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THE GANN FLAT, DALE: THIRTY YEARS ON

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ABSTRACT

A survey of the fauna of the intertidal Gann Flat at Dale in Pembrokeshire (Dyfed) was carried out in 1988. A grid of 29 stations, covering about half of its area, was sampled by digging and sieving sediment through a 1 mm mesh. 111 species were recorded of which 60 were polychaetes, 14 bivalve molluscs, and 12 amphipod crustaceans. Thirty-two species were additions to the Dale Fort Marine Fauna. Multivariate analysis of the species abundance data reveals four distinct assemblages whose locations on the flat appear to be determined by the interaction of tidal level, freshwater influence and sediment type. The distributions of the dominant species which characterised the assemblages are examined and present day distributions compared with those recorded in 1958-1959 by Bassindale and Clark. The most striking changes have been a decline of *Megalomma vesiculosum, Sabella pavonina* and *Arenicola marina,* and a dramatic increase in the abundance of *Neanthes (= Nereis) virens.* Possible reasons for these changed are discussed.

INTRODUCTION

A classic study of the Gann Flat at Dale in Pembrokeshire, Dyfed, was carried out in 1958-1959 by students and staff of Bristol University following a suggestion by the then Warden of Dale Fort Field Centre, Mr J. H. Barrett (Bassindale and Clark, 1960). This study has served as a starting point for students carrying out field work on the Gann Flat for over a generation. However, over the last 30 years Milford Haven as a whole and the Gann Flat in particular have seen many changes. Those conducting marine field courses in the area from either Orielton or Dale Fort centres will have perhaps remarked on the apparent differences between the biological communities of the Gann Flat now and those described by Bassindale and Clark (1960). In the light of the continuing popularity of the Gann Flat as a field study site and the heavy pressure on it from bait digging, we considered it opportune to resurvey the area to assess the changes wrought over 30 years.

We elected to resurvey the fauna of as much as possible of the flat over one set of spring tides in August 1988. In the event, a grid of some 29 stations covering about half the Gann Flat was surveyed (Fig. 1).

The Gann Flat is comprised of varied and patchy substrata. The dominant substrate types are gravel overlain by mud and muddy sand. For a general description of the area and a detailed chart of the Gann Flat and Dale Sands the reader is referred to Bassindale and Clark (1960). Although we were interested in comparing our data with the 1958-1959 study we considered it was inappropriate to limit our investigation to common species which were easily recognisable in the field, as was done in the earlier study. We consider that the loss of direct comparability resulting from our adoption of a different sampling methodology is more than compensated for by the additional information obtained. Because of the limited field time and personnel we decided not to repeat the study of the distributions of common algae (*Enteromorpha* spp., *Ulva lactuca*, *Fucus* spp., *Chorda filum* and *Laminaria saccharina*) reported in Bassindale and Clark (1960).

In this paper we present not only a preliminary description of changes to the Gann Flat fauna since 1958-1959 but also discuss appropriate methods for repeatably surveying such an area and for analysing the data so-collected. We suggest that long-term monitoring of the Gann Flat might be attempted using the techniques presented under the co-ordination of staff of adjacent Field Centres.

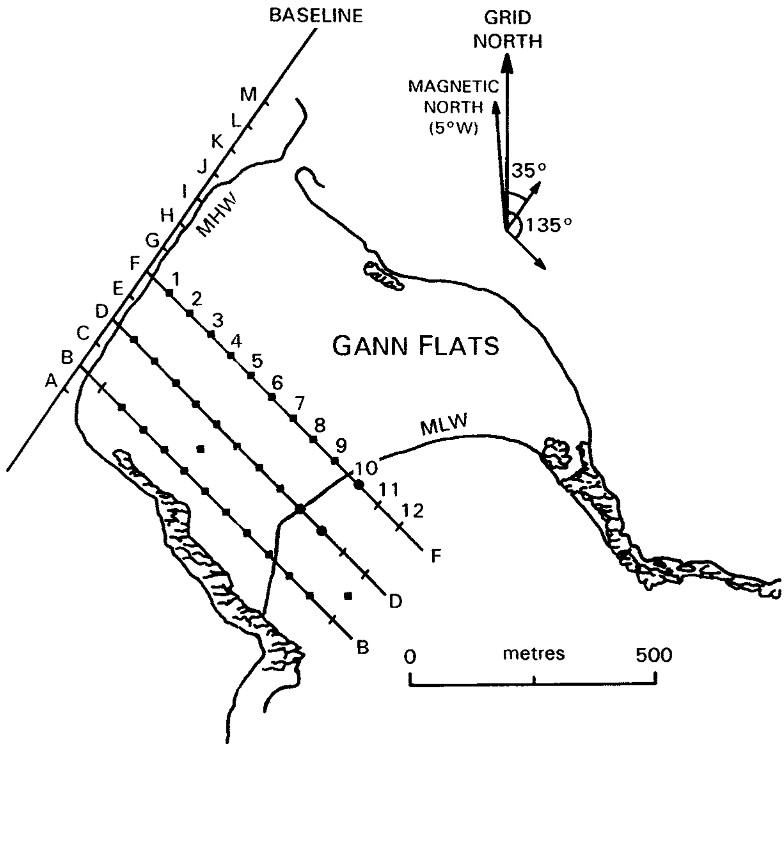

FIG. 1
Map of stations sampled on the Gann Flats showing transects B, D and F, the baseline along the bank bordering the Pickleridge Lagoons, and the 60m grid reference system used in the study. ■ indicates sites where sieved samples were obtained, ● indicates sites which could not be sampled due to standing water.

METHODS

The objective was for five people to resurvey the fauna of as much of the Gann Flat as possible over one set of peri-equinoctial spring tides from 27-30 August 1988. Like Bassindale and Clark (1960), we set out a grid with the intention of sampling a network of stations situated on the nodes at 60 m (200 ft) intervals. In the time available only 29 stations were fully sampled (Fig. 1). The exact positions of stations were located on the ground using ranging poles, a 100 m plastic tape-measure and a sighting compass. Transects were laid down the length of the shore from a baseline running along the top of the shore at 35° to Grid North (Fig. 1). The transects were laid at 100° to the baseline for reasons of local geography and thus, fortuitously, ran south-east.

