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VERTICAL DISTRIBUTION AND GENERAL ECOLOGY OF SOME OF THE COMMON INTERTIDAL ORGANISMS OF THE NORTHUMBERLAND COAST[1]

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INTRODUCTION

THE horizontal distribution and vertical zonation of organisms on the seashore has engaged the attention of marine ecologists for several years. While numerous investigations in different parts of the world have thrown much light on the nature of this distribution and zonation, they have still not removed the need for more intensive as well as extensive studies on different coastal regions for a complete and correct understanding of these phenomena. A part of the exposed Northumberland coast was therefore studied from this point of view during the years 1946-48. General ecological observations were also made on the more common intertidal species of this coast.

The field observations were carried out during the period October 1946 to December 1947, the limits of distribution of the more common species being followed in selected areas throughout the year. The work was completed early in 1948 but publication was unfortunately delayed. Some important papers such as those of Stephenson and Stephenson (1949), Womersley and Edmonds (1952), Chapman and Trevarthen (1953) and Lewis (1955) have appeared subsequent to the completion of this work. The discussion in the present paper has accordingly been revised.

The investigation was made by using a modification of Colman's (1933) traverse method designed to include the advantages of that used by T. A. Stephenson and his colleagues (see Bokenham, Naugebauer and Stephenson, 1938, and Evans, 1947a and 1947b). Sections of the intertidal region were chosen in different parts of the bay extending from low water mark to well above all tide marks, and a number of reference points marked on the rock at known intervals. These points were then accurately levelled correct to one hundredth of a foot using known bench marks for the purpose. Profiles were constructed of the sections chosen and several yards of the shore on either side of each of the sections were examined in detail for the distribution of plants and animals. Scrapings of the rock were examined in the case of very small organisms. The heights of intermediate points along the sections and of points outside the sections wherever necessary, were determined by the use of (1) the reference points mentioned above, and (2) a good handlevel clamped on to or held against a levelling staff so as to slide vertically along it.

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[1] Condensed from part of a thesis accepted for the degree of Doctor of Philosophy of the University of Durham in June, 1948.

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The detailed survey was carried out on the rocky and boulder beaches of Cullercoats Bay. General observations were extended to other selected areas as far as Newbiggin Bay, 15 miles north of Cullercoats.

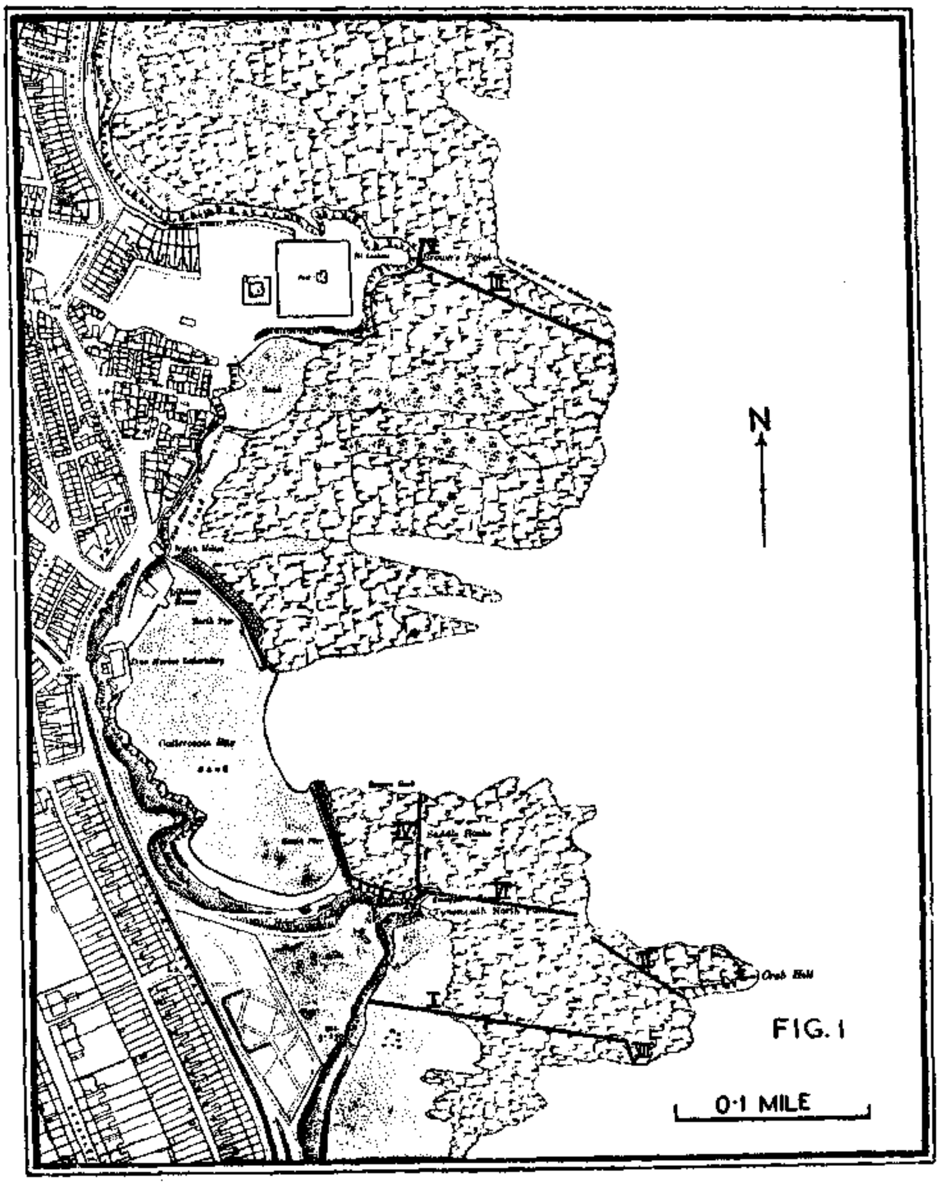


FIG. 1. Map of Cullercoats Bay and its neighbourhood showing the positions of the selected sections (I-VII) in the intertidal region.

The position and approximate directions of the selected sections are indicated in Fig. 1. The latter is taken from the Ordnance Sheet No. NLXXXVI, 5, (1919). The mapping of the sections was done by the Plane Table method.

Altogether seven sections were chosen so as to include as many different kinds of physical features as possible within the area surveyed.

In addition to these sections and the areas including them the South Pier was also levelled and its east face studied in detail. The remaining areas of the rocky, stony and shingly beach between the pipe-line section and the Brown's Point Sections were also periodically examined but not always with reference to accurate tidal levels.

General Environmental Conditions

(a) *Topography of the shore.*

The shore at Cullercoats is divisible into the 'North Side' extending from the North Pier to the Brown's Point rocks, and the 'South Side' extending from the South Pier to the southern end of Smugglers' Cave and Crab Hill rocks. Between these two parts, which are mainly rocky and boulder strewn, is the sandy foreshore guarded on both sides by the piers. In all these three parts, the shore is bounded on the landward side, except where artificial walls are built, by bare cliffs or ledges of rock or by clayey banks. Northward of the Brown's Point rocks the shore consists of rock and shingle for some distance and then passes over into the sandy beach of Whitley Bay. South of the Crab Hill and Smugglers' Cave rocks is a sandy beach extending for a considerable distance towards the River Tyne entrance. Sections I and VII are situated close to this sandy zone.

Crab Hill, on which section II is situated, consists of sandstone and is a continuous stretch of rock with a rough surface but without many boulders or large fissures. This rock is completely submerged at high tide but forms an island when the water reaches the level of Highest Low Water Neaps.

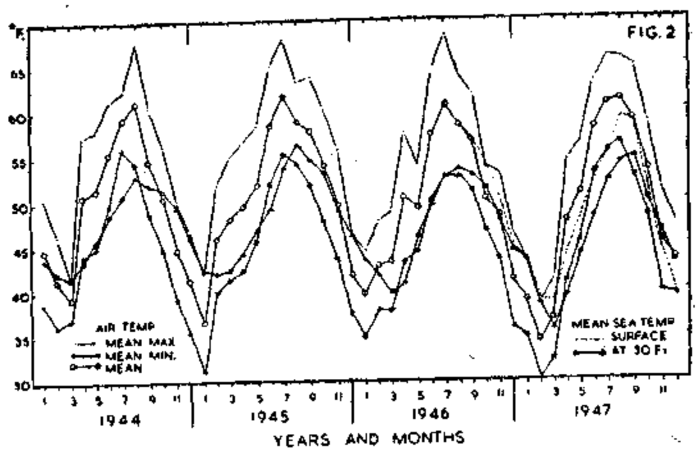
The Smugglers' Cave rocks are partly sandstone and partly limestone with a rough pitted surface. Sections IV and VI are situated on these rocks and parts of the areas traversed by these are covered by silt.

