INVESTIGATIONS ON THE MICROFAUNA INHABITING SEAWEEDS ON ROCKY COASTS

(UNTERSUCHUNGEN ÜBER DIE ALGEN-BEWOHNENDE MIKROFAUNA MARINER HARTBÖDEN)

IV. STUDIES ON THE VERTICAL DISTRIBUTION OF THE FAUNA INHABITING SEAWEEDS BELOW THE PLYMOUTH LABORATORY

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(Text-figs. 1–4)

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Introduction, Material and Methods

The present study forms part of a more extensive one on the ecological factors which govern the distribution of the microfauna inhabiting seaweeds on rocky sea-coasts. This part of marine ecology is lagging far behind other branches. I wish to stress two points in particular: first, that our understanding of the composition of the littoral (intertidal) fauna would increase very much if this fauna can be linked with the true infralittoral fauna, and, secondly, problems involving the synecological aspects of marine biology cannot be approached before more is known about the autecology of the animals composing the cryptofauna (i.e. those living in the shelter of algae) and the causal factors determining their occurrence and distribution within a given area under stated conditions. On this point the work of T. A. Stephenson is especially relevant: as a result of his extensive investigations on the composition of the intertidal flora and macrofauna he has come to stress the importance of autecological rather than of biocenological work on the shore (Stephenson *et al.* 1942; Stephenson, T. A. & A., 1949). Moreover, he has clarified the intertidal terminology and introduced the most useful terms 'supra-' and 'infralittoral fringe'. Since his terminology appears to be the best suited to meet the needs of ecologists, I hope it will be generally applied in future. Most work on littoral ecology has been limited to macro-organisms, but valuable data on the ecology of microfaunas of seaweeds have been supplied by Colman (1940), Kitching, Macan & Gilson (1934), and Dahl (1948). Some ideas on the causes affecting the composition of faunas have been brought forward by Remane (1933, 1940), but with main reference to the bottom fauna. Such 'causal analysis', applied to the microfauna of algae attached to the bottom, is a primary aim of the present study. Dahl (1948) has called attention to the importance of the quantity of detritus, but otherwise almost nothing has previously been attempted in this line.

To establish a numerical basis for comparisons between intertidal and infralittoral samples, a uniform collecting technique is essential. On a rocky substratum the only useful method seems to be that of diving. The same conclusion was reached by Kitching *et al.* (1934), who used a diving-helmet to examine a sublittoral gully in Wembury Bay. Since it was my intention simply to study the population of single tufts of weed, it was possible to carry out the sampling under water (infralittoral and littoral during high water) using nothing but glasses (made by Draeger, Lübeck), flippers (made by Pirelli, Milano), and a belt with pieces of lead fixed to it. The sampling could be carried out only when the sea was fairly calm. A one-litre jar was carried and placed carefully over the clump of weed to be examined, which, when the whole was inside the jar, was torn off at the base as quickly as possible, the hand following and closing the opening of the jar immediately. Since all animals living in seaweeds have a tendency to fasten rather than to loosen their hold if their habitat is disturbed (reaction to wave-shock?), it is likely that my samples contained almost the whole population of the clump. The alga was carefully shaken in formalin, branch by branch, and the derived material examined under a dissecting microscope. All animals were picked out and counted. The nematodes, which were collected for special study, were transferred to glycerin-jelly and mounted on slides for examination.

The whole material was collected just below the Plymouth Marine Biological Laboratory, on the rocks adjoining the men's bathing place (Tinside). The limestone rocks here are broken and fissured, and supply habitats of varying degrees of shelter. For a description of the area see Evans (1947*b*, p. 176:

Tinside to West Hoe). It is only necessary to add that the deposition of sediment is rather heavy along this piece of shore, with important effects. Wave-action being fairly strong the sediment is distributed unevenly, being accumulated in dense tufts of weeds like *Gelidium corneum*, while tall and shrub-like weeds as *Fucus serratus* may be almost free of silt.

The Rivers Tamar and Plym discharge into Plymouth Sound and cause a variable reduction in the surface salinity of the sea water. This effect, however, is large only in winter. Fluctuations in the volume of the more erratic Plym particularly affect Tinside. The silt-laden surface skin of fresh water penetrating far into the Sound, after spells of heavy rain, is a familiar sight from the Laboratory.

No continuous measurements of salinity have been made at Tinside itself, but a fairly accurate picture can be obtained by extrapolating from Milne's data (1938). The salinity values for Tinside can be taken as identical with those for Drake's Island, or somewhat less during wet periods. It is evident that in winter quite large falls in salinity may occur, and appreciable differences daily between high and low water. However, the present work did not start until after 2 or 3 months of settled summer conditions and the winter can be ignored.

From April onwards it can be said that high-water salinities are normally between 32 and 34 ‰ (Typically 33 ‰), and low-water salinities between 31 and 32·5 ‰. The daily (or rather 12 hr.) fluctuation is normally less than 2 ‰. After 2 or 3 days of heavy rainfall inland a temporary fall below 30 ‰ may occur at low tide, but is not likely to have occurred in the summer of 1950 up to the time the work had been completed.

The conditions at Tinside, therefore, as applied to this study, can be regarded as truly marine with some polyhaline influences (see Dahl, 1948). This view is, moreover, supported by the character of the fauna, which is purely marine without any brackish component.