At each station three 1/16 m^2 areas (25 x 25 cm) were extracted to a depth of 15 cm and washed through a 1mm mesh sieve. The animals and other materials so obtained were placed in labelled pots for later sorting and identification. In addition, 1 m^2 was carefully dug over at each station with a fork and all the animals so revealed were picked out and placed in pots for later identification and counting. Three stations (D9, D10 and F10) could not be properly sampled because of standing water although D10 was dug. Station C6 was dug but not sieved.

In the laboratory, the extracted animals from each station were identified and counted. The resultant species/frequency data matrix was analysed using both traditional univariate measures (*e.g.* Shannon-Wiener diversity index) and various multivariate techniques (Clifford and Stephenson, 1975; Kruskal and Wish, 1978; Field *et al.*, 1982; Warwick *et al.*, 1988; Carr, 1991). These included non-metric multi-dimensional scaling ordination (MDS) and cluster analysis performed on the faunal data after a double square-root transform. This transformation was chosen to diminish the influence within the analysis of the more dominant species. It is not as severe as the more conventional logarithmic transformation. Similarity was computed using the Bray-Curtis measure and sites were clustered by the group averaging technique. The significance of differences between groups of sites distinguished by cluster analysis and MDS were determined by analysis of similarities (ANOSIM) and the identities of the species making the largest contributions to dissimilarities between groupings were determined by similarity percentage analysis (SIMPER). In addition to picking out species present in one group but not in the other, the latter technique highlights those ubiquitous species whose numbers differ markedly between them. The results of the analyses were used as the basis for characterising the faunal assemblages.

Usage of generic and species names is based on Howson (1987).

RESULTS

Given the short time available to us only biological data were collected. However, on the basis of a preliminary inspection of the shore, it was expected that the presence of freshwater from the Gann Estuary and the transition from gravelly mud on the western part of the shore to sand on the eastern part would interact with tide level as the dominant physical factors setting the distribution of the fauna. This expectation was to some degree confirmed by the results of multivariate analyses. 111 species of invertebrate were recorded in the sieved samples. 60 of these were polychaete worms, 14 were bivalve molluscs and 12 were amphipod crustaceans (Appendix 1). By contrast, only 27 species were recorded from the dug samples, 26 of which were

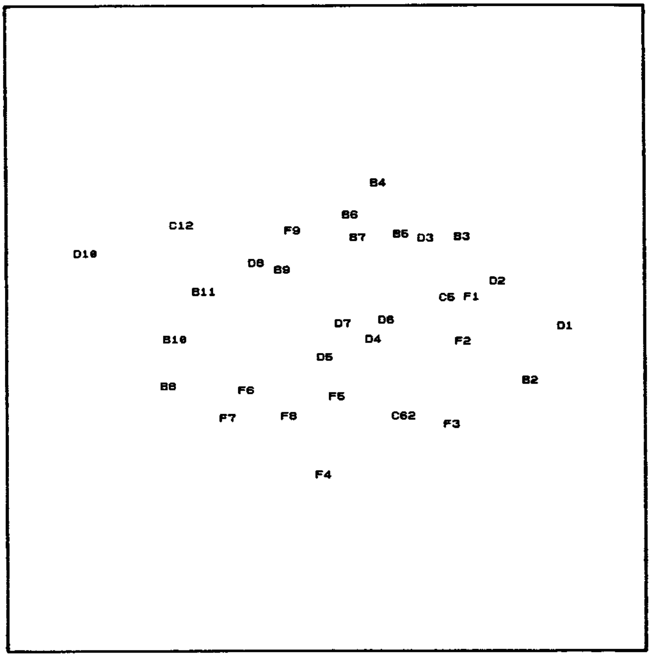

FIG. 2
Multidimensional scaling (MDS) ordination of the faunal data from the dug samples. Sites on the upper shore tend to lie to the right of the plot and sites on the lower shore to the left. See text for details of methods.

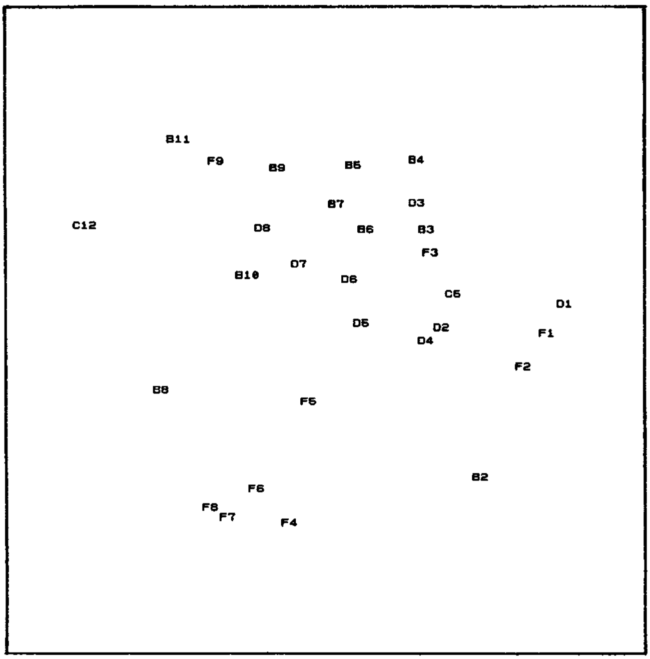

FIG. 3
MDS ordination of faunal data from the sieved samples.

polychaetes (Appendix 2). For analysis, dug and sieved samples were treated separately. While a clear pattern emerged from the analysis of the latter the results from the dug samples were less distinct (Fig. 2) and will not be discussed further.

