PATTERNS OF INTERTIDAL DISTRIBUTION AROUND DALE

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ALL over the world sea shores have the same basic pattern in the distribution of their animals and plants. This has been revealed by the studies of Professor Stephenson of Aberystwyth as a result of work in many parts of the world. His division of the intertidal shore into universal zones proposed in 1949 is generally accepted by shore ecologists. Within this framework wide orderly variation exists. The shores of Dale are no exception and they give a good introduction to the diversity of distribution and detailed pattern that can be found within the main scheme. The forces of weather and sea, acting on all the different kinds of shore-lines, produce a variety of circumstances under which the many species of shore animals and plants live.

By way of setting the scene a few points about the Dale area must be mentioned. The reader is referred to the new Dale Fort Marine Fauna* for further details on this and many other aspects of shore ecology in the Dale area.

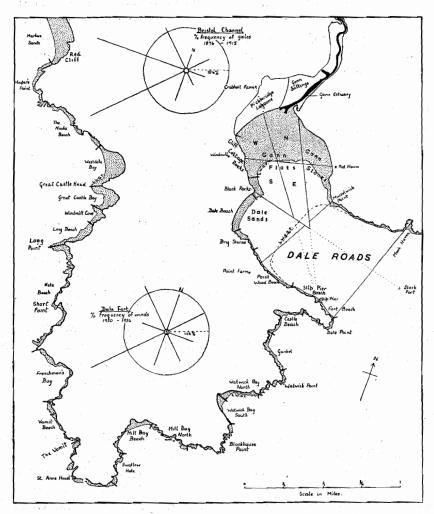
The eight miles of coastline enclosing Dale are, with a few notable exceptions, rocky. The rock is almost entirely Lower Old Red Sandstone marls. This one constant feature would make a detailed study of the area of interest if it were then compared with another area of similar diversity but built up from another rock material.

Sections of coastline are to be found facing in all compass directions. The wave fetch varies from half a mile on to the shores of Dale Roads to three thousand miles in the case of the Atlantic coastline on the west side of the peninsular. The direction in which there is the greatest wave fetch is also that of the prevailing wind, i.e. south-west. The frequency of the winds blowing on to the shores with the shortest wave fetch is only about

^{*} Bassindale, R., and Barrett, J. H. (1957) The Dale Fort Marine Fauna. Proc. Bristol Nat. Soc., 29 (3).

half as great. This results in an accentuation of the factor which is so important in determining intertidal distributions—that of relative wave exposure. Shores can be classified according to their degree of exposure or shelter with respect to wave action. Wave action takes various forms: from the crash of wind-speeded ocean waves with their accompanying splash and finer spray, to the surge of water in gullies and bays protected from the immediate effects of the wind. Extreme conditions are all important. When in September, 1957, the residue of "Hurricane Carrie" was blowing itself out over Britain, the wind at Dale was only a moderate gale, but the accompanying sea-swell which brought huge rollers to the exposed shores was a reminder of the wind that had sunk the barque Pamir in mid-Atlantic. After such conditions boulders weighing several tons are found to have been tossed about on western shores, while much smaller stones remain unmoved on the shores of Dale Roads.

Another most important factor well exemplified at Dale is the effect of varying profile and detailed structure of the shore on intertidal distributions. Rocky shores are made up basically of bedrock or boulders, rocks and stones, or a combination of bedrock and one or more types of the breakdown material. Nearly half the coastline of Dale is bedrock for the complete tidal range. Such shores vary enormously in slope from almost vertical, as seen in places around St. Ann's Head, to the very gentle slope of many other beaches. The difference between the aspect of the shore and the direction of the dip of the rock strata largely determines whether the shore is a more or less smooth slope, as on parts of the south side of Dale Point, or a mass of ridges, pinnacles and gullies as at Watwick Bay. Many of the Dale shores, especially those commonly visited by students, are bedrock for the upper part of the tidal range and broken material lower down. The angle of slope of these shores usually becomes progressively less steep down the tidal range. At Great Castle Head a steep bedrock slope falls to a more or less level boulder strewn surface (wave cut platform) at mean sea level. At the seaward extremity of this, stacks of rock tower up the complete tidal range. At Red Cliff similar stacks are set in sand which reaches up to the level of low water of neap tides. Rocky shore distributions are very much influenced by waterborne sand and, on an exposed coast, sand can have an effect on the zonation of the shore even if it only occurs on the bottom in the sub-littoral, e.g. the Hooks Beach.



