Field Studies (1980) 5, 229–258

PATTERNS OF ANIMAL AND PLANT DISTRIBUTION ON ROCKY SHORES OF THE SOUTH HAMS (South Devon)

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ABSTRACT

The paper describes the basic distribution patterns shown by the common animals and plants on 15 rocky sea shores in the South Hams, and demonstrates the ways in which they may be modified by local characteristics and variables.

INTRODUCTION

THIS paper is the fifth to appear in *Field Studies* concerned with the distribution patterns of animals and plants on rocky sea shores. Whilst inevitably repeating some material contained in the others, its aim is to provide background information for use by people working from Slapton Ley Field Centre. It describes the basic patterns found on 15 shores in the South Hams, from Berry Head to Bantham, and demonstrates the ways in which they may be modified by local characteristics and variables. It does not set out to provide a comprehensive list of the fauna or flora of the area; nor to provide detailed descriptions of the ecology of individual species. The area west of Start Point is covered by the Plymouth Marine Fauna (Marine Biological Association, 1957).

SHORE TRANSECTS

The 15 shores (Fig. 1) were surveyed from low water mark (of the day concerned) to at least the upper lichen zone, well above high water mark. The vertical intervals were established along a transect line, laid at right angles to the slope of the shore, using a 25 cm (or 50 cm) cross-staff (Fig. 2). In use, the base is set on the rock at the lower station and levelled by the observer sighting along the top of the cross-piece, watching the bubble reflected in the mirror.

The distances along the shore between the stations were measured and a profile drawn of each shore (Fig. 3). At each station the rock was examined for five metres either side of the transect line and the abundance of the common organisms assessed on the scales used by Crapp (1973), (see Table 1). The height of each station above Lowest Astronomical Tide (L.A.T) was calculated by reference to the Admiralty Tide Tables (1975 and 1978).

Shore Profiles

The shores (Fig. 1, Table 2), are composed of five main rock types. In the Lower Devonian, the Dartmouth and Meadfoot bed slates and Staddon grits occur whilst, to the north, the Middle Devonian limestone outcrops at Berry Head (Dineley, 1961). The Bolt Head-Start Point, Tinsey Head area is composed of quartz mica and hornblende-chlorite schists. Each rock type has a different hardness and morphology. The softer rocks are subject to active erosion which must affect the distribution and abundance of certain organisms.

In profile there are two principal types of shore. Start Point and Black Cove are examples of precipitous cliffs requiring considerable mountaineering skill for their successful negotiation. In contrast many of the other shores consist of an extensive

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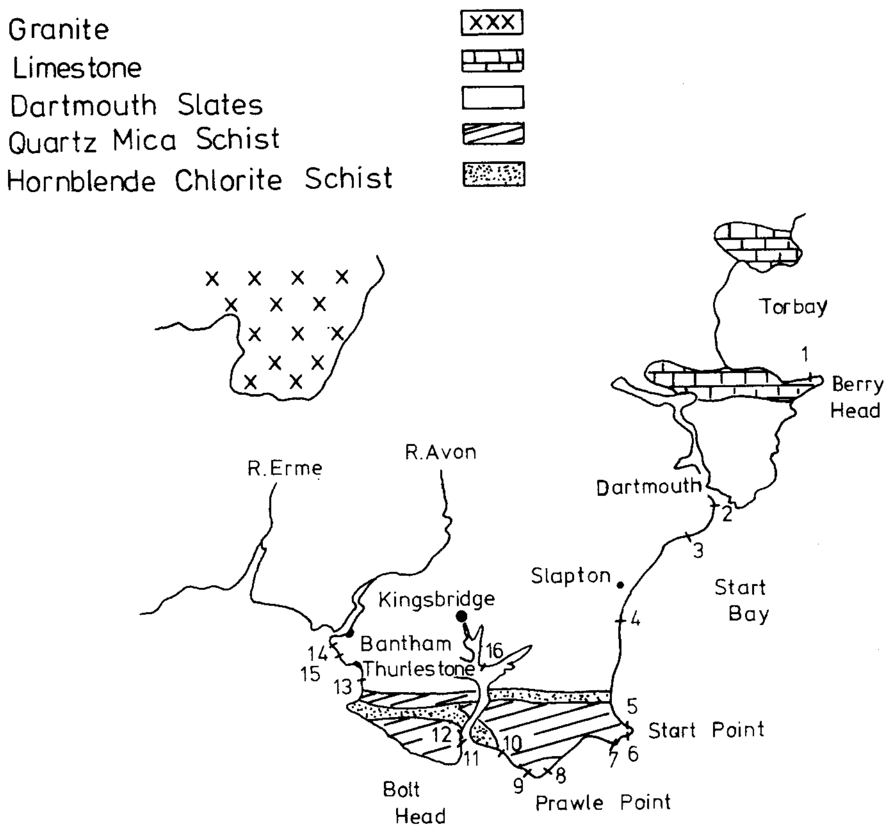

FIG. 1.
The Geology of the South Hams showing the position of the sampling sites. Numbering is the same as in Table 2.

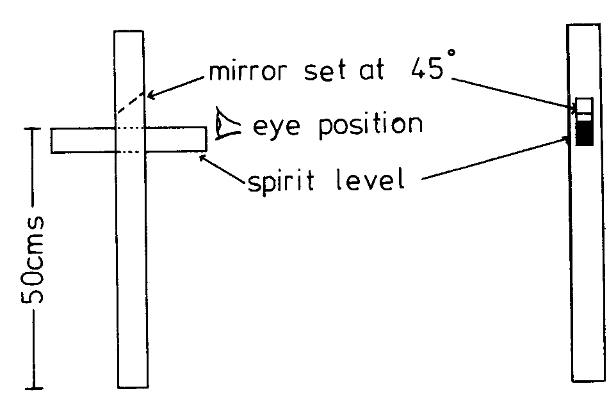

FIG. 2.
Diagram of Cross Staff.

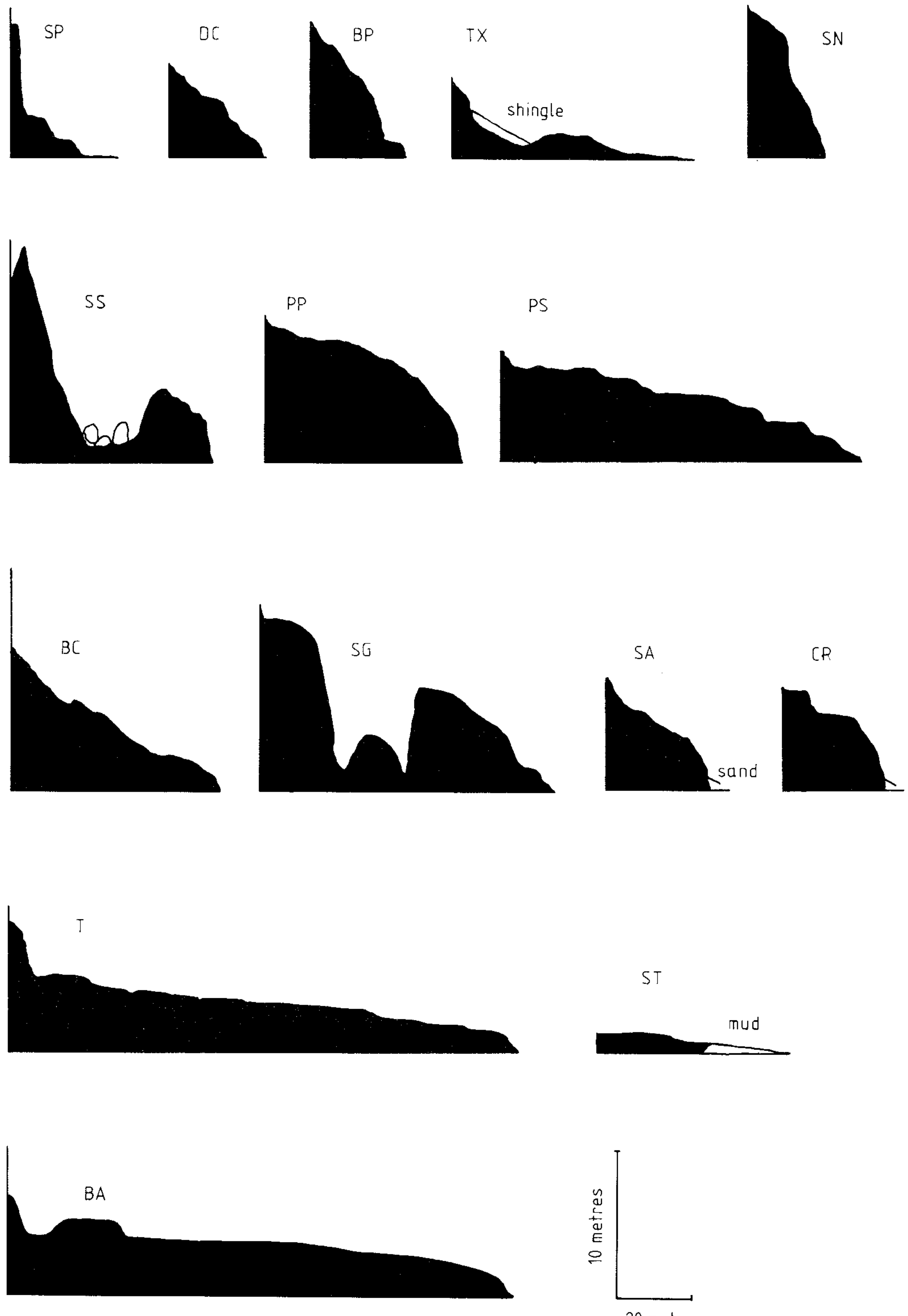

FIG. 3.
Shore profiles for the sampling sites.
(Abbreviations as in Table 2 p.233)

TABLE 1
Abundance Scales for Some Common Littoral Organisms
(cm^{-2} = per square centimetre)

Lichens and other encrusting species:	
Ex.	More than 80% cover
S	50-80% cover
A	20-50% cover
C	1-20% cover
F	Large scattered patches
O	Widely scattered patches, all small
R	Only one or two patches
Seaweeds (algae):	
Ex.	More than 90% cover
S	60-90% cover
A	30-60% cover
C	5-30% cover
F	Less than 5% cover, zone still apparent
O	Scattered plants, zone indistinct
R	Only one or two plants
Barnacles; *L. neritoides* and *L. neglecta*:	
Ex.	More than 5 cm^{-2}
S	3-5 cm^{-2}
A	1-3 cm^{-2}
C	10-100 dm^{-2}
F	1-10 dm^{-2}, never more than 10 cm apart
O	1-100 m^{-2}, few within 10 cm of each other
R	Less than 1 m^{-2}
Limpets and winkles: except *L. neritoides* and *L. neglecta*	
Ex.	More than 200 m^{-2}
S	100-200 m^{-2}
A	50-100 m^{-2}
C	10-50 m^{-2}
F	1-10 m^{-2}
O	1-10 Dm^{-2}
R	Less than 1 Dm^{-2}
Top-shells and dog-whelks:	
Ex.	More than 100 m^{-2}
S	50-100 m^{-2}
A	10-50 m^{-2}
C	1-10 m^{-2}, locally sometimes more
F	Less than 1 m^{-2}, locally sometimes more
O	Always less than 1 m^{-2}
R	Less than 1 Dm^{-2}
Mussels:	
Ex.	More than 80% cover
S	50-80% cover
A	20-50% cover
C	Large patches, but less than 20% cover
F	Many scattered individuals and small patches
O	Scattered individuals, no patches
R	Less than 1 m^{-2}

platform, up to 130 m long and frequently backed at the landward end by a small shingle beach or "head" cliff (Mottershead, 1971). The platforms are formed on old marine erosion surfaces (Orme, 1960) and can carry large numbers of students without causing damage to the shore or personnel.

