ZONATION OF ANIMALS AND PLANTS ON ROCKY SHORES AROUND DALE, PEMBROKESHIRE

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CONTENTS

I. INTRODUCTION

PREVIOUS work on marine biology at Dale includes that of Bassindale (1950, 1958), Barrett (1951), Thomas (1953) Bassindale and Barrett (1957), Bassindale and Clark (1960) and Ballantine (1961). A preliminary account of Dale rocky shores is given by Moyse (1958). The present study is the first general description to appear of the zonation of intertidal organisms on these shores. It is based on detailed transects at sites around the Dale peninsula, at which the general shore surface was examined but such special habitats as rock pools and gullies were ignored. Densities of the species studied were recorded within the five defined degrees of abundance devised by Crisp and Southward (1958) and adopted by Ballantine (1961), rather than as absolute numbers. The quantitative field-work was carried out on the mainland during two separate weeks of spring tides in June and July, 1961; Skomer was visited in August.

The position of the Dale peninsula and the offshore islands is shown in Fig. 1 and the locations and profiles of the mainland shores studied are given in Fig. 2. At these sixteen sites the bedrock is Devonian Old Red Sandstone Marls; the remaining transect, down the south side of Skomer Head, was across Ordovician igneous rocks. The geology of the area is described in Dresser (1959) and in

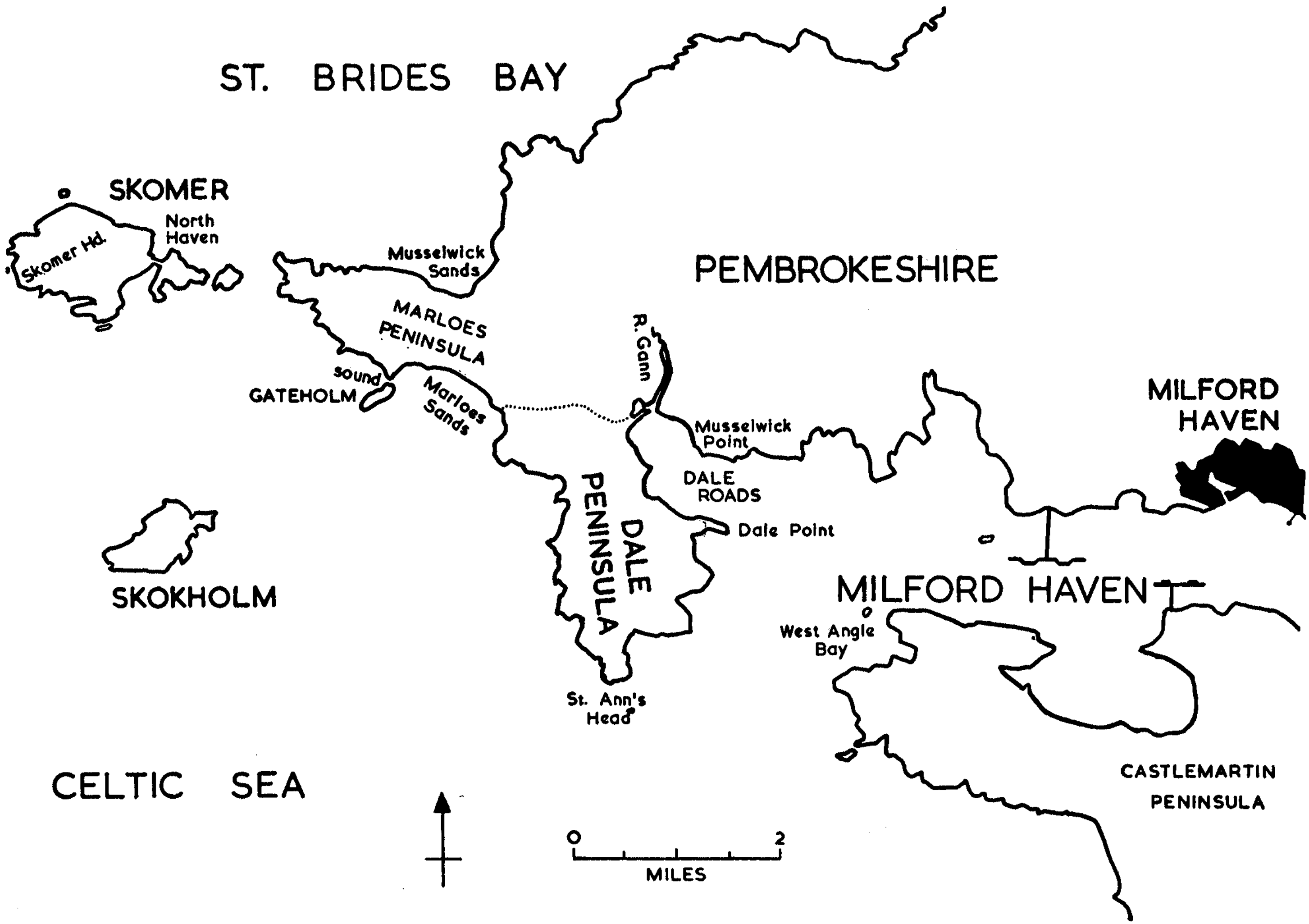


Fig. 1.

Outline map of the area around the Dale peninsula. The dotted line marks the northern boundary of Dale parish.

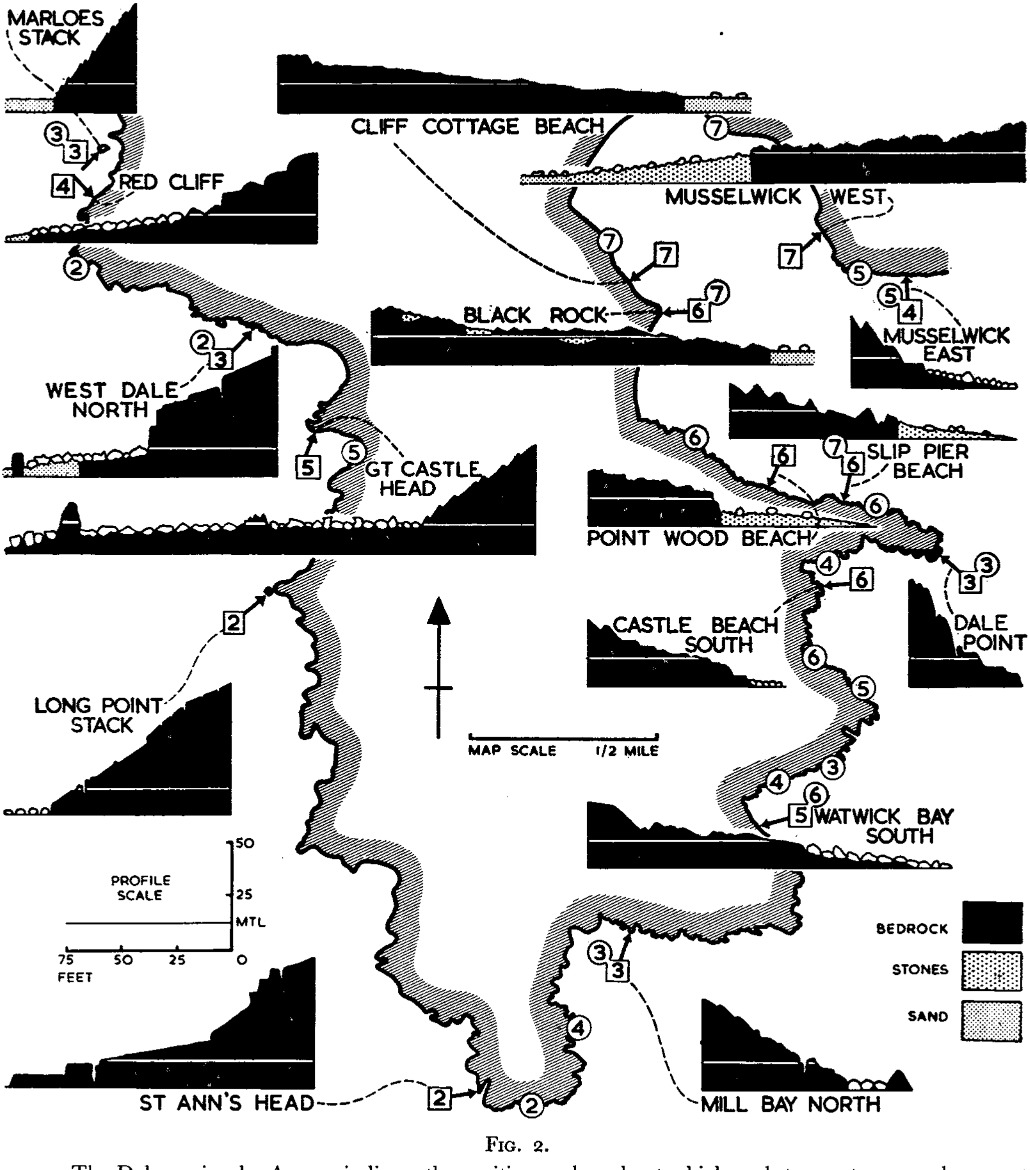


FIG. 2.

The Dale peninsula. Arrows indicate the position and angle at which each transect was made. Numbers give the degree of exposure to wave action, rated according to the biological exposure scale; those derived by the present authors are shown in boxes, while those due to Ballantine (1961) are shown in circles and placed at his survey stations. The profile scale, shown near the bottom left, runs vertically from Chart Datum (approx. ELWS).

Bassindale and Barrett (1957). Oliver (1959, 1960) gives climatic data and Ballantine (1961) discusses the estimation of wave action on its coastline.

The profiles given in Fig. 2 are of the transects selected. These accurately represent the topography of the shore except at St. Ann's Head, where the gentle slopes shown represent oblique traverses across steep rock faces. Skomer Head, which is not shown in Fig. 2, consists of bedrock dipping steeply into the sea.

II. METHODS

On each shore a transect was marked across the rocks, where possible of bedrock, facing the sea and extending from low water of spring tides to the first few flowering plants at the top of the shore. An "L"-shaped instrument having one limb two feet long and a longer sighting limb bearing a spirit level was used to mark stations at two-foot vertical intervals along the transect, referring to Chart Datum as the zero level. This level was established from the observed high or low water on the day of the survey, assuming that the prediction for that date in Admiralty Tide Tables (Admiralty Hydrographic Department, 1961) was reliable in the settled calm weather conditions under which the survey was carried out. As a check the level of a later high water as indicated by the survey marks was compared with its predicted height, and the error revealed was always less than one foot.

When considering the distribution of animals and plants, each station was taken to include a vertical distance of one foot above and below the marked point. The width of the strip studied varied with the nature of the shore, but generally included about ten feet to each side of the line of stations. The inhabitants of rock pools, gullies and crevices, the undersides of stones and the landward faces of boulders and ridges were recorded merely as "present", the only exceptions to this rule being those species (e.g. *Littorina neritoides*) which are normally found only in crevices.

A list was prepared of about sixty of the commonest animals and plants of rocky shores. These were recorded as being abundant (A), common (C), frequent (F), occasional (O) or rare (R) according to the system of Crisp and Southward (1958), whose criteria were used where applicable. These criteria are given by Ballantine (1961) who adds criteria for *Mytilus*, lichens and fucoid algae, and those for *Pomatoceros* and *Spirorbis* are given below. Other species were assessed according to the most appropriate scale (Table 1). Where a distribution

Pomatoceros triqueter

A. 50 or more tubes per sq. dm.
C. 1 to 50 tubes per sq. dm.
F. 10 to 100 tubes per sq. m.
O. Less than 10 tubes per sq. m.
R. Only a few found in 30 minutes' search

Spirorbis spp.

