence is greater over the rougher surfaces and that selective scouring must occur. Both Menard and Boucot (1951) and Johnson (1957) have discussed this problem in terms of sand and shells, and we assume that muddy sands and other ill-sorted sediments with shells will show a somewhat greater tendency to erosion (and shell concentration or removal) than the same sediments without shell material.

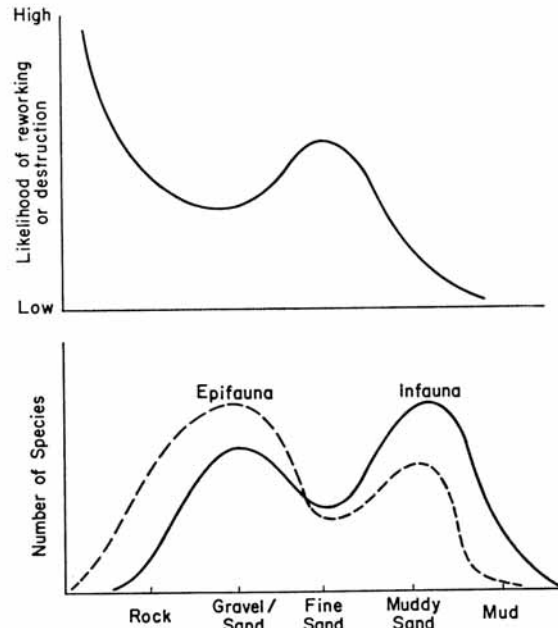
It is possible to generalize much of the information we have presented in the previous section. Text-fig. 2 shows the relationship between the abundance of epifaunal and infaunal species and the different grain sizes of sediment that they may inhabit. Since epifaunal species are more common in the higher energy environments and more exposed to currents, they are more likely to be transported after death. This is especially true of sessile epifauna. Active epifaunal species which inhabit areas of deposition are less likely to be transported after death. Only on sandy beaches are infauna more abundant than epifauna in a high energy environment.

One final point is of particular concern to palaeontologists. We have estimated the numbers of infaunal and epifaunal species which have hard parts and have therefore a chance of preservation as fossils in the Irish Sea. Out of a total of 79 of the more abundant species of infauna on the sea floor off the Isle of Man about 33 per cent. are preservable: out of a total of 56 of the more abundant species of epifauna 58 per cent. are preservable.

Influence of benthos on sediment. If a sediment is conducive to the establishment of life, then the character of the sediment will change. Burrowing organisms will modify existing sedimentary structures and create new organic structures by their burrowing activities and through digestion by deposit feeders and deposition of faeces; further, the increasing abundance of living and dead shelled animals will alter the texture of the sediment so that in extreme cases the sediment becomes a shell bed. The presence of organisms on the surface of the sediment affects its rate of accretion or erosion. At low current velocities, sedimentary particles may be trapped, but at higher velocities erosion may be prematurely induced or accelerated by the development of scouring around the shells. Experiments with shells in a flume tank have demonstrated this process (Johnson

1957). Indeed it is possible that the appearance of shells on a previously stable substratum could lead to its partial or even complete removal, without the need for any other change in the environment.

At the same time the change in the nature of the sediment will have an effect on the composition of the fauna. The larvae of those animals with a pelagic phase do not simply settle wherever they happen to be when the time for settlement arrives but show,



TEXT-FIG. 2. Idealized frequency distribution of infaunal and epifaunal species according to the nature of the substrate. The upper graph indicates the likelihood of transport or destruction of the benthos after death on the different substrates.

more or less, some power of selection. They respond to a suitable substrate and can delay settlement for some time until one is found (Wilson 1952, Smidt 1951, Thorson 1957). One of the stimuli affecting the settlement of many species is the presence of adults of the same species, and the successful settlement of some individuals may lead to the establishment of a larger population of that species. The build-up in the sediment of shells and their possible eventual transformation into a shell bed will have obvious effects on the fauna and may even lead to the complete change from an infaunal to an epifaunal community.

Palaeoecological implications. One aspect of the environment, the substrate, has been taken and its influence and effects on the benthos examined. Geologists understandably

tend to overemphasize the importance of the sedimentary environment since the other two important factors of salinity and temperature are not immediately obvious. The preoccupation in this paper with the substrate and its effects on the benthos should not blind the reader to the importance of these other factors.

We have shown that the chances of transportation of the shells of epifaunal species must be greater than those of infaunal species. From this it could be presumed that the chances of the destruction of epifaunal shells must also be greater. But epifaunal skeletons are usually stronger than infaunal skeletons and to this extent the balance is redressed.

