THE GANN FLAT, DALE: STUDIES ON THE ECOLOGY OF A MUDDY BEACH

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INTRODUCTION

PERHAPS the simplest situation in intertidal ecology is to be found on a homogeneous and uniformly sloping sandy beach where the fauna is limited in variety and the distribution of the animals is clearly related to tide levels. Muddy beaches, on the other hand, usually present a much more complicated ecological situation.

Muddy shores develop only where the water currents are weak enough to permit the deposition of fine particles, and under these conditions there is also a heavy settlement of organic detritus which provides food for a rich and varied fauna. The sheltered condition of these beaches produces many other effects on the fauna. Because the substratum is more stable than that of more exposed beaches, mud tends to be colonized by animals living in permanent burrows or tubes and the surface is marked by signs of the fauna beneath. The weak current permits the development of extensive, gently sloping beds, and the play of the currents over them produces slight variations in level and texture on which the effect of waves, when they do occasionally develop, is marked. This leads to the establishment of a very heterogeneous and patchy substratum and so to an irregular distribution of the fauna.

The relatively simple techniques employed in a study of the ecology of a homogeneous sandy beach are inadequate and may even be misleading on a mud flat. Instead of relating the distribution of animals to tidal level by means of a single line transect, as is usual on the former type of beach, it is necessary to consider the distribution of each species over the whole area of a muddy beach and to relate the distribution to tidal level and to a variety of other physical factors which are reflected in the nature of the substratum.

The Gann Flat at Dale, Pembs., forms a muddy beach with an extremely varied and patchy substratum and fauna. In this preliminary study we have attempted to discover something of the distribution of the more abundant members of the fauna and to suggest reasons underlying that distribution.

The variety of the flora and fauna of the Gann Flat has been emphasized by the records made by numerous workers at the Dale Fort Field Centre and these will be discussed below. In addition, detailed surveys of the Flat have been made by students from Bristol University in late March of 1958 and 1959, and by two summer classes organized by the Field Centre in late August or early September of the same two years. The idea for a survey of the Flat originated with the Dale Fort Warden, Mr. J. H. Barrett, and some preliminary ideas on methods were provided from work carried out with earlier classes by

Mr. J. Moyse. The final shape of the survey was based on preliminary investigations in an inclement period of August 1957 by a "class" consisting of Mr. Barrett, Mr. Moyse, Mr. R. Brehaut of Guernsey and the present authors.

Estimates of the distribution and abundance of the animals have been based on about ten parallel transects taken across the Flat at intervals of about 200 ft. On each transect there were about 20 equidistant stations (determined by pacing) at each of which a count was made with the aid of a metre square. The total population present was then calculated after the results from over

Table 1. *The areas of the Gann Flat at various levels*

For the purpose of the table the Gann Flat is the area limited by the 21 ft. chart contour and the two broken lines in Fig. 1.

Vertical level (feet)	Area exposed in 1,000 sq. m.	Percentage of total area	Vertical level (feet)	Area lying between two adjacent one foot contours in 1,000 sq. m.	Percentage of total area
Below			Between		
21	616	100·0	20 and 21	7·9	1·3
20	608	98·8	19 „ 20	7·9	1·3
19	600	97·5	18 „ 19	7·9	1·3
18	592	96·1	17 „ 18	7·9	1·3
17	585	95·0	16 „ 17	14·6	2·4
16	570	92·5	15 „ 16	13·1	2·1
15	557	90·6	14 „ 15	18·1	2·9
14	539	87·5	13 „ 14	17·1	2·8
13	522	84·8	12 „ 13	20·9	3·4
12	502	81·5	11 „ 12	20·0	3·2
11	481	78·2	10 „ 11	25·6	4·2
10	455	73·9	9 „ 10	23·5	3·8
9	432	70·2	8 „ 9	43·7	7·1
8	388	63·0	7 „ 8	52·8	8·6
7	336	54·6	6 „ 7	81·1	13·2
6	255	41·4	5 „ 6	73·3	11·9
5	181	29·4	4 „ 5	73·4	11·9
4	108	17·5	3 „ 4	71·3	11·6
3	36	5·9	2 „ 3	34·2	5·6
2	2	0·3	Below 2	1·9	0·3

200 stations had been plotted and contoured, by measuring the areas at each density and multiplying by the average density in each area. These totals must be regarded as no more than crude estimates of the population of each species.

In deciding which animals and plants to study the following considerations prevailed. Firstly, the species must be common and, secondly, it should be recognizable in the field. Thirdly, it should be easily counted. Thus plants are at the surface and easily counted, the lug worm, *Arenicola*, can be recognized by its casts and the fan worm, *Branchiomma*, by its tube. Some estimates of animals like *Nephtys* could only be obtained by digging and sieving. For one reason or another some species have had to be ignored despite their abundance, and the results presented here are of only a few selected species.