A. 5 or more per sq. cm.; occurring on 50% of suitable surfaces
C. 5 or more per sq. cm.; on 5 to 50% of suitable surfaces
F. 1 to 5 per sq. cm.; or on 1 to 5% of suitable surfaces
O. Less than 1 per sq. cm.
R. Only a few found in 30 minutes' search.

Table 1.

Species	Scale used	Author
Balanus crenatus	*Balanus balanoides*	Crisp and Southward (1958)
Actinia equina	Topshells, etc.	,, ,,
Littorina saxatilis sub spp. *saxatilis* and *tenebrosa*	*Littorina neritoides*	,, ,,
sub spp. *rudis* and *jugosa*	Other *Littorina* spp.	,, ,,
"Lithothamnia"	Lichens	Ballantine (1961)
All other algae listed	Fucoids, etc.	,,

Table 2. *Species of plants and animals used as indicators of wave-exposure, showing their typical degrees of abundance on shores of exposure grades 1 to 7.*

	←Exposed				Sheltered→		
Exposure grade:	1	2	3	4	5	6	7
Alaria esculenta	A	N—A	N—A	N—A	N	N	N
Porphyra umbilicalis (high-level form)	A	C—A	N—A	N	N	N	N
Laminaria cloustoni	N—O	O—A	R—C	N	N	N	N
Fucus vesiculosus f. evesiculosus	O—A	O—A	O—A	N—C	N	N	N
Lichina pygmaea	N—C	C—A	C—A	R—A	N	N	N
Mytilus edulis	R—A	R—A	R—A	R—F	R—F	N—O	N
Corallina officinalis	A	F—A	F—A	O—C	O—C	N—F	N
Patella depressa	O—C	O—A	O—A	O—A	O—A	N—C	N
Patella aspera	F—A	F—A	F—A	R—A	R—A	N—A	N
Littorina neritoides	C—A	C—A	C—A	C—A	C—A	R—C	N
Laurencia pinnatifida	O—F	O—A	O—A	O—A	O—A	R—A	N
Chthamalus stellatus	A	A	A	C—A	C—A	C—A	R—F
Fucus serratus	N	R—A	R—A	R—A	R—A	A	A
Balanus perforatus	N	N—F	O—A	O—A	O—A	O—A	O—A
Pelvetia canaliculata	N	N	R—F	R—F	F—C	A	A
Nucella lapillus	N	N	R—A	C—A	C—A	C—A	C
Spirorbis rupestris	N	N	N—O	O—F	C—A	C—A	C—A
Gibbula umbilicalis	N	N—A	N—A	C—A	A	A	A
Littorina obtusata	N	N	N	R—F	R—F	F—A	A
Monodonta lineata	N	N	N	R—F	C—A	C—A	C—A
Littorina littorea	N	N	N	N—C	R—C	R—C	A
Fucus vesiculosus	N	N	N	N	R—C	O—C	C—A
Catenella repens	N	N	N	N—O	N—O	F—A	F—A
Fucus spiralis	N	N	N	N	N	R—A	C—A
Spirorbis borealis	N	N	N	N	N	N—F	C—A
Ascophyllum nodosum	N	N	N	N	N	N—A	A
Laminaria saccharina	N	N	N	N—A	N—A	N—A	N—A

N=absent, R=rare, O=occasional, F=frequent, C=common, A=abundant.

was patchy, the score recorded was for the greatest density occurring over at least a square metre. Since it was impossible to spend the prescribed time searching at any one station for a species scoring only "rare", this grade was used infrequently and rather more subjectively.

Lewis (1953) published diagrams showing the horizontal distribution of many plants and animals between the extremes of exposure to wave action. Ballantine (1961) introduced a biological exposure scale based on such changes. He established eight grades of exposure, giving an account of the plants and animals typical of each grade. It was found in the present study that the exposure grade of any shore could be determined merely from the greatest abundance of certain indicator species on that shore. Table 2 lists 27 such species, showing the degree of abundance typical of each grade of exposure to be found in the Dale area. Absence is as diagnostic as abundance, provided that it is not due to unsuitability of the substratum. Table 3 lists the shores studied, showing the

Table 3. *Biological grades of wave-exposure of shores in the neighbourhood of the Dale peninsula, and abbreviations used for these shores in Fig. 3a and Figs. 4 to 12.*

Shore	Abbreviation	Description	Grade
Skomer Head	Sk	extremely exposed	1
St. Ann's Head Long Point Stack	StA LPt	very exposed	2
West Dale North Dale Point Mill Bay North Marloes Stack	WD DPt MB MSt	exposed	3
Red Cliff Musselwick East	RC ME	semi-exposed	4
Great Castle Head Watwick Bay South	GtC WS	fairly sheltered	5
Castle Beach South Black Rock Point Wood Beach Slip Pier Beach	CB BR PW SP	sheltered	6
Musselwick West Cliff Cottage Beach	MW CC	very sheltered	7

exposure grade derived for each from these data. Neither extremely exposed nor extremely sheltered shores are found on the Dale peninsula. In the account of the distribution of plants and animals which follows, wave exposure is referred to in the terms used in this table; thus "exposed shore" means one of grade 3 on the biological exposure scale. To avoid confusion, the "exposure" or uncovering of a plant or animal by the ebbing tide is referred to as emersion.

III. Distributions of species studied

(1) *Flowering Plants (Angiospermae)*

A flora of the peninsula by George (1961) includes marine and maritime angiosperms; these were identified in this survey from Clapham, Tutin and Warburg (1958). The lowest was always either *Plantago maritima, Crithmum maritimum, Spergularia* sp., *Festuca rubra* or *Armeria maritima* (Fig. 3*a*). On the more exposed shores these maritime plants are scattered in a wide zone, but on the very sheltered shores north of Dale Point they quickly give way to scrub or woodland. At Cliff Cottage Beach the branches of trees, particularly ash (*Fraxinus excelsior*) and sycamore (*Acer pseudo-platanus*), are washed by the highest tides.

Beta maritima, Cochlearia officinalis and *Matricaria* sp. were recorded at a few shores, and seen at others at a level higher than the transect; *Crithmum maritimum* is, however, confined to the more exposed shores. The succulent variety of *Plantago coronopus*, typical of the offshore islands (Gillham, 1953), was seen at Long Point Stack.

(2) *Lichens (Lichenes)*

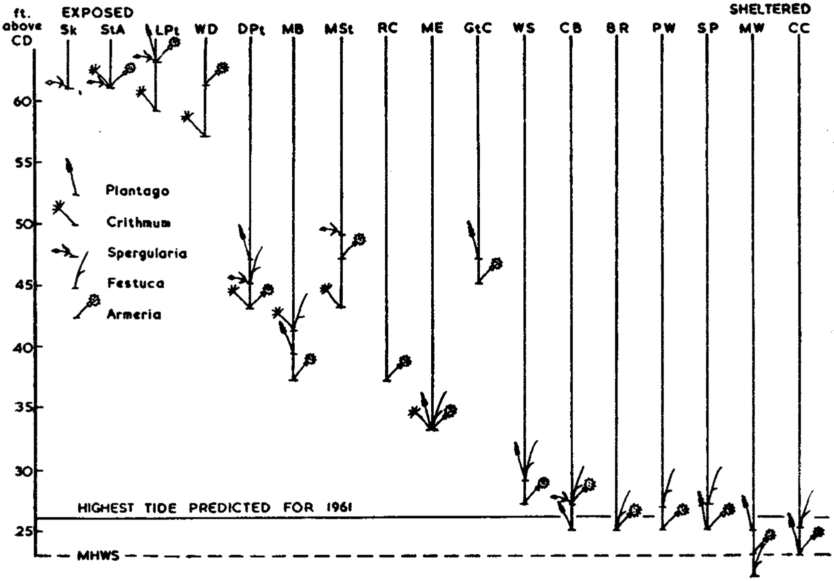
Wade (1960) gives a preliminary list of the lichens of Dale. Those included here were identified from Duncan (1959), but no attempt was made to deal with them in detail. Table 4 lists the levels at which the supralittoral species were recorded on the mainland shores, but they often occurred only above the highest station on the transect; *Pseudophyscia fusca*, for example, was seen at higher levels on most of the more sheltered shores. These lichens occupy narrower zones at lower levels on the more sheltered shores (Fig. 3*b*).

The orange lichens are mostly either *Xanthoria parietina* or *Caloplaca marina* (*Placodium lobulatum*), and the dominant species of *Ramalina* is *R. scopulorum*. *Verrucaria* was divided into a "*V. maura*" group of thin dull black forms and, replacing this from MHWS downwards, "*V. mucosa*" comprising thick, shiny green-black species (Fig. 6). At St. Ann's Head, "*V. mucosa*" extends to well above this level in the shade of a natural arch. It is absent from most of Cliff Cottage Beach, where there is a full cover of Fucaceae. Neither group was recorded from Skomer Head because of the difficulty of distinguishing them on the black rock there, but both are probably present.

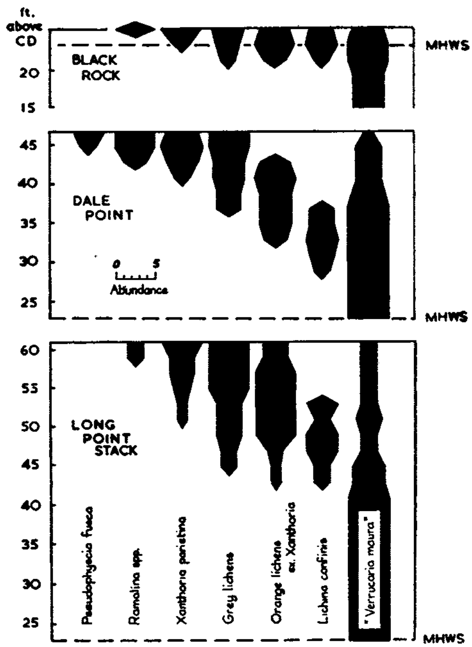
Lichina pygmaea occurs at Dale on the sunlit vertical surfaces of the more exposed shores (Fig. 6) as black rounded patches often 20 cm. or more in diameter; it is sometimes confused with the red alga *Catenella repens*. *Arthropyrenia foveolata* was seen on nearly every shore on the shells of all but the highest barnacles and limpets.

(3) *Brown Algae (Phaeophyceae)* (Fig. 4)

Pelvetia canaliculata in abundance reaches an upper limit about one foot below MHWS; this limit is raised on shaded, north-facing shores where desiccation effects are reduced. Its wider zone on shores of greater exposure is probably due to greater wave splash and the absence of some midlittoral competitors; on the most exposed shores at which it occurs, the plants are



a (above). The lowest flowering plants recorded on each shore. The shores are arranged according to their degree of exposure to wave-action, and are designated by the letters given in Table 3 (p. 6).



b (right). The zonations of supra-littoral lichens on three shores of increasing exposure. Black Rock is sheltered (grade 6), Dale Point exposed (grade 3) and Long Point Stack very exposed (grade 2).