Zonation

If the abundance data for the species on one shore are plotted on the same kite diagram against height above L.A.T. it will be seen that the different species form

TABLE 2

Shore No.	*Name*	*Abbre-viation*	*Survey Date*	*Ht. LW.*	*Map Ref. (SX)*	*G.N. Direction*	*Rock Type*	*Ballantine*	*Access*
1	Shoalstone Point	SP	9.4		939568	0°N	Limestone	4	/
2	Dartmouth Castle	DC	26.2	0.4	886502	70	Hard Slate	2	/
3	Blackstone Point	BP	11.4	0.6	888495	90	Hard Slate	2	/
4	Torcross, Limpet Rocks	TX	27.1		824416	90		4	/
5	Start Point N	SN	27.1	1.1	830372	355	Quartz mica schist	3	X
6	Start Point S	SS	12.1	0.6	830370	185	Quartz mica schist	2	X
7	Peartree Point	PP	11.1	0.4	819366	240	Quartz mica schist	2	/
8	Prawle, Stack Point	PS	10.1	0.6	776353	150	Hornblende chlorite schist	4	/
9	Prawle, Black Cove	BC	6.4	0.7	771352	240	Hornblende chlorite schist	2	WC
10	SE Gara	SG	7.4	0.6	753368	240	Hornblende chlorite schist	2	/
11	Splat Cove Point	SA	10.4	0.8	731376	50	Hard Slates	5-6	/
12	Castle Point	CP	10.4	0.8	735381	160	Hard Slates	4-5	/
13	Thurlestone	T	13.1	0.8	674410	270	Soft Slate	5	/
14	Bantham A	BA	26.1	1.0	659434	255	Soft Slate	6	/
15	Bantham B	BB	5.6	0.9	661432	290	Soft Slate/Quartz boulders	6	/
16	Saltstone	ST	20.6	0.7	746408	180	Soft Slate	7	X

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clearly defined zones (see Lewis, 1964; Stephenson, 1949). At Bantham the most obvious zones, in order from the top of the shore, are characterised by:

Lichens
Pelvetia canaliculata
Fucus spiralis
Barnacles/limpets
Ascophyllum nodosum
Fucus vesiculosus
Fucus serratus
Laminaria spp

These zones are related to the twice daily rise and fall of the tide. Variation in the tidal movement to produce spring and neap tides (see Fig. 4) is caused by the combined gravitational forces of the sun and moon. Spring tides occur at the new and full moons, when the sun and moon are acting more or less in a straight line, and neap tides at the first and last quarters when they are more or less at right angles to the earth (Defant, 1958).

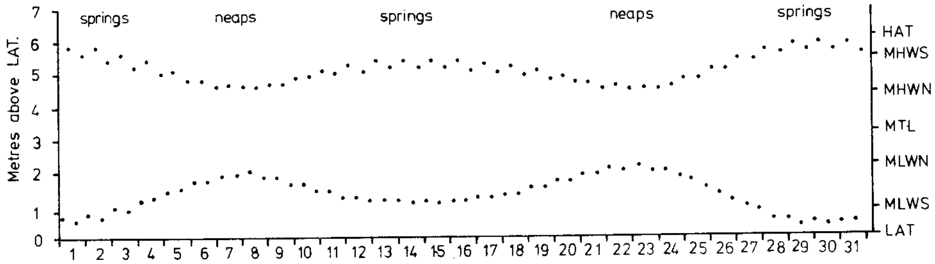


FIG. 4.
Predicted heights of high and low Tides for January 1978 plotted to show the spring/neap cycle. The figure also shows diurnal inequalities between successive tides. Abbreviations as in fig 5.

If the percentage time out of water is plotted against height up the shore (Fig. 5) it may be seen that organisms at the top will spend considerably longer emersed than submersed. They will also have to cope with wide fluctuations in temperature, salinity, light intensity and oxygen availability. Sea water by contrast provides a relatively constant medium for life. It is the changes in environment from the low to the high shore which give rise to the distribution of organisms into zones. Lewis (1964) and Newell (1970) discuss the adaptations which enable organisms to live on the high shore. The heights of the stations on each shore are referred to L.A.T. at Devonport except for Shoalstone Point where the tidal levels at Torquay are used. Although tidal data are available for Dartmouth and Salcombe they refer to the harbours and may not necessarily be correct for sites outside the estuaries. The mean tidal levels, e.g. MLWS, as measured from L.A.T. are not exactly the same at any of the shores. Therefore, exact comparison of the vertical range of organisms on different shores cannot be made. Tidal levels were taken from Admiralty Tide Tables (1975) and are given in Fig. 5.

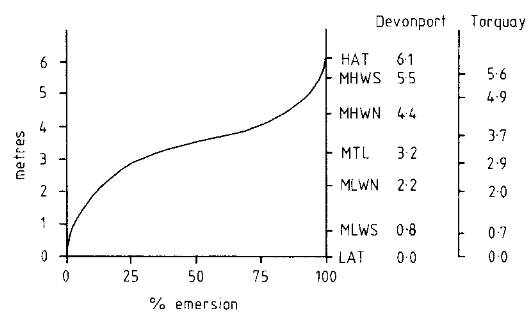


Fig. 5.

The theoretical emersion percentage (time spent out of water given calm conditions) for January 1978 at Devonport plotted against the height above the Lowest Astronomical Tide. The tidal levels for Devonport and Torquay are also given.

HAT = Highest Astronomical Tide
MHWS = Mean High Water Springs
MHWN = Mean High Water Neaps
MTL = Mean Tide Level
MLWN = Mean Low Water Neaps
MLWS = Mean Low Water Springs
LAT = Lowest Astronomical Tide

Wave exposure

The basic pattern of zonation is repeated on almost every rocky shore. However, there is considerable variation in the type of community found as a result of the exposure of shores to wave action. The degree of "exposure" depends on the slope, aspect and geographical position of the shore. The size of waves is related to the distance the wind can blow over the sea, so a shore with a wide aspect to the open sea is potentially more exposed than one in a landlocked bay.

The sheer physical battering of the waves has three main effects on the community found on an exposed shore:

1. A reduction in the number of species present.
2. A change in the species, e.g. absence of dense seaweed cover and topshells and presence of *Fucus vesiculosus* var *linearis*.

3. The vertical uplifting of certain species by the more frequent swash of waves keeping the rock wet for a longer period.

Although it is difficult to make direct measurements of exposure to wave action, Ballantine's (1961) exposure scale may be used for the comparative description of different shores since it uses the relative abundance of selected indicator species. The exposure scale is reproduced diagrammatically in Fig. 6. Within limitations it works well in this area. Not all the species used by Ballantine are present, e.g. *Alaria esculenta* is absent. Ballantine exposure grades have been given to the shores and these are listed in Table 2.

Water movement

A current of water, e.g. a tidal stream, may have a similar effect on the littoral community as exposure to wave action, (Lewis, 1968). Where the current is strong,

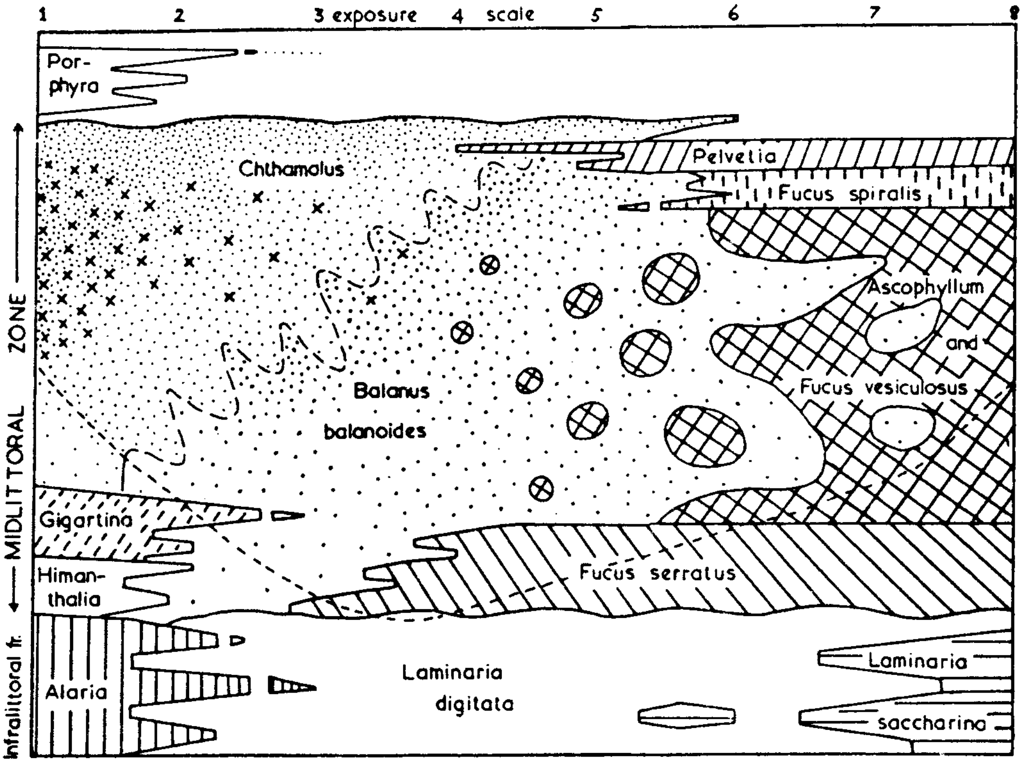


FIG. 6

The changes in distribution and zonation of the barnacles and algae with exposure. Based on shores in the Dale area. Pembrokeshire, except the extremely sheltered shore. Vertical scale according to Stephenson's universal scheme. Horizontal scale of exposure (sheltered to the right) with the approximate positions of the exposure scale given.

X = *Fucus vesiculosus* f. *linearis*

——— = upper limit of "Lithothamnia".

From Ballantine (1961)

sheltered shore species are replaced by a community more characteristic of an exposed shore. This is seen clearly in Plates 1 and 2, and may well influence the distribution of organisms at Dartmouth Castle where the species are characteristic of an exposed shore, but do not extend as far up the shore as would be expected as a result of wave action alone. Kitching *et al.* (1967) observe that there is a higher number of species in sub-littoral tidal rapids than in more sheltered conditions.

Species Notes

1. ***Patella*** spp. (Fig. 7). Three species of limpet, *Patella vulgata, P. depressa* and *P. aspera* are known to occur in the area (Fretter & Graham, 1962 and 1976). Although it is possible to separate some large specimens by external characters alone, positive identification necessitates removal of the animal from the rock and even then it is sometimes impossible due to the probable occurrence of hybrids. Limpets are thus considered here as a single entity. *Patella* is most abundant on exposed shores where it may be found up to H.A.T. and tends to be smaller than on sheltered shores. A very small population of large limpets is found on the Saltstone. The decrease in abundance below MLWN at Bantham B is associated with an increase in the cover of *Ascophyllum nodosum.*

2. ***Littorina*** spp. (Fig 8) Periwinkles.

L. neritoides is well adapted physiologically and behaviourally to live at the top of the shore (see Fretter & Manly, 1977; Newell, 1970). On exposed shores where there are suitable crevices it may be found up to 5 m above H.A.T. e.g. at Black Cove.

L. saxatalis agg.: Heller (1975*a*) has shown that, in Wales, the Rough Winkles formerly known as *L. saxatalis* Olivi comprise four sympatric species, *L. patula, L. neglecta, L. rudis,* and *L. nigrolineata.* To which Hannaford Ellis (1978:1979) has substituted *L. arcana* for *L. patula.* All four of these species occur in the South Hams

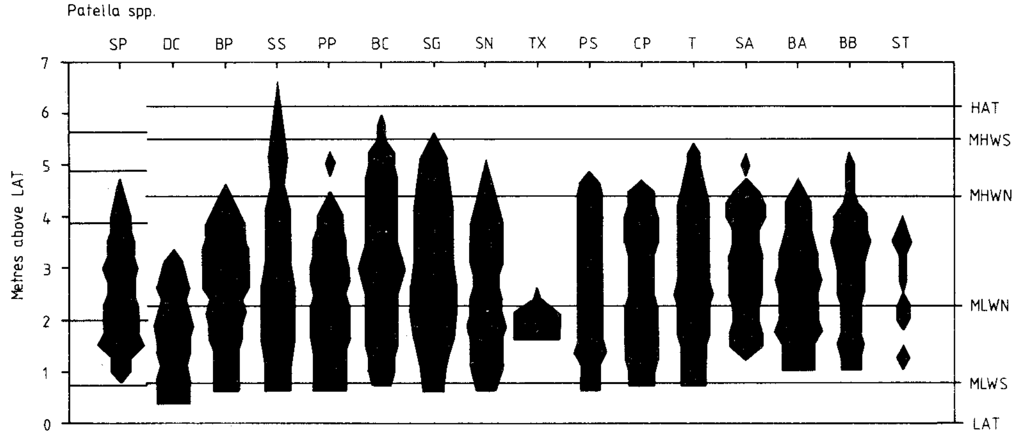


Fig. 7.