1. MULTIVARIATE ANALYSIS OF COMMUNITY STRUCTURE

Multidimensional scaling

The MDS plot for the sieved samples (Fig. 3) shows two primary groupings of sites with four sites (B2, B8, C12 and F5) which lie separately. The larger, upper group consists of the remaining stations on transect B, all of those on transects C and D, and stations F1, F2, F3, and F9. The smaller, lower group comprises the remaining stations from transect F. This major split reflects the substantial difference between the sand dwelling fauna of much of transect F and that inhabiting the poorly sorted muddy gravel on the others. The species responsible for these differences will be considered below. Within the larger group, stations in the high shore cluster to the lower right-hand side of the plot while those in the lower shore lie to the top and the left. Three sites, D1, F1 and F2 lie apart from others in the high shore grouping. These are in areas influenced by fresh water from the Gann Estuary and/or seepage from the Pickleridge Lagoons which lie immediately to the north-west of the 'baseline' in Fig. 1.

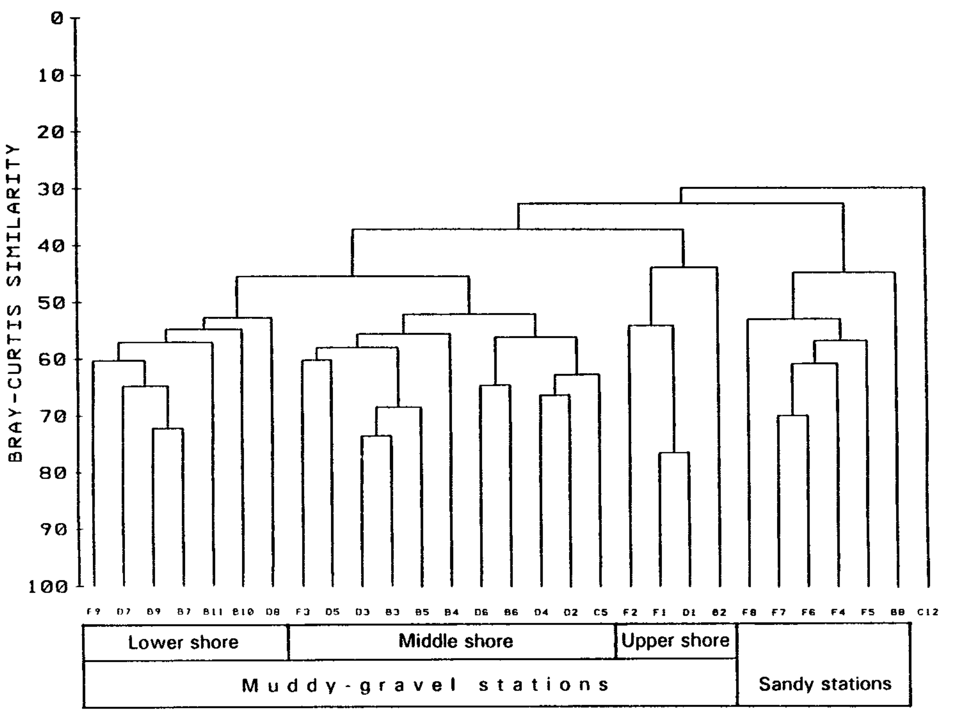

FIG. 4
Dendrogram for hierarchical clustering of faunal data from sieved samples. The four principal clusters are labelled.

Cluster analysis

Cluster analysis of the sieved samples (Fig. 4) supports the results of the MDS showing three distinct groups of sites at the 45% level of Bray-Curtis similarity. Although a few minor differences exist from the MDS pattern, the analysis nevertheless separates the gravelly mud sites both from those on sand and those influenced by fresh water. Within the muddy sites there is a clear division between middle and lower shore sites at the 50% level of Bray-Curtis similarity. The four groups distinguished in Figure 4 were found to be significantly different ($P<0.01$) using analysis of similarities. Site C12, which was close to MLWS, stands alone.

Similarity percentage analysis

Similarity percentage analysis (SIMPER) was performed to determine the identity of the species responsible for the different groupings distinguished by the MDS and cluster analysis. In addition to picking out species present in one group but not in another, this technique highlights those ubiquitous species whose numbers differ markedly between them. The results, which serve to confirm the validity of one's rather more subjective viewing of faunal lists, were used as the basis for characterising the faunal assemblages. The distribution of some of the more important species will also be considered independently.

Muddy-gravel stations

Middle shore

As the chart in Bassindale and Clark (1960) shows, by far the greatest area of the Gann Flat lies below mid-tidal level and as such most of the sites sampled must be regarded as being in the middle to lower shore. In discussing the fauna of the muddy gravel area we will consider the mid-shore sites first and then compare them with those on the lower and upper shore. The mid-shore sites were characterised by moderate numbers of the polychaetes *Scoloplos armiger* (Fig. 5a), *Notomastus latericeus* (Fig. 5b), *Glycera tridactyla* (Fig. 5c), *Melinna palmata* (Fig. 5d), *Ampharete acutifrons* (Fig. 6a), *Caulleriella zetlandica* (Fig. 6b), *Pygospio elegans* (Fig. 6c), the oligochaete *Tubificoides benedii* (Fig. 6d), and the bivalve *Cerastoderma edule* (Fig. 7a).

Lower shore

At the lowest stations, numbers of species tended to be higher than in the middle shore (Figure 10). Species characteristic of the middle shore were still present but their relative importance often changed; for example, numbers of the polychaetes *Euclymene oerstedii* (Fig. 7b), *Caulleriella zetlandica* (Fig. 6b), and *Myriochele oculata* increased significantly. On the other hand species such as the polychaete *Pygospio elegans* (Fig. 6c), the oligochaete *Tubificoides benedii* (Fig. 6d) and the bivalve *Cerastoderma edule* (Fig. 7a) which were present in moderate numbers in the middle shore declined in abundance towards the lowest sites. Other species which were rare in the mid-shore were increasingly prominent near low water (e.g. *Lumbrineris gracilis, Dexamine spinosa, Cirriformia tentaculata*), the most notable example being *Lanice conchilega* (Fig. 7c). A similar trend was shown by the gastopod *Calyptraea chinensis* although the distribution of this species may have owed more to the presence of solid substrata, such as small rocks or shells, to which it could attach.