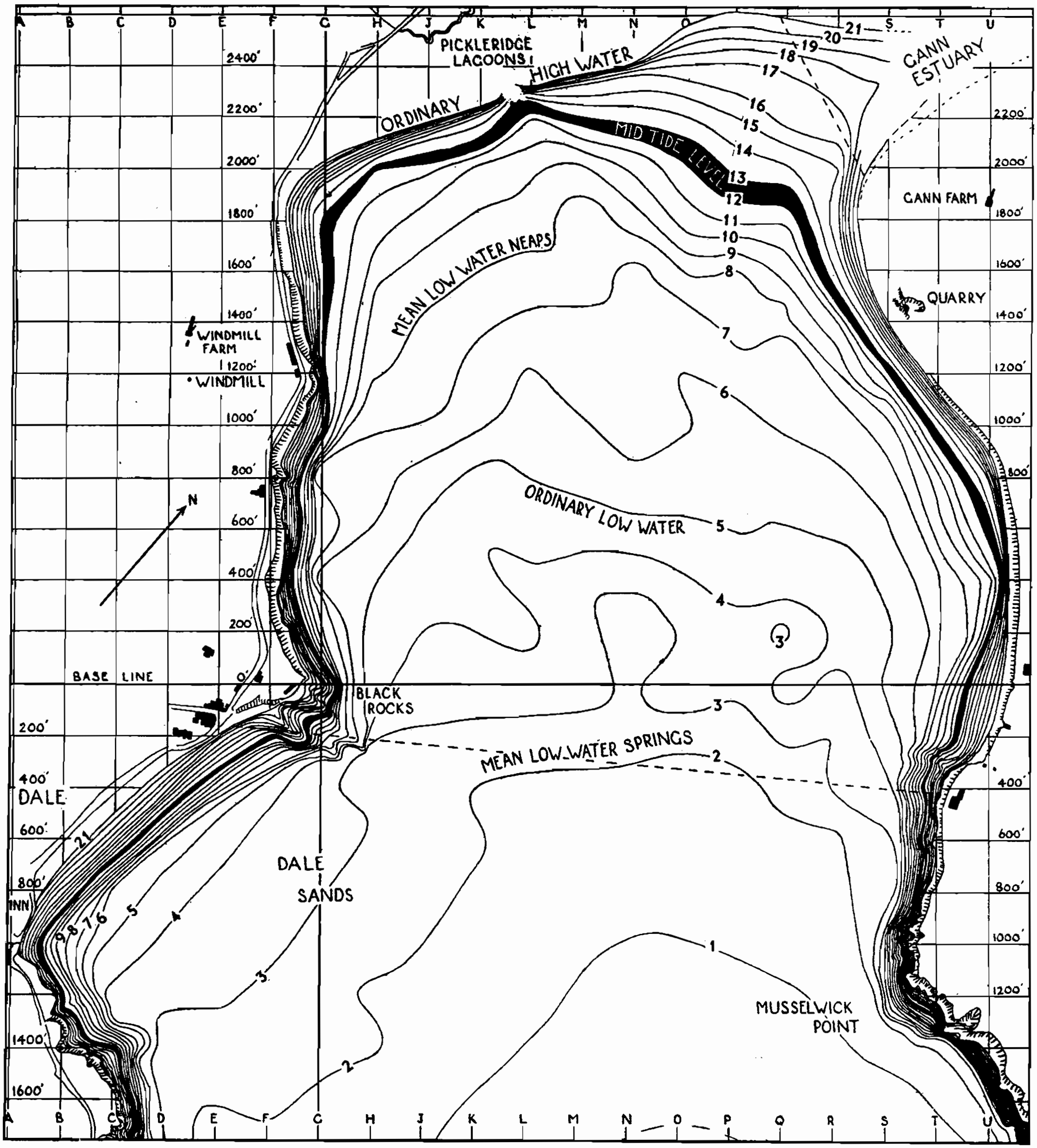

Fig. 1.
A chart of the Gann Flat and Dale Sands showing tide levels in feet above Chart Datum. The base lines and 200′ grid are from a survey by the Haverfordwest Rural District Council in 1957. The contours were drawn from survey data provided by the Council Surveyor and are reproduced with permission. Chart Datum is 12·03′ below Newlyn Ordnance Datum and the limits of the Flat are indicated by the 21′ chart contour and by arbitrary broken lines.

In addition to the biological data, a physical survey of the Flat was made in 1957 by the Haverfordwest Rural District Council and the Surveyor has most courteously permitted us to copy the data and to publish charts based on them.

GENERAL DESCRIPTION OF THE AREA

Dale Bay is a rectangular inlet extending about one and a quarter miles in a north-westerly direction from the mouth of Milford Haven, and it is about half a mile wide. The sides of the Bay are steep rocky shores but the head of the Bay consists of low lying land in which are the Pickleridge Lagoons and the Gann Saltings. It is through the Saltings that a brook, the river Gann, flows into the Bay.

Table 2. *Areas of the Gann Flat covered at chosen tide levels*

	Level above Chart Datum (feet)	Percentage Area Covered	Percentage Area Exposed
Mean Low Water Spring tides	2·2	1·5	98·5
Approximate Low Water Ordinary tides	5·0	29	71
Mean Low Water Neap tides	8·1	64	36
Mid Tide Level	12·6	84	16
Mean High Water Neap tides	17·2	95	5
Approximate High Water Ordinary tides	21·0	100	0

The data available do not permit consideration of levels higher than 21 ft. and they would, in any case, only affect the area near the Gann mouth. Their influence on the steep cliffs surrounding the Flat amount only to a few per cent of the total area involved.

Although the side walls of the Bay plunge steeply into the sea, the floor shelves very gently from the head of the Bay so that spring tides expose the Gann Flat of over 600,000 square metres (0·238 square miles); there is also a low lying extension of the Flat called Dale Sands on the south-western side (Fig. 1).

Reference to Figs. 1 and 2 and Tables 1 and 2 indicates that the shape of the Flat is of a flat plain with sloping sides. Thus only 16 per cent. of the Flat lies above mid-tide level, and mean low water of neap tides exposes only 36 per cent. of the area. Ordinary tides expose 71 per cent. and the remaining 29 per cent. (nearly one third of the area and the most productive region) is only available for examination on really low tides. This feature of the Flat is clearly illustrated in the final column of Table 1. Starting at high water (21 feet above datum) a drop of one foot in the tide level exposes 1·3 per cent. of the area. This rate increases very slowly until the drop from 10 to 9 feet still exposes only an additional 3·8 per cent. From 9 to 7 feet this proportion increases until below 7 feet a fall of one foot exposes about 12 per cent. additional area and this rate of exposure continues and is much enhanced at the lowest levels by large areas of Dale Sands which are not included in the Gann Flat area proper.

On the flatter part of the Gann Flat there is a low sandy ridge which runs down the middle of the Flat separating an eastern basin in which flows the

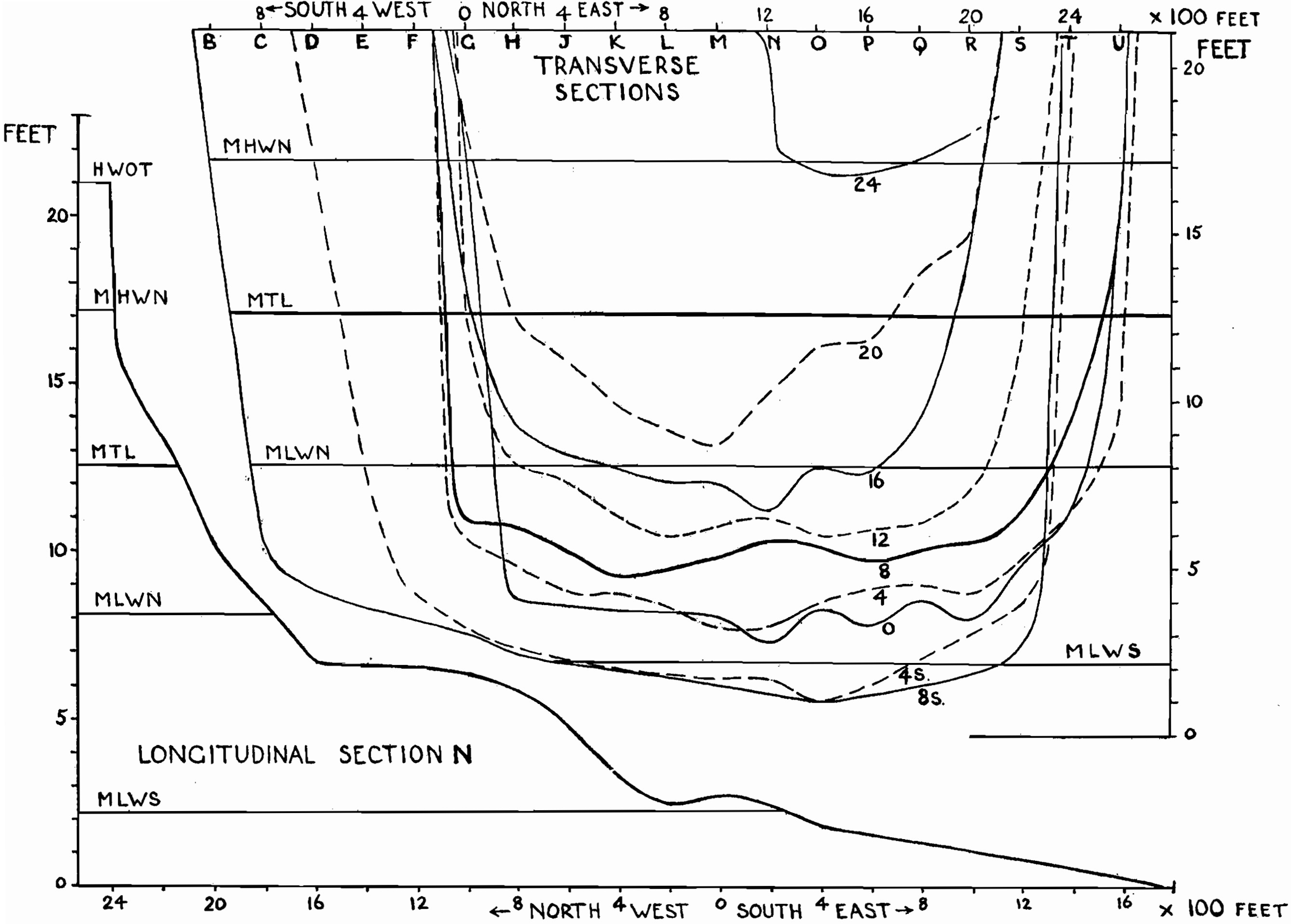

FIG. 2.