Distribution of *Patella* spp. on different shores plotted against height above LAT. The width of the kite histogram is proportional to abundance class. Tidal levels as in Fig 5. Except for Shoalstone Point the shores are arranged so that the sheltered shores are to the right.

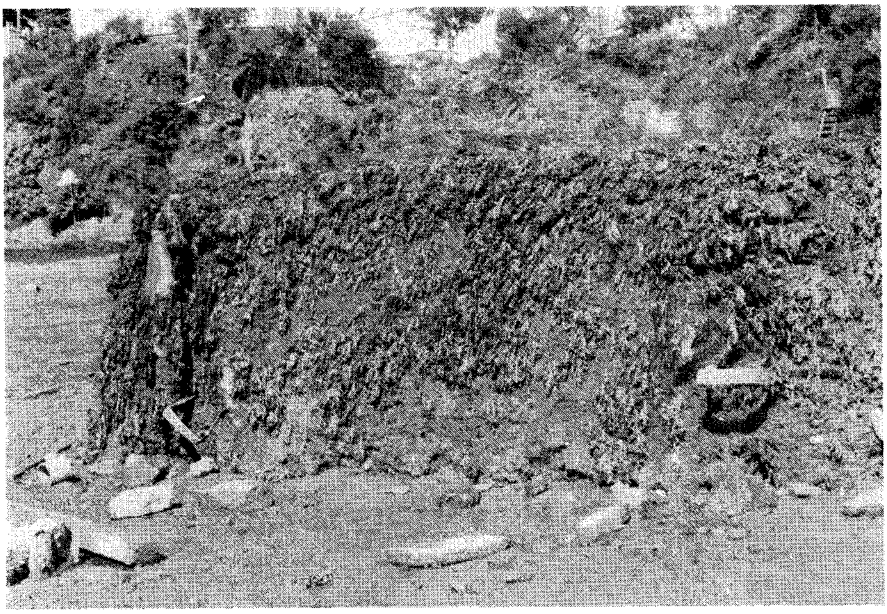


PLATE I(a)

Photograph of a jetty in a wave sheltered, slow water area of the Kingsbridge estuary at N.G.R. SX740429. The vertical end of the jetty is dominated by the large fucoids *Fucus serratus* and *Ascophyllum nodosum* of the form typical of very sheltered shores. There are large numbers of epiphytic red and brown algae; large encrusting sponges e.g. *Myxilla incrustans* and polyzoa including *Alcyonidium gelatinosum*. The area is covered with flocculent mud.

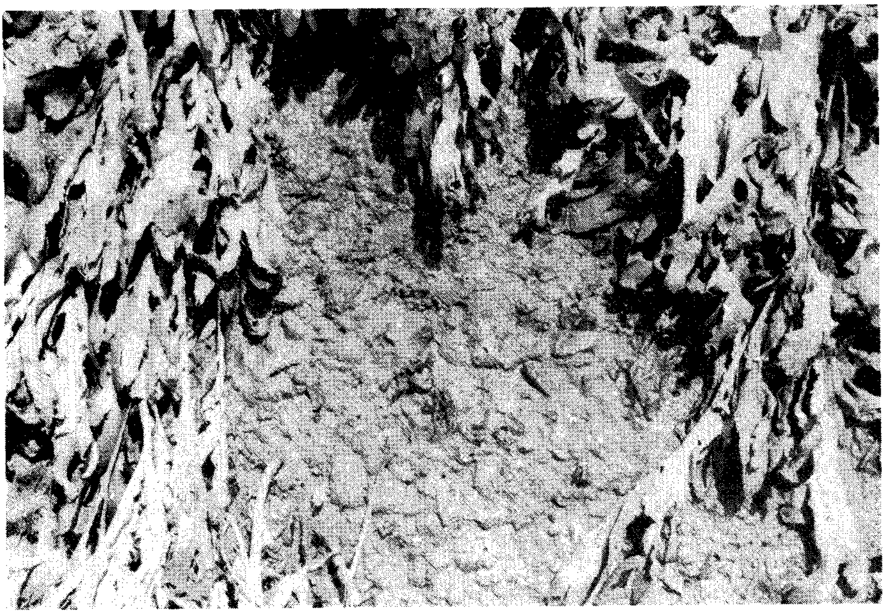


PLATE I (b)

Close up of vertical surface showing sponges and two species of *Fucus*.

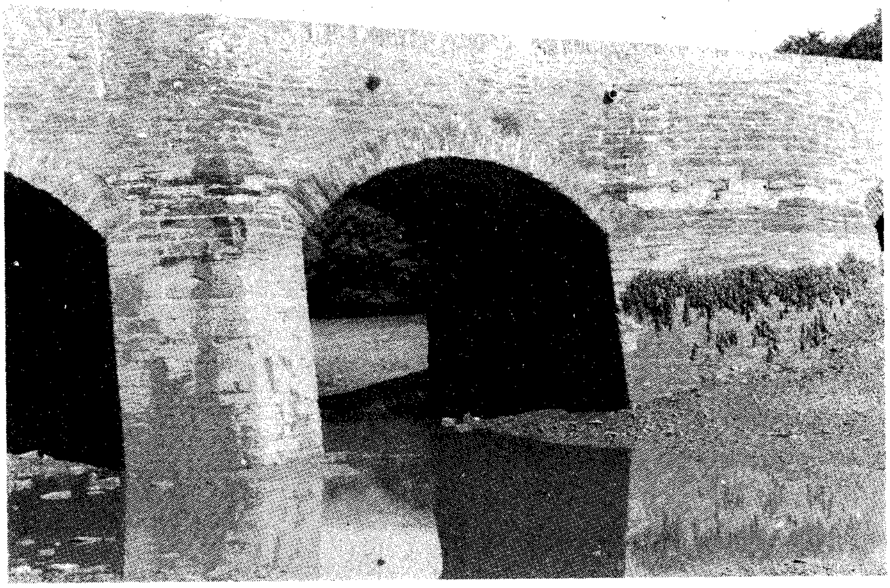


Plate II (a)

Less than one km away from the jetty (Plate I) is the bridge which carries the A379 across the Bowcombe Creek. The supports are at the same tidal level as the jetty but are scoured by a rapid tidal current. The Fucoid algae are confined to sheltered sides of the bridge (see Fig 2a) and are completely absent from the interior of the arches. The vertical surfaces inside the arches are dominated by barnacles, principally *Balanus* sp. and *Elminius modestus* (see below).Small colonial ascidia and thick growths of hydroids are also present. Note that the barnacles are orientated across the current.

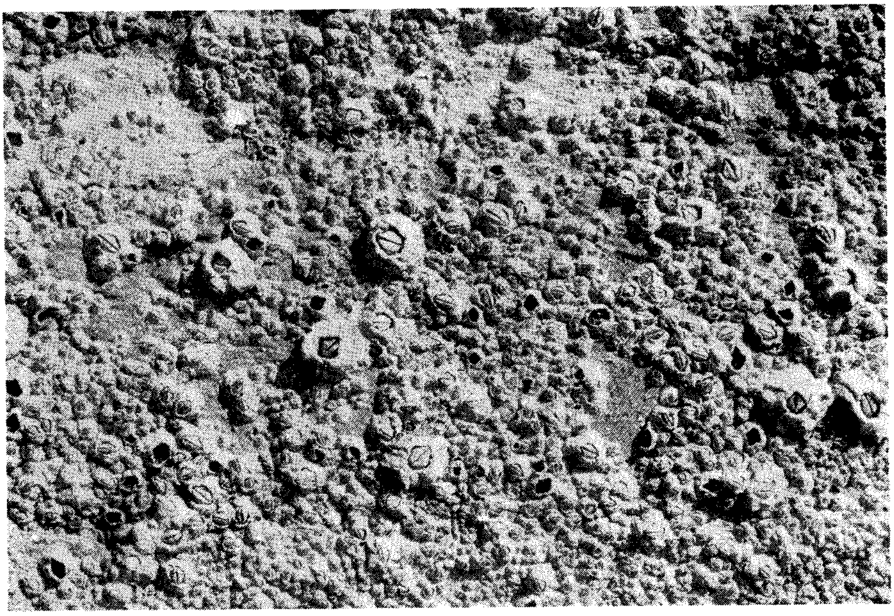
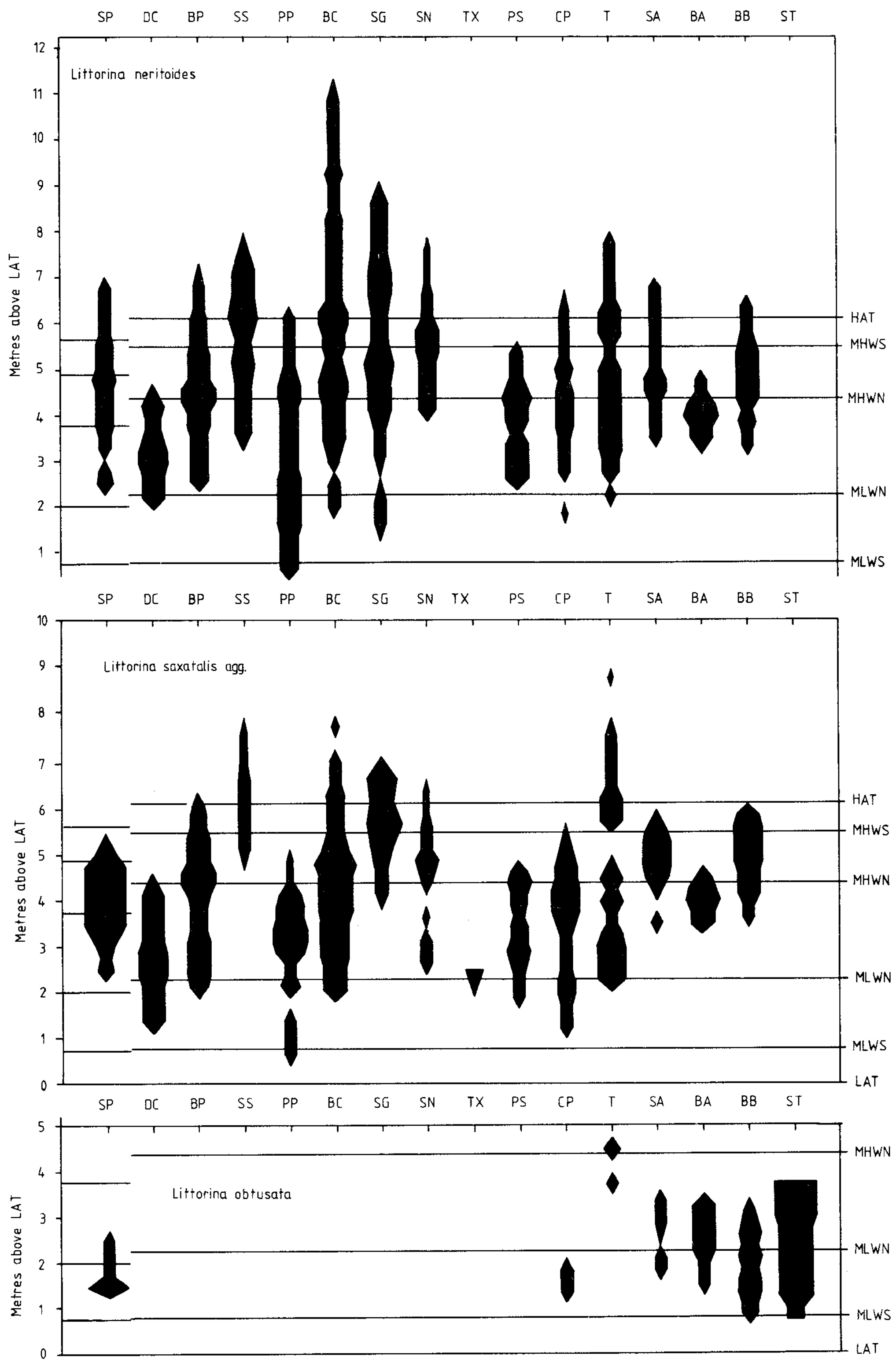