FIG. 3

Table 4. *Distribution of supralittoral lichens*

		Exposed															Sheltered
Shore:		StA	LPt	WD	DPt	MB	MSt	RC	ME	GtC	WS	CB	BR	PW	SP	MW	C C
Highest station surveyed		69	61	61	47	41	51	37	33	49	31	27	25	27	27	25	25
Pseudophyscia fusca	lower limit	×	×	×	44	×	×	×	×	×	×	×	×	×	26	×	24
Ramalina spp.	upper ,,	+	+	+	+	+	+	+	+	+	+	+	+	×	+	+	+
	lower ,,	68	58	56	42	34	46	28	28	42	26	24	24	×	24	22	22
Xanthoria parietina	upper ,,		+		+		+						+	26			
	lower ,,		50		40		50						22	24			
Orange lichens (ex. *Xanthoria*)	upper ,,		+		44		+						+	+			
	lower ,,		42		32		46						20	24			
Orange lichens (inc. *Xanthoria*)	upper ,,	+		60		+		+	+	+	+	+			+	+	+
	lower ,,	52		50		28		26	26	38	24	24			22	20	22
Grey encrusting lichens	upper ,,	62	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	lower ,,	54	42	50	36	28	44	32	26	38	24	24	20	24	20	20	22
Lichina confinis	upper ,,	66	54	58	38	+	46	32	32	44	28	26	+	×	24	22	+
	lower ,,	54	42	42	28	26	32	26	24	26	24	24	20	×	20	20	22
"*Verrucaria maura*"	upper ,,	+	+	58	+	36	+	+	32	42	+	+	22	26	+	+	24
	lower ,,	18	6	20	16	16	16	18	18	16	14	18	12	20	18	18	18

Figures are feet above Chart Datum (MHWS is 23ft. above C.D.). + = upper limit above highest station surveyed, × = absent at all stations surveyed. (At some localities *Xanthoria* has been recorded separately from the other orange lichens.)

scattered individually, and are often present only in patches of *Lichina pygmaea* or anchored in crevices.

Fucus spiralis is present only on sheltered and very sheltered shores, with the highest plants amongst the *Pelvetia*. Like *Pelvetia*, its zone is higher on shaded than on sunlit shores; on rocks bordering sand at Castle Beach, however, some plants were seen as low as MTL, perhaps because of the scarcity of limpets there.

Ascophyllum nodosum is found on bedrock and boulders firmly embedded in the substratum, often covering the entire rock surface in a zone 100 feet wide horizontally on the most sheltered shores. On the jagged but gently sloping Slip Pier Beach transect, although abundant over most of its usual range it never completely covers the shore, while at Point Wood Beach it is stunted and occurs only on the flatter upper parts of the shore. *Ascophyllum* was not found at Castle Beach, although it is known to have been present there a few years ago.

Fucus vesiculosus occurs on exposed shores as the bladderless form *evesiculosus*; few intermediates occur between this and the "normal" form found in shelter, because of the rarity of the species on shores between these extremes. The "normal" form occurs in gullies and patches of stones on very sheltered shores; it is more abundant on those sheltered shores where *Ascophyllum* is absent, but on no shore does it form a dense zone.

The form *evesiculosus* normally occurs only on rocks facing the sea, where it receives wave surge and splash at low water. It is rare or absent at steep sunlit shores such as Dale Point, which although rated as exposed dry rapidly at low water in calm summer conditions. Its abundance at Red Cliff may be due to the shaded aspect or to the swell at that Atlantic shore. Plants are rare and at a high level on Marloes Stack, perhaps because *F. vesiculosus* does not tolerate sand abrasion. Occasional hybrids between *Fucus spiralis* and *F. vesiculosus* were found on several shores, for example Great Castle Head.

Fucus serratus occupies a narrow zone on the lower part of the shore, but extends higher and often to MLWN where this region is relatively damp and free from limpets. On the fairly shaded Slip Pier Beach it spreads to MTL or even higher. At lower levels it gives way abruptly to *Laminaria* spp. on most shores.

Laminaria saccharina extends further into shelter than *L. digitata* and on moderately exposed shores it is often present only when there is sand nearby. It is absent from the Point Wood Beach transect, but was seen in the water at a lower level.

Laminaria digitata may cover the rocks in exposed and moderately sheltered situations, forming a wide zone which usually extends a few feet onto the shore. The plants sometimes reach higher levels in damp gullies.

Himanthalia elongata was recorded from the mainland only on three west coast headlands, although it has since been observed at West Angle Bay (Fig. 1). It is absent from Skomer Head, but abundant in the North Haven of Skomer, where *Pelvetia* and *Fucus spiralis* also occur. Thus it appears to need water from the open sea, but to be intolerant of great exposure.

Alaria esculenta is essentially sublittoral and typical of the most exposed shores. It has a zone similar to that of *Laminaria*, and replaces this species completely at Skomer Head.

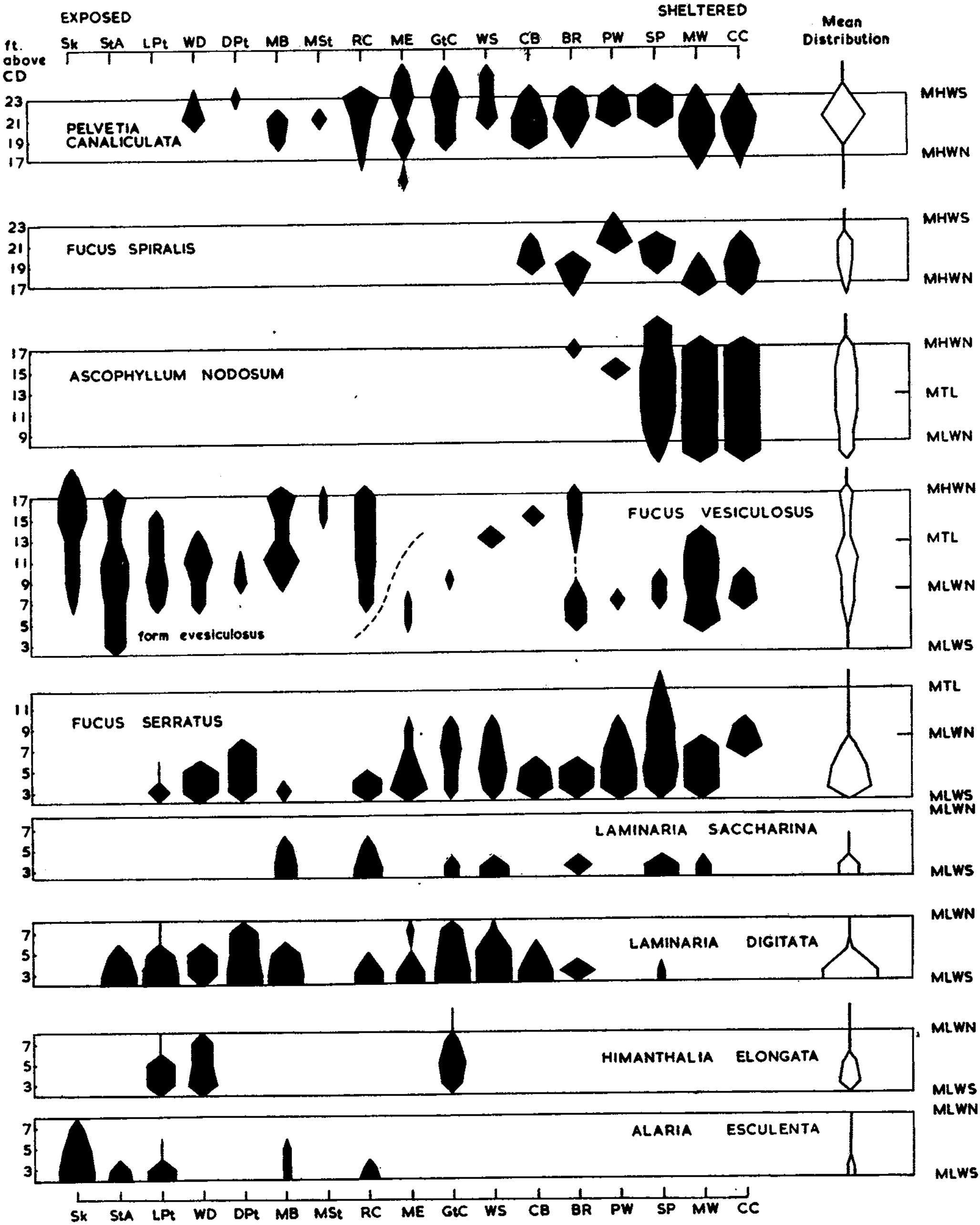


FIG. 4.

Distribution of brown algae (Phaeophyceae) on the transects studied (see Fig. 2). The shores are arranged according to their degree of exposure to wave action, rated according to the biological exposure scale, and are designated by the letters given in Table 3 (p. 6). The scale of abundance is given in Fig. 8 (p. 18). The interrupted line divides the "normal" form of *Fucus vesiculosus* from f. *evesiculosus*.

(4) *Green Algae* (*Chlorophyceae*) (Fig. 5)

These were recorded as a single category, neither listing nor separating the component species. Greatest abundances were found on stones towards the lower parts of moderately sheltered shores; on the more exposed sites these plants are often confined to the shells of the larger limpets.

(5) *Red Algae* (*Rhodophyceae*)

Porphyra umbilicalis occupies a distinct zone astride high water mark on the most exposed shores at Dale, and also occurs abundantly below MTL on more sheltered shores. These zones are never continuous, and only the upper one was surveyed (Fig. 6). At Long Point Stack and Skomer Head the zone is wide and dense, and must be kept moist by surf during neap tides; its particularly high level at St. Ann's Head is probably due to shade as well as wave splash. Grazing by limpets may prevent its spread below MHWN.

The low-level *Porphyra* occurs on flat rocky surfaces partly covered by sand or stones, e.g. at Marloes Sands. There the plants, which are exploited commercially for "laverbread", probably thrive because limpets seem to be deterred by the sand.

Catenella repens (Fig. 6) occupies a zone at the same level as *Lichina pygmaea*, with which it may be confused; but it is confined to shaded rocks and is intolerant of wave exposure. Beneath *Ascophyllum* and *Fucus spiralis*, *Catenella* may form an undergrowth almost covering the rock surface.

The midlittoral red algae studied were *Laurencia pinnatifida*, *Gigartina stellata*, *Rhodymenia palmata*, *Corallina officinalis* and the "lithothamnia" (Fig. 5). None extend much above MHWN except on shores with a northerly aspect, and all tolerate considerable wave exposure, but none occur at Marloes Stack, probably because of sand abrasion there. On shores covered by Fucaceae they probably fail in competition for space and light, and are generally scarce; "lithothamnia" extend higher, however, in the damp conditions under the weed. All except *Laurencia* occur abundantly in rock pools above their upper limit on the open shore.

Laurencia pinnatifida generally forms a zone above the other red algae, with a lower limit above low water, while *Gigartina stellata* often extends below MLWS, with a lower limit visible not much below this level. *Rhodymenia palmata* is frequently attached to other weeds, especially *Laminaria* spp., and extends some distance below low water. *Corallina officinalis* occupies a zone centred below the midlittoral, and probably below MLWS, but occurs as high as MHWN in damp gullies.