Longitudinal and transverse sections of the Gann Flat, with vertical scales giving heights above Chart Datum. The longitudinal section is along the line N. in Fig. 1, the horizontal scale giving distances from the intersection of line N. and the S.W.—N.E. Base Line through Black Rocks. The transverse sections are numbered by their distances (in 100 ft.) from the S.W.—N.E. Base Line, the horizontal scale giving distances across the Flat from the N.W.—S.E. Black Rocks Base Line. (Based on survey data provided by the Haverfordwest Rural District Council and published by permission.)

main part of the discharge from the Gann Estuary and Pickleridge Lagoons, and a western basin which takes some of the seepage through the shingle from the Lagoons. Most of the drainage from the Gann Estuary and Pickleridge Lagoons is of sea water which floods in at high tide so that nowhere are brackish water effects very marked. Most of the water drains away across the surface but in flatter areas shallow pools remain throughout the intertidal period (Fig. 3b).

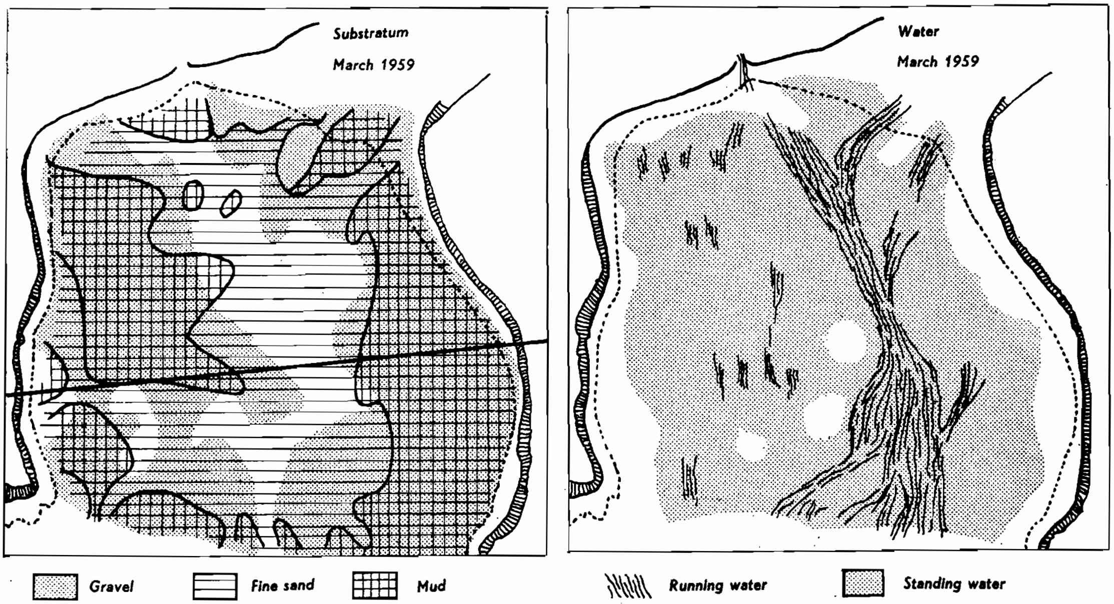

FIG. 3.
Diagrams showing (a) the nature of the substratum and (b) the distribution of surface water on the Gann Flat.

The underlying stratum of the area is a thickness of fluvioglacial gravel on which the fine sand and mud of the Flat has been deposited. The gravel which contains some large stones, forms a wide strip down each side and occupies some two thirds or more of the area. The fine sand down the middle is flanked by muddier sand and both sand and mud extend across the gravel areas (Fig. 3a). Pure mud, unmixed with stones, occurs rarely and although a patch is known in the east corner of the Flat its limits have not been determined.

THE FLORA (ALGAE)

No detailed examination of the Gann Flat flora has been published although a few records for this area are included in the lists published by Thomas (1953) and in the *Phycological Bulletin* (Burrows *et al.*, 1957).

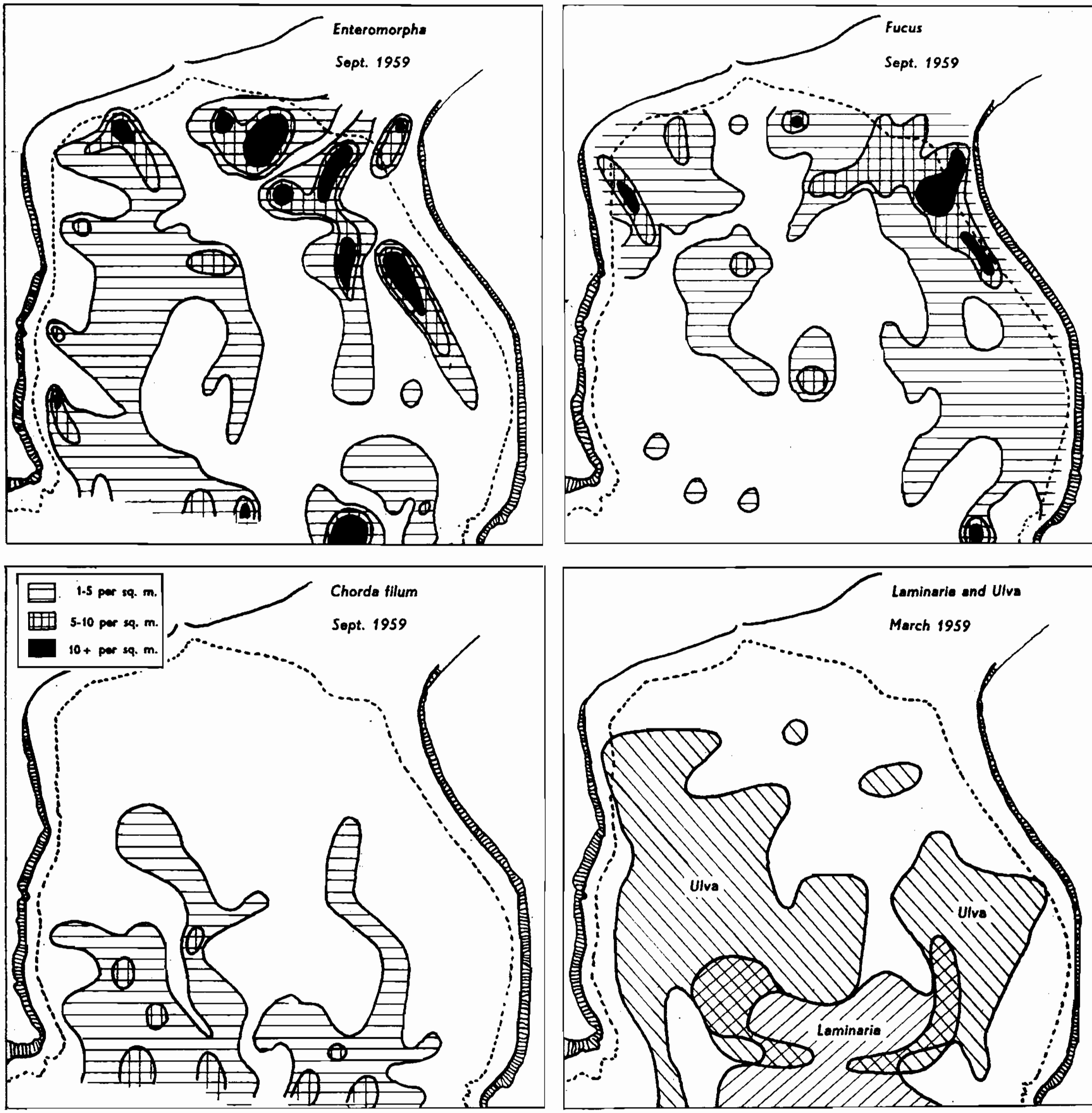

FIG. 4.