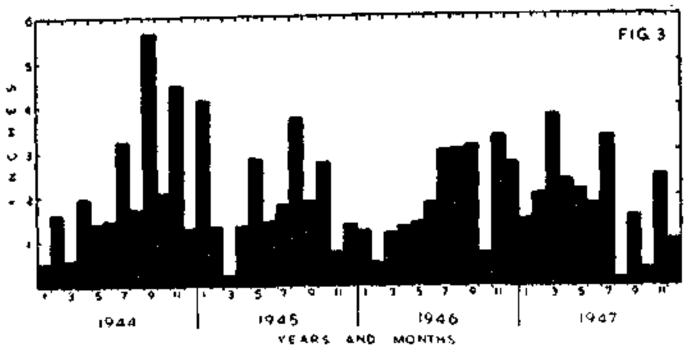
The Brown's Point rocks on the northside of the bay are of rough surfaced sandstone. Section III passes for the most part over the main rocks but partly also over a short zone of stones and shingle. Section V northward of Brown's Point, is for a short distance, on a continuation of the same rocks but has its main stretch in a region of boulders and shingle.

All these rocks are much exposed. Relatively sheltered spots are largely confined to the regions of boulders and stones which are less frequent on the Brown's Point rocks than on the rocks of the South side of the bay. A good part of Section VI is in an area which is the most sheltered in the upper shore of the bay.

(b) *Sea and air temperatures and rainfall.*

The intertidal organisms at Cullercoats are in general exposed to somewhat lower sea and air temperatures than in the south and west of England. Fig. 2 shows the monthly mean values of sea and air temperatures for the period 1945-47.





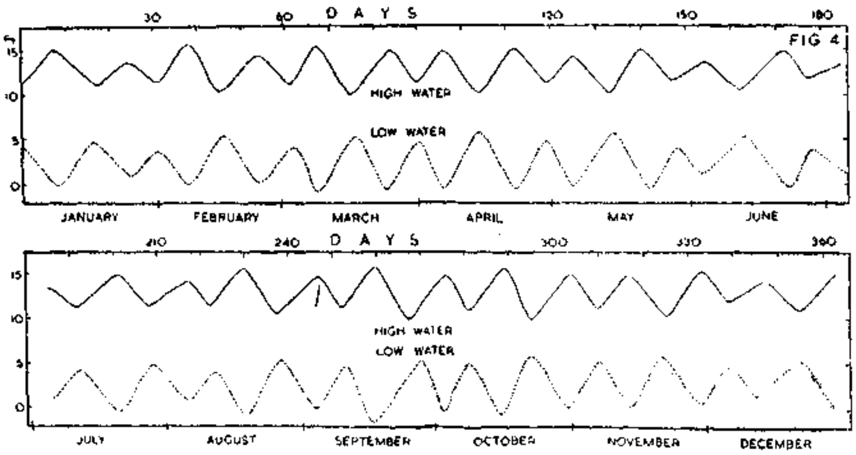


FIG. 2. Monthly sea and air temperatures at Cullercoats for the years 1944 to 1947.

FIG. 3. Monthly totals of rainfall recorded at South Shields from January 1944 to December 1947.

FIG. 4. Extreme tidal limits of all the tidal periods during 1947 showing roughly, the periodicity and frequency of continued submergence and emergence at the various intertidal levels.

Fig. 3 shows the rainfall data at Cullercoats (South Shields) for the same period.

(c) *Wind, Turbidity and Wave action.*

The prevailing winds are westerly. Both turbidity and wave action are important factors at Cullercoats and on the whole of the Northumberland coast on account of its exposed nature, the strong winds and the mainly sandy and muddy nature of the sea bottom near the shore.

(d) *Tidal levels and Exposure to the air.*

The tidal information has been taken or calculated from data given in the Admiralty tide tables for 1947 for the River Tyne entrance. Tidal levels were checked on several occasions with bench marks and were found to agree well with the predictions on calm days.

The theoretical range of the tide varies between 17.4 ft. and 4.1 ft. having a mean value of 13.84 ft. for spring tides and 7.09 ft. for neap tides. The Highest High Water and the Lowest Low Water both occurred on the same day in September and reached a height of 15.8 ft. and −1.6 ft. respectively; the Lowest High Water occurred in the months of September and October stopping at 9.9 ft. above C.D. (Chart Datum), while the Highest Low Water occurred in October and November and was 5.8 ft. above C.D. Low Water Springs at Cullercoats always occur early in the forenoon or during night and therefore, except during Summer, the effect of insolation is very low on the lower parts of the beach.

The terms 'Lowest High Water Neaps' and 'Highest Low Water Neaps' have been used here as equivalent to the terms 'Extreme High Water Neaps' and 'Extreme Low Water Neaps' used by Evans (1947a and 1947b). The latter terms are likely to be misleading as they might mean the 'Highest High Water Neaps' and the 'Lowest Low Water Neaps' respectively and therefore should be omitted.

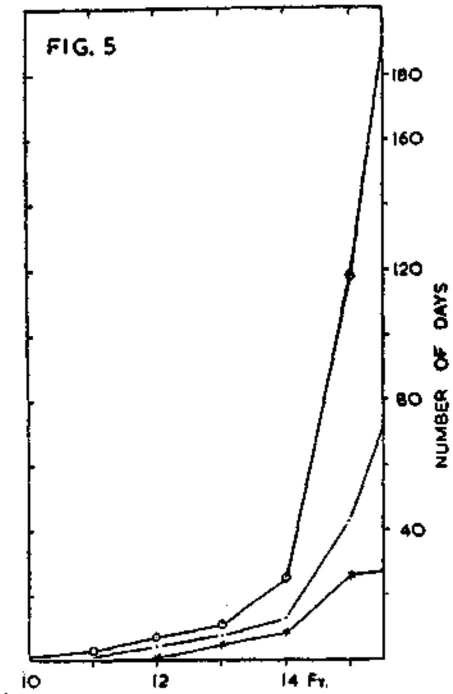
The percentage exposure to the air at different levels of the shore was calculated by Colman's (1933) method. But instead of choosing exactly 380 hours for each period as Colman did, the full relevant tidal period is taken into account, beginning from the extreme tide immediately preceding the equinoctial date and ending with the similar next extreme tide.

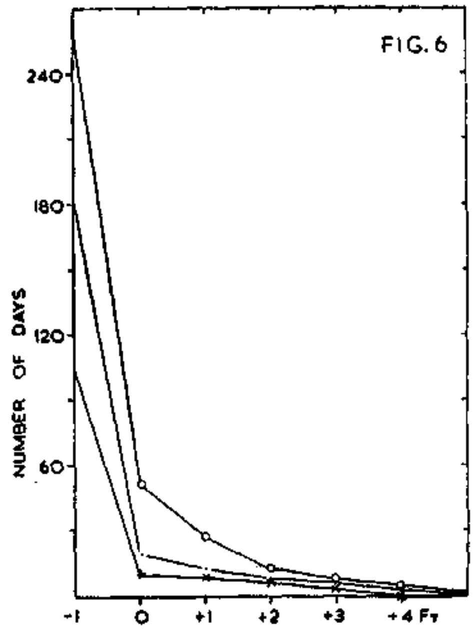
Colman (1933), Fischer-Piette (1936) and Chapman (1943) have drawn attention to the importance of 'non-tidal exposure' or continued emergence from water during the neap tide periods as one of the causal factors for critical zonational levels. This factor arises only above the level of the Lowest High Water Neaps and increases towards higher levels. But, as Chapman points out, it is not the regularity of the increase that is important but the significant changes at certain levels, in the rate of its increase. A method is suggested here for detecting these levels in this type of work: Fig. 4 shows roughly the lengths and frequency of such continuous emergence at various levels at Cullercoats. The figure is obtained by plotting against the days of the year the heights of the Highest and Lowest High Waters of all the tidal periods and joining them by a smooth curve, and gives a rough idea of the relative lengths of continued exposure at the various heights. The results are also shown in Fig. 5. The graph shows significant changes in the rate of increase between 13 ft. and 14 ft., and 14 ft. and 15 ft. above C.D.

Like the continued emergence factor is the continued submergence factor which is operative below the level of the Highest Low Water Neaps. The lower curve in

Fig. 4 is obtained like the emergence factor curve, by plotting against the days of the year, the heights of the highest and lowest low waters of all the tidal periods of the year and joining them by a smooth curve. The rough values thus obtained are plotted against intertidal heights in Fig. 6. The significant changes in the rate of decrease are here seen between -1 ft. and 0 ft., and between 0 ft. and $+2$ ft.

From Fig. 4 it is also possible to count the number of tidal periods in the year which reach their extreme limits at various heights on the shore.