"Lithothamnia" is a convenient term used by many ecologists (e.g. Southward, 1953 and Lewis, 1957) for all the encrusting corallines of the family Melobesiae; in this study the component species were not distinguished, although the form growing under cover of Fucaceae was seen to have a different colour and texture from that on exposed shores. "Lithothamnia" often spread up the shore as fine streaks in damp crevices, which are occupied at a higher level by *Littorina* spp. On exposed shores *L. neritoides* is replaced by the alga in such crevices at low levels, but is still present in empty barnacle shells. Yet lower, "lithothamnia" may blanket rock surfaces completely in the absence of sand

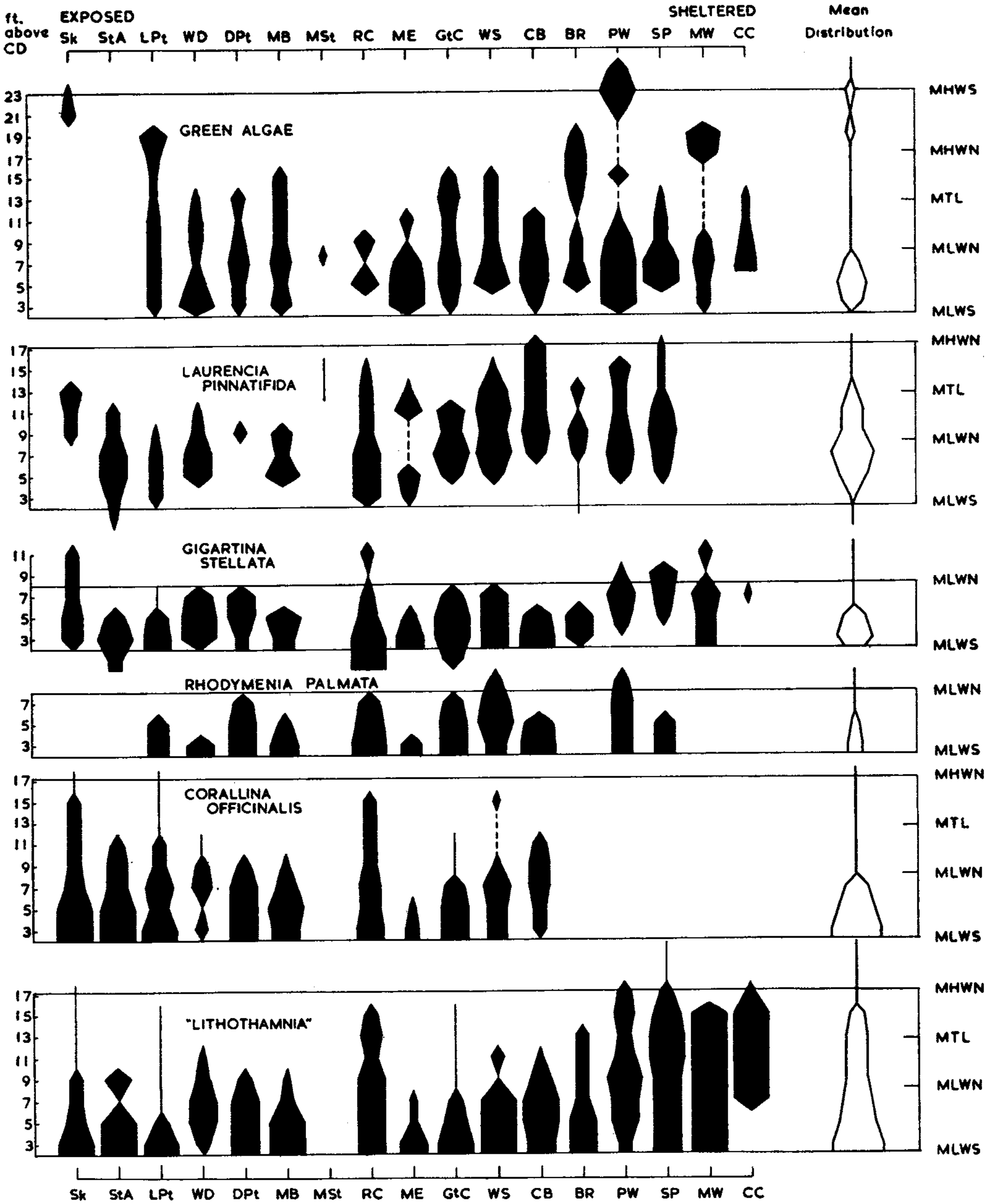


FIG. 5.

Distribution of green and red algae (Chlorophyceae and Rhodophyceae), shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

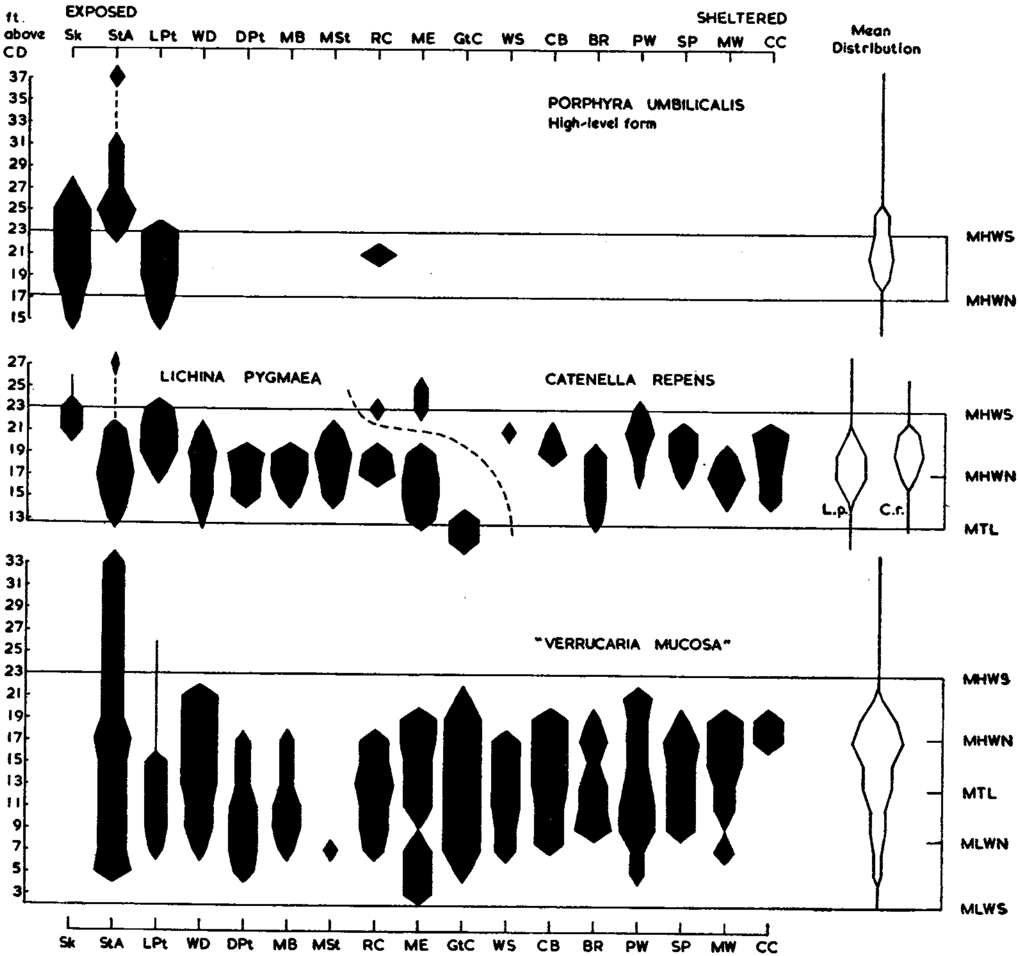


FIG. 6.

Distribution of some intertidal algae and lichens, shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

abrasion or severe desiccation, excluding barnacles and limpets. *Spirorbis* spp. and *Pomatoceros triqueter* are, however, able to grow on or in the algal thallus, and many bryozoa and sponges compete successfully with it for space.

(6) *Barnacles* (*Cirripedia*) (Fig. 7)

In a distant view of a rocky shore a definite "barnacle line" can be seen above which barnacles are so few as to be unnoticeable; this line lies, at Dale, at about twenty feet above Chart Datum, but is absent on the shores covered with Fucaceae. *Chthamalus stellatus*, the highest shore barnacle, may be locally numerous above the barnacle line, especially in moist crevices and on long gentle slopes where the waves at high water wash far up the rocks.

Chthamalus often reaches a maximum abundance of five or more per square cm. near MHWN. Above this level its numbers diminish rapidly, and below it more gradually. In the presence of *Balanus balanoides* its density is reduced to little more than one per square cm. As this still ranks as abundant on the scale used in the survey, the zonation diagrams present a misleading uniformity of width. On the exposed Marloes Stack *Chthamalus* is strikingly abundant at its normal high level but is absent just below MTL where *B. balanoides* is abundant. It is probable that *Chthamalus* cyprids, which settle in late summer and over-winter as small spat, cannot withstand the sand abrasion which is severe at lower levels here in winter; the cyprids of *B. balanoides* settle in spring and the spat grow rapidly during the calmer summer. Spat were not counted during the survey.

Changes in the zonation of *Chthamalus* observed when moving from exposed to sheltered shores are similar to those seen in moving from south to north. In the extreme south-west of England *B. balanoides* is scarce or absent and *Chthamalus* extends down to a low level on the shore (Southward and Crisp, 1956), while on the west coast of Scotland *Chthamalus* is found only high on the shore and in shelter may be separated from *B. balanoides* by a zone of bare rock (Lewis and Powell, 1960). Further north still, it is absent.

On Skomer Head, specimens both of *Chthamalus* and *Balanus balanoides* are considerably larger than elsewhere, perhaps because they feed better in constantly moving water.

Elminius modestus, an immigrant species from Australasia, was first recorded in this area from Dale Roads in 1951 (Bassindale and Barrett, 1957). It is still (1961) absent from the open coast but is spreading within Milford Haven. Bassindale (1958) recorded "two or three individuals" from Watwick Bay, whereas it is now common over most of that shore; it has also increased in abundance at Dale Point, demonstrating that it can tolerate exposed conditions and might be expected to appear in due course on similar shores outside the Haven. Its method of spreading is discussed by Knight-Jones and Stevenson (1950), Crisp (1958), and Crisp and Southward (1959). It often extends into the sublittoral.

Balanus balanoides has an upper limit which seems to be higher on the more exposed shores, and also on two sheltered shores (Slip Pier Beach and Point Wood Beach) which are shaded; at Watwick Bay South it clearly extends higher on shaded than on sunlit rock surfaces.

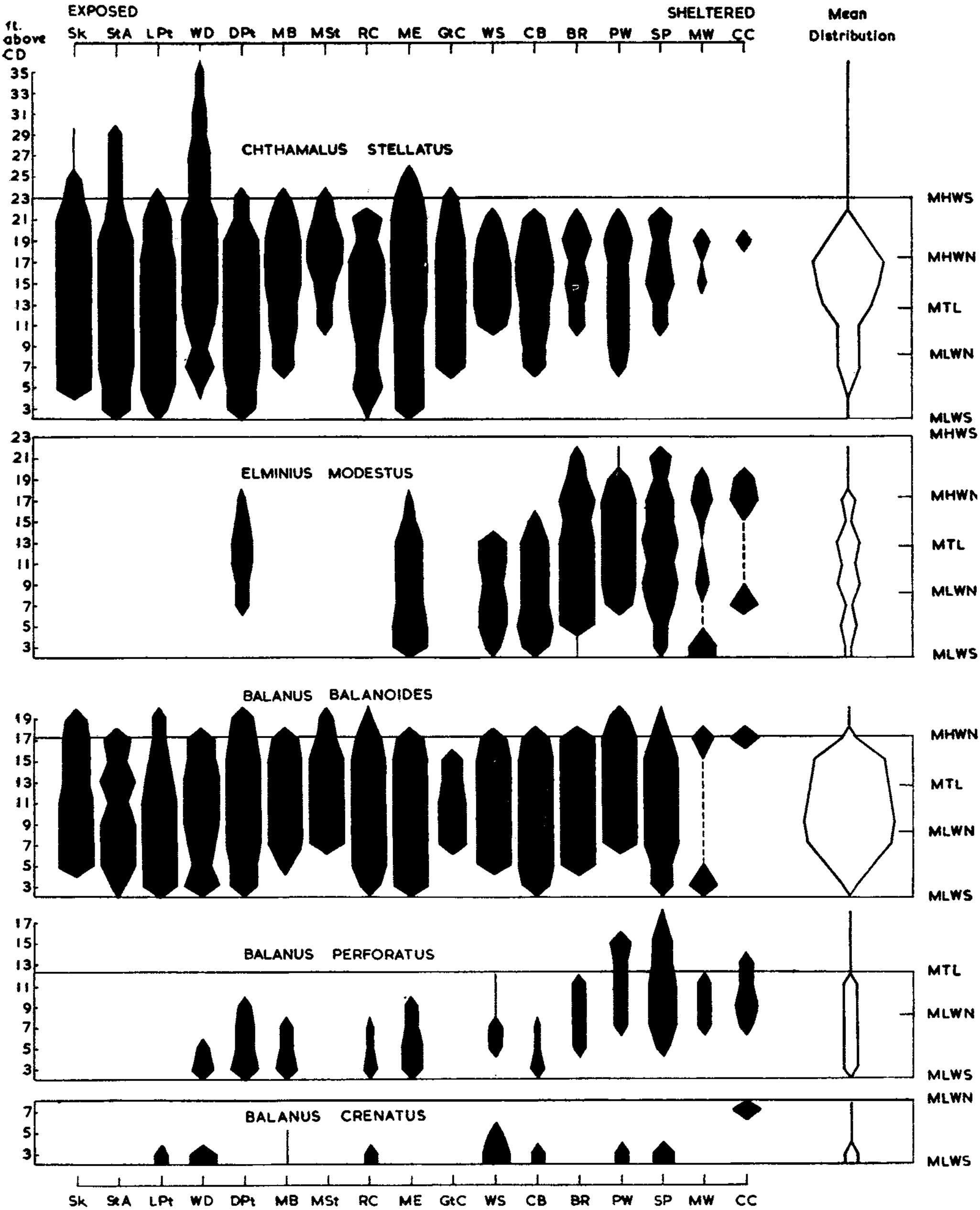


FIG. 7.