Upper shore

As the highest sites were approached, the number of species declined although at some the number of individuals was higher than in either the middle or lower shore.

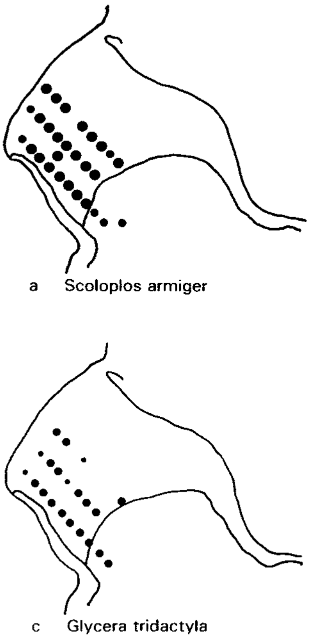

FIG. 5

Distribution and abundance of the polychaetes: a) *Scoloplos armiger*, b) *Notomastus latericeus*, c) *Glycera tridactyla*, and d) *Melinna palmata*. • = 0-10m^{-2}, • = 11=100m^{-2}, ● = 101-1000m^{-2}, ● = 1000+m^{-2}.

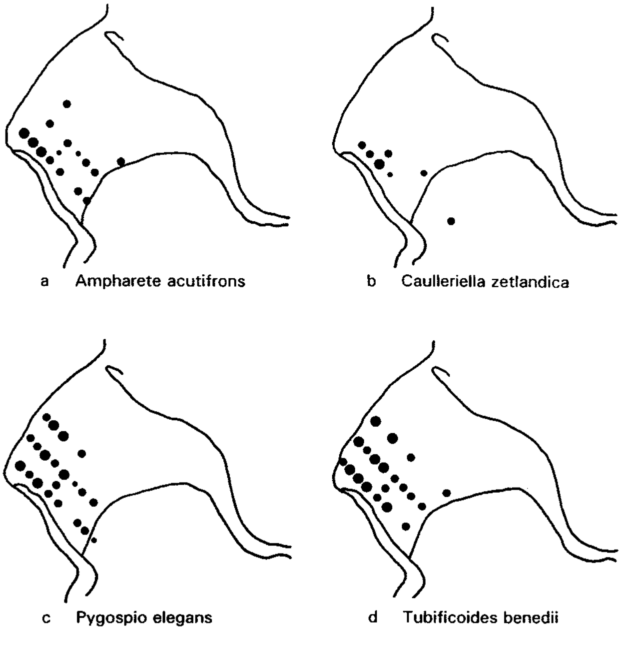

FIG. 6

Distribution and abundance of the polychaetes: a) *Ampharete acutifrons*, b) *Caulleriella zetlandica*, and c) *Pygospio elegans*, and d) the oligochaete *Tubificoides benedii*. Abundance scale as for Fig. 5 (above).

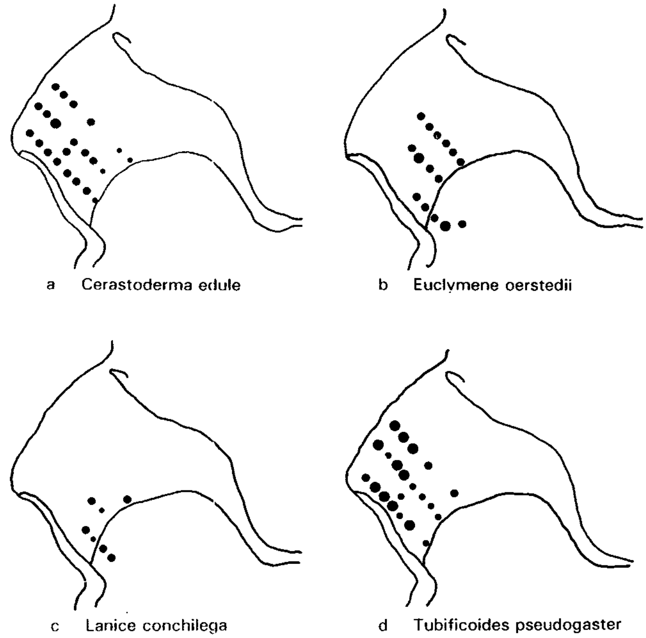

FIG. 7

Distribution and abundance of a) the bivalve *Cerastoderma edule,* b) and c) the polychaetes *Euclymene oestedii* and *Lanice conchilega,* and d) the oligochaete *Tubificoides pseudogaster.*
• = 0-10m^{-2}, • = 11=100m^{-2}, ● = 101-1000m^{-2}, ● = 1000+m^{-2}.

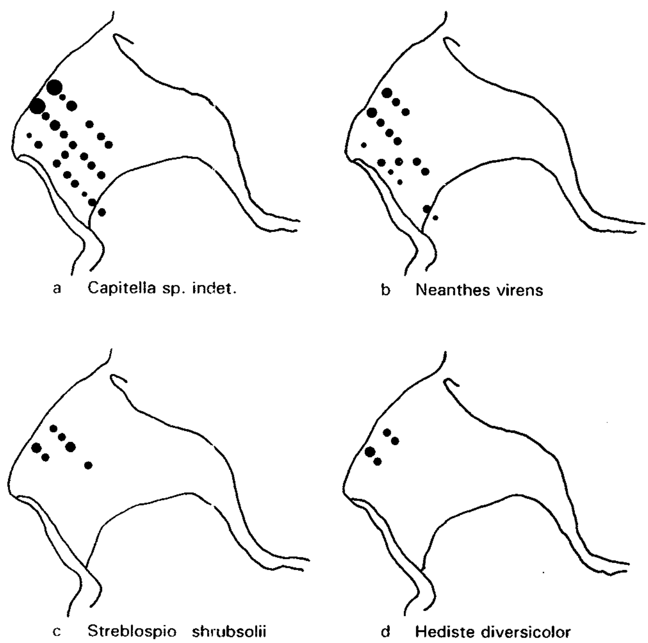

FIG. 8

Distribution and abundance of the polychaetes: a) *Capitella* sp., b) *Neanthes virens,* c) *Streblospio shrubsolii,* and d) *Hediste diversicolor.* Abundance scale as for Fig. 7 (above).