It is difficult to arrive at an accurate estimate of the proportion of epifaunal to infaunal species. Thorson (1957) has shown that the number of epifaunal and infaunal species are much the same in the Arctic seas but that epifaunal species may greatly outnumber infaunal species in tropical waters. He estimates that overall, epifaunal species may be about four times as abundant as infaunal. The considerable reduction in the proportion of epifaunal species in polar water is the result of the excessively cold waters during the polar winters, and is not typical of the geological past. For this reason it seems that there should have been even more epifaunal species in the geological past and that they should form a high proportion of the preserved fossil record.

Epifauna may be found *in situ* in isolated cases in the geological record, principally at unconformities or disconformities and in bioherms. They will probably be more abundant than infauna (although reworked) on the rocks flanking and immediately above such structures, and in the earlier rather than the later stages of infilling of a basin. They will also occur more commonly in sediments of transgressing rather than regressing seas.

Another factor which influences the picture of the fossil state is the evidence, derived from the benthos of the Irish Sea, that even under favourable conditions of preservation between one-half and two-thirds of the major species of the benthos are *not* preservable as body fossils. More analyses of this kind are required from different environments but the results underline what every palaeontologist knows empirically, and emphasize all too clearly the difficulties to be faced in the reconstruction of the ecosystem of a fossil community. It would seem to be a whimsical fact that the fossil communities most likely to be preserved *in situ*—the infaunal—are most likely to have fewest members of the original living community preserved as fossils.

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REFERENCES

- BUCHANAN, J. B. 1958. The bottom fauna communities across the continental shelf off Accra, Ghana (Gold Coast). *Proc. zool. Soc. Lond.* **130**, 1–56.
- CHAPMAN, G. and NEWELL, G. F. 1947. The role of the body fluid in relation to movement in soft-bodied vertebrates. I, The burrowing of *Arenicola*. *Proc. R. Soc.* **134B**, 431–5.
- HJULSTROM, F. 1935. Studies of the morphological activity of rivers as illustrated by the River Fyris. *Bull. geol. Instn Univ. Upsala*, **25**, 221–527.
- IDELSON, M. 1930. A preliminary quantitative evaluation of the bottom fauna of the Spitzbergen Bank. *Trudy. morsk. nauch. Inst.* **4**, 3.
- INMAN, D. L. 1949. Sorting of sediments in the light of fluid mechanics. *J. sedim. Petrol.* **19**, 51–70.
- JOHNSON, R. G. 1957. Experiments on the burial of shells. *J. Geol.* **65**, 527–35.

- JONES, N. S. 1940. The distribution of the marine fauna and bottom deposits off Port Erin. *Proc. Trans. Lpool biol. Soc.* **53**, 1-34.
- 1951. The bottom fauna off the south of the Isle of Man. *J. Anim. Ecol.* **20**, 132-44.
- 1952. The bottom fauna and the food of flatfish off the Cumberland coast. *Ibid.* **21**, 182-205.
- 1956. The fauna and biomass of a muddy sand deposit off Port Erin, Isle of Man. *Ibid.* **25**, 217-52.
- MENARD, H. W. and BOUCOT, A. J. 1951. Experiments on the movement of shells by water. *Am. J. Sci.* **249**, 131-51.
- PETERSEN, C. G. J. 1913. Valuation of the sea. II, The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Dan. biol. Stn.* **21**, 1-42.
- PURDIE, E. G. 1964. Sediments as substrates. In IMBRIE, J. and NEWELL, N. D. *Approaches to Paleocology*. Wiley, New York.
- SANDERS, H. L. 1956. Oceanography of Long Island Sound, 1952-1954. X, The biology of marine bottom communities. *Bull. Bingham oceanogr. Coll.* **15**, 345-414.
- SAVILOV, A. 1961. Ecologic characteristics of the bottom communities of invertebrates in the Okhotsk Sea. *Trudŷ. Inst. Okeanol.* **46** (R).
- SCHAFFER, W. 1956. Wirkungen der Benthos-Organismen auf den Jungen Schichtverband. *Senckenberg. leth.* **37**, 183-263.
- SMIDT, E. 1951. Animal production in the Danish Waddensea. *Meddr Kommn Danm. Fisk. -og Havunders., Ser. Fiskeri*, **11** (6), 1-151.
- THORSON, G. 1957. Bottom communities (sublittoral or shallow shelf). In *Treatise on Marine Ecology and Paleocology* (ed. J. E. HEDGPETH). *Mem. geol. Soc. Am.* **67**, 461-534.
- WELLER, J. M. 1959. Compaction of sediments. *Bull. Am. Ass. Petrol. Geol.* **43**, 273-310.
- WILSON, D. P. 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Anals Inst. océanogr., Monaco*, **27** (2), 49-156.
- ZENKEVITCH, L. 1963. *Biology of the seas of the U.S.S.R.* London.

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