The distribution of *Ulva lactuca, Laminaria saccharina, Enteromorpha* spp., *Chorda filum* and *Fucus* spp. on the Gann Flat.

Although the rocky fringes of the Gann Flat carry a normal algal flora, the main cover being provided by the characteristic series of fucoids, the open flats provide a relatively unsuitable environment for the development of a dense plant cover. Nevertheless scattered plants are present over the greater part of the flats where small stones are available for attachment, and there is much plant growth in the more elevated and stony areas in the corners of the bay, particularly near the Gann mouth.

The results of surveying some dominants appear in Fig. 4. Near the Gann mouth is a complex association of *Fucus spiralis*, *F. vesiculosus*, *F. ceranoides* and *F. serratus* with various hybrids. *F. serratus* is particularly well developed near Musselwick. *Laminaria saccharina* is usually found in a wide band from Black Rock to Musselwick but in the summer of 1959 its place was largely taken by *Chorda filum* (Fig. 4).

THE FAUNA

(1) *A General Survey of the Population*

The rocky shores down the sides of the Flat support a normal sheltered-water rock fauna particularly rich at Black Rock and Musselwick. Representatives of this fauna are to be found on large stones all across the upper part of the Flat. However, the Flat itself, consisting as it does of small stones intermingled with gravel, mud and sand, offers an environment suitable only to species specialized for this situation. As most of the Flat lies below mid-tide level the fauna is rich and consists mainly of polychaete worms with some bivalve molluscs, except where the Flat extends southwards on to Dale Sands where a fine bed of the razor shell, *Ensis*, and the burrowing heart urchin, *Echinocardium*, occupy a low lying bed of muddy sand.

Animals living on the surface (hermit crabs, shore crabs, periwinkles, *Calyptraea* etc.)—the epifauna—are scarce. The rich infauna of burrowing and tubicolous species consists of two main types—the filter feeders and the deposit feeders. The first filter food from the sea water, e.g. some bivalve molluscs such as *Venerupis* and worms such as *Sabella* and *Branchiomma*. The deposit feeders feed at the surface (*Lanice* and *Amphitrite*) or deeper down (*Arenicola*, *Audouinia*). Carnivorous species like *Nephtys*, nemertine worms and *Priapulus* are a third group.

Bassindale and Barrett (1957) list over 150 species from the Gann Flat and many species are doubtless still unrecorded. Most phyla are represented and the following notes give some indication of the constitution of the fauna.

PORIFERA. The only sponge which may be properly regarded as a Flat species is the yellow or orange *Suberites domuncula* which is not uncommon and is often associated with hermit-crabs.

COELENTERATA. Six species of hydroid have been identified from stones and weeds but there are probably many more present. The growth varies from year to year and was good in 1958. *Obelia* and *Aglaeophenia* are the most conspicuous; *Hydractinea* is found regularly on shells inhabited by the hermit crab.

The Scyphozoan *Lucernaria* occurs on algae but is rare.

Anemones are more characteristic of rocky shores but some are mud living forms. Five species have been recorded including two which live in the sand, *Halcampa* and *Peachia* (both rare), and *Cereus pedunculatus* which is found commonly on the Flat around Black Rock and across Dale Sands, being attached to small stones a few inches below the surface, spreading its disc on the surface of the muddy sand.

PLATYHELMINTHES. Two species of the large, highly coloured but delicate, free living Polyclad flatworms have been found on the Flat. The triclad, *Procerodes ulvae*, lives near the Gann mouth and is characteristic of beaches over which fresh water flows.

NEMERTINEA. Detailed investigation might show that these carnivores are much more abundant and important on the Flat than the meagre records so far indicate.

ANNELIDA. No oligochaetes are recorded. The whole of the Gann Flat is emphatically dominated by polychaetes. Over 40 species are already recorded, some in large numbers. Although many polychaetes are found on Dale Sands, their importance is somewhat diminished where the more uniform texture of the muddy sand supports razor shells and the burrowing heart urchin.

Notable among tubicolous worms are *Branchiomma*, *Melinna*, *Lanice*, *Owenia*, *Sabella* and the maldanids, while among burrowing but more or less sedentary species *Arenicola*, *Amphitrite*, *Audouinia*, *Cirratulus*, *Glycera* and others are important. Among more actively burrowing species *Nephtys*, *Marphysa*, *Goniada* and *Perinereis* are abundant.

Among interesting even if relatively rare species are: the brackish water, *Nereis diversicolor; Aphrodite aculeata*, the sea mouse, which is occasionally found near low tide level; the very large *Marphysa sanguinea; Flabelligera affinis*, which wanders around in a mucous tube through which the chetae project to permit locomotion and which is frequently found, when small, on the surface of the urchin *Psammechinus miliaris; Pectinaria* which builds so neat a tube of carefully chosen sand grains, and *Amphitrite edwardsi* whose burrow occasionally houses the commensal scale worm *Lepidasthenia argus*.

SIPUNCULOIDEA. These carnivorous animals are represented by two species on the Flat, one of which is notable for having on its body a species of the Kamptozoan, *Loxosomella phascolosomata*. The commoner species *Golfingia elongatum* is sparsely distributed over a wide area near L.W.M.

PRIAPULOIDEA. Not unlike the Sipunculoids, the voracious carnivore *Priapulus* is distinguished by a curious cluster of terminal outgrowths of unknown function. It is very rare on the Flat and is normally a sublittoral species.

ARTHROPODA. Ostracods and copepods may be well represented on the Flat but preliminary efforts to collect them by a flotation technique have failed. Two interesting parasitic species of copepod occur—the bright red *Mytilicola* living in the intestine of the common mussel and *Sabelliphilus* (recorded only twice from the Gann Flat and only twice previously in Britain in 1877 and 1888) living on the tentacles of *Sabella*.

Barnacles are not found on soft bottoms but *Balanus balanoides* and *Elminius modestus* can tolerate muddy conditions and live on the larger stones. The parasitic species, *Sacculina carcini*, occurs occasionally on shore crabs.

The most numerous of the Crustacea—the Malacostraca—includes species which live as epifauna on the Flat and one Order, the Amphipoda, is particularly well represented. Of some 40 Malacostraca so far recorded, more than a dozen are amphipods and these small animals live a generally scavenging life in the surface sand or under small stones. The species of *Gammarus* and *Marinogammarus* require close examination in the light of recent work on this group and several species including brackish water representatives are probably present. Among sand hoppers, which are notably common in the sand near H. W. M. on Dale Beach and at the head of Dale Bay, three genera have been recorded (*Talitrus*, *Orchestia* and *Talorchestia*). There are only a few records of the swimming types of Malacostraca; mysids, particularly *Praunus flexuosus*, are commoner in summer than in spring; the shrimp, *Crangon vulgaris*, and prawns (*Palaemon* and *Leander* spp.) are common at low water springs. The shore crab, *Carcinus maenas*, and the hermit-crab, *Eupagurus bernhardus*, are abundant; the burrowing sand crab *Corystes* is occasionally found near L.W.M. but otherwise crabs are rare.

Among other Malacostraca, *Nebalia bipes* is interesting for its mixture of primitive and specialized characters and *Jaera albifrons* for its tolerance of reduced salinities.

MOLLUSCA. Gastropod molluscs are not characteristic of soft bottoms but of the 21 species listed for the Gann Flat a few are common. Large *Littorina littorea* and *Calyptraea chinensis* are widely scattered near low water, *Buccinium undatum* is frequently and *Turritella communis* occasionally exposed by extreme tides while a few species of opisthobranchs and nudibranchs are occasionally seen, particularly *Aplysia*.