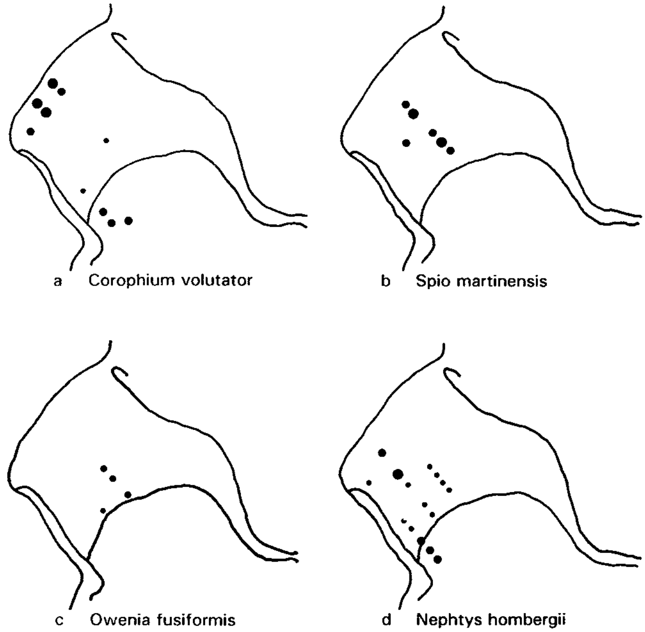

FIG.9
Distribution and abundance of a) the amphipod *Corophium volutator*, and the polychaetes: b) *Spio martinensis*, c) *Owenia fusiformis*, and d) *Nephtys hombergii*. • = 0-10m^{-2}, • = 11=100m^{-2}, ● = 101-1000m^{-2}, ● = 1000+m^{-2}.

This was due to the dominance of the oligochaetes *Tubificoides pseudogaster* (Fig. 7d) and *Tubificoides benedii* (Fig. 6d) and/or the polychaete *Capitella* sp. (Fig. 8a). On the upper shore some of the characteristic mid-shore species such as *Caulleriella zetlandica* (Fig. 6b) and, to a lesser extent, *Ampharete acutifrons* (Fig. 6a) declined in abundance. However, the highest densities of *Neanthes virens (= Nereis virens)* (Fig. 8b) were found at this level.

Freshwater influenced upper shore stations

As mentioned above, at the more easterly high level sites there was a suite of species normally associated with estuarine conditions. These species were the annelids *Streblospio shrubsolii* (Fig. 8c), *Hediste diversicolor (= Nereis diversicolor)* (Fig. 8d), and *Tubifex costatus* which were restricted to sites D1, D2, F1 and F2 and the amphipods *Melita palmata* and *Corophium volutator* (Fig. 9a) which were also common at the top of transect B.

Sandy stations

On transect F only sites F3 and F9 cluster with the main group. The freshwater influenced sites F1 and F2 have been discussed above thereby leaving sites F4-F8 for discussion. Of these, sites F4, F6, F7 and F8 group together and can be considered to have a typical sand fauna characterised by the polychaete *Spio martinensis* (Fig. 9b, n.b. this species was absent from F8), the amphipods *Ampelisca brevicornis* and *Urothoe poseidonis* and the bivalves *Angulus tenuis* and *Fabulina fabula*. The dominant species of the mid-shore muddy gravel such as the polychaetes *Pygospio elegans*, *Glycera tridactyla*, *Melinna palmata* and *Ampharete acutifrons* were all absent from these sandy sites. Elements of both the muddy gravel and the sand fauna were taken at site F5 which lies between the main grouping and the sand grouping on the MDS plot (Fig. 3).

2. UNIVARIATE MEASURES OF COMMUNITY STRUCTURE

Having carried out the MDS analysis, we will restrict our discussion of common, but less useful univariate measures of community structure such as diversity indices. The lowest sites (below MLWS) tended to have the highest number of species (Fig. 10) and to be more diverse (in terms of the Shannon-Wiener index) than those higher up the shore (Fig. 11). Among the least diverse sites were those in the upper shore influenced by fresh water. Although both the magnitude of the Shannon-Wiener diversity index and the number of species per sample were correlated with distance down the shore ($P<0.001$), neither evenness nor numbers of individuals showed any such correlation. Overall the univariate measures tell us little more than could be determined from a brief visual inspection of the data.

Table 1. *Shannon-Wiener diversity index and evenness, number of species and total number of individuals per square metre at each site sampled.*

Site	Diversity Index	Evenness	Number of species	Total nos. m^{-2}
B2	2.13	0.927	10	176
B3	2.36	0.699	29	2255
B4	2.34	0.780	20	858
B5	2.68	0.726	40	3081
B6	2.73	0.849	25	469
B7	3.08	0.860	36	1002
B8	2.64	0.811	26	490
B9	2.94	0.785	42	1226
B10	2.59	0.736	34	1744
B11	3.21	0.799	56	2361
C5	2.15	0.795	15	512
C12	2.55	0.825	22	696
D1	2.17	0.714	21	4685
D2	2.13	0.738	18	1391
D3	2.36	0.700	29	3987
D4	2.26	0.814	16	693
D5	2.04	0.651	23	1333
D6	2.19	0.745	19	1178
D7	2.87	0.814	34	1301
D8	2.30	0.646	35	1844
F1	1.84	0.679	15	2894
F2	1.71	0.649	14	1306
F3	2.23	0.692	25	3113
F4	1.85	0.702	14	352
F5	1.96	0.625	23	1050
F6	2.24	0.792	17	682
F7	2.07	0.668	22	1167
F8	2.50	0.924	15	203
F9	3.04	0.812	42	1428