Map of the Dale Peninsula, showing the named beaches (after Bassindale and Barrett)

By courtesy of The Bristol Naturalists' Society

Other points to note about the Dale area are that low water of spring tides occurs at just after midnight and noon, so that the lowest zones of the shore are exposed at the hottest part of the day (although not the coldest part of the night). Compared with other parts of the British Isles the weather of Dale may be briefly characterized as being windy and sunny and with a low rainfall and few frosts.

The Shore Zones

Stephenson's universal zones may be briefly set out with their dominant inhabitants as follows:

The Supra-Littoral Fringe

Lichens and Littorinas

The Mid-Littoral Zone

Barnacles or Brown Algae

The Infra-Littoral Fringe

Laminarias

The supra-littoral fringe is the upper shore—not covered by every high tide but more often reached by splash and spray. Its depth varies enormously according to the degree of exposure. The mid-littoral zone occupies the greater part of the shore proper and varies a little in depth, being slightly extended in an upward direction in conditions of exposure. The lower shore or infra-littoral fringe is only uncovered by low water at spring tides. The lower limit of the infra-littoral is the lowest point to which the tide falls and below this is the sub-littoral zone. It is important to note that the dividing lines between the shore zones are not definable in terms of tidal level as they vary according to the exposure.

The Supra-Littoral Fringe

The supra-littoral fringe, by definition, starts at the top of the barnacle zone, which is usually a quite distinctly marked line. The upper limit of the zone is not at all easy to mark, but the beginning of the flowering plant zone is a convenient boundary. The zone is remarkably consistent in its component species and can be seen very well at Dale Point, Watwick Point and Castle Beach in the basic form. The lichen zone is most distinctive. Even when seen from a mile or more away the three colour bands, black, orange and grey are evident. The lowest—black—usually overlaps with the topmost barnacles, thins out above after a varying distance and is succeeded by the usually narrower orange zone. Above these the grey

zone reaches for sometimes fifty feet up the cliff. The make-up of the zones varies somewhat and altogether many species of lichens are involved. The most important of the black lichens is *Verrucaria maura* with *Lichina confinis* playing an important but still subsidiary role in increasing exposure. The orange lichens are mainly represented by *Caloplaca spp.* and *Xanthoria parietina*. In conditions of shelter *Caloplaca* soon disappears. The grey zone is more diverse, different lichens appearing with different conditions. Some of the commonest ones are: *Lecanora spp.*, *Ramalina spp.*, *Pseudo-physcia fusca*, and *Lecania prosechoides*.

Even on the most sheltered shores the three colour zones are often found to be quite distinctly marked, although exceedingly narrow. Greys and blacks overlap but orange is there in the intermediate region. Where flowering plants including trees, grow down the cliff far enough to be washed by the spring tides, the grey and sometimes orange zones are absent, as in parts of the Cliff Cottage and Point Wood beaches. There is a tendency for the black zone to be more extensive in shaded than sunlit conditions. Although on some cliffs there is almost complete coverage of the rocks by lichens, in other places five per cent. cover or less is found. This seems to be due to the fast weathering of the Old Red Sandstone surface in these places, so that lichens which are slow growing are flaked off before covering a large area. This is particularly noticeable on some of the most exposed west coast cliffs.