By contrast with the Gastropoda, the Lamellibranchia are typical of sand and mud flats and are here second in importance only to the polychaetes. Some 30 species have been recorded including *Nucula*, *Chlamys*, *Venus*, *Tellina*, *Venerupis*, *Cardium*, *Mya* and *Barnea*, and the razor shells (*Ensis siliqua*) which dominate a great area of Dale Sands.

ECHINODERMATA. This group of rock-living animals does include soft bottom specialists of which the Gann Flat has three notable representatives. The burrowing brittle star *Acrocnida*, and the burrowing heart urchin *Echinocardium* are both found on Dale Sands; *Acrocnida* also occurs in the more stony conditions across the low tide region of the Flat itself. The burrowing sea cucumber *Leptosynapta* is found in a small patch of gravel at L.W.M. near Musselwick.

CHORDATA. Fishes are well represented in the waters of Dale Bay and many species swim over the Gann Flat at high tide. Of typical shore species a few gobies and blennies are present; the lesser sand eel, and various pipe fish also occur. The tunicates are represented by two compound ascidians, *Botryllus schlosseri* and *Botrylloides leachi*, which are very common on stones and algae at L.W.E.S.T. The Enteropneust *Saccoglossus* is a notable species and occurs in patches near extreme L.W.M. on Dale Sands and towards Musselwick.

(2) *The distribution of some common species.*

Arenicola marina (L.)

Professor G. P. Wells has published a long series of papers on the biology and habits of *Arenicola* and much of this work is summarized in a recent article (Wells, 1957).

The occurrence and distribution of *Arenicola* on the beaches around the coast appears to depend upon the presence of suitable conditions for feeding, respiration and burrowing. For feeding, *Arenicola* requires that there should be a heavy deposition of organic detritus onto the substratum. This requirement is particularly well met on the intertidal zone of rather muddy beaches; fast water currents prevent the deposition of either silt or organic detritus on coarse sandy beaches. The animal is able to draw a respiratory current of water through its burrow only when it is submerged, but it is able to absorb oxygen from the air providing it is damp. However, its penetration to the higher tidal levels on the beach is ultimately limited by the length of time it can withstand exposure. Relatively little is known about the preferences of substratum of *Arenicola*, except that it generally avoids fine mud or particularly coarse substrata. The worm does not secrete a tube, but merely consolidates the walls of its burrow with mucus, so that it cannot live in shifting sands. It is possible, too that the worm is unable to burrow into certain types of substratum. Adult worms burrow to a depth of 12 inches or more and a layer of dense, impenetrable material, such as hard clays may be sufficient to prevent *Arenicola* colonizing parts of a beach although the surface substratum appears to be suitable for them (Chapman and Newell, 1949). Within these limits *Arenicola* is tolerant of a wide range of soft substrata. It is also tolerant of a wide range of salinities and is one of the characteristic species of estuaries.

The influence of both intertidal level and variations in the character of the substratum on the distribution of *Arenicola*, as well as tolerance of a wide range of salinities, can clearly be seen on the Gann Flat. Lugworms are distributed over almost the whole beach and in the Gann estuary, but the greatest numbers occur around the periphery of the Flat at about L.W.N.T. (Fig. 5) although many of the worms in these peripheral populations are small. This is a somewhat lower tidal level than is usual for them on most beaches in Britain, France and Germany, where the greatest density of *Arenicola* is usually about M.T.L. The reason for occupying a lower tidal level on the Flat than elsewhere is probably because the level of the beach rises abruptly above L.W.N.T. and the substratum becomes coarser. The *Arenicola* bed is far from continuous, and is interrupted in places by patches of unsuitable substratum. The narrow trench of fine mud near the Gann Stones is devoid of *Arenicola* and so are the areas of shingle near the mouth of the Gann (cf. Fig. 3a).

The area of gravel and stones near the slipway at the west corner of the beach has only a few *Arenicola* and these are confined to small isolated patches of sandy mud lying between the stonier areas.

An estimate of the number of lugworms over an area can be made by counting the number of worm castings. We have found, by digging out all the worms in a sample area, that there is a good correspondence between the number of casts and the number of worms. Since all the castings are

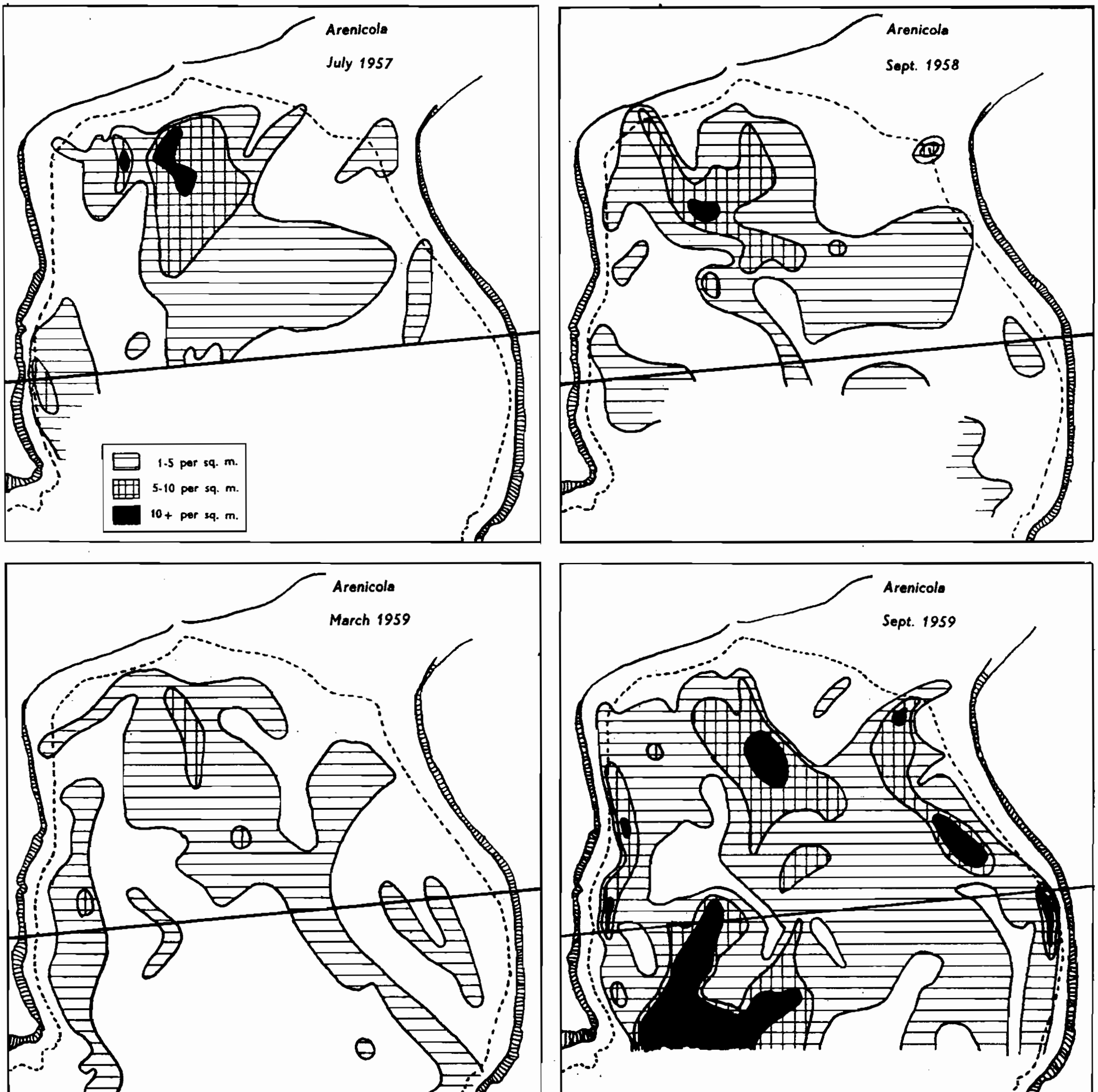

FIG. 5.