Plate II (b)

Close-up of the vertical surfaces inside the bridge arches


SP DC BP SS PP BC SG SN TX PS CP T SA BA BB ST
Littorina neritoides
Littorina saxatalis agg.
Littorina obtusata
Metres above LAT
HAT
MHWS
MHWN
MLWN
MLWS
LAT

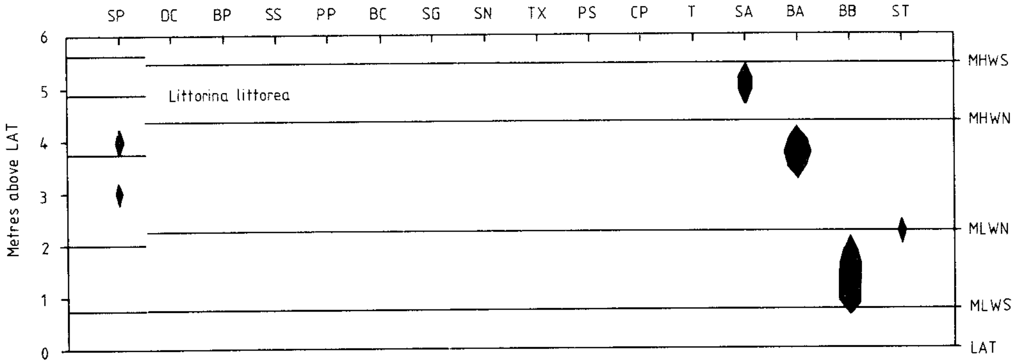


Fig. 8.
Distribution of *Littorina* spp.
(See also figs 5 and 7)

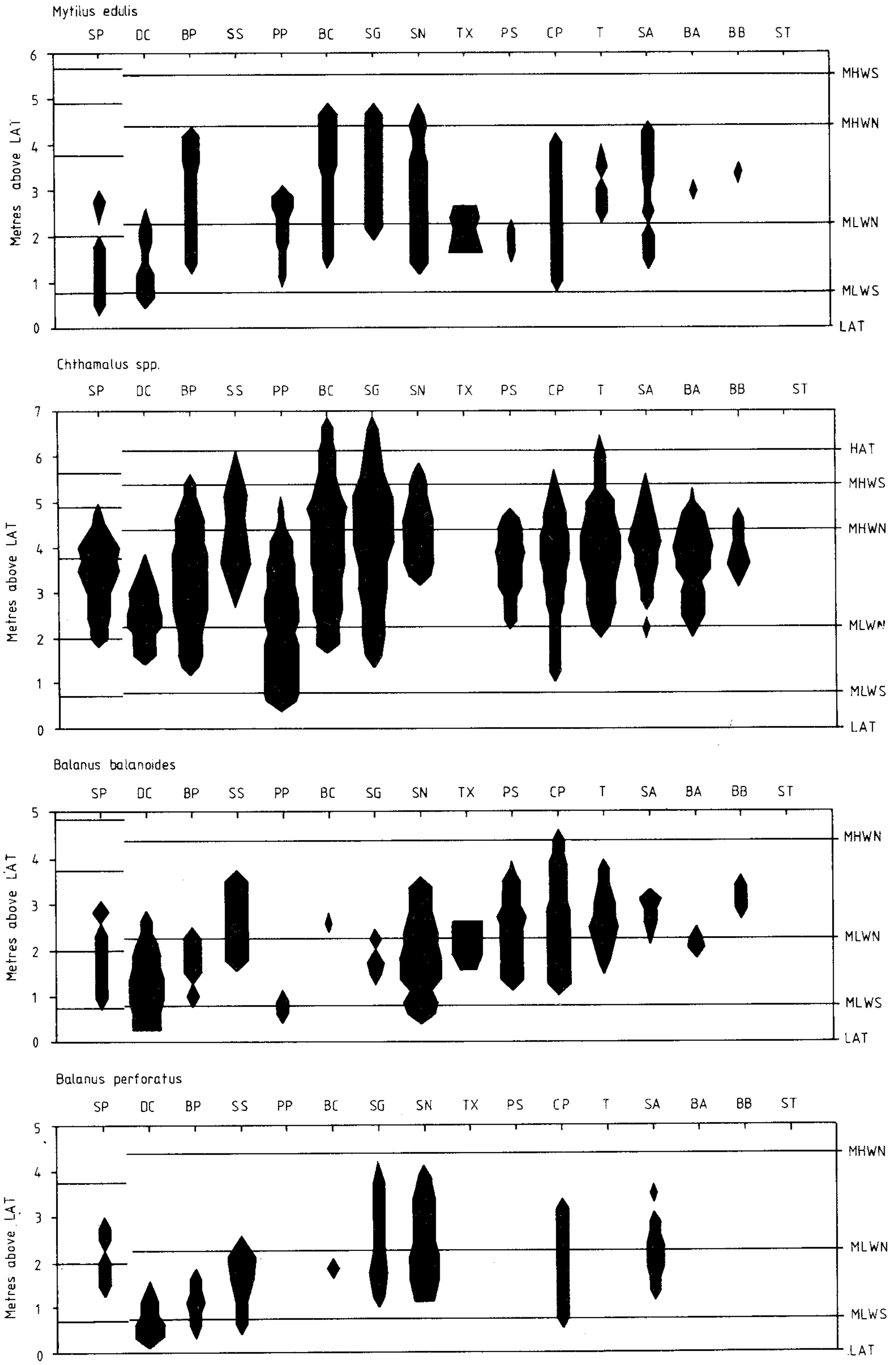
though firm identification requires examination of the internal anatomy. A full description of *L. arcana* was published in 1979 (Hannaford Ellis, 1979). The species were not separated in this survey. The five species probably inhabit different zones. *L. neglecta* for example is specialised to live in empty barnacle shells and the discontinuous distribution of *L. saxatilis* agg. shown on some shores, e.g. Peartree Point, probably reflects the distribution of the different species. These winkles are absent from the Saltstone, since the top of that shore lies below MHWN and all the species occur above this level in the locality. Elsewhere in the Kingsbridge Estuary *L. rudis* is present under cobbles on the high shore.

L. littorea, the Edible Periwinkle, may be found up to the MHWS level on sheltered shores. It is present at Thurlestone but was only found in gullies and rock pools which were ignored in the surveying method used.

Sacchi and Rastelli (1967) (see Goodwin and Fish 1977 in English) have separated the Flat Periwinkle, *L. obtusata* (=*L. littoralis*), into two species, *L. obtusata* and *L. mariae.* It is difficult to separate them reliably without examining the internal anatomy, so for the purposes of the survey both species are treated together. In a sample of 500 snails taken from Bantham on 15 September 1978, *L. mariae* was confined to *Fucus serratus* and *L. obtusata* to *Ascophyllum nodosum.* Sixteen snails were not positively identified. *L. obtusata* agg. is found in close association with the fucoid algae on which it feeds and is thus only abundant on sheltered shores.

3. ***Mytilus edulis*** (Fig. 9). Mussels were found in low densities, frequently confined to crevices, at all the shores except for Black Cove and the Saltstone. In two restricted areas at Torcross and Peartree Point mussels are abundant and at the latter, the area covered by them has been steadily expanding over the last eight years (*Centre staff observations*). It has been suggested that this type of distribution pattern may be related to predation by dogwhelks, *Nucella lapillus.* The dogwhelks feed preferentially on either barnacles or mussels allowing the other species to increase in density. There is insufficient data from this survey to refute or confirm this suggestion.

4. **Barnacles** (Fig. 9). The settlement of barnacle spat is inhibited by the presence of the larger algae (Crothers, 1976) and barnacles are most common on more exposed shores where there is less algal cover.


Mytilus edulis
SP DC BP SS PP BC SG SN TX PS CP T SA BA BB ST
Metres above LAT
MHWS
MHWN
MLWN
MLWS
LAT
Chthamalus spp.
SP DC BP SS PP BC SG SN TX PS CP T SA BA BB ST
Metres above LAT
HAT
MHWS
MHWN
MLWN
MLWS
LAT
Balanus balanoides
SP DC BP SS PP BC SG SN TX PS CP T SA BA BB ST
Metres above LAT
MHWN
MLWN
MLWS
LAT
Balanus perforatus
SP DC BP SS PP BC SG SN TX PS CP T SA BA BB ST
Metres above LAT
MHWN
MLWN
MLWS
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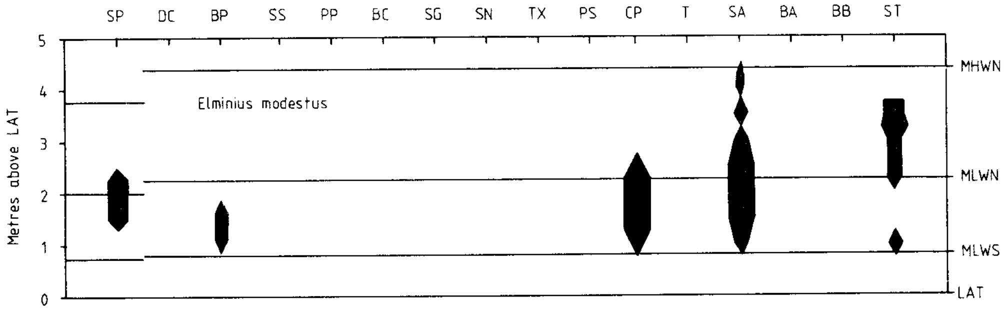


FIG. 9.
Distribution of Barnacles and Mussels
(See also figs 5 and 7).

Southward (1976) has shown that two species of *Chthamalus, C. montagui* and *C. stellatus,* occur in South Devon. The barnacles on most shores of the South Hams are very small and the frequency with which the plates are fused together or deformed makes accurate field identification unreliable. *Chthamalus* spp. occur on all but the most sheltered shore of the Saltstone and on exposed shores may be uplifted well above H.A.T. The lower limit of the distribution of *Chthamalus* spp. may be controlled by interspecific competition for space with *Balanus balanoides* (Connell, 1961). *B. balanoides* occurs below *Chthamalus* spp., but is not completely replaced by it on exposed shores as in Pembrokeshire (Ballantine, 1961; Connell, 1974). The upper limit of the range of *Balanus balanoides* may be controlled by desiccation of both adults and spat (Foster, 1971). The vertical range of *Balanus* is extended upwards on North-facing shores, e.g. Start Point N. The low population of *Balanus* at Splatcove Point is probably related to the abrasion of spat by sand particles suspended in the tidal current moving in and out of the Kingsbridge Estuary.

Elminius modestus was introduced to this country from Australasia by 1947 and was first recorded at Salcombe in 1949. Most of the shores in this survey were previously examined in 1970 by Mr. B. Petts and *E. modestus* was not recorded at that time. *E. modestus* is now present in small numbers in sheltered situations on almost every shore but is common only in the Kingsbridge Estuary, (see also Crisp, 1958). *Balanus perforatus* is present in crevices on many of the shores surveyed but is rarely found on smooth rock. At S.E. Gara it occurs higher than on other shores because of the large number of deep crevices in the rock.

Verruca stroemia, Balanus improvisus and *B. crenatus* all occur on shores in the South Hams but are not sufficiently common in the intertidal zone for the survey data to be plotted.