The type of weathering of the rock is a controlling factor in the Littorina zone also. The tiny Littorina neritoides and the larger ridged L. saxatilis are present in the lower part of the lichen zone. Quite often the honeycomb weathering of the rock results in an abundance of small irregularities which these animals, especially L. neritoides, favour. The abundance of this species, in given conditions of exposure, is directly related to the suitability of the rock surface in this way. However, it decreases in numbers on the most sheltered shores and is absent from the Cliff Cottage and Point Wood beaches which are the most sheltered. It attains a large size in regions which are at the same time exposed to wave action but shaded from the sun and otherwise not liable to drying out, e.g. parts of St. Ann's Head. The range of L. saxatilis is lower than that of L. neritoides and it inhabits more open situations. Its numbers are reduced in very dry areas (sheltered sunlit shores) and in extreme exposure.

The familiar upper shore brown algae, Pelvetia canaliculata and Fucus spiralis, come within the supra-littoral fringe in the terms of the definition given above, although in some ways they have closer connections with the mid-littoral zone. This in any case is a convenient point at which to deal with them. They represent perhaps as well as any other species the extreme importance of wave action in determining zonation pattern. On the most sheltered beaches Pelvetia is present as a dense zone of growth on the rock, whether the rock surface be horizontal or vertical. Within its zone its coverage often approaches one hundred per cent., and it can tolerate the close proximity of stones, gravel or sand as seen in parts of the Cliff Cottage beach. In all these sheltered situations its vertical range is exceedingly narrow-often only a foot for the main zone with a very few plants straggling as much as one foot above or below the zone. As more exposed situations are approached, several things happen to this pattern. Firstly, in relation to absolute tidal level, its mean distribution moves up the shore a foot or more. Secondly, the plants cover a wider range, as much as six feet for the main zone with extreme plants being separated vertically by as much as ten feet. Thirdly, the individual plants are smaller and more widely spaced. All this can be seen at Great Castle Head. In extreme exposure *Pelvetia* disappears altogether. Occasionally single plants are found surviving on most exposed shores but in unusual circumstances. For instance, Pelvetia tufts growing in Lichina pygmaea patches are not uncommon; and on boulder shores at the exposed Red Cliff and West Dale Bay Pelvetia grows only in conditions of local shelter, on the landward side of large boulders or on smaller boulders protected by larger ones. Similarly, it occurs on the sides of gullies even on the south western corner of St. Ann's Head.

The distribution pattern here described for *Pelvetia* is also seen but to a lesser extent in *Fucus spiralis*. This species, however, disappears with an increase in exposure long before *Pelvetia*. On shaded shores which are sheltered enough to have *Fucus spiralis*, a red alga, *Catanella repens*, extends into the supra-littoral and is found even where *Pelvetia* has almost one hundred per cent. coverage. Its short growth forms a ground flora between the plants of the larger brown weed. But *Catanella* is not present on sunlit shores to anything like the same extent as on shaded.

The Mid-Littoral Zone

This is the middle shore with its millions of barnacles or carpet of Fucaceae. The familiar series Ascophyllum nodosum, Fucus vesiculosus and F. serratus on the sheltered shore, or Chthamalus stellatus, Balanus balanoides and B. perforatus on the exposed shore, are the characterizing species in the extremes. On shores of intermediate exposure, slight differences of aspect or slope tip the balance in favour of barnacles or algae on neighbouring rock faces, often resulting in a distribution pattern of extreme complexity. But as well as these six species there are others which play an important part in forming the basic pattern of the mid-littoral zone, and a host of yet others filling in the details of the total picture.

On the typical sheltered shore, such as Cliff Cottage beach, the mid-littoral starts with Ascophyllum nodosum. This, the largest of the mid-littoral brown algae, here exists in great tangles of weed many feet in length and since the shore is here so gently sloping the horizontal extent of the species can be as much as a hundred feet. The epiphytic red alga Polysiphonia fastigiata which grows on it in large tufts is tolerant to a smaller tidal range than its host—the higher Ascophyllum plants having less of the epiphyte. Another feature which is responsible for colour banding within the Ascophyllum zone is the variable production of receptacles by this plant. In the early part of the year (March, April) the upper third of the Ascophyllum zone is seen to be richly covered with fruiting bodies giving it an orange brown colour. The rest of the zone is a greenish brown colour. Where ridges of rock or isolated pinnacles stand proud of the generally sloping surface, the Ascophyllum plants are stunted or entirely lacking. It is presumed that these irregularities effectively increase wave action.