Distribution of barnacles (Cirripedia), shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

Balanus perforatus occurs on rocks up to MLWN, and higher on shaded shores kept damp by abundant *Ascophyllum*. The Pembrokeshire coast is its northern limit; it is abundant at Musselwick Sands (Fig. 1), though not at Dale, but absent from Cardigan Bay and coasts further north. Unlike other shore barnacles, *B. perforatus* is rarely seen on loose rocks. The few specimens occurring below low water at Dale are larger than those from the shore.

Balanus crenatus is essentially a sublittoral barnacle, and the highest individuals often occur on the undersides of boulders. It is absent from the most exposed shores, probably because of the extensive growth of "lithothamnia".

(7) *Winkles* (*Littorinidae*) (Figs. 8 and 9)

Littorina neritoides is well known to show greater size, abundance and vertical range on shores of increased exposure to wave action. It is often most abundant in the upper part of the *Chthamalus* zone, occupying all available crevices including empty barnacle shells. Above this level there may be another dense zone where honeycomb erosion provides shelter in the splash zone. Such depressions may be caused by ages of browsing by the winkles themselves (Fox, 1955). Although it is concluded that the Skomer Head transect is far more exposed than any on the mainland, *L. neritoides* does not extend far above high water there, probably because of the greater smoothness of the igneous rocks.

Littorina obtusata is always found on fucoid algae, but has a distribution more limited than theirs. *Fucus serratus* harbours the winkle in shelter, but lacks it at exposed sites; it is also found on *F. spiralis* on shaded shores or where the plant occurs below MHWN. *L. obtusata* is always numerous at Dale on *Ascophyllum*. Records were not kept of the distribution of the various colour forms of this species, but such differences seemed to be of the sort observed elsewhere (Barkman, 1955). It would be interesting to combine an investigation of the zonation of these colour varieties with studies of their genetics.

Littorina littorea is locally abundant on certain sheltered and very sheltered shores around Dale, and like *Monodonta* is almost confined to gentle slopes.

Littorina saxatilis. B. L. James has made a special study of this winkle, distinguishing four subspecies. He has kindly communicated observations which are incorporated into this account, and in an Appendix he has added brief descriptions of the four subspecies. Diagrams are given (Fig. 9) for each of the exposure grades recognized in the area, since few of the shores studied by James coincide with those included in this survey.

L. saxatilis tenebrosa occurs at a high level on the more exposed shores, though on a given shore it never extends as far as the highest *L. neritoides*. While its upper limit is generally raised by greater exposure, it is not very high on Skomer Head as the rock there is probably too smooth.

L. saxatilis saxatilis replaces *L. s. tenebrosa* at lower levels on shores exposed to wave action, and extends further into shelter. It is less numerous at the most exposed sites. At Skomer Head its lower limit was MTL, but at St. Ann's Head it reached MLWS. *L. s. saxatilis* occurs almost exclusively in empty barnacle shells, replacing *L. neritoides* in this habitat below MLWN.

L. saxatilis jugosa occurs in the *Pelvetia* zone on sheltered shores, where it is abundant at Dale. *L. saxatilis rudis* coincides with it on these shores, but extends

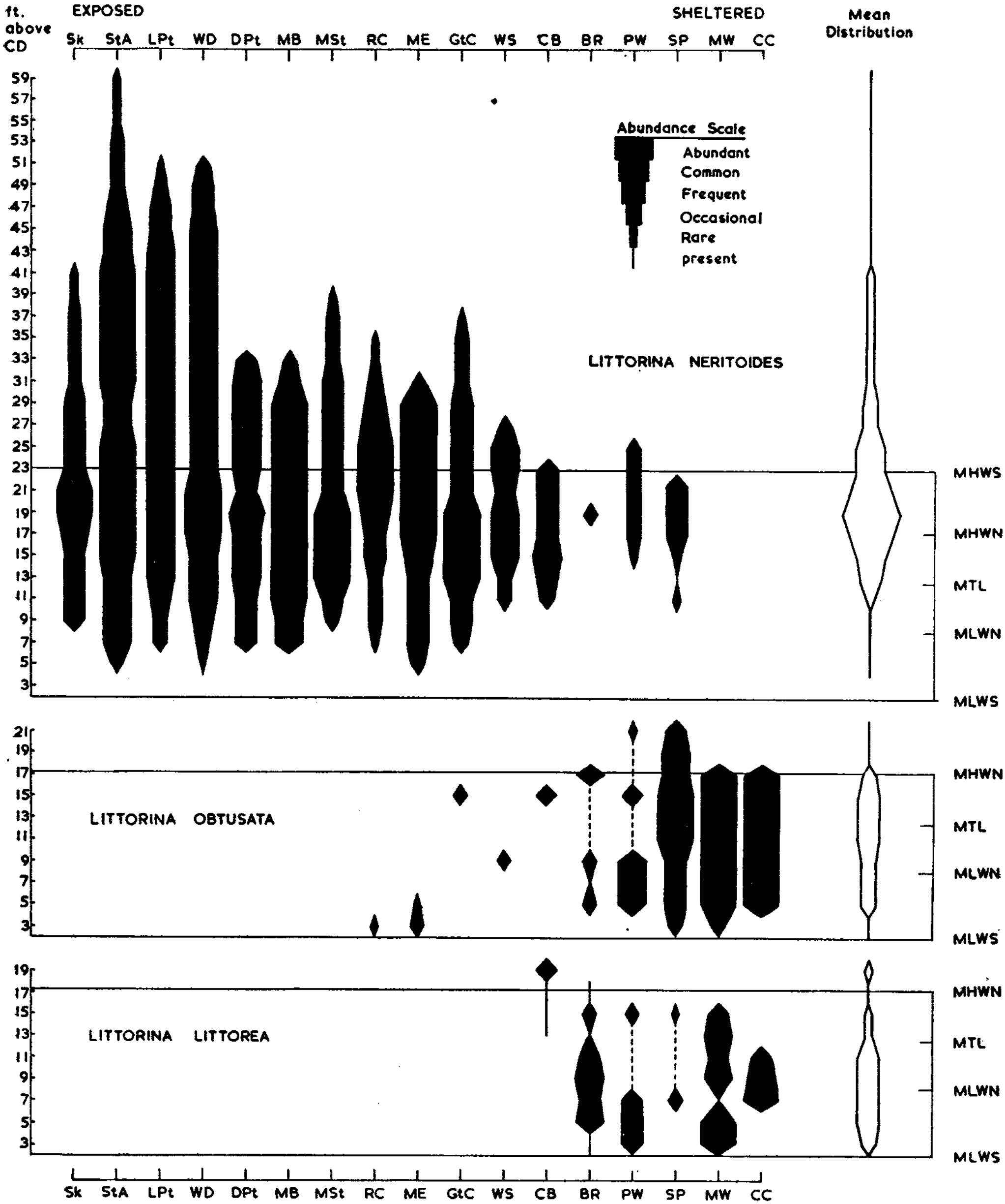
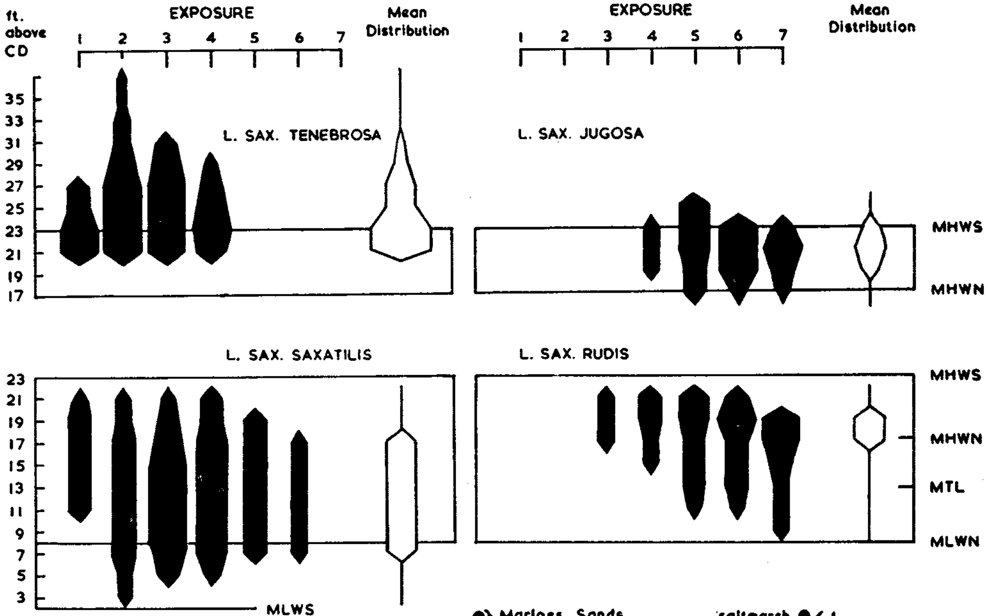
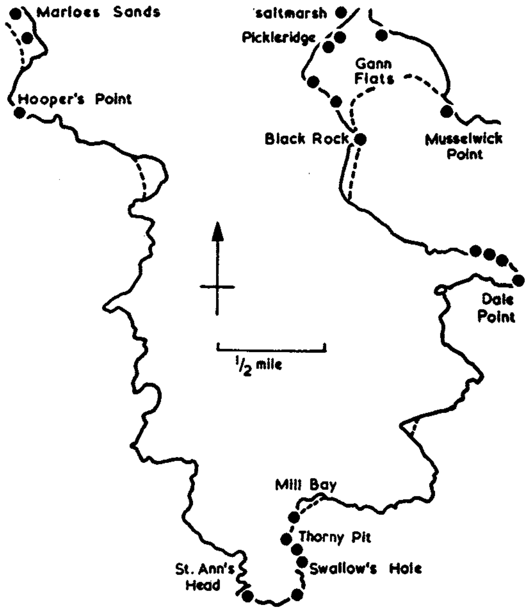


FIG. 8.
Distribution of some winkles (Littorinidae), shown as in Fig. 4 (p. 11). The solid histograms show abundance, as in the inset scale. The "mean distribution" histograms have a width proportional to the number of shores on which that species was Abundant (or Common, where rarely or never abundant).





Shores visited in studying the distribution of *Littorina saxatilis* subspp.