The distribution of the lugworm *Arenicola marina* on the Gann Flat.

washed away at each high tide the population measured by the number of castings is liable to be underestimated rather then the reverse. This source of error is most obvious in the stream of water that runs across the Flat and may account in part for the low density of *Arenicola* recorded in the stream beds. The greatest density recorded by this method was 40 per sq. m. (rather small individuals) in September 1959, at one spot near the Gann mouth. The average density is, of course, very much less.

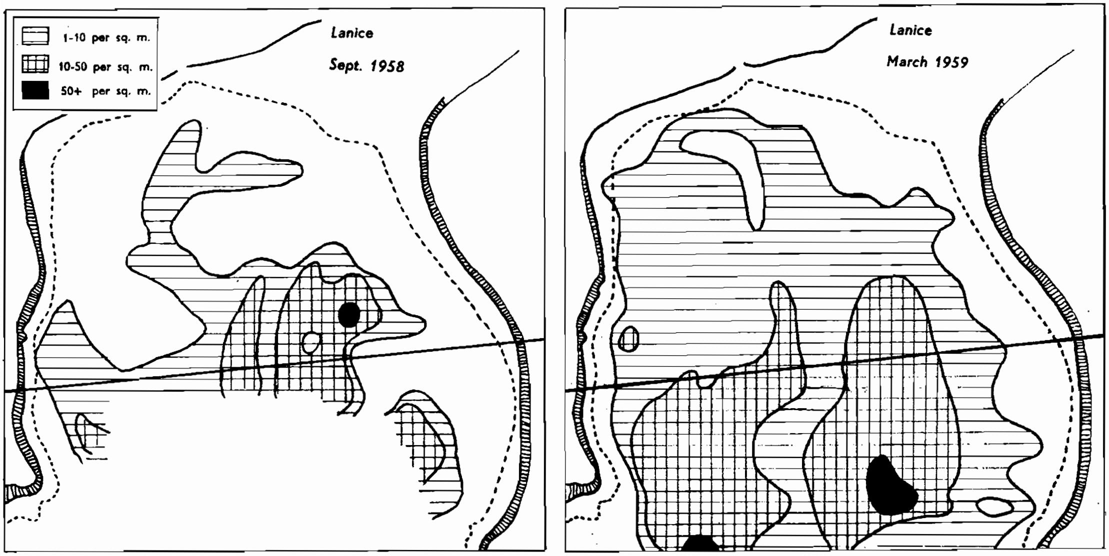

FIG. 6.
The distribution of the worm *Lanice conchilega* on the Gann Flat.

Lanice conchilega (Pallas)

This terebellid worm, like *Arenicola*, feeds on surface detritus, though instead of feeding in bulk, as *Arenicola* does, *Lanice* picks up individual fragments and conveys them to its mouth by means of its long extensible tentacles (Dales, 1955). The particles are sorted out by the lips, the smaller ones are ingested and the larger fragments are either rejected or used in the construction of the tube. The tube is constructed of coarse sand grains, small fragments of stone and shell plastered together with mucus. Its open end has a very characteristic frilled lip on one side, which hangs like a flap over the mouth of the tube, and possibly prevents the animal from drying when the beach is exposed. The mouth of the tube projects no more than an inch or two above the surface but the other end may be buried at a considerable depth.

The worms live in a great variety of substrata, from clean sand to muddy gravel, and on the Gann Flat it may be found almost anywhere below L.W.N.T. except in the area of shingle around the mouth of the Gann and in the coarse muddy gravel along the N.E. side of the flats (Figs. 3a and 6). It occurs in lower numbers on the sand bank in the centre of the beach than in the muddy or sandy gravel on either side of it. This worm has to emerge from its burrow in order to feed and it has been found that its numbers tend to be greatest near L.W.S.T. and in the shallow sub-littoral (Dales, 1955). This trend is reflected in the estimated population of *Lanice* on the Gann Flat. It has been found that on the upper part of the beach, including only a small area below L.W.M.O.T., the population is about 900,000 whereas that of the whole

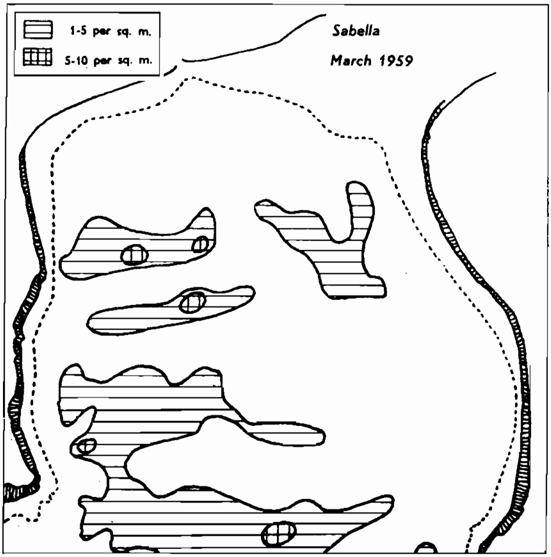

FIG. 7.
The distribution of the fan worm *Sabella pavonina* on the Gann Flat.

beach, including the area exposed only at spring tides, is about 3,000,000. It will be noticed too that *Lanice* extends in numbers further up the beach in the drainage area from the lagoon and the Gann estuary, where it is probably always submerged.

The tube of *Lanice* is sometimes found to be empty so that our counts of tubes may over-estimate the population of worms, but this inaccuracy is not likely to obscure general trends in the population.

Sabella pavonina (Savigny)

The sabellid worms feed on suspended detritus which is filtered from the currents of water drawn through the tentacular crown by ciliary activity (Nichol, 1930). The filtered particles are carried along tracts on the inner side of the tentacles and are sorted into three size groups at the base of the tentacular filaments. The largest particles are discarded, the smallest particles pass into the mouth and are ingested, while the medium sized particles pass in a string of mucus to the collar where they are wound around the lip of the tube which is constantly being added to in this way. The worms live in the lower part of the intertidal zone and in the shallow sub-littoral where suspended detritus is most abundant. Furthermore they are confined to comparatively still water, presumably because of the size and delicacy of the branchial crown, and so are found only where there is a muddy substratum.

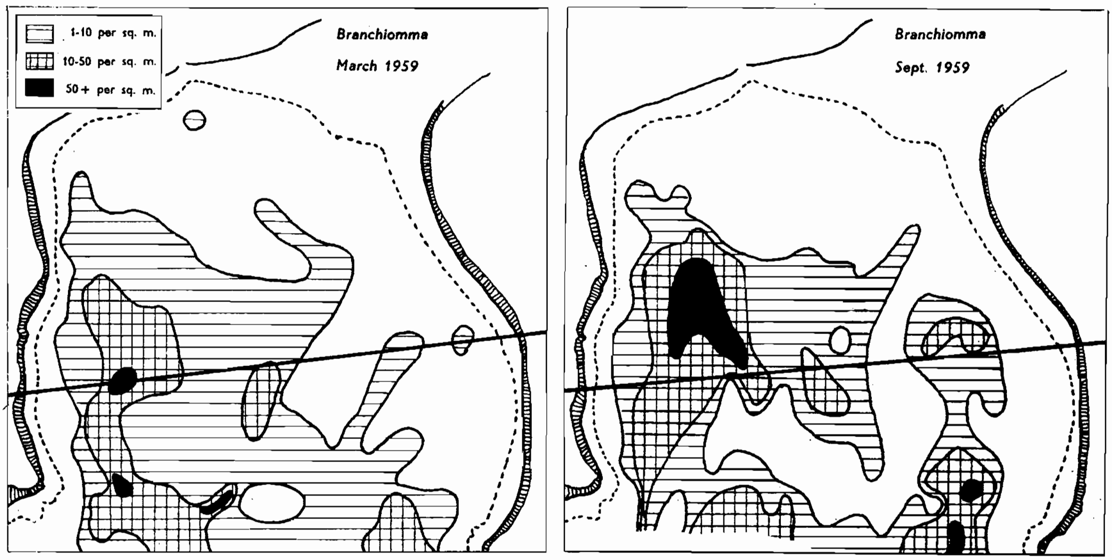

FIG. 8.
The distribution of the fan worm *Branchiomma vesiculosum* on the Gann Flat.