5. Time of continuous exposure of various intertidal levels at Cullercoats during the year 1947.

6. Time of continuous submergence of various intertidal levels at Cullercoats during the year 1947.

DISTRIBUTION AND GENERAL ECOLOGY OF SOME OF THE COMMON ORGANISMS

(a) *General Remarks.*

The intertidal algae are comparatively poorly developed in the region studied, especially above the 'Laminarian Zone.' The fucoids are rather sparsely distributed and not very well grown. *Fucus serratus* is the most abundant and best developed; *F. spiralis* occurs only as patches of stunted plants and *F. vesiculosus* is also localised in its distribution; *Pelvetia canaliculata* is absent. Several normally common species of red and green algae are either unrepresented or are poorly grown and confined to particularly sheltered situations.

The fauna is also not very rich. Several common species are poorly represented and erroneous impressions of their vertical distributions would have been obtained if Colman's *limited* traverse method *alone* had been used for the survey.

(b) *Vertical distribution of the common species.*

The extreme limits of vertical distribution of the common species studied in the different sections is summarised in Tables I and II.

TABLE I

Limits of Distribution (in Ft. above C.D.) of some of the common organisms at Cullercoats. (Downward arrows indicate below and upward arrows above the levels given)

(a) ANIMALS

a	b	c		d		e		f	
No.	Species.	Sects. I & VII. U.L.	L.L.	Sect. II U.L.	L.L.	Sect. III U.L.	L.L.	Sect. IV U.L.	L.L.
	PORIFERA								
1.	*Grantia compressa* ..	1.4		—		2.9	↓1.5	2.8	0
2.	*Leucosolenia botryoides* ..	1.5		—		2.8	↓1.5	2.8	0
	COELENTERATA								
3.	*Actinia equina*	6.4	↓0	9.6	↓0	10.9	↓0	9.7	↓0
4.	*Dynamena pumila* ..	1.6	2.8	2.8		3.2	1.0	4.5	0
	ANNELIDA								
5.	*Fabricia sabella* ..	3.9		3.6	↓0	5.8	↓0	6.6	↓0
6.	*Pomatoceros triqueter*	5.0		2.6	↓0	4.9	↓0	5.1	
	ECHINODERMATA								
7.	*Asterias rubens*	1.5		0.8		1.6	↓0	—	
	MOLLUSCA								
8.	*Anomia ephippium* ..	1.5		—		4.1	1.0	3.1	0
9.	*Gibbula cineraria* ..	6.4		1.0	↓0	6.1	↓1.0	—	
10.	*Hiatella gallicana* ..	—		—		—		2.8	↓0
11.	*Lacuna pallidula*	—		—		7.3	1.0	7.2	↑0
12.	*L. vincta* ..	3.9		2.8		8.2	↓0	6.2	↓0
13.	*Littorina littoralis* ..	8.9		—		7.3	↓4.3	7.5	3.5
14.	*L. littorea* ..	11.5	↓2.1	9.9	↓1.9	10.8	↓2.3	14.0	0.9
15.	*L. neritoides* ..	12.4	4.2	9.9	1.9	24.5	3.9	21.9	5.2
16.	*L. saxatilis rudis* ..	11.9	2.1	9.9	9.7	15.3	3.8	14.5	4.9
17.	*L. saxatilis rudissina* ..	—		9.9	9.4	23.5	10.9	21.8	11.5
18.	*L. saxatilis saxatilis* ..	12.4	1.9	9.9	↓1.9	12.4	1.1	13.0	0.9
19.	*Margarites helicinus* ..	3.9		2.8	0	5.3	↓0	6.1	↓0
20.	*Mytilus edulis* ..	9.3		9.9	↓0	14.9	↓1.1	12.9	↓0
21.	*Nucella lapillus* ..	11.9	↓0	9.9	↓0	8.2	↓0	9.9	↓0
22.	*Patella vulgata* ..	9.7	0.7	9.9	1.0	16.9	1.1	13.4	↑0
23.	*Patelloida virginea* ..	1.4	↓0	1.5	↓0	2.4	↓0	1.4	↓0
24.	*Rissoa parva* ..	3.9	↓0	2.8	↓0	8.1	↓0	8.1	↓0
25.	*Turtonia minuta* ..	3.9		2.1	↓0	6.3	↓0	6.2	↓0
26.	*Zirfaea crispata* ..	2.2	↓0	—		—		—	
	CRUSTACEA								
27.	*Balanus balanoides* ..	12.4	1.5	9.9	↓1.0	14.9	1.0	12.2	↑0

No.	Species.	g		h		i		j	
		Sect. V		Sect. VI		South Pier		Extreme	
		U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L.L.
	PORIFERA								
1.	*Grantia compressa*	—		—		—		2.9	↓0
2.	*Leucosolenia botryoides* ..	—		—		—		2.8	↓0
	COELENTERATA ..								
3.	*Actinia equina* ..	8.5	2.4	7.6	↓2.4	7.7		10.9	↓0
4.	*Dynamaena pumila* ..	—		3.5	2.4	—		4.5	↓0
	ANNELIDA								
5.	*Fabricia sabella* ..	—		5.6	↓2.4	—		6.6	↓0
6.	*Pomatoceros triqueter* ..	5.9	2.4	6.8	↓2.4	—		6.8	↓0
	ECHINODERMATA ..								
7.	*Asterias rubens* ..	—		2.4		—		2.4	↓0
	MOLLUSCA ..								
8.	*Anomia ephippium* ..	—		—		—		4.1	↓0
9.	*Gibbula cineraria* ..	4.8	2.4	6.9	2.4	—		6.9	↓0
10.	*Hiatella gallicana* ..	—		—		—		2.8	↓0
11.	*Lacuna pallidula* ..	5.3	2.4	8.2	2.4	—		8.2	↑0
12.	*L. vincta* ..	5.8	2.4	5.8	2.4	—		8.2	↓0
13.	*Littorina littoralis* ..	4.2	2.4	11.4	2.9	—		11.4	2.4
14.	*L. littorea* ..	3.1	2.4	11.4	2.4	10.1		14.0	↓0.9
15.	*L. neritoides* ..	24.5	5.8	19.9	13.0	20.8	6.3	24.5	1.9
16.	*L. saxatilis rudis* ..	15.8	2.4	8.5	5.9	16.8		16.8	↓2.1
17.	*L. saxatilis rudissima* ..	24.2	11.8	19.9	8.4	18.0	9.3	24.2	9.4
18.	*L. saxatilis saxatilis* ..	14.2	2.4	11.4	2.9	13.2		14.2	0.9
19.	*Margarites helicinus* ..	4.1	2.4	—		—		6.1	↓0
20.	*Mytilus edulis* ..	13.1	2.4	10.9	↓2.4	12.1		14.9	↓0
21.	*Nucella lapillus* ..	8.6	2.4	9.8	↓2.4	7.6		11.9	↓0
22.	*Patella vulgata* ..	16.7	2.4	14.1	2.4	14.6		16.9	↑0
23.	*Patelloida virginea*	—		—		—		2.4	↓0
24.	*Rissoa parva* ..	7.1	2.4	6.3	↓2.4	—		8.1	↓0
25.	*Turtonia minuta* ..	—		5.9	2.4	—		6.3	↓0
26.	*Zirfaea crispata* ..	—		—		—		2.2	↓0
	CRUSTACEA								
27.	*Balanus balanoides* ..	13.1	2.4	12.9	2.4	14.2		14.9	0

(c) *Seasonal changes.*

Some of the sections particularly Sections III and IV were closely watched throughout the year to determine possible changes in the limits of the vertical distribution of the different organisms from season to season ; general observations were extended to the other areas also.

There was no appreciable change seen in the case of most of the organisms. Most of the changes which did occur concerned the algae and were the result of the settling of a new generation of plants in the spring.

The following are the species which showed seasonal changes to a marked degree :—(1) *Porphyra umbilicalis*, (2) *Rhodymenia palmata*, (3) *Nucella lapillus*, (4) *Balanus balanoides*, (5) *Asterias rubens*, (6) *Enteromorpha compressa*, and (7) *Ulva linza*. The changes noticed in respect of the first four of these will be mentioned

Table II

Limits of distribution (in ft. above C.D.) of some of the common organisms at Cullercoa s.