Still confining attention to the Cliff Cottage beach, it is found that Fucus vesiculosus occurs as a zone below the Ascophyllum but there is always a wide area of overlap. In gullies where bedrock is overlain by loose stones, Ascophyllum gives way to Fucus vesiculosus which here extends up to the F. spiralis zone. F. serratus occurs lower still and its area of overlap is smaller. On the most sheltered parts of this beach barnacles are indeed absent, but at points where the effects of exposure begin to appear Elminius modestus is the first barnacle on the scene. Limpets are common but not abundant and are all Patella vulgata. The few dogwhelks, Nucella lapillus, living here in the absence of their usual food of barnacles or

muscles are often to be found feeding on limpets. Most of the common shore Littorinas and Gibbulas are plentiful on this beach, living most successfully amongst the weeds. L. littoralis reaches an abundance of 120 per square foot, using Ascophyllum not only for shelter but as food and a surface on which to lay its eggs. L. littorea occurs in localized patches towards the bottom of the zone apparently in relation to local detritus collections. Gibbula umbilicalis is common under the weeds whilst G. lineata is found where the algal cover is less complete.

Dale Point is a typical example of a moderately exposed mid-littoral zone. The Fucaceae occur only as scattered plants or patches in local shelter. The barnacles are indeed dominant here: Chthamalus stellatus is always the highest species, Elminius modestus appears slightly lower, and below this Balanus balanoides appears and rapidly becomes the dominant species. B. perforatus appears quite gradually at the bottom of the barnacle belt. Two plants which have a close superficial resemblance to each other occur in the upper part of the mid-littoral here. Both form distinct patches of tufted growth about half-an inch high. Close examination shows that they never compete for space as the one, Catanella repens, always occurs in damp shady situations while the other—the lichen Lichina pygmaea—occurs in the open sunny sites.

The larger Littorinas and the Gibbulas are present but only in very small numbers. The danger of being washed away here is very real. Limpets on the other hand being independent of shelter are here abundant—both *Patella vulgata* and *P. aspera*. In cracks and crevices many sponges and anemones find a living.

On the beaches between Dale Fort and Dale village in intermediate exposure conditions the two types of mid-littoral zonation are superimposed to give a beach richer in species than the two extremes combined. Where the rock slope is gentle algae predominate but on steeper faces barnacles appear. Another feature of this beach which increases its wealth of species is the loose stoney nature of its lower levels, which provide shelter for many species, especially Crustacea. Many of the larger stones bear the appropriate Fucaceae but the quantity varies from year to year according to the severity of onshore winter winds.

These three types of mid-littoral zonation are the commonest but variations are to be seen. In really severe exposure as at St. Ann's Head various species disappear, e.g. Gibbulas and the larger Littorinas, but new types appear. Fucus vesiculosus var. evesiculosus, a tough stunted plant well suited to withstand a pounding sea, is one of these. At Red Cliff, on stacks of grey-green Silurian rock, Mytilus edulis becomes a dominant midlittoral species. It is tempting to try to relate this to rock chemistry, as neighbouring Old Red Sandstone stacks have few mussels.

The Infra-Littoral Fringe

This narrow zone varies considerably but the Laminarias are always present if the substrate is rocky. Even if the rock consists only of small stones Laminaria saccharina can exist, as on the shores of Dale Roads. L. digitata and the larger species such as Saccorhiza polyschides appear on the solid rocks. But besides these and other large brown algae the infralittoral fringe is an area of Rhodophyceae. Many occur in the lower midlittoral but in the present zone they assume more dominant proportions. Exposure favours the genera Lithothamnion and Lithophyllum which may completely cover the rock surfaces as at Gt. Castle and St. Ann's Heads. In areas where the infra-littoral is rocky and sheltered as at Castle Beach and Gunkle, the number of species of animals and plants is enormous. Every inch of rock surface is utilized. Tubeworms, bryozoa, sponges, tunicates and hydroids abound and, hidden away in crevices, the rarer gastropods and treasures like the Devonshire cup coral are to be found.