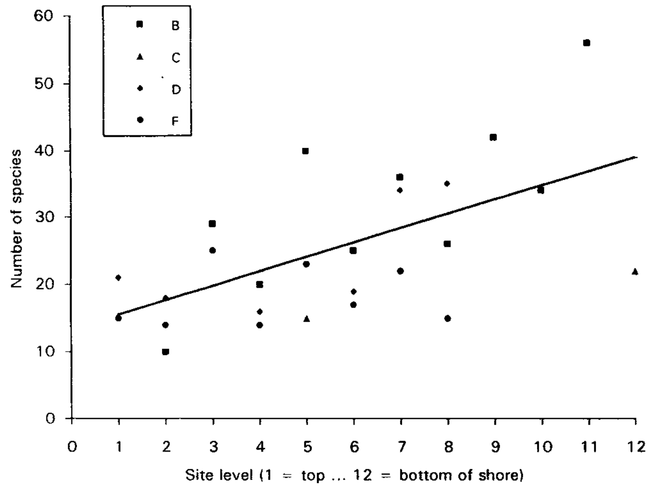

FIG. 10
Relationship between the number of species in the sieved samples and the level on the shore from which the samples were collected. The line of best fit is drawn through the data.

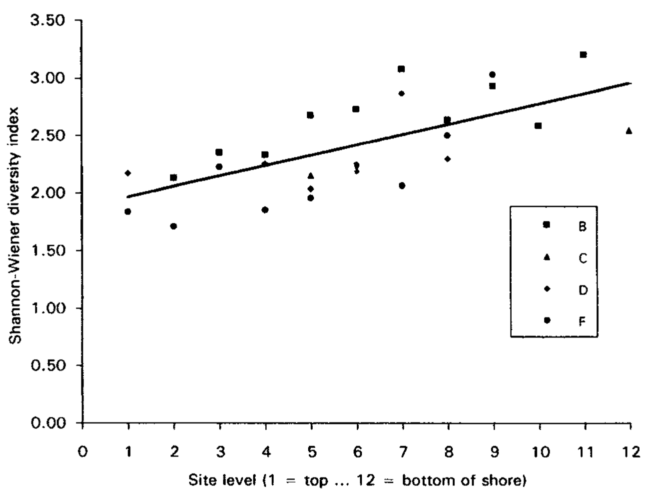

FIG.11
Relationship between the Shannon-Wiener diversity index calculated for the sieved samples and the level on the shore from which the samples were collected. The line of best fit is drawn through the data.

3. CHANGES IN SPECIES DISTRIBUTION SINCE 1957-1959

Full lists of species recorded in both dug and sieved samples are presented as Appendices 1 and 2, and the average densities of the 20 commonest species are listed as Appendix 3. It is apparent that there have been substantial changes in the fauna since the surveys of Bassindale and Clark (1960), although interpretation of these changes is not straightforward. Differences in methodology must be borne in mind, Bassindale and Clark relying on surface evidence or hand-digging, the 1988 survey being largely based on the extraction of fauna by washing over a 1.0 mm mesh sieve. The latter method clearly results in the collection of species of small body size not considered by Bassindale and Clark, and of the smaller individuals of species upon whose distribution patterns they commented. The 1988 survey covered only the western side of the flat, so that reduction in the number or total absence of a species in this survey cannot be taken as necessarily applying to a Gann Flat as a whole.

At the time of Bassindale and Clark's surveys, the western part of the flat was dominated by the sabellid polychaete *Megalomma vesiculosum* (as *Branchiomma vesiculosum*), with patches of high densities of *Owenia fusiformis* and, lower down the shore, *Melinna palmata* and *Euclymene oerstedii* (as maldanids) towards the centre of the flat. *Arenicola marina* was present over much of this area, though often absent from much of transect D of the 1988 survey, and showing considerable temporal variability in its distribution pattern and maximum densities. *Lanice conchilega* showed a comparable temporal variation, being widespread over the area in March 1959, but being absent from all but the lowest part of the western side of the flat in September 1958. *Sabella pavonina*, described by Bassindale and Clark as preferring the muddy sediments of sheltered conditions, was reasonably abundant in patches down the western part of the flat, and *Nephtys hombergii* was also widespread.

By 1988, the fauna of the western part of the flat had changed considerably. The sabellids *Megalomma vesiculosum* and *Sabella pavonina* had declined dramatically in numbers, being represented by 1 and 3 individuals respectively in all the samples taken. Much of the area was dominated by the large nereid *Neanthes virens*, which was absent at the time of Bassindale and Clark's work, and is, indeed, not recorded in the first edition of the Dale Fort Marine Fauna (Bassindale & Barrett, 1957) (first recorded in the area in 1962 — Crothers, 1966). *Melinna palmata* was found to be much more widespread than in the earlier surveys, whilst *Euclymene oerstedii* also occupied a larger area, but was limited to the lower stations. *Owenia fusiformis* would appear to occupy a distinct patch similar to that reported by Bassindale and Clark. *Arenicola marina* was virtually absent from transects B, C and D, though present at densities of up to 3 m^{-2} at some stations along transect F. It would appear, therefore, to be rather less widespread in its distribution than at any one of the 4 survey dates of Bassindale and Clark. *Lanice conchilega* was limited to the lowest stations in 1988, and had a rather more restricted distribution than that found on either of the earlier sampling dates. The general distribution pattern of *Nephtys hombergii* was similar in 1988 to that in March 1959.