(b) Plants

a	b	c		d		e		f		g		h		i		j	
No.	Species	Sects. I & VII		Sect. II		Sect. III		Sect. IV		Sect. V		Sect. VI		South P er		Extreme	
		U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L.L.	U.L.	L..L
	Chlorophyceae																
1.	*Enteromorpha minima* ..	18.3	5.4	—		16.9	10.9	18.5	11.5	18.2	11.5	18.2		21.1	10.6	21.1	5.4
2.	*Ulva linza* ..	—		—		6.5	1.1	8.5	3.2	7.5	2.4	8.1	2.4	—		8.5	↓0
	Rhodophyceae																
3.	*Callithamnion sp.* ..	9.6		9.6		11.1		—		9.8	1.5	9.5	2.4	7.6		11.1	1.5
4.	*Chondrus crispus?* ..	2.4	0	1.5		1.1 & 13.7 ?	↓0 9.6	4.5		13.7 ?	9.6 ?	—		—		4.5 13.7?	↓0 9.6
5.	*Gigartina stellata* ..	2.0 - 1.1		2.8	↓0	8.2	↓0	6.1		7.0	2.4	6.3	↓2.4	6.3		8.2	1.1
6.	*Laurencia pinnatifida* ..	—		—		8.2		8.3		8.1	2.4	—		4.3		8.3 (opt. 5.9)	↓0
7.	*Lomentaria articulata* ..	—		—		8.2		8.3		7.9	2.4	—		4.0		8.3	↓0
8.	*Porphyra umbilicalis* ..	—		9.7	9.3	16.2	2.6	12.4	3.2	16.2	2.4	14.3	2.4	14.7		16.2	2.4
9.	*Rhodymenia palmata* ..	3.9		2.8	↓0	4.7		3.6		2.9	2.4	4.5	↓2.4	—		4.7	↓0
	Phaeophyceae																
10.	*Ascophyllum nodosum* ..	6.4	4.4	—		—		—		—		9.5	5.7	—		9.5	4.4
11.	*Fucus serratus* ..	3.9	1.1	2.8	↓0	9.5		9.4		4.6	2.4	8.7	2.4	5.8		9.5	-1.1
12.	*F. spiralis* ..	9.7	9.5	—		13.9	11.4	14.3	11.9	14.2	13.3	12.6	9.6	14.3	13.2	14.3	9.5
13.	*F. vesiculosus* ..	9.7	5.5	—		—		—		12.4	11.5	10.6	6.7	—		12.4	5.5
14.	*Laminaria cloustoni* ..	-0.7		0.3		0.1		0.8		—		—		—		0.8 -0.7	
15.	*L. digitata* ..	1.5		2.8		2.6		3.7		—		3.0		—		3.7	↓0
16.	*L. saccharina* ..	0.6		0.8		2.4		1.0		—		2.4		—		2.4	↓0

under the respective heads in the ecological accounts of the species. The changes relating to the rest are as follows :—*Asterias rubens.* The lower part of the pipe-line beach (area of sections I and VII) was kept under observation with particular attention to this species and it was found that while large numbers of *Asterias* occurred up to 1.5 ft. above C.D. during non-summer months, hardly any could be found above M.L.W.S. during August and September. It is probable that there is a downward migration of these starfishes from the littoral during the warmest months of the year. Similar summer migrations have been noticed in the case of *Asterias rubens* by Huntsman (1918) in Nova Scotia, and in *Pisaster ochraceus* and *Evasterias troschelli* by O'Donoghue (1924) in Departure Bay, British Columbia. Hewatt (1937) in Monterey Bay, found that ' a generally lower level is obtained by *Leptasterias aequalis* during the breeding season ' (late spring).

Enteromorpha compressa and *Ulva linza.* During the winter and early spring both these plants were absent from the rocks in most parts of the beach. By midsummer the plants had formed a dense covering on the rocks of the lower beach between M.T.L. and H.L.W.N. downward. Towards the higher levels the density was gradually lower, *Ulva linza* having its upper limit below L.H.W.N. while *E. compressa* occurred, though sparsely, to beyond M.H.W.N. Correlated with the appearance of the thick covering of these green weeds and of *Porphyra* on the lower beach was an elevation of the upper limits of distribution of *Rissoa parva*, *Lacuna vincta* and *Margarites helicinus.* Errant forms such as *Idotea granulosa* and amphipods not found on weed-free rocks in other seasons were also found now sheltering under these plants. By next December both the species had mostly disappeared.

(d) *Ecology of selected species of Plants and animals.*

(i) PLANTS

Fucus spiralis : This species forms not a dense belt, but a characteristic zone of sparse, stunted plants just below or within the *Enteromorpha minima* zone which forms the highest intertidal algal zone common to both exposed and sheltered rocks. Though nowhere abundant, a greater number of plants occur and thrive better where *E. minima* is absent. Of the local fucoids, *F. spiralis* is the most tolerant of surf action. It is associated with large populations of *Hyale nilssoni*, acarines, and of juvenile *Littorina saxatilis* (usually) and *L. littoralis* (occasionally).

F. spiralis ranges from just below M.H.W.S. to below L.H.W.N. Its most usual occurrence is between just below M.H.W.S. and M.H.W.N.

Ascophyllum nodosum : Cotton (1912), Rees (1935), Lyle (1920), Johnson and Skutch (1928) and Gibb (1939) report the species from both sheltered and exposed localities. Kitching (1935), David (1941) and Evans (1947a, 1947b) find that it prefers relatively sheltered localities. In Cardigan Bay, (David, 1941 and Evans, 1947a) it prefers a long, fairly level beach with shelter and surf. This seems to be the case at Cullercoats also. *A. nodosum* also seems to require a film of silt on the rock when the latter is very rough and rugged, as pointed out by Hatton (1938). It is nowhere found on steep slopes except when very well sheltered. There is a wide gap between *F. spiralis* and this species, probably because both are so sparsely represented, but, as David (1941) suggested (for Aberystwyth), the steepness of the shore at the higher levels (a feature which is common at Cullercoats and of which *F. spiralis* is tolerant) may be responsible for this. The same may explain the low upper limit of the species when compared with other areas. *F. vesiculosus* seems to mix freely with *Ascophyllum*, very often occurring on the same boulder.

The species extends from just below L.H.W.N. to just above M.L.W.N. and is more flourishing at the lower levels of its distribution than at the higher.

Fucus vesiculosus : This species is also poorly represented at Cullercoats, though better developed than *F. spiralis*. It is definitely much more tolerant of broken ground and boulders than any other of the fucoid species here. Kitching (1935) found on the Argyll coast that it survived on all slopes between 0° and 90°, was scarce and stunted on overhanging surfaces, and ranged from positions of the most extreme shelter to very wave-beaten coasts, frequently however, being sparse on the latter except when the shore was broken. He found that in sheltered parts *Ascophyllum* replaced *F. vesiculosus* though the latter was represented by a few plants at a higher level than *Ascophyllum*. David (1941) in Aberystwyth noticed signs of great competition between these two species ; he found that *F. vesiculosus* was frequently an epiphyte on *Ascophyllum* when it occurred above (E) H.L.W.N. and suggested that *F. vesiculosus* would grow higher up but for the crowding by *Ascophyllum nodosum*. This seems to be correct because, at Cullercoats, while both species are sparsely distributed, *F. vesiculosus* does occur at higher levels than *Ascophyllum* where the latter species is absent.

Fucus serratus : This is by far the best developed of the fucoid species of this coast. It is absent in highly exposed positions and unprotected steep slopes. Where it does not form a wide belt it may occur, but always patchily, in crevices or other places offering some protection. Kitching (1935) found it on the Argyll coast from wave beaten to very sheltered situations. Evans (1947a) in Cardigan Bay found that it definitely avoided steep slopes unless very protected but grew fairly well on boulders and was tolerant of fine sand ; on horizontal rocks the species was poor if surf was strong. This is also true for Cullercoats. Increasing shelter raises the upper limit of *F. serratus* to some extent. The range of optimum distribution of the species is variable according to conditions.

Laminaria digitata : Laminaria digitata occurs in both exposed and sheltered regions and the upper limit of distribution is lowered with increased exposure to surf. Evans (1947 b) describes this condition as being ' tolerant of a wide range of conditions of surf.' It seems however, that where the upper limit of distribution is lowered and the plants are submerged almost continuously, they are not exposed to the action of surf although they are to that of backwash. These two forms of physical disturbance may be expected to have different effects on the plants.

Laminaria saccharina : This species comes next to *L. digitata* in its vertical extension and does not thrive in exposed situations. In very exposed places the species seems to be absent even in the regions (just below the low tide mark) of the backwash to which the surf effect is reduced in the case of submerged plants. The distribution of the species falls in line with the findings of Evans (1947 a & b) and Kitching (1935) in other localities.

Laminaria colustoni : According to Evans (1947a) in Cardigan Bay this species is more tolerant of exposed situations than *L. saccharina*. But here if we judge from its distribution above Low Water Mark, it is definitely less tolerant of exposed situations than *L. saccharina*. Its upper limit is below that of *L. saccharina* in all exposed situations where both occur. Both however, have about the same upper limits in some sheltered situations. In a more or less permanently submerged state this species is present in some of the exposed situations where *L. saccharina* is altogether absent, this showing perhaps a greater tolerance to the effects of backwash. The extreme upper limit noticed at Cullercoats was slightly above M.L.W.S. but only a few plants extended beyond 0.3 ft. above C.D.

Rhodymenia palmata : In many places this species forms a characteristic zone emerging above the *Laminaria* belt and is one of the commonest of the Rhodophyceae on the shore near the low water mark. It varies in size and intensity of colour being generally larger and darker in sheltered situations. It seems to be very tolerant of broken ground such as boulders and even small stones but is smaller in the latter case. In specially sheltered positions the region of maximum density lies at a higher level than elsewhere. The optimum limit of upper distribution is about half way between M.L.W.N. and M.L.W.S.