Grade 1. Grassholm (Skomer Head).
2. St. Ann's Head, Hooper's Point (St. Ann's Head, Long Point Stack).
3. Dale Point (Dale Point, Marloes Stack, Mill Bay North, West Dale North).
4. Mill Bay South, headlands near Thorny Pit and Swallow's Hole, Dale Fort Beach (Red Cliff, Musselwick East).
5. Boulders on Marloes Sands, Gateholm Sound (Great Castle Head, Watwick South).
6. Slip Pier hard-lying (Slip Pier Beach, Black Rock, Point Wood Beach, Castle Beach).
7. Shores around Gann Flats (Cliff Cottage Beach, Musselwick West).

FIG. 9.

Distribution of *Littorina saxatilis* subspecies. Diagrams are given for each of the biological grades of wave-exposure occurring around Dale (see p. 6), from data collected at the shores listed. The inset map indicates shores visited by James; those named in parentheses were surveyed by the authors, Skomer Head and Gateholm Sound are shown on Fig. 1 (p. 2), while Grassholm lies to the west of Skokholm. Abundance scale in Fig. 8 (p. 18).

to lower levels, reaching a maximum abundance in the *Fucus spiralis* zone. On exposed shores, *L. s. rudis* is less numerous, but extends lower so that it overlaps with *L. s. saxatilis* although not sharing its habitat. On some shores of an intermediate degree of exposure, all four subspecies are found.

(8) *Top-Shells* (*Trochidae*) (Fig. 10)

Monodonta lineata has a distribution largely determined by the slope of the shore. On semi-exposed shores it is confined to areas which are relatively flat, while in greater shelter it occurs on steeper slopes but is still absent from the steepest. There are few steep slopes on the most sheltered shores at Dale, and *Monodonta* is probably scarce on these shores because of the abundance of Fucaceae. It is found at a high level on sheltered, shaded shores, and it may also extend down to the *Laminaria* zone, being often quite abundant at that level among stones too mobile for the attachment of *Laminaria* or *Fucus serratus*.

Gibbula umbilicalis is less dependent on shelter and gentle slopes than *Monodonta*, and does not extend so far up the shore; the highest individuals usually occur in rock pools.

Gibbula cineraria occurs in the sublittoral fringe, appearing on the shore only at the upper limit of its range. The highest individuals are usually hidden under stones, and the absence of this species from the more exposed shores may be due partly to the absence there of loose stones.

(9) *Limpets* (*Patellidae*) (Fig. 11)

Patella vulgata seems the most ubiquitous of the macroscopic shore animals at Dale. On the more sheltered shores it is scarce on open surfaces above MHWN, although stragglers are found in shaded gullies. It extends higher in greater exposure, particularly on a shaded wave-washed slope at St. Ann's Head. Where the substratum is suitable the lower limit of *P. vulgata* is MLWS, but at Skomer Head it is absent from the lower shore and becomes abundant only above MHWN. It probably fails in competition with *P. aspera* here (see below). At West Dale North and Castle Beach South, *P. vulgata* flourishes below MLWS where "lithothamnia" are absent.

Ballantine (1961) found that *P. vulgata* becomes less abundant in shelter. This was found to be generally so in the present survey, but because of their large size in the very sheltered localities, the limpet biomass in a given area is probably greater than on more exposed shores.

Patella depressa at Dale is near the northern limit of its geographical range, and is nowhere abundant. It appears to prefer vertical sunlit surfaces, and the fluctuation in its lower limits between the shores studied is probably due to the scarcity of such sites at this level. It is most numerous between MTL and MLWN; according to Orton and Southward (1961) it occurs at a higher level in Cornwall.

Patella aspera is the dominant limpet at the lowest levels on most of the more exposed shores, and it is found much further up the shore in rock pools. At Skomer Head it extends abundantly up to and beyond MHWN, possibly because desiccation is less at such wave-beaten sites. The few specimens of *P. aspera* seen

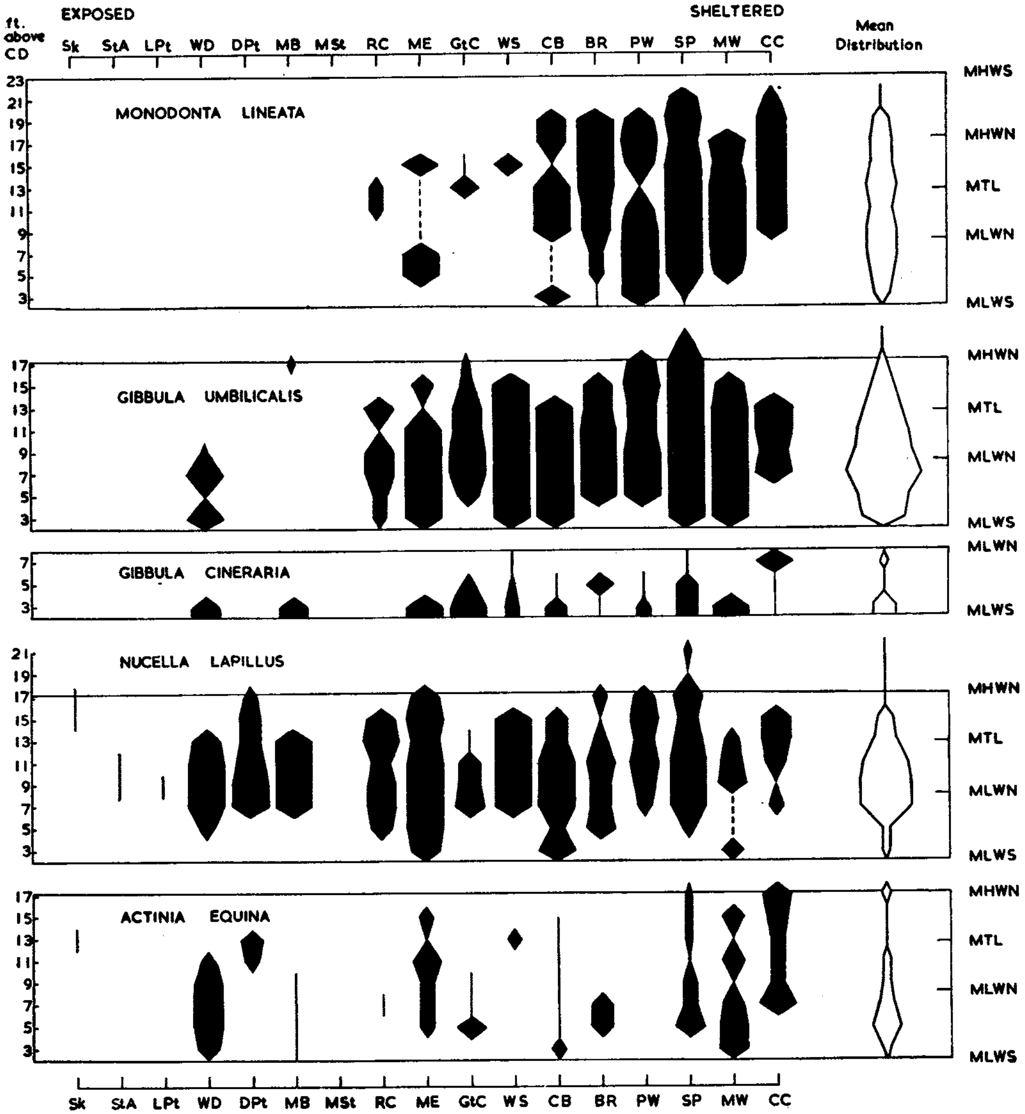


FIG. 10.

Distribution of top-shells (Trochidae), *Nucella lapillus*, and *Actinia equina*, shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

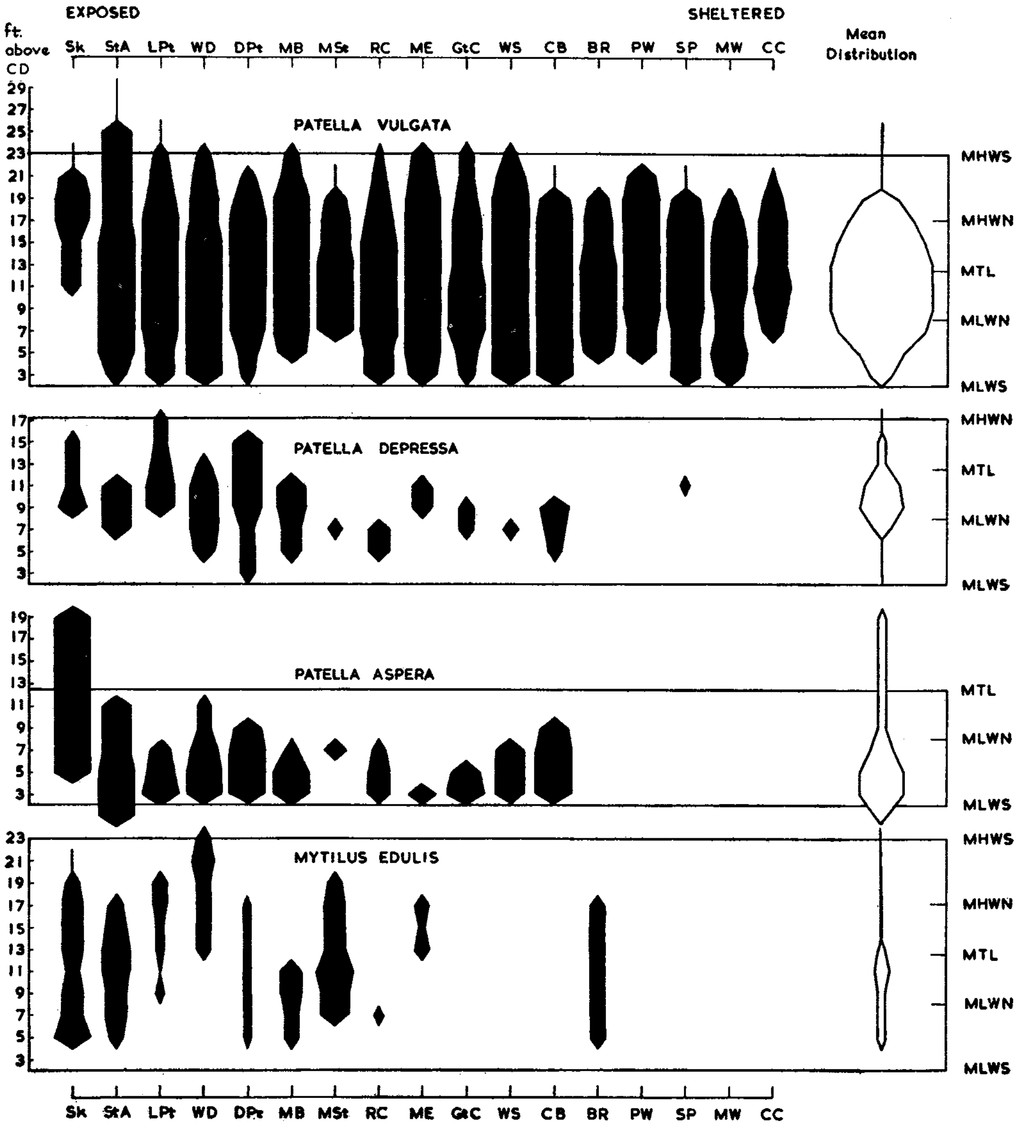


FIG. 11.

Distribution of limpets (Patellidae) and *Mytilus edulis*, shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

on sheltered and very sheltered shores at Dale were in rock pools on Slip Pier Beach and at Black Rock.

The limpets found on some shores with shells encrusted by "lithothamnia", and having "homes" in dense patches of these algae were all *P. aspera*, so this species seems a little more tolerant of "lithothamnia" than *P. vulgata;* but, in general, heavy growths of "lithothamnia" prevent the downward spread of *Patella* spp.