Although the Gann Flat represents a region of still water where there is a constant deposition of silt and where there is a considerable amount of detritus in suspension in the water, there are no dense beds of *Sabella* (Fig. 7). The greatest numbers occur on the very protected S.W. part of the beach in mud or muddy gravel. Areas of sand or sandy gravel appear to be avoided by the worms (cf. Fig. 3a).

Sabella tubes are always occupied. As soon as the worm dies the tube must fill up with mud and disintegrate.

Branchiomma vesiculosum (Montagu)

This sabellid has similar feeding habits to *Sabella*, and like it is confined to the lower part of the beach, but having much stubbier tentacles it is able to withstand stronger water currents and is generally found to replace *Sabella* on beaches with coarser substrata and so is one of the commonest and most conspicuous polychaetes on the Gann Flat. Its tube projects an inch or two above the surface and is easily recognizable. The method by which *Branchiomma* builds its tube is unknown but it must certainly differ from the method of tube-building used by *Sabella* because a *Branchiomma* tube is encrusted with small stones, shell and coarse sand grains, none of which could have been filtered out of the water by the tentacular filaments.

Branchiomma is widely distributed over the beach below M.L.W.O.T. (the 5 ft. level) (Fig. 8). The largest estimated population recorded for the upper part of the beach was two million and for the whole beach more than three and a half million in the late summer of 1959 (Table 3).

Table 3. *Estimated populations on the Gann Flat of some common species (in thousands)*

A. UPPER BEACH (north of the line shown in Figs. 5 to 8).

	1957	1958		1959	
Species	Summer	Spring	Summer	Spring	Summer
Arenicola marina	502	—	516	274	971
Lanice conchilega	640	808	878	910	—
Branchiomma vesiculosum	1,503	244	1,685	722	2,179
Sabella pavonina	22	—	26	131	—
Mytilus edulis	—	1,533	584	1,364	1,781

B. WHOLE BEACH.

	1959 Spring	1959 Summer
Arenicola	345	1,746
Lanice	3,216	—
Branchiomma	1,797	3,643
Sabella	213	—

Owenia fusiformis (Delle Chiaje)

Owenia is one of the less conspicuous polychaetes on the beach, though it occurs in fairly large numbers. It lives in a sandy tube about 10-12 cms. long and no more than 2-3 mm. wide. The top of the tube may project a little above the surface of the sand, but more often, during the day and at low tide, it is retracted beneath ground level. Although technically a "sedentary" worm, *Owenia* is muscular and able to burrow through the sand carrying its tube, which fits it tightly like an extra skin. To do this it must retain a firm hold on the tube and it is not surprising that each segment carries enormous numbers of uncinate hooks (variously estimated at numbering a total of 150,000 to 450,000 per segment), nor that it is extremely difficult to extract a worm undamaged from its tube (Watson, 1901).

Although the tubes generally project above the surface, they are not always visible and are not easily recognizable in the field. The population and distribution of *Owenia* can be studied only by digging up the worm. The distribution of *Owenia* on the Gann Flat is not entirely known, but the greatest numbers, rising to 80 per sq. m. around L.W.M.O.T., are in the rather muddy sand in the centre of the beach (Fig. 9). In the more gravelly substratum at the mouth of the bay, they tend to be replaced by *Clymene* and *Melinna*. The worms are stated (Watson, 1901, Dales, 1957) to be very hardy in the laboratory and an abundant supply of muddy sand is more important than good oxygenation of the water. This agrees with their distribution on the beach, for they appear to avoid the areas of clean sand, which are too high up the beach, and also to avoid areas of gravelly mud, through which presumably they would have some difficulty in burrowing as well as in finding suitable particles out of which they build their tube.

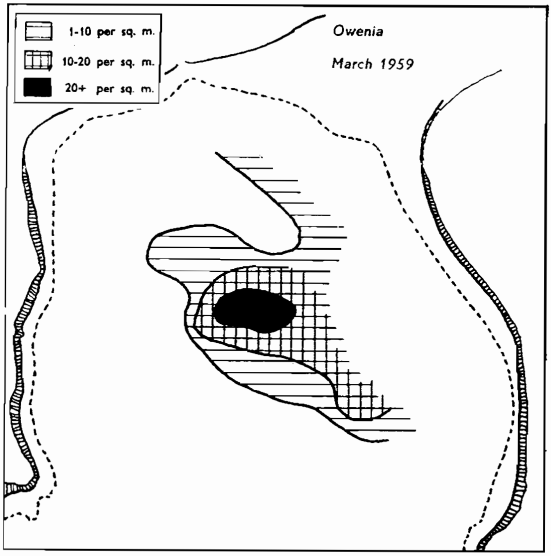

Fig. 9.
The distribution of the tube worm *Owenia fusiformis* on the Gann Flat.

Nephtys spp.

Nephtys is a carnivorous polychaete that burrows in the sand. Only two species, *N. hombergi* Lamarck and *N. cirrosa* Ehlers, are common in beaches on the south and west coasts of Britain and they occupy fairly distinct habitats (Haderlie and Clark, 1959, Clark and Haderlie, 1960). The former species inhabits rather muddy sand in which between about 2 and 6 per cent. of the constituent particles are less than 0·125 mm. in diameter. It is unable to live in much muddier deposits than this because its gills become clogged. *Nephtys cirrosa* generally lives in substrata containing between 4 and 50 per cent. particles smaller than 0·125 mm., but it will tolerate coarser substrata, providing that the larger particles are not composed of sharp shell fragments; or it will tolerate a higher proportion of fine particles, so long as there is also a high percentage of coarse ones. Substrata of the last type, containing relatively large amounts of both coarse and fine material, are referred to as "poorly sorted"; those in which the particles are more nearly uniform in size are "well sorted". Poorly sorted substrata are a comparative rarity, but where they exist the ecological requirements of both *N. hombergi* and *N. cirrosa* may be met simultaneously and the two species live side by side. Fine substrata, suitable for *N. hombergi*, are found in the lower reaches of estuaries and in the sub-littoral zone. The coarser substrata in which *N. cirrosa* lives are characteristic of the open coast.

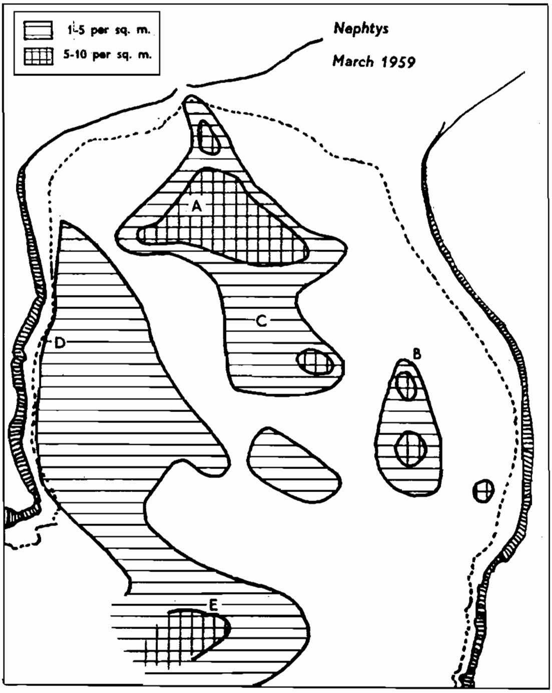

FIG. 10.