New young plants of *Rhodymenia* appeared in spring all over the lower part of the rocky and boulder beach and grew through the summer. The upper limit however, was the same as before, but by December, only the plants in sheltered localities and pools were surviving.

Porphyra umbilicalis : The history of this species also was closely followed throughout the year. In winter and early spring it was present mostly at high water mark (above L.H.W.N.). In June *Porphyra umbilicalis* appeared all over the beach in the lower regions also. By August it was very abundant, forming a characteristic covering to the rock, especially on the lower half of the beach along with *Enteromorpha compressa* and *Ulva linza.* On the Crab Hill and Smugglers' Cave rocks the new generation and the older generation which was found throughout the Winter months became one continuous zone though the new generation was always distinct because of its darker colour. On the Brown's Point rocks, there was a considerable gap left between the high water level forms and the newly settled low water level forms of *Porphyra.* By early December all the low water level forms disappeared on most of rocks. While the first appearance of the plants was noticed on the most exposed rocks, the first disappearance was also noticed in the same situations.

P. umbilicalis is tolerant of steep slopes and can stand very high exposure. But its distribution is always patchy and never in a dense or continuous belt. The low water form is more tolerant of broken ground than the high water form and much less tolerant of exposure.

The species is extremely tolerant of surf action and texture of substratum. It is frequently found with *Enteromorpha* spp. and often grows on limpet shells ; the low water forms sometimes occur as epiphytes on the fucoids. The winter form ranged between 16.2 ft. and 9.8 ft. above C.D. except on Crab Hill rock where it was found slightly further below L.H.W.N. The spring forms extended down to 2.4 ft. above C.D. and had their optimum upper limit just below M.T.L.

Gigartina stellata : This species occurs in variable quantities in all the areas studied and shows considerable tolerance to the nature and angle of slope of the substratum. On exposed rocks where *Fucus serratus* and *Laminaria* are absent or sparse, *G. stellata* is the dominant form forming along with *Chondrus crispus,* a characteristic belt of weed and silt with an optimum upper limit at a few inches above

M.L.W.S. In boulder regions it is mixed with *Rhodymenia palmata* and the *Laurencia-Lomentaria* community and becomes part of the underflora of *F. serratus* and *Laminaria digitata*. On exposed horizontal rock it does not extend much above M.L.W.S., but in sheltered situations under *Fucus*, in cracks and crevices, and on vertical surfaces it extends up to 8.2 ft., above C.D. (above M.T.L.) As a rule its occurrence above the M.L.W.S. level is patchy and never in the same density as below this level. In several situations the contour of the upper limit of *G. stellata* is found to follow closely the contour of the wash zone of the waves at this level and as the surf action is not the same at all points it seems likely that the emergence from water or the desiccation factor is the limiting cause for this upper limit.

Gigartina and *Fucus serratus* seem to be competing with each other for space as, in some sheltered places, the latter species is dominant and *G. stellata* becomes a member of the underflora. In other places which are very exposed *F. serratus* yields place completely or largely to *G. stellata.*

Enteromorpha : There are at least three species of *Enteromorpha* at Cullercoats, viz. *E. compressa, E. minima* and *E. intestinalis.* The first two are the more dominant and exhibit zonation, (on open rock). *E. minima* prefers rocks and boulders at the high tide level and forms a characteristic zone immediately above and including *F. spiralis.* It is tolerant of slopes, poorly developed in highly sheltered situations and absent on overhanging surfaces. There seems to be a close inverse correlation between the abundance of this species and of *F. spiralis*, the former being very sparse or absent where the latter is relatively well developed. The roughness or smoothness of the substratum also does not seem to matter much but it is most abundant on moderately smooth and sloping substrata. There is invariably a thin layer of silt in the *E. minima* zone with small nematodes forming the most abundant element of the fauna. In the recolonization observations (Seshappa, 1956) the development of some fucoid sporelings in the zone of *E. minima* and their later diminution in numbers indicated a possible competition between the two species. The optimum lower limit of *E. minima* is mostly near M.H.W.N.

E. compressa is also a very common species throughout the year in rock pools and on damp rocks, but is especially abundant during spring and summer. In some places no plants of this species were found on the rocks during March but by May they were appearing on the rocks and had increased in the pool both in exposed and sheltered situations. By June *E. compressa, Ulva linza,* and *Porphyra umbilicalis* together formed a characteristic zone in the lower littoral region. While *Ulva linza* and *P. umbilicalis* both disappeared in late autumn and early winter, patches of *E. compressa* continued to survive in sheltered places and moist localities.

Laurencia Pinnatifida : This species almost always occurs in association with *Lomentaria articulata,* occasionally including also patches of *Callithamnion* spp. and forming the *Lomentaria-Laurencia* community recognized by several authors (e.g. Cotton, 1912 ; Rees, 1935 ; Kitching, 1935 ; and Gibb, 1938 and 1939), as occurring on exposed and moderately exposed coasts. At Cullercoats *L. pinnatifida* is very common in exposed situations. Where present on flat rock it is always confined to crevices or underflora.

Callithamnion : Two species of *Callithamnion, C. arbuscula* (?) and *C. turneri* (?) occur at Cullercoats, sometimes mixed with *Laurencia* and *Lomentaria* but often independently and extending much higher in vertical distribution. *Plumaria elegans* is also sometimes associated with these two species. Like the members of the *Laurencia* group, *Callithamnion* prefers vertical surfaces and crevices at the edges of ledges. It is absent on small stones and not well developed on boulders; the presence of silt does not seem to favour any of the species of *Callithamnion*.

Corallina: Both *Corallina officinalis* and *C. squamata* are present, the latter being the rarer and confined to lower tidal levels, occurring either amongst other weeds or singly. *C. officinalis* is more abundant on exposed rocks and extends up to M.T.L. In pools it goes higher up to M.H.W.N. and nowhere extends beyond this level. It is often found forming a characteristic patch on damp, silt-free, barnacle-covered rock; but is also found in patches in silty areas occupied by *Fabricia sabella* and *Gigartina stellata*. The *Corallina* association is described as typical of exposed coasts (Cotton, 1912), replacing the *Laurencia* association when the surf is too intense for the latter. In Cardigan Bay (Evans, 1947a), it is one of the most tolerant of the littoral algae with regard to wave action. The distribution of *Corallina* at Cullercoats agrees with these findings.

(ii) ANIMALS.

Balanus balanoides: The species is abundant in all the regions examined, subject to the occurrence of suitable local conditions and gives a characteristic appearance to the mid-beach, *Chthamalus stellatus* being absent. The ecology of this species in other places has been studied by several authors in the past, notably by Moore (1935 and 1938), Fischer-Piette (1929 etc.), Hatton (1938), Kitching (1935), Kitching and Moore (1939) and Evans (1947a and 1947b). It favours exposed rock irrespective of the angle of slope and, in the absence of surf, prefers regions most frequently washed by strong currents. The texture of the rock is important and although new spat are found to settle on practically every kind of surface available within tidal range, they thrive only on rough rock. The limits of vertical distribution are also affected by the amount of exposure or shelter in a given locality; the upper limit is raised and the lower limit is lowered where there is much surf action thus increasing the intertidal range of the species; conversely, the lower limit is raised and the upper limit lowered with increased shelter. The occurrence of silt and profuse weed is unfavourable to barnacles. All these points are easily verified at Cullercoats.

The vertical range of adult *Balanus balanoides* here lies between M.L.W.S. and M.H.W.S., stopping at and following closely the upper limit of the continuous *Gigartina* belt. There is in many places a clear upper barnacle line but this is often disturbed where *Enteromorpha minima* occurs. In such situations the upper limit of optimum density is roughly about M.H.W.N. while elsewhere it may rise a little higher.

Nucella lapillus: *N. lapillus* is found in varying numbers in all the areas studied. Normally this species is most abundant in boulder-strewn areas and creviced rock, being very frequent in each case on vertical surfaces covered with barnacles.

Silty covering, smooth surfaces, and *Rhodochorton* or *Enteromorpha* beds are not frequented by *Nucella*, probably because of the absence of barnacles in these situations, and also the absence, frequently, of a firm foothold for creeping. Evans (1947a) says that the species is poor on the limestone rocks at Tinside, West Hoe in the Plymouth neighbourhood. Much of the rock to the north-east of the Smugglers' Cave is magnesian limestone and has a very small population of *Nucella*.

In vertical range *N. lapillus* extends from slightly above M.H.W.N. down to E.L.W.S. The abundance gradually decreases between M.L.W.N. and M.L.W.S., and not many are found below this latter level. During the season of barnacle settlement *Nucella* was found in numbers at all levels within the zone of dense barnacle populations.

Patella vulgata : This is one of the commonest animals on the shore. An account of its intertidal distribution with reference to size and sex frequencies at various levels on the shore at Cullercoats, has been published elsewhere (Das and Seshappa, 1947).