5. **Other animal species.** Topshells are confined to the more sheltered shores, e.g. Bantham and Thurlestone, and may be present in large numbers. The group shows a distribution pattern similar to that around Milford Haven (Moyse & Nelson Smith, 1963; Nelson Smith, 1967). The order from the top of the shore is *Monodonta lineata, Gibbula umbilicalis, G. cineraria* and *Calliostoma zizyphinum.* The last two species are mainly sub-littoral in distribution (see Williams, 1965; Fretter & Graham, 1977). Dog whelks, *Nucella lapillus,* are present on all shores and may be important predators on some.

An energetic search of the intertidal zone, particularly below MLWS, will rapidly produce a long species list but many of the species found will be confined to specialised habitats, e.g. under stones.

6. **Lichens.** Only a limited number of lichens were surveyed as accurate identification frequently requires the use of chemical tests (Ferry & Sheard, 1969). The general pattern of distribution on the shores of the South Hams is much the same as that described by Lewis (1964), and Ferry and Sheard (1969), although not every species is found on every shore. The usual order of the most common species from the top of the shore is:

Lecanora atra/L. gangaleoides	Fig. 10
Anaptychia fusca	not figured
Ochrolechia parella	not figured
Ramalina siliquosa	Fig. 10
Xanthoria parietina	Fig. 11
Caloplaca thalincola	Fig. 11

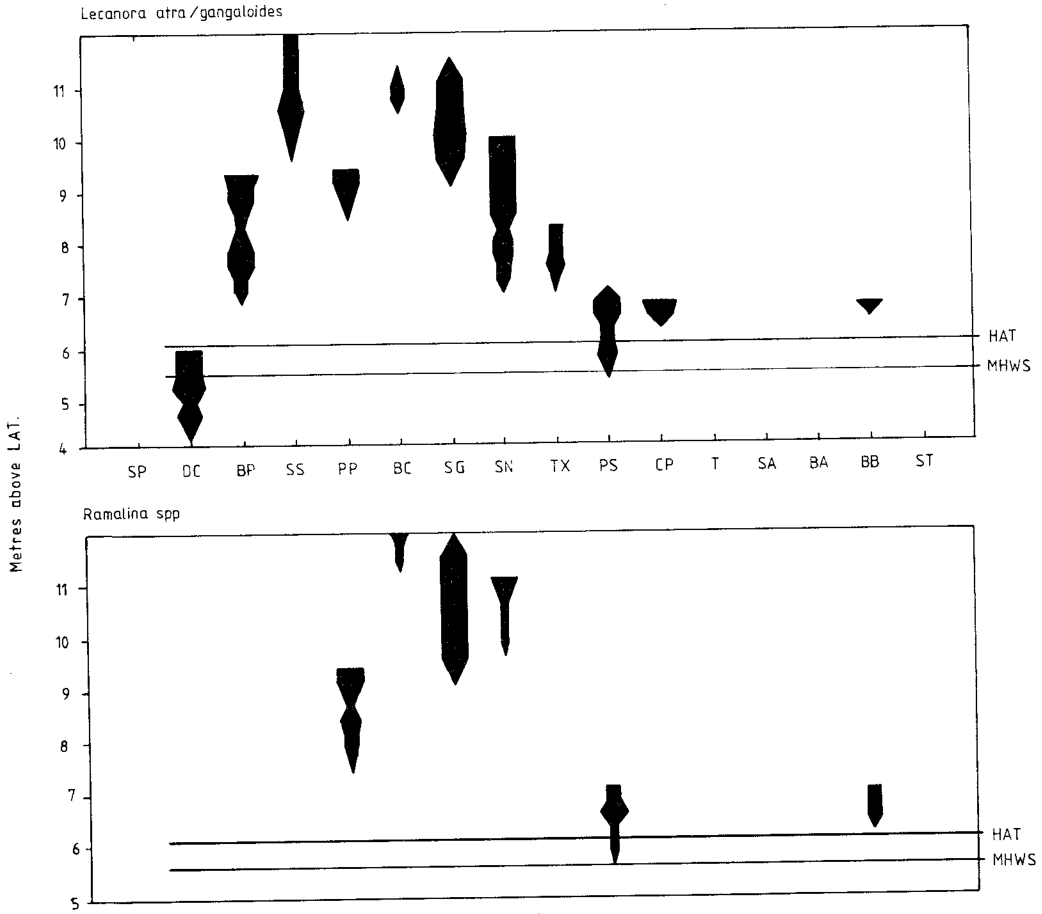


FIG. 10.
Distribution of *Ramalina* spp. and *Lecanora* spp.
(See also figs 5 and 7).

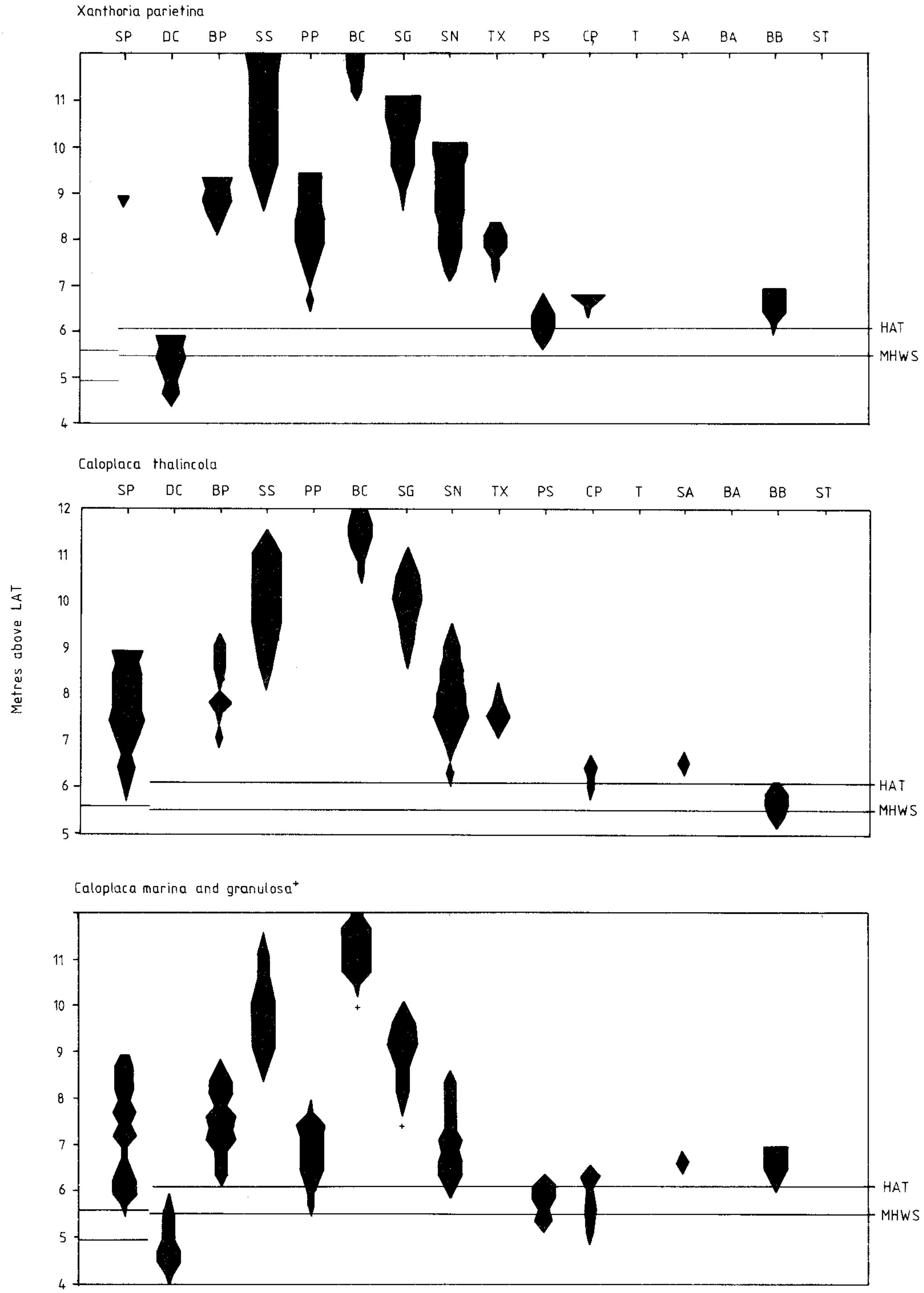
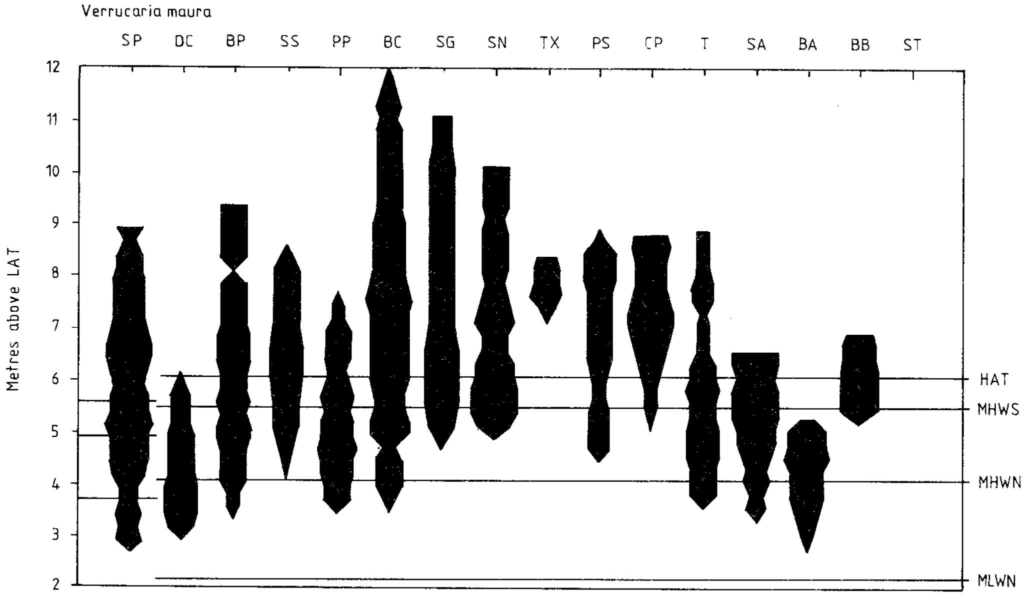
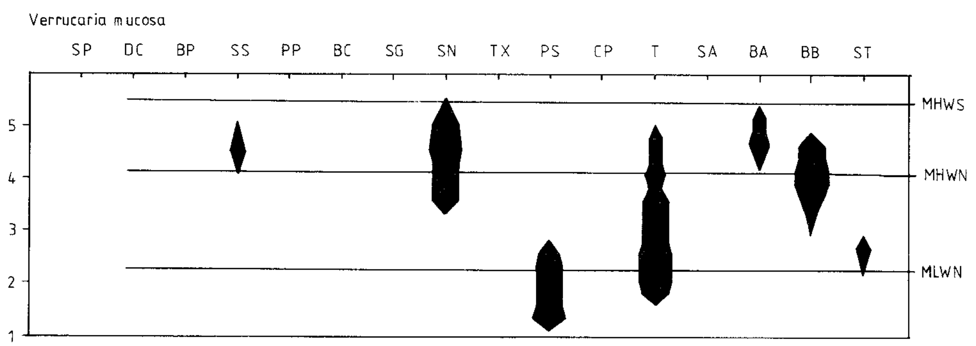


FIG. 11.
Distribution of *Caloplaca* spp. and *Xanthoria* spp.
(See also figs 5 and 7).