(10) *Other Mollusca*

Nucella lapillus, the dogwhelk (Fig. 10), is most abundant on shores of intermediate exposure; this has also been observed by Lewis (1953, as *Thais*) and Ballantine (1961). In extreme exposure it is scarce and confined to crevices. It is absent from Marloes Stack, probably because of the steep slope from which dislodged individuals would be washed away with little chance of returning. Changes in the size and shape of the shell associated with different degrees of exposure are seen well at Dale (Bassindale and Barrett, 1957). *Nucella* feeds mainly on barnacles, but does not extend up the shore so far as these, perhaps because it is less able to withstand desiccation.

Mytilus edulis (Fig. 11) was seen almost exclusively on the more exposed sites surveyed at Dale, but is not confined to rocky shores; its extensive distribution on the Gann Flat is discussed by Bassindale and Clark (1960). The only record for mussels on a sheltered rocky shore is from the nearby Black Rock, where they are very small, as they are also at the much more exposed Skomer Head, West Dale North and Dale Point. On the Gann Flat, and also on the exposed Marloes Stack, they are large. *Mytilus* appears from this survey to thrive best on sunny shores free from the larger algae; it also occurs sublittorally.

(11) *Serpulidae* (Fig. 12)

Spirorbis borealis is found on *Fucus serratus* and occasionally on *F. vesiculosus* but it cannot extend as far up the shore as these algae, nor can it tolerate as much wave-exposure. *S. borealis* is abundant on the two very sheltered shores studied, but only rare or occasional on the sheltered shores.

A recent revision of this genus (de Silva and Knight-Jones, 1962) has made it possible to include in this survey three further species, *Spirorbis tridentatus* Levinsen (previously regarded as a variety of *S. borealis*), *Spirorbis pagenstecheri* Quatrefages (described in Fauvel, 1927, but often confused with *S. spirillum*), and *Spirorbis rupestris* Gee and Knight-Jones (1962). These species settle mainly on rocks, occurring further up the shore when these are kept damp by a covering of large algae. They are all less abundant on the more exposed shores, and are absent from Marloes Stack, possibly because of sand abrasion. *S. spirillum* is found only sublittorally, and is thus excluded from this account.

Spirorbis tridentatus is probably the most tolerant of exposure and is locally abundant at Long Point Stack; here, as it is almost completely covered by "lithothamnia", it was at first mistaken for *S. rupestris* until scraping revealed the characteristic three longitudinal ridges. *Spirorbis pagenstecheri* is usually ridged in this way, but is the only middle-shore species to coil in an anticlockwise direction. It occurs up to MHWN under algae and damp boulders, and even higher in tide pools; it can be found abundantly on *Laminaria* sublittorally off the Slip Pier.

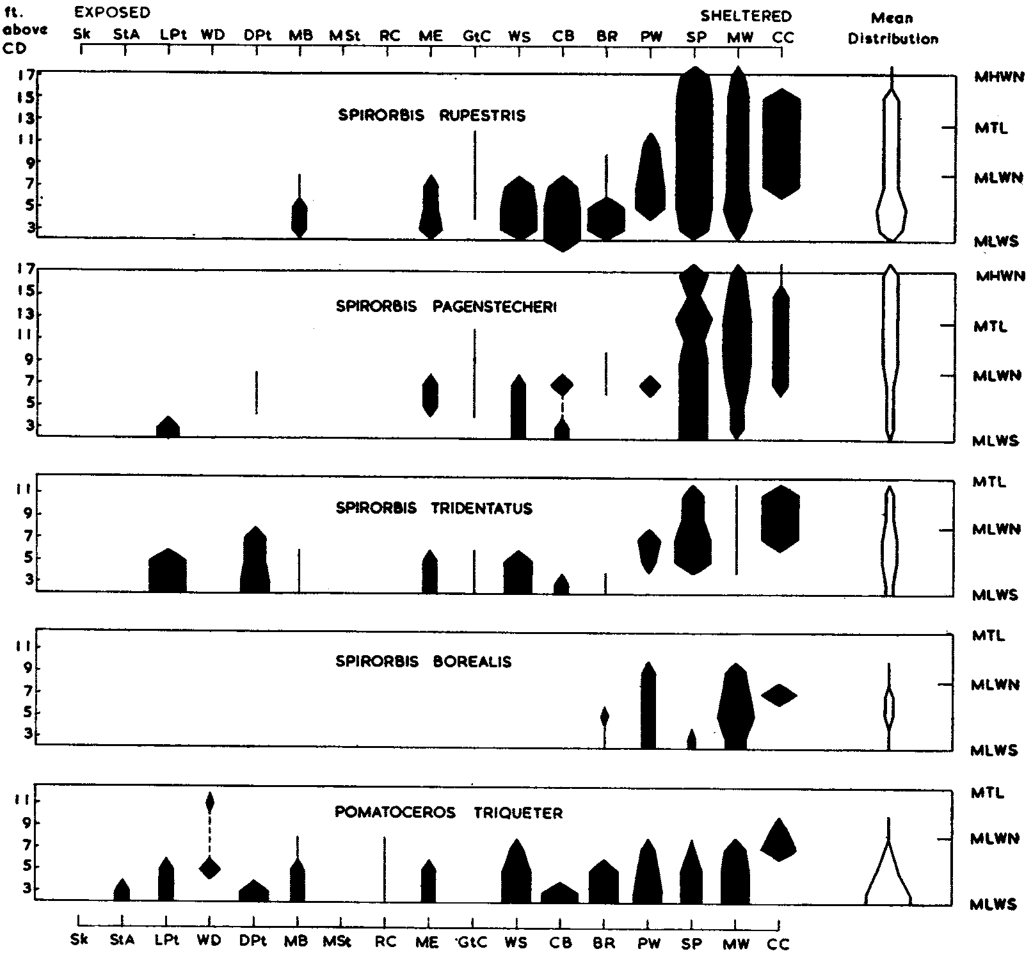


FIG. 12.

Distribution of Serpulidae, shown as in Fig. 4 (p. 11) (abundance scale in Fig. 8, p. 18).

Spirorbis rupestris is larger than the others, has a smooth tube, and normally occurs on and embedded in one of the "lithothamnia", a common dull purple form probably *Lithophyllum incrustans*, which is found mostly in gullies but not on the undersides of boulders. On the shores of intermediate exposure the upper limit of the *S. rupestris* zone agrees with that of this alga, but on exposed shores the tube-worm is usually absent even where "lithothamnia" are abundant, perhaps because these are of a different species.

Pomatoceros triqueter is most abundant below low water, but extends on to the shore as far as MLWN. With its stout tube it is able to survive on quite mobile stones, as can be seen at Slip Pier Beach.

(12) *Actinia equina* (Fig. 10)

This is the only sea-anemone included in the survey. Most specimens occur in rock pools or on the sides of damp gullies, and on rock surfaces the greatest numbers are found under cover of weed; yet some are found on steep slopes which face south and dry out severely.

IV. Components of the shore population

The study of intertidal zonation has recently been reviewed by Southward (1959) who gives a full bibliography. Two basic approaches can be recognized, the synecological and the autecological. In the first, the shore is considered as a number of zones and sub-zones, defined by the presence or abundance of certain indicator species. Studies of this type have been highly developed by the late Professor Stephenson with Mrs. Stephenson (1949 and 1954) and their co-workers, particularly Evans (1947*a*, 1947*b*, 1949 and 1957) and Lewis (1953, 1954, 1955 and 1957). They devised a scheme, shown slightly modified in Fig. 13*a*, applicable to most rocky shores of the world. The midlittoral zone is dominated by barnacles and limpets or on more sheltered shores by Fucales, and lies more or less between two critical levels. Below its lower limit is the infralittoral fringe created by the invasion of the shore by such essentially sublittoral (=infralittoral) forms as "lithothamnia," sponges and Bryozoa. These are largely intolerant of desiccation, temperature changes or strong light. The upper limit of the midlittoral zone lies just above MHWN, above which the many species which need to be wetted by almost every tide cannot survive in the open.

The autecological approach, used by many workers notably Colman (1933) and Southward (1953), involves the study of the zonation of individual species, and may thus be referred to as species zonation (concerned, for example, with the *Laminaria digitata* or *Littorina neritoides* zone). These zones rarely correspond with the Stephensonian zones; for example, *Littorina neritoides* is often the dominant winkle of the supralittoral littorinid zone, but it may on the same shore be even more abundant in the midlittoral barnacle zone. Since no two species have precisely the same distribution, there are virtually as many zones as species on the shore.

The present study is of individual species, but these may be grouped into categories with similar zonation (Fig. 14), following with slight modifications the component scheme proposed by Lewis (1953). These components are

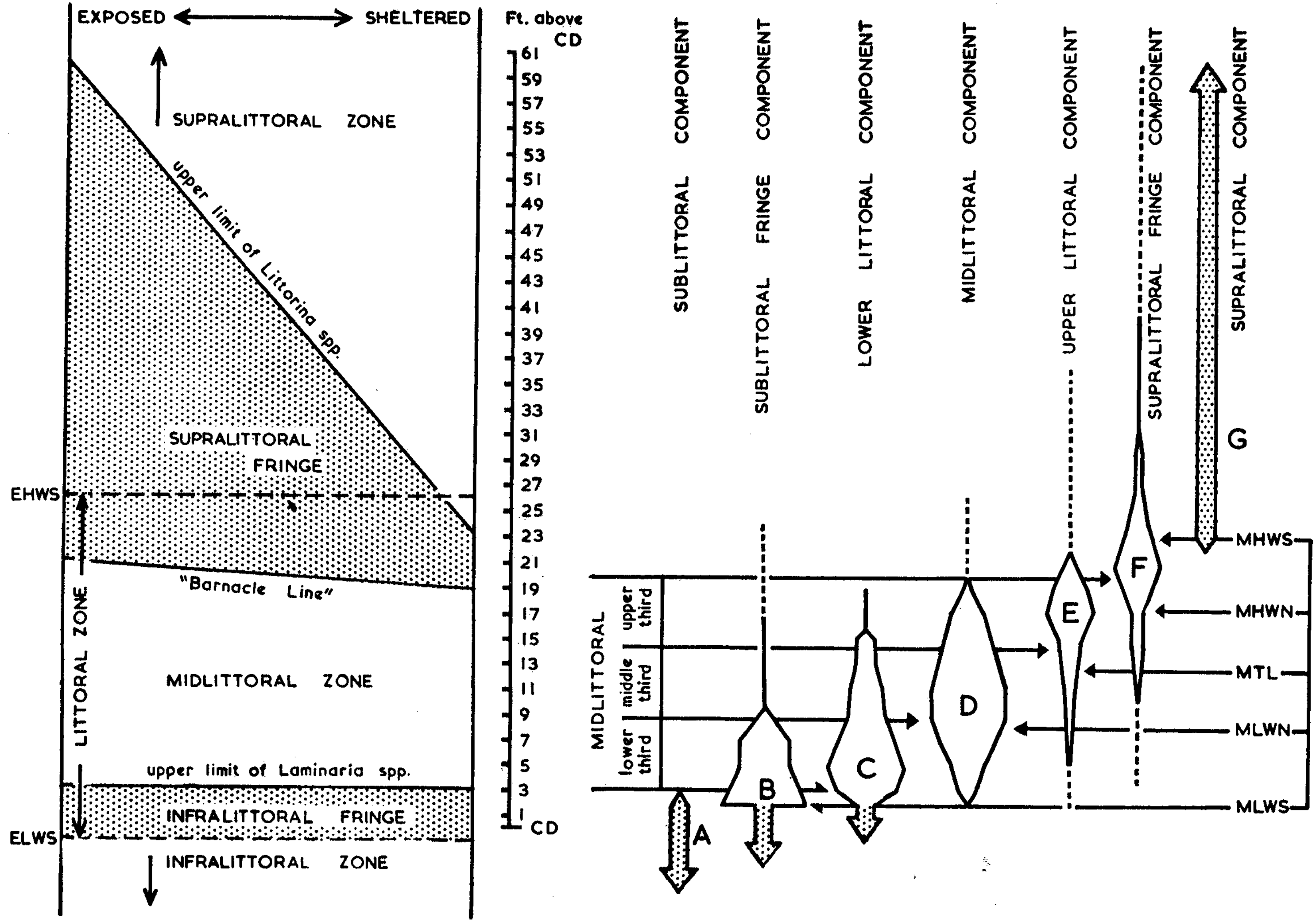


FIG. 13.

a (left) The biologically defined universal shore zones, modified from Stephenson and Stephenson (1949) to show their limits on Dale shores between the extremes of exposure to wave action.

b (right). Components of the shore population at Dale, shown against the same vertical scale as Fig. 13*a*. Data derived from Fig. 14 (opposite).