P. vulgata lives under conditions of extreme shelter as well as of extreme exposure to surf. In some sheltered localities however, especially below the mid-tide level, the density is low when compared with exposed situations at the same level. Coincident with this occurrence is a relatively better development of the larger fucoid and other weeds in such situations. Frequently also, in these localities quantities of silt combined with beds of *Rhodochorton rothii* etc. occur and these are unfavourable to *Patella*. Hatton (1938) noticed a denser settlement of *Patella* on exposed surfaces than on sheltered ones. Evans (1947b) suggests the filtering effect of the algal fronds must be important in this respect. While the presence of algae may be responsible for the scarcity of *Patella* in sheltered situations, an abundance of *Patella* may be responsible for the absence of algae in exposed situations, the two species thus having a reciprocal effect upon each other.

P. vulgata is very tolerant of the angle of slope and the texture of the substratum, occurring on rough as well as smooth and on overhanging as well as vertical and horizontal surfaces. Broken ground is tolerated up to a point. A rough surface seems to be essential for spat survival.

L. littorea : This is a shelter-loving species and when occurring on continuous rocky ground, is confined to horizontal and gently sloping surfaces and to the sheltered sides ; where weeds are relatively well developed or there is considerable amount of silt the number is relatively small. The species is not tolerant of fine grit or sand. The extreme range of vertical distribution is from about M.L.W.S. to M.H.W.S. No specimens were seen at E.L.W.S. anywhere and in most places the upper limit is reached round about M.H.W.N.

Littorina littoralis : This is the most shelter-loving and the least abundant of the Littorinids at Cullercoats. The scarcity of the species is correlated with the general scarcity of fucoid algae on the mid-beach.

The vertical distribution, like the horizontal, is also determined by the nature of the substratum and the degree of fucoid growth. The upper limit at Cullercoats lies at 1 ft. below L.H.W.N. and the lower limit between M.L.W.N. and M.L.W.S. The area of abundance lies in the neighbourhood of M.T.L.

Littorina saxatilis : This species was studied in some detail but an account of the same has however, not been included in this paper.

Littorina neritoides : This species occurs along with *L. saxatilis* in the ' Littorina zone ' and among the barnacles on exposed rocks in the ' Balanoid zone '. A peculiar feature is noticed in this species, especially on the Crab Hill. *L. neritoides* occurs as occasional individuals as low as 1.9 ft. above C.D., becomes more frequent above H.L.W.N., but occurs in numbers only in the crevices and among barnacles on the ledges near the top of the rock. The specimens at the lower levels look quite normal and have a well developed spire; the colour is black or dark brown with sometimes a white streak on the last whorl. The specimens at the top on the other hand, are frequently stunted, with a rounded off spire and with an ash-grey colour. Search in similar situations elsewhere has also revealed the frequent occurrence of this peculiarity. The reason for this must lie perhaps in that *L. neritoides* shows an upward migration on the shore (Lysagt 1941). The young probably settle at all levels in the range of distribution of the species and all travel upwards to the *Littorina* zone which alone seems to be their proper *niche*. On Crab Hill, this upward journey of the snails is limited by the fact that the rocks do not extend beyond High Water Neaps. The snails, therefore, have to settle down at the highest levels available and may be affected in some way by continued daily submergence after their reaching adult size.

The zone of greater abundance of *L. neritoides* is above M.H.W.S. Evans (1947b) found specimens 'definitely' below M.T.L. at Church Reef and down to M.L.W.S.+ 2 ft. at Blackstone Point. Lysagt (1941) found the species to below M.T.L. on Plymouth break-water. In Cardigan Bay Evans (1947a) found the zone of abundance to lie above M.H.W.S. 'though occasional specimens did occur as low as M.L.W.N.' During the present work, the lowest level at which specimens were recorded was 1.9 ft. above C.D. i.e. the lower limit may be said to lie between M.L.W.N. and M.L.W.S. The upper limit varies with the amount of surf and the nature of the rock and weed cover.

Gibbula cineraria: This species inhabits the stony and shingly areas near the low water mark. It is extremely shelter-loving and is completely absent on continuous rock; even in the stony areas it is almost invariably found underneath the stones or in the sheltered crevices at their sides. Large masses of sand, fine silt and thick weed cover, are unfavourable. The optimum upper limit of distribution is about M.L.W.N. but occasional specimens do extend higher up, in highly sheltered situations.

Mytilus edulis: This is found in varying numbers in all the areas surveyed. The best population in Cullercoats, both from the number of individuals per unit area and the average size per individual, occurs on the top of the Crab Hill rock. While small individuals occur all over, down to low water mark, the larger sizes and numbers are restricted to situations where there is a considerable amount of surf-effect without much mechanical force.

In vertical distribution, *Mytilus edulis* may be said to extend from M.H.W.S. to below M.L.W.S. At the higher levels it is found only in moist crevices. The optimum distribution is variable from L.H.W.N. downwards.

General Discussion and Conclusions

(a) *Vertical Zonation:* The division of the seashore into a number of vertically disposed biological zones has long been recognized by marine ecologists, the zonation being most marked in the case of plants and sessile or semi-sessile animals. There is, however, considerable variation in the number of zones recognized and in the pattern of their arrangement from region to region and author to author (see for example, King and Russell, 1909; Pearse, 1913; Johnson and York, 1915; Hewatt, 1937; Stephenson, 1939 and 1949; Doty, 1946; Evans, 1947a, 1947b and 1949; Womersley and Edmonds, 1952; Ricketts and Calvin, 1952; Chapman and Trevarthen, 1953; and Lewis, 1953 and 1955). An excellent historical summary of the work on zonation is given by Ricketts and Calvin (1952).

In 1939, Stephenson suggested a fundamental plan of zonation for the British coasts in general, consisting of the 'Littorina', 'Balanoid' and 'Laminarian' zones from above downwards. Evans (1947a and 1947b) found it easy to fit the observed distribution of the intertidal organisms in Cardigan Bay, and the Plymouth neighbourhood into this plan. On the Northumberland coast, there appear to be (on a first examination), four clear zones namely, *Littorina, Upper Algal, Barnacle*, and *Lower Algal*. The distribution of organisms in these four zones would be as follows :—

(1) *Littorina Zone :* This corresponds to the *Littorina* zone of Cardigan Bay and Plymouth neighbourhood (Evans). It occurs from about M.H.W.S. upward and is characterised by *Littorina neritoides* and *L. saxatilis* var. *rudissima*. *Ligia oceanica* occurs in crevices. Lichens may be also present.

(2) *Upper Algal Zone :* This occurs roughly between M.H.W.N. and slightly above M.H.W.S. The zone is characterised mainly by *Fucus spiralis* and *Porphyra umbilicalis* (H.W. variety). *Enteromorpha minima* is an invariable component of the zone though this species may occur higher up also. *L. saxatilis* var. *rudissima* is characteristic on bare vertical cliffs. *Mytilus edulis*, *L. saxatilis* var. *rudis*, *Patella vulgata*, and *Balanus balanoides* also occur in varying densities where the algae are sparse or absent. At the lower levels are *L. littoralis, L. littorea* and *Nucella lapillus* penetrating into this zone in certain situations.

(3) *Barnacle Zone :* This occurs typically between M.H.W.N. and M.L.W.N. but may extend upward or downward at both ends according to circumstances. When the upper algal zone is not well developed, the *barnacle* zone and the *Littorina* zone may become contiguous. In extreme shelter, even the *Littorina* zone may be less prominent than usual as it would then get mixed up with the upper algal zone.

Balanus balanoides is the only barnacle occurring in quantities at Cullercoats and this with *Patella vulgata* gives a characteristic appearance to the mid-shore. The other important animals occurring in this zone are *L. saxatilis, L. littorea, L. littoralis, N. lapillus, M. edulis* and *Actinia equina*.

(4) *The Lower Algal Zone :* This is the lowermost part of the shore and is characterised by an algal growth of variable extent (with upper limit at about M.L.W.N. or lower) consisting of *Laminaria, Rhodymenia Palmata, Gigartina stellata, Laurencia pinnatifida, Lomentaria articulata, Fucus serratus* and *Corallina*. Practically all the species of animals mentioned for the *Laminarian* zone of Cardigan Bay occur here. In addition may be mentioned the sponges, various species of gastropods, bivalves and several other encrusting or sedentary forms.

The author's main arguments in favour of the above plan of zonation in preference to the three-zone plan are as follows :—

(i) The name *Laminarian* zone implies a relationship with species of *Laminaria* but is used to include regions of the lower shore beyond the upper limit of *Laminaria* itself. Species such as *Fucus serratus, Gigartina stellata*, and *Corallina*, sp. often extend far beyond the upper limit of *Laminaria*, and they are not restricted to the absolute lower limit of the barnacles. The term *Lower Algal Zone* would be appropriate as it would allow the inclusion of all species of the lower shore and provide also for all possible variations in the upward extent of the zone.