The distribution of the burrowing worm *Nephtys hombergi* on the Gann Flat. The letters A to E show where samples of the substratum were taken for analysis (Table 4).

Table 4. *Mechanical analysis of substrate samples taken at Stations* A *to* E. (Fig. 10).

Stn.	V. Fine Sand <0·125 mm.	Fine Sand 0·125-0·25 mm.	Medium and Coarse Sand >0·25 mm.
A	8·43	66·46	25·11
B	14·52	82·63	2·82
C	9·96	30·93	59·10
D	48·57	16·71	38·73
E	13·00	86·62	0·37

The Gann Flat, with its very patchy and poorly sorted substrata, is one of the few beaches around the coast to contain both species of *Nephtys* though, since the beach tends to be muddy, *N. hombergi* predominates over *N. cirrosa*. It is clear that the distribution of these worms bears very little relation to tidal level, but is determined by the nature of the substratum. The greatest number of *N. hombergi* occur at the head of the sand bank (Fig. 10, Station A) but the numbers fall abruptly a little lower down (Station B) where the bank becomes muddier. The seaward end of the bank is gravelly and supports only a few

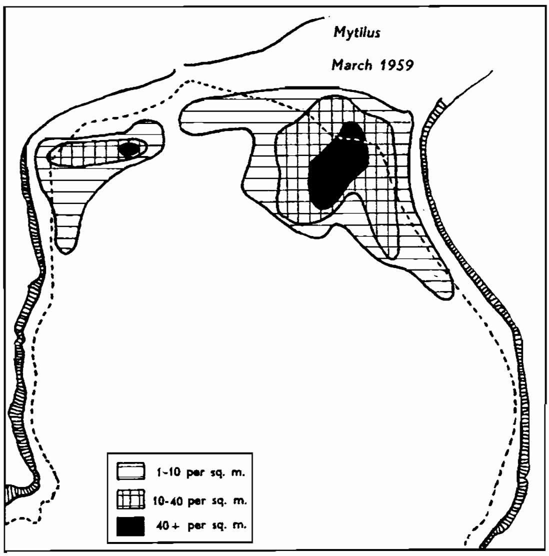

FIG. 11.
The distribution of the common mussel *Mytilus* spp. on the Gann Flat.

N. hombergi except in a patch of sandy gravel at the eastward corner of the beach and in the sub-littoral sand bank off Dale Beach (Station E). All the muddier parts of the Flat (e.g. Station D) contain too high a proportion of fine particles even for *N. hombergi*. *Nephtys cirrosa* has an even more patchy distribution and its density is too low at only 1 or 2 per sq. m. for very reliable conclusions to be drawn about the factors limiting its occurrence. It is restricted to a few areas of clean sand or sandy gravel.

Mytilus spp.

The mussel, *Mytilus*, lives on rocks and so its distribution on the Gann Flat is severely limited by the lack of suitable substrata. The chief populations are on the boulders around the mouth of the river Gann and in the stones near the western slipway; both areas are at about H.W.N.T. Even in these limited areas, where the mussel beds are not particularly dense, there is an aggregate of something like a million and half mussels in most years (Fig. 11; Table 3). Both *M. edulis* and *M. galloprovincialis* are present in a proportion of about 2 to 1, but the counts include both.

DISCUSSION

The distribution of some of the more numerous species on the beach bears some relation to intertidal level, that of others is more closely related to the nature of the substratum. These two factors, tide and substratum, are, of course, not entirely independent of each other and the type of substratum is determined by the strength of currents, the rate of tidal movements, the exposure to wave action, etc. All species of animal live in a definable habitat even if some features of it have very broad limits and other features are very narrowly defined.

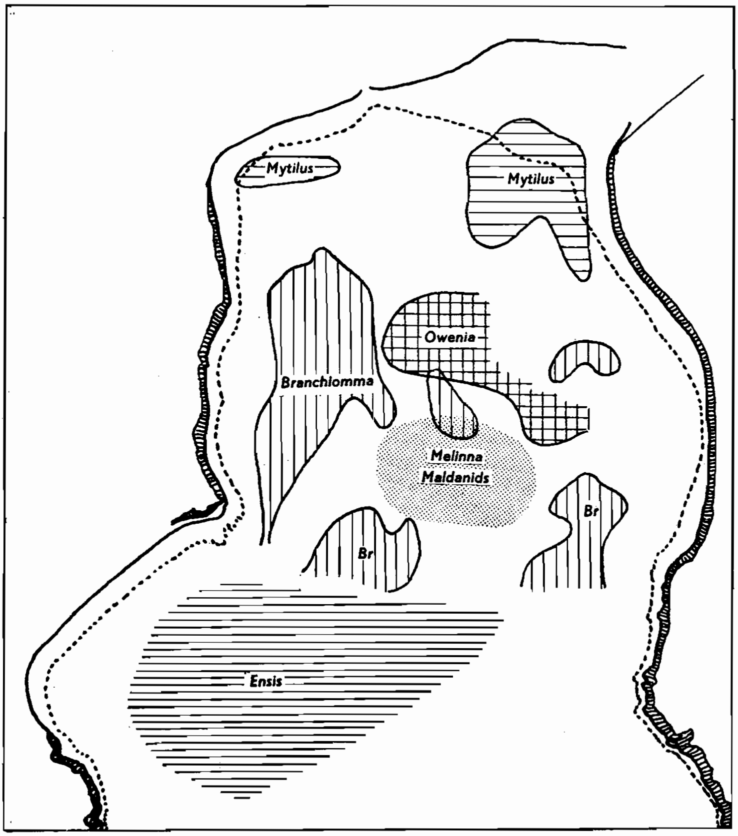

FIG. 12.

The distribution of the dense populations of the chief suspension feeders on the Gann Flat.

Lanice is a species which tolerates almost the entire gamut of substrata available on the Gann Flat, but it is essentially confined to the lower part of the intertidal zone. A few specimens occur up to mean tide level but the bulk of the population lies below M.L.W.N.T., and dense populations occur only below low water of ordinary tides—except where water runs permanently across the beach, and then the worms are able to live in large numbers in the higher intertidal levels.

Arenicola is another example of a species whose distribution is strongly influenced by the tidal level, but it tolerates a narrower range of substrata than *Lanice* and is almost entirely excluded from the muddier and stonier areas of the beach.

Sabella, on the other hand, is a species the distribution of which is almost entirely dependent upon the existence of a fairly fine, muddy substratum. Its distribution over the Gann Flat is therefore patchy, reflecting the variable nature of the substratum there. *Nephtys hombergi* is also tolerant of a wide range of tidal levels but is confined to fine sand. Its distribution on the Flat is accordingly very limited and, like that of *Sabella*, is patchy.

It is almost an axiom of ecology that there is little or no interspecific competition in any habitat, but it is not always apparent that this is so. One interesting feature of the Gann Flat is that, despite the rich and varied fauna living on it, species which use the same food source do not occur in numbers in the same area. This is best exemplified by those animals which filter detritus from the water. The areas occupied by the densest populations (more than 10 per sq. m.) of *Mytilus*, *Branchiomma*, *Owenia*, *Melinna* and maldanids, and *Ensis* are shown in Fig. 12; all are segregated. There are of course zones of overlap, not shown in the Figure, where mixed populations occur, but in none of them is any species at all numerous. As we have already shown, the distribution of each species may be related to the tidal level or to the nature of the substratum, or to a combination of these and other factors, and the distribution of these animals is a reflection of the mosaic of habitats available on the beach; but the net result is a parcelling out of the resources of the area among a few species, each dominant in a particular area and suffering little competition from other species for its food supply.

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