Caloplaca marina	Fig. 11
Lichina confinis	Fig. 12
Verrucaria maura	Fig. 12
Lichina pygmea	Fig. 12
Verrucaria mucosa	Fig. 12

There is considerable overlap between the zones, although on steep shores, e.g. Peartree Point, the upper and lower borders of a zone may be sharply defined, producing a band of colour. Other species include *Arthopyrenia haldytes* which occurs on every shore pinpricked into the shells of barnacles and limpets. The two major factors controlling the extent and position of the lichen zones are aspect and exposure to wave action. A comparison of Start Point North (aspect North) and South East Gara (aspect South West) shows that the abundance and vertical extent of most lichen species is decreased at the former. The effect of a northerly aspect is usually to increase the upper limit of lichens and the limited zone of lichens at Start Point North is probably a reflection of lower exposure. At Black Cove, where many of the lichens extend further up the shore than at South East Gara which has the





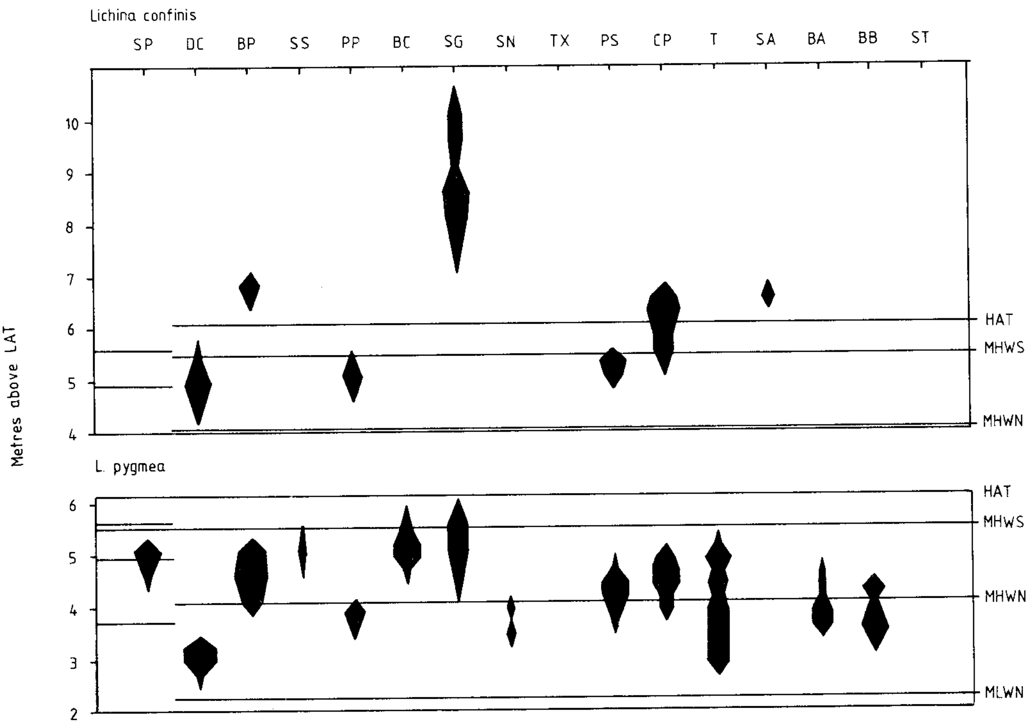


Fig. 12.
Distribution of *Lichina* spp. and *Verrucaria* spp.
(See also figs 5 and 7).

same exposure and aspect, the even topography of the rock may allow the waves to wash further up the shore than the more broken profile at South East Gara. Substantial areas of the rock slab at Black Cove are free of lichen covering where the surface of the soft hornblende-chlorite schist has been eroded by sub-aerial processes. A more detailed discussion of the littoral and the supralittoral lichens of the South Hams will be found in Hawksworth (1973, 1979).

7. **Fucoid Seaweeds.** The fucoids are more common on the sheltered shores or on the back slopes of gullies. *Pelvetia canaliculata* is not extensive on any shore and usually occurs in a very narrow band between MHWS and MHWN. *Fucus spiralis* is found just below *P. canaliculata* and is not common on any shore. There is frequently an area between *F. spiralis* and the next large seaweed to be found, *F. vesiculosus* at MHWN, which is dominated by barnacles and limpets and grazed clean by the latter (see Fig. 13). The bladderless form, *F. vesiculosus* var. *linearis,* occurs at Start Point North and a few stunted plants may be found at Peartree Point. *F. serratus* is confined to the lowest part of sheltered shores and may be abundant below MLWN. *Ascophyllum nodosum* occurs with *F. vesiculosus* on sheltered shores and is the dominant alga on the Saltstone.

8. **Other Seaweeds.** *Laminaria digitata* occurs below MLWN on most shores (Fig. 15) but is replaced by *Laminaria saccharina* on the Saltstone. *Enteromorpha* spp. and *Ulva lactuca* usually occur under the shelter of the more robust fucoids. In exceptional situations *Enteromorpha* may become very abundant on a part of the shore for part of

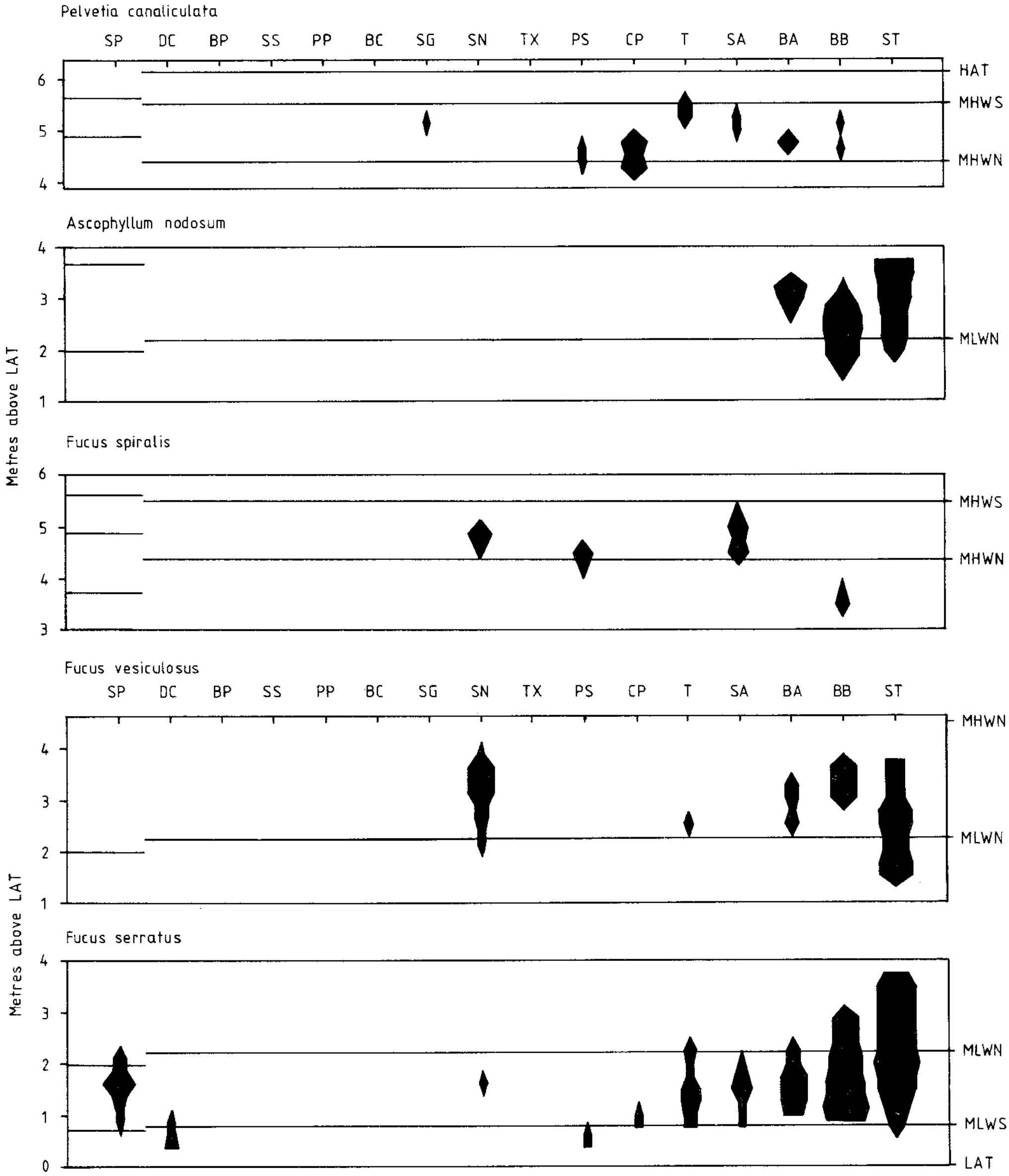


FIG. 13.
Distribution of Fucoid Seaweeds
(See also figs 5 and 7).

the year, e.g. where the limpets are removed by pollution, by hand or by the influence of freshwater. It may be regarded as a primary coloniser and its rapid growth allows it to take advantage of disturbed situations. The red seaweeds (Fig. 15) are to be found for the most part under the larger fucoids or on the low shore, e.g. *Palmaria palmata*. Some species of the Rhodophyta are more resistant to desiccation and may extend considerable distances up the shore, e.g. *Laurencia pinnatifida*, albeit in a stunted form and frequently restricted to cracks and crevices which afford some protection against grazing by limpets and where moisture is trapped.

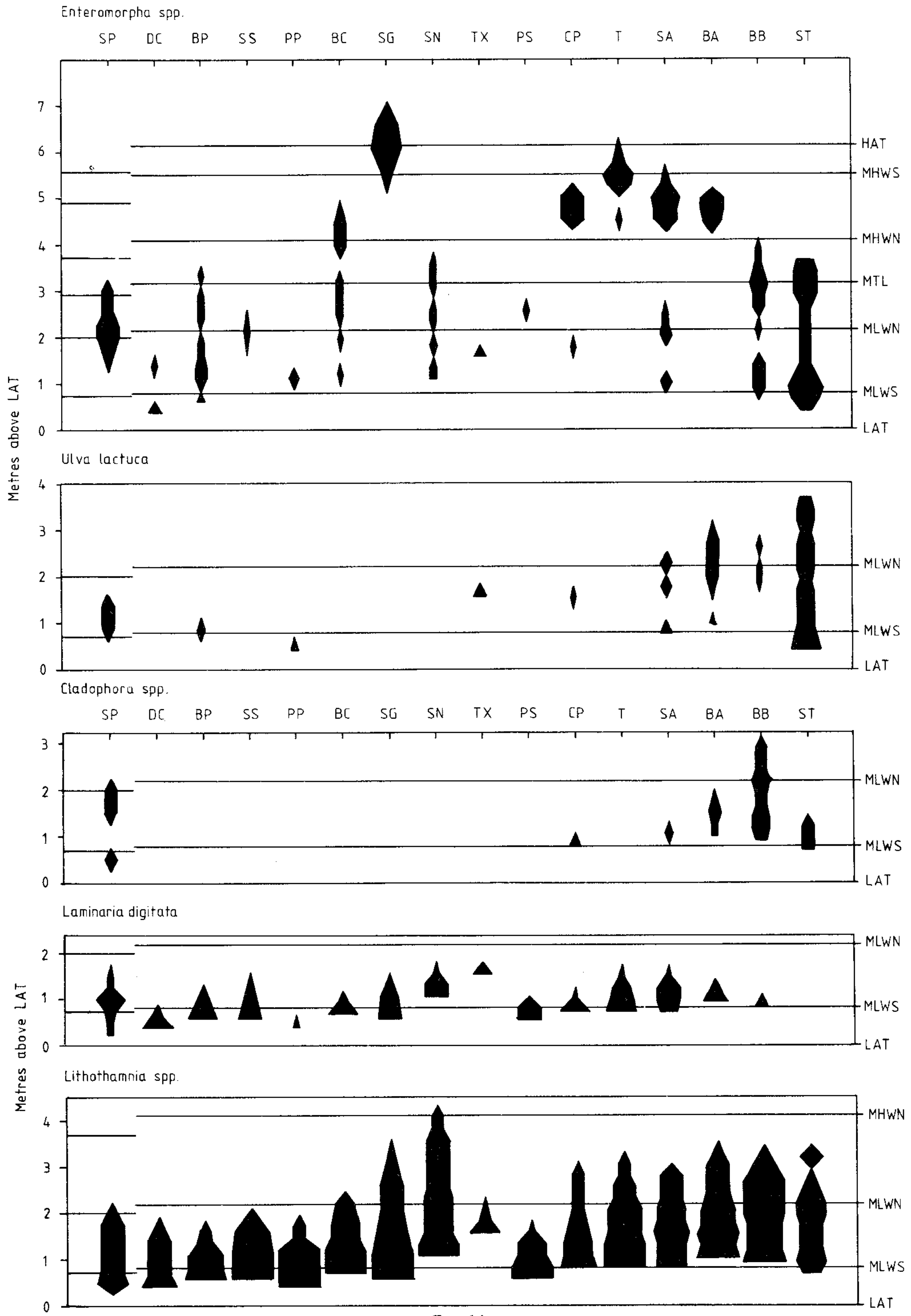


Fig. 14.
Distribution of some other seaweeds
(See also figs 5 and 7).