(ii) The occurrence of a belt of algae between the *Littorina* and the barnacle zones is found to be more a rule than an exception on the Northumberland coast, though the extent and density of this belt may vary. The absence of weeds in the upper shore can in most cases be correlated with peculiarities of rock configuration. It is natural therefore, to consider the occurrence of the upper algal zone as a primary condition while Evans considered that as a secondary condition in Cardigan Bay ; but even his basic plan itself indicates the presence of patches of algae in the lower part of the *Littorina* zone and the upper part of the *Barnacle* zone. The frequent references to algae in the upper shore in the literature and also the frequency of algae noticed by the author during casual examination of the upper shore in some places on the British coasts lead him to the belief that the existence of an upper algal zone must be considered a primary condition for the British coasts.

(iii) The ' Balanoid ' zone would include part of the upper algal zone in most places and the name would therefore lose its significance if it did not strictly refer to the zone of abundance in quantity. In Cullercoats this zone of abundance is often limited by the limits and densities of the algal belts both in the upper and lower shore. In high exposure, the algal zones may be highly reduced and the barnacle zone may be very extensive ; in high shelter, the reverse may happen.

In 1949, Stephenson and Stephenson introduced a new scheme, the *universal scheme* of zonation. This scheme, in essence, designates the regions above and below the effective intertidal belt of the shore as the *Supralittoral* and *Infralittoral* zones (the latter being actually a submerged zone), the effective intertidal region itself being divided into three zones called *Supralittoral fringe*, *Midlittoral* zone, and *Infralittoral fringe*, corresponding roughly to the *Littorina*, *Balanoid* and *Laminarian* zones respectively of the earlier fundamental plan (Stephenson, 1939 and Evans, 1947a). The Supralittoral fringe would extend from the upper limit of the Littorinas to the upper limit of barnacles in quantity, the midlittoral zone being marked by the latter above and the upper limit of the Laminarian or lower algal belt below. Some workers, notably Womersley and Edmonds (1952) have not been able to accept this scheme in full but many others, have found it easy to apply it in their surveys in different parts of the world. Mention may be made in this connection, of the works of Chapman and Trevarthen (1953), Guiler (1953), Lewis (1953and 1955) and Purchon and Enoch (1954). Even in the case of Womersley and Edmonds (1952), the Stephensons (see Lewis, 1955, p. 287) are satisfied that the difference is rather one of interpretation than of fact. The extensive work of Lewis (1955) on the British coasts has however brought out a point of difficulty regarding the identity of the upper limit of the midlittoral zone on some of these coasts, which becomes obscured by the presence of an algal belt or a bare zone which may sometimes be interpreted as midlittoral and sometimes as supralittoral. This is the difficulty noticed by the present author also, although in most situations on the Northumberland coast the upper algal belt is clearly above the barnacle line. Otherwise the present author also finds no difficultyin fitting the distribution of organisms on the Northumberland coast into the universal scheme. This coast must belong to the *Balanus*—type of zonation described by Lewis (1955, p. 273) and the upper algal zone will have to be considered mostly as part of the supralittoral fringe. This may not be so elsewhere but then the Universal scheme is meant to be so flexible and convenient that all such variations can be easily superimposed on the scheme.

(b) *Critical levels :* Apart from the gross pattern of vertical zonation discussed in the previous section, there is the question of the intertidal levels at which there may be sudden changes in the composition of the organisms both qualitatively and quantitatively. Such critical levels have been looked for and recognized by various authors in different localities (Colman, 1933 ; David, 1941 ; Evans, 1947 a & b ; Hewatt, 1937 ; Doty, 1946 ; and Chapman, 1943). Colman (1933) found three such levels in Wembury Bay, viz. between M.L.W.S. and E.L.W.S., between M.L.W.S. and M.L.W.N. and at L.H.W.N. (allowing in each case 2 ft. for splash). Evans (1947a) found five important levels in Cardigan Bay, but after a study of six localities near Plymouth in comparison with this locality, he (1947b) concluded that the positions of critical levels change according to local variations in surf-action, rock-configuration, illumination etc. Nevertheless, he considered the existence of critical levels an actuality and that in general, the following three regions of the shore might be described as more critical than others for organisms : (i) from M.L.W.S. (or just below this) to M.L.W.N. ; (ii) just below M.L.W.N. ; and (iii) from E. (lowest) H.W.N. to M.H.W.S.

In the light of these findings, the results from Cullercoats were also examined for the detection of critical levels by the method used by Colman (1933). The species considered are the same as in Table IV. Considering the data in the same manner as Colman did, it is interesting to notice from Table III that while there are two maxima for the lower limits of species on the shore, namely between -1 ft. and 2 ft. above C.D. and between 7 ft. and 12 ft. above C.D., as many as six maxima are apparent for the upper limits of species. The latter are at the following mean heights above C.D. : (a) 3.5 ft. (0.5 ft. below M.L.W.N.) ; (b) 5.5 ft. (1.5 ft. above M.L.W.N. and 0.3 ft. below H.L.W.N.) ; (c) 7.5 ft. (slightly below M.T.L.) ; (d) 9.5 ft. (0.4 ft. below L.H.W.N.) ; (e) 13.5 ft. (1 ft. below M.H.W.S.) and (f) 15.5 ft. (1 ft. above M.H.W. S.)

TABLE III

Number of species and limits of species in relation to tide levels in Cullercoats Bay. (Total number of species 43.)

Height rel. to C.D. in ft.	Lower limits	Upper limits	Total limits	Total species	Difference between Total Species and total limits
17-20	0	0	0	3	3
16-19	0	3	3	6	3
15-18	0	3	3	6	3
14-17	0	8	8	11	3
13-16	0	6	6	12	6
12-15	0	8	8	14	6
11-14	0	6	6	16	10
10-13	0	5	5	17	12
9-12	3	4	7	19	12
8-11	3	10	13	26	13
7-10	3	9	12	26	14
6-9	0	12	12	29	17
5-8	2	5	7	30	23
4-7	3	9	12	34	22
3-6	3	5	8	35	27
2-5	4	12	16	39	23
1-4	5	8	13	38	25
0-3	11	8	19	39	20
—1 to 2	12	1	13	36	23
—2 to 1	11	1	12	34	22

While some of the above maxima may be compared to those in the data of Colman and Evans there are others which have to be interpreted either as offshoots from the main maxima or as entirely new ones. One is tempted to feel that such a confusion might only increase if the number of species considered is also further increased. It is still possible however, to distinguish among the above levels some which are more critical than the others by a reference to the totals of both the lower and upper limits of the species. From this it is seen that the most critical level on the shore is at a mean height of 0.9 ft. above M.L.W.S. This mainly affects the lower limits of intertidal animals and plants. The next critical level is at a mean height of 0.5 ft. below M.L.W.N. and marks mainly the upper limits of a large number of sublittoral organisms. A maximum noticed at a mean height of 5.5 ft. above C.D. must be considered an offshoot from the previous maximum. The most critical level on the upper shore lies at about a mean height of 0.4 ft. below L.H.W.N., corresponding to the similar level in the data of Colman and Evans. The total species figures also justify this view. The maxima beyond this level are of minor importance but the minor critical level in the upper shore may be said to lie round about M.H.W.S. The maxima (e) and (f) of the upper limits can however, be related to the non-tidal exposure factor mentioned on page 171.

The zone of maximum survival of species is indicated by the difference between the total species and total limits and lies at a mean height of 0.5 ft. above M.L.W.N. This is therefore the least critical level for intertidal species. This corresponds to the least critical level revealed in Colman's work also but after allowing 2 ft. for the splash zone. Evans found the least critical level to be 1.2 ft. above H.L.W.N. at Cardigan Bay and to lie between H.L.W.N. and L.H.W.N. in all localities near Plymouth.

(c) *Relation of species to percentage exposure to the air :—*

Table IV summarises the recorded ranges of intertidal species in terms of percentage exposure to the air from Cardigan Bay (Evans, 1947b) and the Plymouth neighbourhood (Evans, 1947b) in comparison with the observed ranges of 43 species of plants and animals at Cullercoats.

The following points may be specially noted from the Table :

(1) In general the zonation may be said to be of about the same kind in all the three localities ; forms like *Fucus serratus*, *F. spiralis*, *Littorina saxatilis* and *Patella vulgata* are remarkably similar both in the absolute range and in the position of the upper and lower limits in all the three localities.