Of the other species of polychaete mentioned by Bassindale and Clark, all but *Cirratulus cirratus* and *Flabelligera affinis* were recorded in 1988. *Glycera tridactyla* was widespread over the western part of the flat, whilst *Hediste (= Nereis) diversicolor* was restricted to the upper shore and *Amphitrite edwardsi* and *Cirriformia (= Audouinia) tentaculata* to the lower shore. The 1988 sampling techniques resulted in the collection of 39 species not previously recorded from Gann Flat. Several of these species, such as the polychaetes *Anaitides mucosa*, *Notomastus latericeus* and *Ampharete acutifrons* were present in reasonable numbers in 1988, and are of a body size likely to have been collected using the hand-digging technique of Bassindale and Clark. Whether this should be interpreted as an indication of their appearance at Gann Flat since 1959, or of an increase in their abundance from low levels in 1959, remains an open question.

The other polychaete species recorded in the 1988 survey, but not mentioned in Bassindale and Clark (1960) are of small body size, and like the three species of oligochaetes, would not have been sampled using their collecting methods. Relatively few species of molluscs were recorded in 1988 (14 species, compared with 30 reported by Bassindale and Clark), but little can be made of this in view of the restricted area sampled in 1988. Amongst the Crustacea, *Carcinus maenas* and *Crangon crangon* were widespread in 1988, though estimates of the numbers of the latter may have been unreliable due to the possible addition of animals to the samples during the washing process. The 12 amphipod species taken in 1988 were all too small to have been collected by Bassindale and Clark (1960).

Discussion

The most striking changes to have occurred since the surveys of Bassindale and Clark (1960) relate to the dramatic decline of the tube-living sabellids *Megalomma vesiculosum* and *Sabella pavonina* and, less certainly, of the burrow-dwelling *Arenicola marina*. Whilst all three of these species were previously widespread over the western part of the flat, in 1988, this area was dominated by *Neanthes virens*, accompanied by sub-surface deposit feeders such as *Notomastus latericeus*, *Scoloplos armiger* and *Caulleriella zetlandica*. Of these species, only *Neanthes virens* would certainly have been noticed by Bassindale and Clark, had it been present when they were working on the flat.

The cause of the increase in the abundance of *N. virens* and the time-scale involved cannot be readily determined. We cannot be certain whether the arrival of this species, and its subsequent popularity as a bait species, has led to a change in the granulometry of the sediment, or if a change in the sediment made the area more suitable for colonisation by *N. virens*. Nevertheless, the development of an abundant *N. virens* population has had important implications for the macrobenthic community of the muddy gravel areas of the Gann Flat. *N. virens* is probably the most sought-after angling bait used in the British Isles and, as a result, digging can be intense. *Arenicola* is generally much more readily available and thus, while one might expect some bait collection to have taken place when the area was dominated by this species, the intensity would have been far lower than at present. When a hole is dug in the muddy gravel, spoil is left on the surface and with the incoming tide some of the finer sediment particles are winnowed away. This effectively increases the gravel content of the surface material. In time the hole itself beings to fill with mud, and thus, in the short term, pockets of fine sediment surrounded by gravel develop. These characteristic "pock marks" cover much of the western side of the Gann Flat but decrease in abundance with distance from public access points.

Physical disturbance plays an important role in the maintenance of diversity in sediment dwelling communities. Highly disturbed assemblages tend to be dominated by opportunists but as the time over which communities are stable increases so these opportunistic species are progressively replaced by more efficient competitors. At some intermediate level of disturbance there is maximal diversity (Huston, 1979). In intertidal situations any pattern resulting from disturbance will tend to overlie those resulting from variation in shore height, sediment type, etc. It would be reasonable to expect patchy disturbance to reduce the number of species recorded at the expense of the larger and longer-lived animals. The mechanisms of species reduction will vary; some animals will die following damage, while suspension feeders could be expected to suffer as a result of their feeding mechanisms becoming clogged by the increased level of suspended fine sediments. Physical burial of species with limited powers of movement back to their normal feeding position close to the sediment surface might also be significant, particularly for some tube-building species. All of these consequences of disturbance of the sediment would tend to affect adversely species such as *Megalomma vesiculosum* and *Sabella pavonina,* whilst favouring the sub-surface deposit feeders such as *Notomastus latericeus* and *Scoloplos armiger.* The mobile omnivorous *Neanthes virens* is also well suited to this physically disturbed environment.

As part of a study of a broad range of estuaries in the south-west of England, Warwick *(personal communication)* showed that the fauna of the Gann Flat was clearly different from the other 40 sites which he investigated. This is because it is comparatively unusual to find the combination of sediment types found in this area in (almost) fully marine conditions. Thus, despite high levels of disturbance the area must be seen as having a high conservation value. While some reduction in the intensity of anthropogenic disturbance (field course collection, bait digging, etc.) might be seen as desirable it would be interesting to assess the extent to which moderate levels of bait digging might actually promote species diversity.

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REFERENCES

BASSINDALE, R. and BARRETT, J.H. (1957). The Dale Fort Marine Fauna. *Proceedings of the Bristol Naturalists' Society*, 29(3), 227-328.

BASSINDALE, R. and CLARKE, R.B. (1960). The Gann Flat, Dale: Studies on the ecology of a muddy beach. *Field Studies* **1**, (2), 1-22.

CARR, M.R. (1991). User Guide to PRIMER *(Plymouth Routines in Multivariate Ecological Research).* Plymouth Marine Laboratory, Plymouth, 90 pp.

CLIFFORD, H.T. and STEPHENSON, W. (1975). *An Introduction to Numerical Classification.* Academic Press, New York.

CROTHERS, J.H. (Ed) (1966). Dale Fort Marine Fauna (Second Edition) *Field Studies* **2** supplement 169pp.

FIELD, J.G., CLARKE, K.R. and WARWICK, R.M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37-52.

HOWSON, C.M. (Ed.) (1987). *Directory of the British Marine Fauna and Flora.* Marine Conservation Society, Ross-on-Wye. 471 pp.