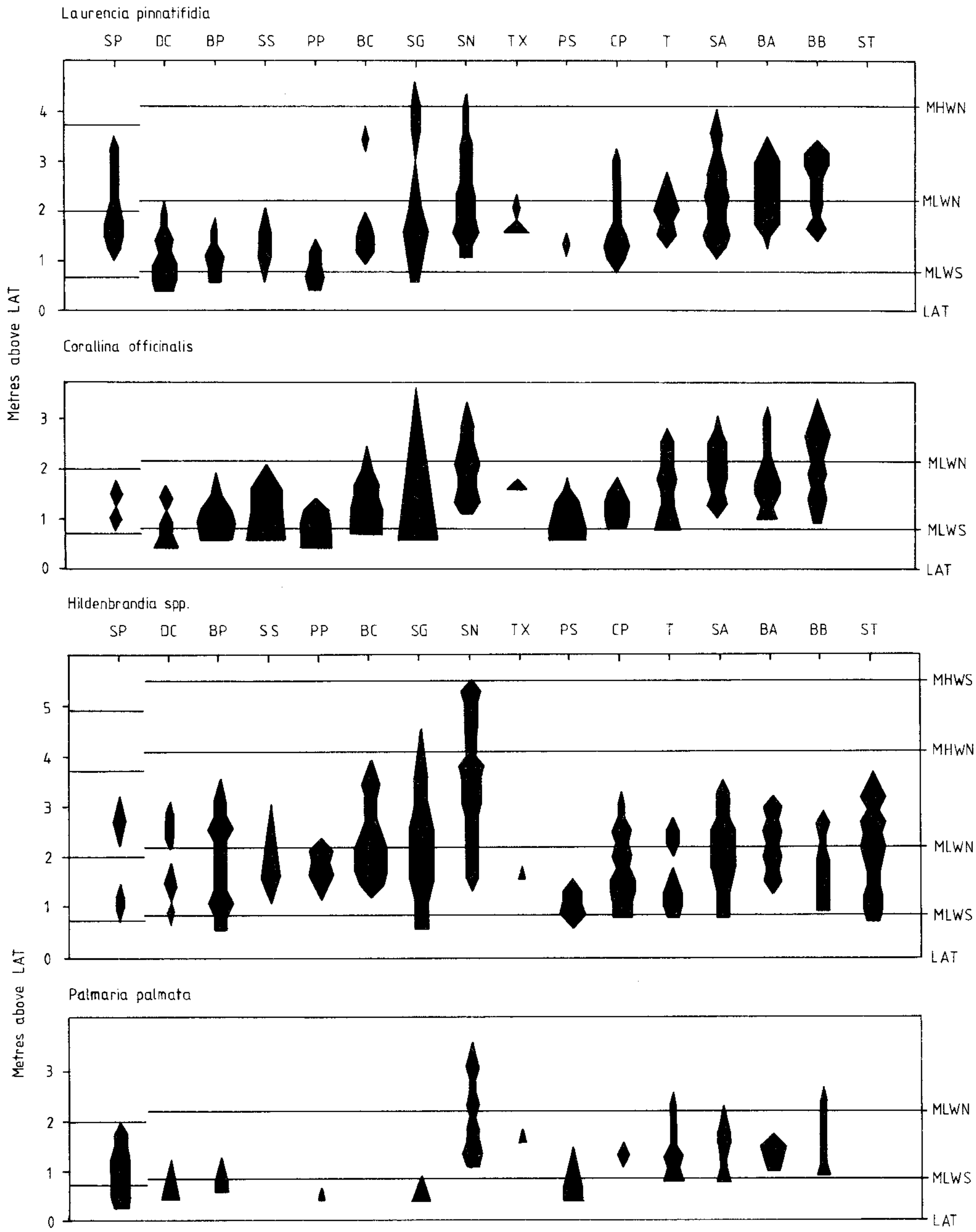


FIG. 15.
Distribution of Red Seaweeds
(See also figs 5 and 7).

MODIFYING FACTORS

The basic pattern of zonation on all rocky shores is much the same when related to tidal level and exposure. However, on some shores large differences in population and pattern may be produced by the operation of subsidiary modifying factors. Examples of these are given on the next three pages.

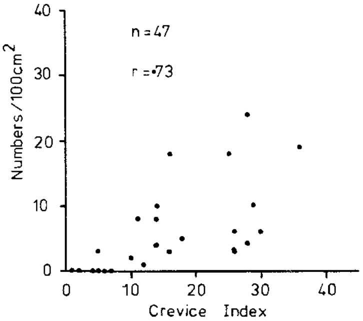


FIG. 16.

The population of *Littorina saxatilis* agg. and *L. neritoides* 100 cm^{-2} plotted against Crevice Index. Crevice index is the % frequency of crevices occurring in a sample of 100×1 cm^2 using a flexible transparent quadrat. n = number of samples, r = correlation coefficient, p = >.001.

1. **Rock type**

Three principal rock types are found in the South Hams. Limestone, the softest rock to chemical erosion, is only found at Shoalstone Point so it is to this rock that Piddocks (boring Bivalves) are confined. The other shores surveyed are comprised of slates and grits or schists (Fig. 2). Some of the softer slates are being rapidly eroded at the top of the shore by subaerial erosion processes (e.g. freeze-thaw) and are totally barren of life. At Bantham a contrast to bare rock of this type is provided by large boulders of quartz-mica schist close by, which are well covered by dense lichen growth.

Littorinid populations may also be affected by rock type. *L. neritoides* and "*L. saxatalis* agg." are found clumped in high shore rock crevices. The number of Littorinids 100 cm^{-2} on some shores is directly related to the number of crevices (see Fig. 16) and the crevice density may limit the population. The maximum size of snails is also directly proportional to mean crevice size (Raffaelli & Hughes, 1978). Crevices may provide protection against displacement by wave action, desiccation and predation. Desiccation seems likely to be the most important factor as Littorinids may frequently be observed grazing on the rock surface in damp or humid conditions.

Heller (1975*b*) has shown that there is a significantly higher proportion of the red varieties of *L. rudis* and *L. nigrolineata* on old red sandstone rocks in Wales than on rocks of different colours and suggests that predation by rock pipits, *Anthus spinoletta,* may favour cryptic colour varieties. A similar change in the frequency of colour morphs may be observed on rocks of different colours at Bantham where white, black and reddish rocks occur in close proximity. However, the difference in colour frequencies is not as clear cut as that reported by Heller and the situation needs further investigation.

2. **Vertical and Horizontal Surfaces**

At Start Point there is a set of unused steps leading down the North face of the Point to MLWN. The surfaces were surveyed using suitable sizes of quadrat and the results are summarised in Fig. 17, and shown in Plates 3 and 4. *Fucus* spp. grow exclusively on the horizontal surfaces. In contrast, barnacle and limpet species have a higher population and are uplifted by up to $1\frac{1}{2}$ m above their horizontal range on the vertical surfaces. Horizontal surfaces are more likely to retain puddles of water

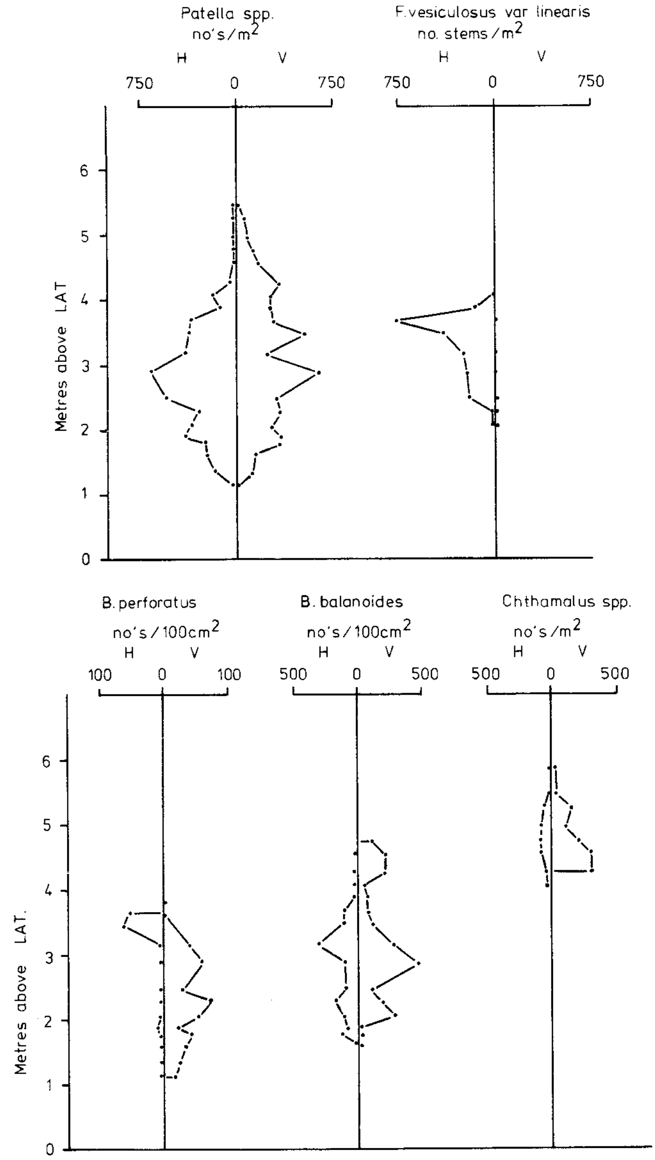


FIG. 17.
Population per unit area of five species on horizontal (H) and vertical (V) rock surfaces at Start Point North.

and sporeling survival may account for the marked difference in population of Fucoids between the surfaces. Vertical surfaces are more shaded and more exposed to wave action and the difference in the population and range of *Chthamalus* spp. and *Patella* spp. may be due to the resulting variation in temperature, desiccation and exposure. The decrease in *B. balanoides* below 4 m corresponds with the increase in *Fucus vesiculosus* var *linearis* population and it is probable that the *B. balanoides* spat is swept off the rocks by the movement of the *Fucus* in the waves. Above 4 m *F. vesiculosus* var *linearis* disappears and the population of *B. balanoides* increases. In contrast *B. perforatus* only exists on the horizontal surfaces under *F. vesiculosus* stems.

Plate III
General view of the steps at Start Point North.

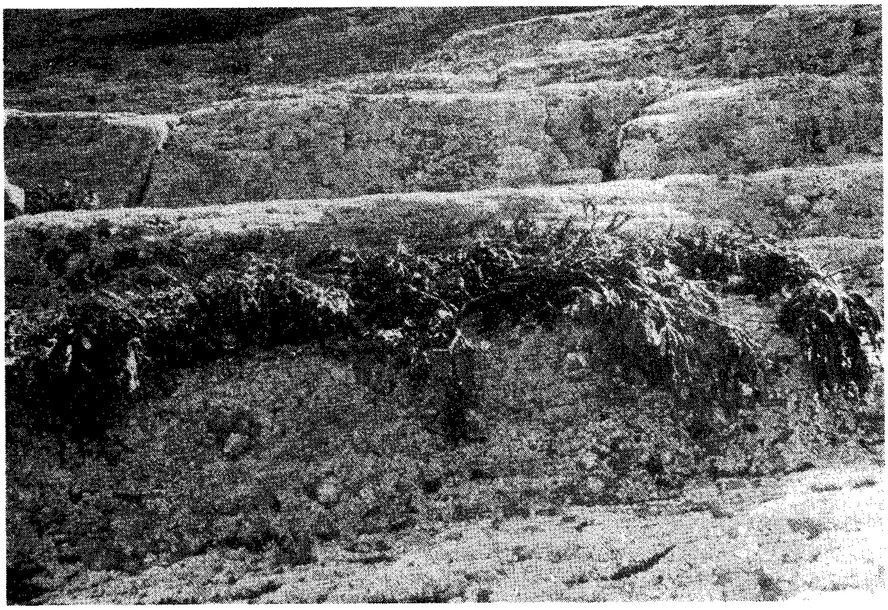


Plate IV.
Close up of one step. Very few stems of *Fucus vesiculosus* var *linearis* occur on the vertical surfaces which are more exposed to wave action than the horizontal surfaces (see also Fig. 17).