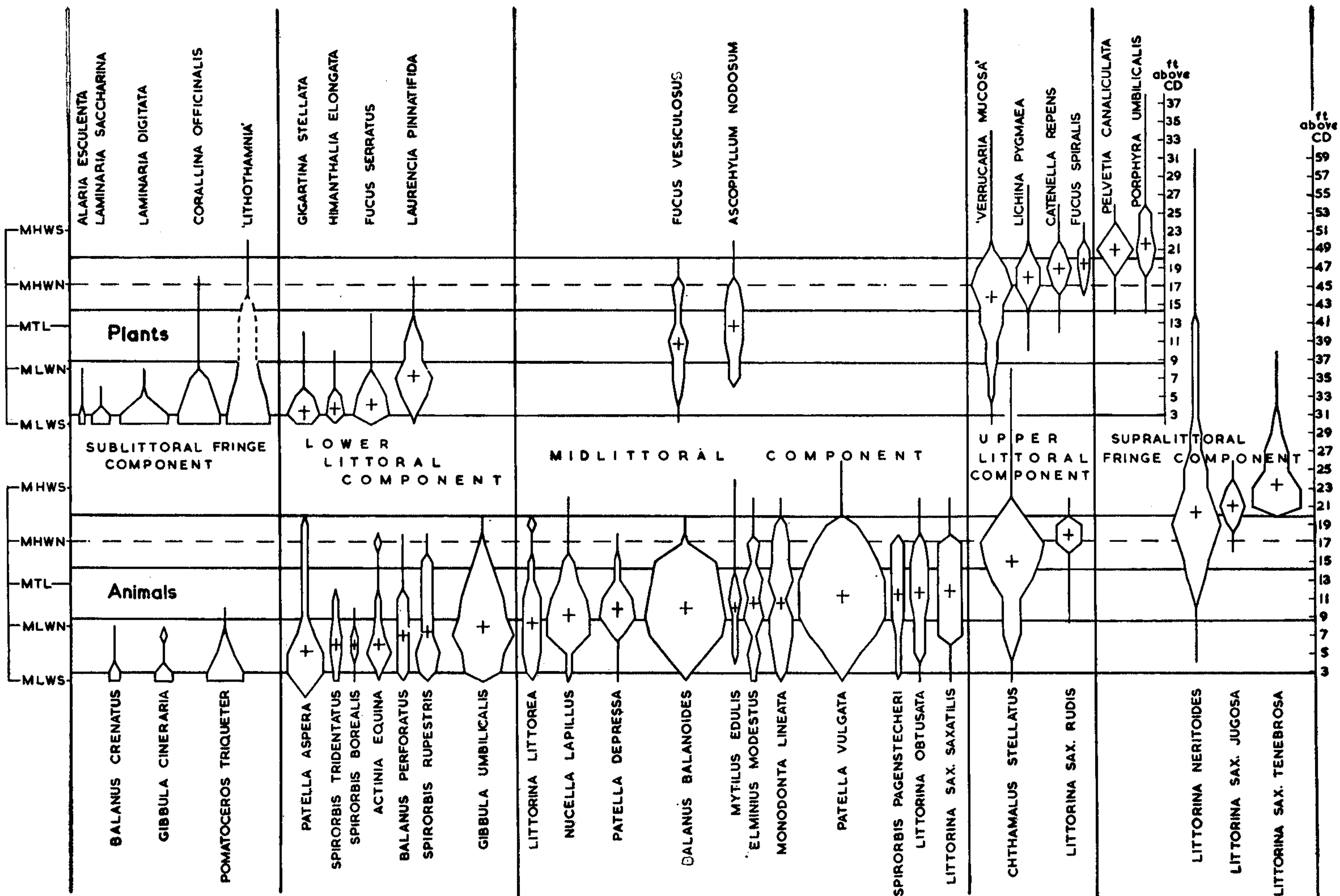


Fig. 14.

The mean distribution of littoral plants and animals at Dale, derived from Figs. 4-12 and arranged to show the variations in patterns of distribution within the five major components of the littoral population. The centre of abundance of each species is shown by a cross.

named according to that Stephensonian zone in which the centres of abundance of the included species lie; this centre of abundance is the level which divides the diagram of mean distribution of a species into upper and lower halves of equal area.

The sublittoral component contains most of the benthic animals found abundantly offshore and occurring on the shore only occasionally or rarely, although they are sometimes stranded there in great numbers after gales. Their centres of abundance lie below the lowest level of the tide. Those of the sublittoral fringe component may also have centres of abundance below low water, but they are abundant or at least common both offshore and in the lowest part of the tidal zone, and some may be found in rock pools quite high up the shore.

The midlittoral zone can be divided into three equal parts, following Womersley and Edmonds (1952); this keeps together, in the three corresponding components, species with mean distribution diagrams which are of similar shape because they are related similarly to the main critical levels delimiting this zone. Those of species centred in the upper, lower and middle thirds will be respectively like kites, inverted kites and lozenges (Fig. 13*b*). Thus the lower littoral component contains species centred in the lower third of the midlittoral, but with lower limits often extending into the sublittoral. Their upper limits are generally no higher on shores subjected to greater exposure, but they may extend further up the shore in rock pools and damp gullies. Species centred in the middle third extend a little further up the shore in exposure, and during periods of neap tides are subjected to a few days' emersion. The upper littoral component contains species with zones which are often wider on more exposed shores, and all tolerate emersion for a week or more.

The supralittoral fringe component comprises species which may extend into the midlittoral, but which must be tolerant of weeks or even months of desiccation during calm weather. Above these, with centres of abundance above the supralittoral fringe, are the flowering plants and lichens forming the supralittoral component, with zones both higher and wider on exposed shores (Figs. 3*a*, 3*b*). Many are not strictly part of the shore population, but are often confined to the neighbourhood of the sea; most are probably intolerant of much actual immersion in sea water.

It is difficult to include every shore animal in this scheme; for example, *Carcinus maenas* migrates up and down the shore with the cycles of tides and seasons (Naylor, 1962). The narrowness of the zones of species restricted to high levels on sheltered shores is not well shown, and in a somewhat arbitrary division it is not, for example, very clear whether *Pelvetia* should be placed in component E or F. The species included in any one component are not similarly zoned for the same reasons, for while many may be limited particularly at their upper limits by physical conditions, their lower limits will more often be determined by changes in the biotic environment, affecting each species differently. Littoral zonations may also be considerably modified by different tidal regimes (Doty, 1946) and amplitudes (Mokyevsky, 1960). With these reservations it is felt that this scheme helps the understanding and teaching of species zonation. It is only necessary to recall the category into which a given species falls to have a fairly accurate impression of its distribution on the shore from the patterns indicated in Fig. 13*b*.

ACKNOWLEDGEMENTS

The authors wish to express their thanks to Mr. J. H. Barrett, Warden of Dale Fort Field Centre, for suggesting this survey and for his editorial patience. They also wish to thank Professor E. W. Knight-Jones for advice in drafting this account and Mr. B. L. James for kindly supplying information about his original work on *Littorina saxatilis*.

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APPENDIX

SUBSPECIES OF *Littorina saxatilis* AROUND DALE

by B. L. JAMES

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Many features of its anatomy, shell characters and distribution suggest that *Littorina saxatilis* should be divided into four subspecies. Their superficial characters are given here as an aid to field identification in this area, referring to the sizes of sexually mature forms only. A more detailed account, including data collected from other areas, will be published separately.

Littorina saxatilis (Olivi, 1792) subsp. *rudis* (Maton, 1797)

Shell large, thick and heavy, 8-22 mm. long. Six whorls, spire tall and moderately acute; shell surface often lined or banded. Shell aperture relatively large but somewhat elongated, with the shell angle (the angle between the lip of the aperture and the body whorl) more acute than in any other subspecies. A dark reddish-brown form with darker lines, which is common in shelter at Dale, may be confused with *Littorina littorea;* the latter however has more whorls, a more acute spire and shell angle, and lines more numerous and finer than in *L.s. rudis.*

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L. saxatilis (Olivi, 1792) subsp. *jugosa* (Montagu, 1803)
Shell medium-sized and fairly thick, 5-15 mm. long. Five whorls, spire tall and more acute than any of the other subspecies; shell surface smooth or slightly grooved. Shell aperture large and nearly circular, its angle a right angle.

L. saxatilis (Olivi, 1792) subsp. *tenebrosa* (Montagu, 1803)
Shell medium-sized, thin and often fragile, 4·5-12 mm. and exceptionally 14 mm. long. Four, five or siz whorls, the spire often very long and obtuse; surface often deeply grooved. Shell aperture very large and nearly circular, shell angle a right angle.

L. saxatilis (Olivi, 1792) subsp. *saxatilis* (Johnston, 1841)
Shell very small, thin and fragile, 1·5-4·5 mm. long. Four whorls, spire always very obtuse terminally, although its height is variable; surface usually very smooth, often with a tessellated colour pattern. Shell aperture comparatively small but nearly circular, shell angle a right angle.

The shell characters of *L. s. saxatilis* are fairly constant, but those of the other subspecies vary according to the degree of exposure of the shore. In shelter they tend to have small, narrow shell apertures, tall and acute spires and smooth shells; under exposed conditions the aperture is wide and much larger, the spire low and blunt, and the shell surface more grooved. Shells may also be thinner and smaller in exposure, and at lower levels in the vertical range. Of the three, *L. s. tenebrosa* is the most and *L. s. jugosa* the least subject to variation. However, at three semi-exposed stations to the south of Mill Bay *L. s. jugosa* was present and was most unusual in having a thin deeply grooved shell with a short blunt spire and a wide aperture. These specimens reached a maximum length of only 7 mm. and were clearly equilavent to the "exposed" forms of *L. s. tenebrosa* and *rudis*. This is the only record known to the author of *L. s. jugosa* on a semi-exposed shore, and the only locality where an "exposed" form of this subspecies has been recorded.

Key to L. SAXATILIS *subspecies at Dale* (*adults*)

1. Shell longer than 15 mm. **L. s. rudis**
   Shell 15 mm. or shorter 2
2. Shell aperture elongated, with shell angle acute (the angle between the lip of the aperture and the body whorl) **L. s.rudis**
   Shell aperture almost circular, with shell angle a right angle 3
3. Spire acute, shell thick, and marked only by fine shallow grooves. **L. s. rudis**
   Spire acute, shell thick and without colour patterns or groooves. Up to 15 mm., not found above EHWST. **L. s. jugosa**
   Spire obtuse, shell thin. 4
4. Aperture very large (¾ shell length or more); shell usually coarsely grooved with prominent sharp ridges. Up to 15 mm., extending well into supralittoral **L. s. tenebrosa**
   Aperture rather small (about ½ shell length); shell smooth or slightly ridged, often with a tessellated pattern. Always less than 5 mm., usually within empty barnacle shells. **L. s. saxatilis**

NOTE ADDED IN PROOF: Dr. J. R. Lewis' 'The littoral zone on rocky shores' [*Oikos*, **12**(2), 280-301, 1961] proposes a modification of the scheme of Stephensonian zonation discussed here.

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