HUSTON, M. (1979). A general hypothesis of species diversity. *American Naturalist*, 113, 81-101.

KRUSKAL, J.B. and WISH, M. (1978). *Multidimensional Scaling.* Sage Publications, Beverley Hills, California.

WARWICK, R.M., CARR, M.R., CLARKE, K.R., GEE, J.H. and GREEN, R.H. (1988). A mesocosm experiment on the effects of hydrocarbon and copper pollution on a sublittoral soft meiobenthic community. *Marine Ecology Progress Series*, **46**, 181-191.

APPENDIX 1
Species recorded from sieved samples

CNIDARIA
Halcampa chrysanthellum
Anemone indet. 1
Anemone indet. 2

NEMERTEA
Lineus indet.
*Tubulanus superbus**†
*Oerstedia dorsalis**

SIPUNCULA
Golfingia vulgaris

ANNELIDA
POLYCHAETA
Gattyana cirrosa
Harmothoe imbricata
Harmothoe indet.
Sigalion mathildae
Sthenelais boa
*Eteone longa**
Anaitides mucosa
Glycera tridactyla
Goniada maculata
Microphthalmus indet.*†
*Typosyllis variegata**†
*Odontosyllis ctenostoma**†
*Parapionasyllis minuta**†
*Exogone hebes**†
*Exogone naidina**†
*Autolytus brachycephalus**
Autolytus prolifera
Hediste diversicolor
*Neanthes virens**
Perinereis cultrifera
Platynereis dumerilii
Nephtys cirrosa
Nephtys hombergii
Marphysa bellii
Nematonereis unicornis
*Lumbrineris gracilis**†
Orbinia indet.
*Scoloplos armiger**
Aricidea indet.
*Aricidea minuta**†
*Aonides oxycephala**†
*Malacoceros tetracerus**†
Polydora ciliata
*Polydora cornuta**†
*Polydora quadrilobata**†
*Pseudopolydora pulchra**†
Pygospio elegans
*Spio filicornis**†
Spio martinensis
*Spiophanes bombyx**†
*Streblospio shrubsolii**†
*Caulleriella zetlandica**†
Cirriformia tentaculata
Tharyx indet.*†
Capitella indet.
*Heteromastus filiformis**†
*Mediomastus fragilis**†
Notomastus latericeus
Euclymene oerstedii
*Scalibregma inflatum**
*Myriochele oculata**†
Owenia fusiformis
Pectinaria indet.
Melinna palmata
*Ampharete acutifrons**†
Amphitrite edwardsi
Lanice conchilega
Polycirrus indet.*†
Terebellidea juv. indet.
Fabricia sabella
OLIGOCHAETA
*Tubifex costatus**†
*Tubificoides benedii**†
*Tubificoides pseudogaster**†

CHELICERATA
PYCNOGONIDA
*Endeis spinosa**
Anoplodactylus indet.

CRUSTACEA
AMPHIPODA
Calliopius laeviusculus
Leucothoe incisa
*Leucothoe spinicarpa**†
Talitridae indet.
*Urothoe poseidonis**†
Dexamine spinosa
Ampelisca brevicornis
Gammaridae indet.
Melita palmata
Aoridae indet.
Corophium volutator
Phtisica marina
ISOPODA
Sphaeroma indet.
TANAIDACEA
Leptognathia indet.
CUMACEA
*Bodotria pulchella**†
Bodotria scorpioides
DECAPODA
Crangon crangon
Carcinus maenas

MOLLUSCA
POLYPLACOPHORA
Lepidochitona cinereus
GASTROPODA
Gibbula cineraria
Gibbula umbilicalis
Calyptraea chinensis
Philine indet.
PELECYPODA
Mytilus edulis
Lucinoma borealis
Thyasira flexuosa
*Mysella bidentata**†
Cerastoderma edule
*Cerastoderma glaucum**†
Angulus tenuis
Fabulina fabula
Tellinidae indet.
Macoma balthica
Abra alba
Tapes decussatus
Venerupis senegalensis
Chamelea gallina

ECHINODERMATA
Amphiura brachiata
Amphipholis squamata

* = Additions to Dale Fort Marine Fauna list (Bassindale & Barrett 1957)
† = Additions to Dale Fort Marine Fauna (Crothers 1966)

APPENDIX 2
List of species in dug samples.

ANNELIDA
POLYCHAETA
Sigalion mathildae
Sthenelais boa
Anaitides mucosa
Glycera tridactyla
Goniada maculata
*Neanthes virens**
Perinereis cultrifera
Nephtys cirrosa
Nephtys hombergii
Marphysa bellii
Nematonereis unicornis
Orbinia indet.
*Aonides oxycephala**†
*Spio filicornis**†
Cirriformia tentaculata
Notomastus latericeus
Arenicola marina
Euclymene oerstedii
Owenia fusiformis
Melinna palmata
*Ampharete acutifrons**†
Amphitrite edwardsi
Lanice conchilega
Megalomma vesiculosum
Sabella pavonina
*Myxicola infundibulum**

ECHINODERMATA
Amphiura brachiata

* = Additions to Dale Fort Marine Fauna list (Bassindale & Barrett 1957)
† = Additions to Dale Fort Marine Fauna (Crothers 1966)

APPENDIX 3
Average densities of the 20 commonest species found in the sieved samples

Species	**Average No. m^{-2}**
Scoloplos armiger	238
Tubificoides benedii	182
Capitella indet.	123
Crangon crangon	108
Tubificoides pseudogaster	100
Caulleriella zetlandica	76
Pygospio elegans	62
Notomastus latericeus	51
Melinna palmata	43
Neanthes virens	40
Ampharete acutifrons	36
Spio martinensis	30
Euclymene oerstedii	29
Corophium volutator	26
Myriochele oculata	25
Cerastoderma edule	20
Carcinus maenas	17
Glycera tridactyla	15
Streblospio shrubsolii	15
Polydora quadrilobata	14