It would appear that physical conditions at some other stage of the life cycle control the distribution of *B. perforatus*. Desiccation may limit the population of *B. perforatus*, whereas the abrasion by *Fucus* limits *B. balanoides* in this area.

Similar changes in population and distribution as a result of changing aspect can be observed if the backs and the fronts of rocky ridges are accurately surveyed. This has been previously discussed by several authors (e.g. Ferry & Sheard, 1969; Lewis, 1961). In general the more extreme conditions of a south facing rock will depress the upper vertical range of each species.

3. Limpets and Fucoids

Limpets feed by grazing algae and detritus from rock surfaces. Whilst limpets do not feed on the larger fucoid plants, high populations may prevent their establishment by grazing the algal sporelings from the surface. When limpets are removed, the area of bare rock may be rapidly colonised by *Enteromorpha* spp. followed by *Fucus* spp. (Fretter & Graham, 1962; Southward, 1964). The border between the fucoid and the limpet-dominated regions of the shore is frequently abrupt but does not necessarily occur at the same height on every shore, e.g. Bantham.

A complex series of factors other than height above L.A.T. and exposure probably control the end result of the fucoid/limpet balance and Southward (1964) suggests that there is a cyclical relationship between the two populations. As the fucoids approach the upper limit of their vertical range the balance is tipped in favour of the grazers, dramatically altering the character and species composition of the rock surface. Small seasonal variations in spat/sporeling success will probably result in vertical fluctuation of the limpet/fucoid border from year to year. On steeper shores this change may not be noticeable, but on the more gentle slopes of the wave cut platforms minor changes in this balance could markedly alter the character of the shore.

Unfortunately there are insufficient data from previously marked permanent quadrats to describe this quantitatively and the nature, causes and extent of such changes are speculative. However, there are marked differences between the patterns of distribution of limpets in the two types of habitat. A barnacle/limpet area and another dominated by *Ascophyllum nodosum* at Bantham B within a ±50cm vertical range were surveyed using randomly placed 0.06 m^2 quadrats. Although there is no significant difference in the population of limpets m^{-2}:

A. nodosum zone	$\bar{x} = 60$	$\sigma = 5.21$
Barnacle-limpet zone	$\bar{x} = 52$	$\sigma = 2.68$

Limpets under *A. nodosum* are markedly clumped into small grazed patches whereas the population is more evenly dispersed in the barnacle/limpet area. A length frequency histogram (Fig. 18) shows that there is a higher proportion of small limpets under *A. nodosum* but limpets attain a larger size (60 mm length max.) there. Jones (1948) in Southward (1964) reports that limpets under dense cover grow faster, whilst larger populations may be found on barnacle/limpet dominated shores. Although there are distinct peaks in Fig. 18 these do not necessarily represent distinct age classes. Amongst the barnacles smaller limpets are present in the rock pools which were excluded from the survey. It is likely that recruitment to the population on the rock surface takes place from these pools.

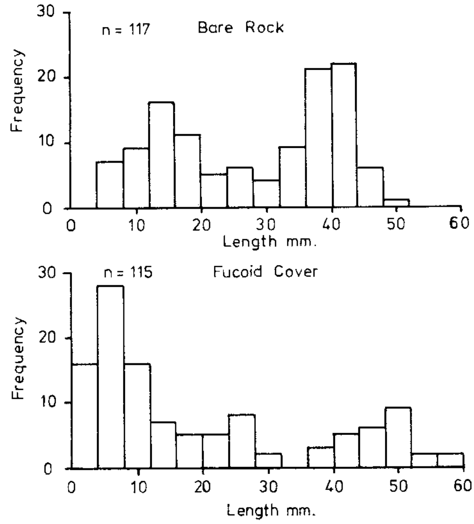


Fig. 18.

Length frequency histograms for limpet populations in areas 1. dominated by fucoid seaweeds 2. bare of fucoids. (Length class = 4 mm)

Discussion

The combined effects of tidal movement and exposure to wave action control the overall distribution of animals and plants on rocky shores. At any one site a complex series of subsidiary factors may influence and modify the basic zonation pattern.

In addition to the factors discussed above, sand scour, spat success, seasonal variation and disturbance by man may influence the ecology of organisms on the shore. It is tempting to regard the results of each rocky shore survey as a fixed ecological fact but each pattern of distribution and abundance is a reflection of the balance of ongoing processes, such as grazing, which are of great intrinsic interest but are frequently difficult to examine and demonstrate, particularly in short-term surveys. Small alterations in this balance of processes may well alter the fine character of shores for many years after an event, but unfortunately there are insufficient data to allow an accurate description of these processes to be made.

Rocky shore surveys based on a transect of the shore and semi-quantitative assessment of the abundance of certain selected species have often been used in the past to provide data for monitoring change. Surveys of this nature present many problems which are difficult to overcome in practice. Field identification of certain groups e.g. barnacles and filamentous brown algae, can be well nigh impossible. Moreover, changes in the taxonomic status of groups, e.g. *L. saxatilis* agg. (Heller, 1975*a*) or revised keys to species, may complicate comparisons with earlier surveys.

There are inherent problems in the use of abundance scales. These are designed to provide repeatable and semi-quantitative data on a wide range of shore types. The scales are broadly based on "logarithmic" series and are thus more sensitive to change in populations at lower densities. Whilst the scales are relatively easy to apply there are several serious disadvantages. Firstly, the division of population density into abundance classes results in a loss of information. Whilst the scales may smooth out minor local discrepancies, significant changes in population between two sites or sampling occasions may then be masked. If the data for vertical and horizontal surfaces at Start Point are plotted using abundance scales (Fig. 19) much of the information is lost.

Moreover, tests on the "repeatability" of shore transect methods using different workers on different days show that estimates of population may differ by up to one abundance class, that is by a factor of ten, and in some cases even more (Baker, 1976; Field Studies Council staff course, 1978). Part of this error results from subjective differences in the estimation of abundance by different workers. Although the survey technique ostensibly takes into account an area up to five metres either side of the transect line, the structure of many shores is such that minor differences in the relocation of a station may produce major differences in abundance class. This problem can be overcome by permanently marking each station, a laborious and time-consuming process.

Lastly, published information on rocky shore surveys is based on at least five different versions of abundance scales, Crisp and Southward (1958), Ballantine (1961), Moyse and Nelson-Smith (1963), Crapp (1970) and Crapp (1973). Although differences between scales may be small, it is frequently difficult to make direct comparisons between published information.

Presence/absence data can equally well be used to establish the vertical range of a species and are usually sufficient to make broad comparisons between shores. The maximum abundance of an organism on any particular shore in quantitative terms, i.e. no. m^{-2}, can be used as effectively as traditional methods to establish exposure (Ferry & Sheard, 1969). Where it is necessary, fewer permanent stations could be used to accurately assess the changes in abundance of selected species between sampling stations and would be more likely to produce reliable, repeatable data. The disadvantage may be that more time is needed to complete a survey but such an approach may prove more profitable than traditional methods.

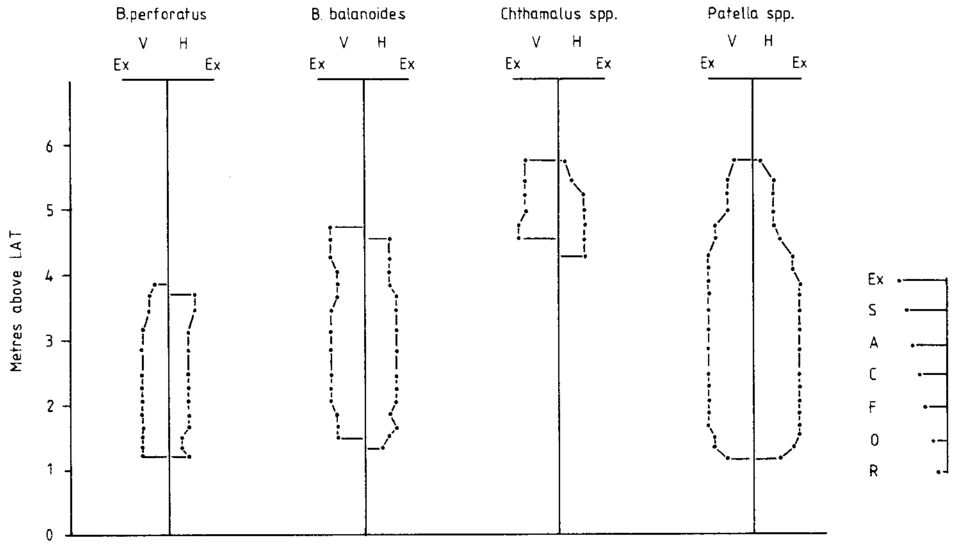


FIG. 19.
The data for the population per unit area (see fig 17) converted to abundance classes and plotted against height above LAT.

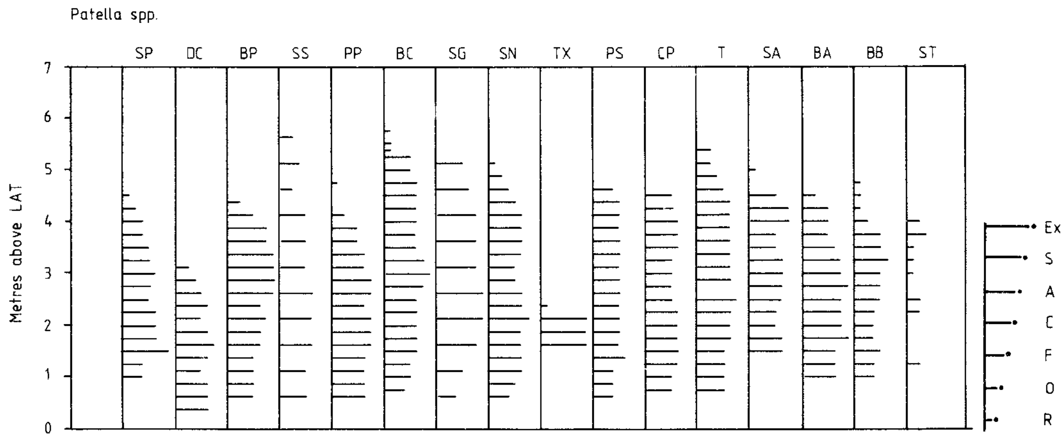


FIG. 20.
The abundance of *Patella* spp. plotted against height above LAT drawn as an interrupted bar chart.

A note on the representation of data

Data from rocky shore surveys have traditionally been represented by kite diagrams. The width of the kite is proportional to the abundance of the species at each station. Although the symmetry of such kites is visually attractive, it is quicker and mathematically correct to plot the data from a discontinuous transect of this type in the form of a bar chart as in Fig. 20.

Conclusion

The shores of the South Hams provide one of the finest teaching grounds for marine biology in the country and this work was conceived as a background to courses at Slapton Ley Field Centre. The authors hope that it may prove useful to studies elsewhere and stimulate interest and discussion in the underlying processes which produce the zonation patterns seen on rocky shores. These frequently give the illusion of permanency, but the pattern observed is the result of a constant interplay of past and present physical factors and biological events.

ACKNOWLEDGEMENTS

The paper would not have been written without the encouragement and patience of Mr. J. H. Crothers. Dr D. H. Dalby and many staff of the Field Studies Council have provided help, information and stimulating discussion. Miss L. Dakin and Miss B. Gillam provided valuable comments on the intelligibility of the draft.

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