(2) Nine out of the twenty comparable species have considerably higher upper limits at Cullercoats than at Cardigan Bay. These are *Fucus vesiculosus*, *Gigartina stellata*, *Laminaria digitata*, *L. saccharina*, *Balanus balanoides*, *Gibbula cineraria*, *Littorina littorea*, *Mytilus edulis*, and *Nucella lapillus*. Of these the upper limits of *L. littorea*, *B. balanoides*, and *F. vesiculosus* are nearly the same at Cullercoats as in the Plymouth neighbourhood. The upper limit of *L. digitata* also is nearer that at Plymouth than at Cardigan Bay. As these species include both surf-loving and shelter-loving forms it appears that in both the extent of surf action and the degree of local shelter available Cullercoats and the Plymouth locality exceed the Cardigan Bay region. It is known that the surf-loving forms such as *Balanus balanoides*, *Littorina neritoides* etc., have their upper limits raised and lower limits lowered with

TABLE IV

Percentage exposure to the air, of organisms in Cullercoats, Cardigan Bay and Plymouth area.

No.	Species	Cullercoats		Cardigan Bay (Evans 1947a)		Plymouth area (Evans 1947b)	
		U.L.	L.L.	U.L.	L.L.	U.L.	L.L.
	PLANTS						
1.	*Ascophyllum nodosum*	57	28	71	15	83	10
2.	*Callithamnion* sp.	70	7	—		—	
3.	*Chondrus crispus* ?	? H.W. 89)	58)	—		—	
		L.W. 29)	0)	—		—	
4.	*Enteromorpha compressa*	84	0	—		—	
5.	*Ent. minima*	100	37	—		—	
6.	*Fucus serratus*	57	0	56	0	58	0
7.	*F. spiralis*	98	57	96	55	94	56
8.	*F. vesiculosus*	82	37	63	8	83	5
9.	*Gigartina stellata*	50	0	26	0	39	0
10.	*Laminaria cloustoni*	3	0	4	0	—	
11.	*L. digitata*	23	0	20	0	25	0
12.	*L. saccharina*	12	0	4	0	—	
13.	*Laurencia pinnatifida*	50	0	60	0	56	0
14.	*Lomentaria articulata*	50	0	—		—	
15.	*Porphyra umbilicalis*	100	12	100	0	—	
16.	*Rhodymenia palmata*	32	0	35	0	47	0
	ANIMALS						
17.	*Actina equina*	70	0	—		—	
18.	*Anomia ephippium*	26	0	—		—	
19.	*Asterias rubens*	12	0	—		—	
20.	*Balanus balanoides*	98	0	83	0	96	0
21.	*Dynamena pumila*	29	0	—		—	
22.	*Fabricia sabella*	43	0	—		—	
23.	*Gibbula cineraria*	44	0	21	0	33	0
24.	*Grantia compressa*	17	0	—		—	
25.	*Lacuna vincta*	50	0	—		—	
26.	*L. pallidula*	50	0	—		—	
27.	*Leucosolenia botryoidlis*	15	0	—		—	
28.	*Littorina littoralis*	73	0	81	4	85	2
29.	*L. littorea*	95	0	71	7	93	1
30.	*L. neritoides*	100	9	100	20	100	13
31.	*L. saxatilis rudis*	100	11)	100	8	100	7
32.	*L. sax. rudissima*	100	56)				
33.	*L. sax. saxatilis*	95	4)				
34.	*Margarites helicinus*	40	0	—		—	
35.	*Mytilus edulis*	99	0	61	0	—	
36.	*Nucella lapillus*	78	0	62	0	93	0
37.	*Patella vulgata*	100	0	100	0	100	0
38.	*Patelloida virginea*	12	0	—		—	
39.	*Pomatoceros triqueter*	44	0	—		—	
40.	*Rissoa parva*	50	0	—		—	
41.	*Turtonia minuta*	42	0	—		—	
42.	*Hiatella gallicana*	15	0	—		—	
43.	*Zirfaea crispata*	12	0	—		—	

increasing surf action. The more extended lower ranges of *L. neritoides* at Cullercoats would then suggest that this locality is even more exposed than Plymouth. Yet the elevation of the upper limit of *Gibbula cineraria* suggests a higher degree of local shelter also. Evans (1947a) suggests that the lower limit of *G. cineraria* at Cardigan Bay, when compared to Plymouth, may be due to the fact that the species is nearing the northern limit of its distribution. This obviously does not hold good as its upper limit at Cullercoats goes still higher in spite of the higher altitude. The sparseness of that species at Cardigan Bay may, on the other hand, be a more likely explanation.

(3) The ranges of *Ascophyllum nodosum* and *Fucus Vesiculosus* are much reduced at Cullercoats compared with the other two localities. This discrepancy must almost definitely be due to the scarcity of both these species at Cullercoats. It should be noted, however, that the distribution of these two species also differs to some extent between Cardigan Bay and the Plymouth neighbourhood. But the coincidence of the upper limits of *F. vesiculosus* between Cullercoats and the Plymouth neighbourhood is remarkable.

Summary

(1) A detailed study was made, using a modification of Colman's traverse method, of the vertical and horizontal distribution of the common intertidal organisms in selected areas of the rocky and boulder beaches near Cullercoats.

(2) The general environmental conditions are described and the tidal data are analysed. A method is suggested for the calculation of the continued submergence and emergence factors.

(3) No appreciable seasonal changes were noticed in the limits of vertical distribution of most of the organisms studied.

(4) Some aspects of the general ecology and distribution of some of the common species of plants and animals are discussed.

(5) Four zones can be recognized in the intertidal regions of the Northumberland coast with reference to distribution of organisms, viz: *Littorina, Upper Algal, Barnacle* and *Lower Algal*. But these can be easily fitted into the Universal scheme of zonation (T.A. and Anne Stephenson, 1949), the *Upper Algal* zone being mostly part of the supralittoral fringe.

(6) The results of the study of the vertical ranges of 43 species of plants and animals are examined for critical levels on the shore and are compared with similar data available for Cardigan Bay and Plymouth neighbourhood. In general, the vertical distribution of organisms seems to be somewhat similar in all the three localities. There are three chief critical levels for the intertidal organisms at Cullercoats, viz. just above M.L.W.S., just below M.L.W.N., and just below L.H.W.N. The least critical level is between M.L.W.N. and H.L.W.N.

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Systematic List of the Species Mentioned

(A) Plants

1. *Chlorophyceae.*
   - *Cladophora rupestris* KUTZ.
   - *Enteromorpha compressa* GREV.
   - *E. minima* NAEG.
   - *Ulva linza* AGARDH.

2. *Rhodophyceae.*
   - *Callithamnion* LYNGB. spp. (*C. turneri*? AGARDH and *C. arbuscula*? LYNGB)
   - *Chondrus crispus* LYNGB.
   - *Corallina officinalis* LINN.
   - *Corallina squamata* ELLIS.
   - *Gigartina stellata* BATT.
   - *Laurencia pinnatifida* LAMOUR.
   - *Plumaria elegans* SCHMITZ.
   - *Polysiphonia fastigiata* GREV.
   - *Porphyra umbilicalis* AGARDH.
   - *Rhodochorton Rothii* NAEG.
   - *Rhodymenia palmata* GREV.

3. *Phaeophyceae.*
   - *Ascophyllum nodosum* LE JOL.
   - *F. serratus* LINN.
   - *F. spiralis* LINN.
   - *F. vesiculosus* LINN.
   - *Laminaria cloustoni* EDMONDS.
   - *L. digitata* LAMOUR.
   - *L. saccharina* LAMOUR.
   - *Pelvetia canaliculata* DENE and THUR.
   - *Pilayella littoralis* KJELLM.

(B) Animals

1. *Porifera.*
   - *Grantia compressa* (FABR.).
   - *Leucosolenia botryoides* (ELLIS and SOLANDER).

2. *Coelenterata.*
   - *Actinia equina* LINN.
   - *Dynamena pumila* (L.).

3. *Annelida.*
   Fabricia sabella EHRENBERG.
   Pomatoceros triqueter (LINN.).

4. *Echinodermata.*
   Asterias rubens LINN.

5. *Mollusca.*
   Anomia ephippium LINN.
   Gibbula cineraria (LINN.).
   Hiatella gallicana (LAMARCK).
   Lacuna pallidula (da COSTA).
   L. vincta (MONTAGU).
   Littorina littoralis (L.).
   L. littorea (L).
   L. neritoides (L).
   L. saxatilis (OLIVI).
   L. saxatilis var. *rudis* (MATON).
   L. saxatilis var. *rudissima* BEAN.
   L. saxatilis var. *saxatilis* JOHNSTON.
   Margarites helicinus (FABRICIUS).
   Mytilus edulis LINN.
   Nucella lapillus (LINN.).
   Patella vulgata LINN.
   Patelloida virginea (MULLER).
   Patina pellucida (LINN.).
   Rissoa parva (da COSTA).
   Skeneopsis planorbis (FABRICIUS).
   Turtonia minuta (FABRICIUS).
   Zirfaea crispata (LINN.).

6. *Crustacea.*
   Balanus balanoides (LINN.).
   Chthamalus stellatus (POLI.).
   Hyale nilssoni (RATHKE).
   Idotea granulosa RATHKE.
   Ligia oceanica (LINN.)
   Tigriopus fulvus (FISCHER).

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