As regards the relation of shore organisms to tidal levels in the Plymouth area, reference is made to Colman (1933), Moore (1935), Evans (1947*b*), etc., who were dealing primarily with the macrofauna and flora. Certain heights and ranges are taken from these authors.

All tidal levels here are given in metres and are referred to *Chart Datum* for the Plymouth area (see The Admiralty Tide Tables). The position of some of the standard levels (see Hartley & Spooner, 1938) is as follows:

E.H.W.S.T.	+5·10	E.L.W.N.T.	+1·78
M.H.W.S.T.	4·78	M.L.W.N.T.	1·40
M.H.W.	4·26	M.L.W.	0·75
M.H.W.N.T.	3·73	M.L.W.S.T.	+0·06
E.H.W.N.T.	3·24	E.L.W.S.T.	−0·47
M.T.L.	2·49		

The seaweeds investigated in this work were collected in the following ranges (which should not be taken as the actual distribution limits):

Ceramium sp.	+2·75 to +0·80
Lomentaria articulata	+1·90 to +1·75
Fucus serratus	+2·00 to +0·20
Porphyra laciniata	+1·95 to +1·50
Gigartina stellata	+2·00 to +1·00
Cladophora rupestris	+3·25 to +2·50
Gelidium corneum	+2·75 to +1·10
Nitophyllum punctatum	−0·70 to −3·00

The material was obtained during a stay at the Plymouth Laboratory between 14 July and 17 August 1950. I wish to thank all members of the Laboratory's staff, above all Mr F. S. Russell, F.R.S., not only for their readiness to help and for all sorts of advice, but also for the spirit prevailing at Plymouth which makes work so easy and the Laboratory itself the most excellent of its kind in Europe. My visit was made possible by financial support from several private institutions and the 'Bundesministerium für Unterricht', at Vienna.

My special thanks are due to Dr A. G. Lowndes, Plymouth, and Prof. L. Pesta, Vienna, who determined the copepods dealt with here. I am also grateful to Dr H. Caspers, Hamburg, for the identification of the chironomid larvae, and, for taxonomic help, to Dr Mary Parke (algae), Dr Vera Fretter (gastropods), Mr G. M. Spooner (amphipods), all of Plymouth, and Prof. A. La Greca (polychaetes), Naples. My thanks are also due to Mrs A. Volsøe for her assistance in writing the paper in English, and to Mr G. M. Spooner for his critical rearrangement and correction of the manuscript.

General Remarks on the Vertical Distribution of the Fauna of Intertidal Seaweeds

The vertical distribution of littoral animals and plants has been studied best in macro-organisms. The zonation of seaweeds, barnacles, limpets, periwinkles, etc., and thus the degree of exposure to air and wave-action which they can endure, is more or less directly observable on the shore. This is due not only to the size of the organisms, but also to the fact that the rocks which serve as a substratum for them may not change appreciably in composition and texture down the length of the shore. The influence of the substratum on the distribution of these organisms may be almost negligible, and the vertical gradients of air-exposure and surf-action reveal themselves clearly in the well-defined zoning (or distribution limits) of the animals and plants in question.

The situation is quite different for micro-organisms inhabiting seaweeds.

The different species of algae serving as substratum for the microfauna show such different features in height, shape and consistency that exposure and wave-action, even within a very restricted area, by no means act uniformly on their inhabitants. It is obvious that the animals inhabiting a dense tuft of *Gelidium corneum* or *Lichina pygmaea* are much more sheltered against desiccation or wave-shock than those living on *Fucus serratus* or *Ascophyllum nodosum*. Therefore, if we suppose that both types of plants might extend over the same vertical range on a rocky coast, the upper level of some littoral animals might well be much higher in *Gelidium* and *Lichina* than in *Fucus* and *Ascophyllum*. Hence it follows that the vertical distribution of the microfauna could be studied best within one single kind of seaweed extending over a sufficiently large vertical range. Numbers of animals per weight or area-unit of the plant from different levels would then be directly comparable.

It is, however, not very often that the conditions are suitable for this kind of investigation in the littoral and upper infralittoral: even within a very limited area of the seashore there is normally a variety of algae some of them forming very narrow belts. To get a fairly true and complete picture of the vertical distribution of the microfauna in the whole area under consideration, the populations of different seaweeds must be studied together. A direct numerical comparison between samples from different weeds is hardly possible owing to their great differences in structure. The best that can be done is to express the vertical distribution of the microfauna in terms of *average 'dominance-values'* (see p. 158) from as many and as different samples as possible. This procedure, it should be remembered, cuts down the differences between single populations and gives an average picture only of the vertical distribution, the reliability of which can be improved by increasing the number of samples.

Different organisms are subjected in a different way to the factors of tidal exposure. The prototypes of littoral zonation: seaweeds, barnacles, periwinkles, etc., are either sessile, hemi-sessile or very slowly moving organisms. They cannot counteract rapid changes of environmental conditions by moving about. We have to presume, therefore, that the animals must be able to endure any condition to be expected in the inhabited area (as proved, for example, by Jacubowa & Malm, 1931, for several bottom-animals, in their ability to withstand anaerobic conditions). In the littoral area the habitat of these animals is either a well-defined 'zone' or has at least one well-defined upper or lower limit. The same conditions should apply to members of the microfauna which are truly sessile, e.g. Bryozoa and Hydrozoa, or hemi-sessile like the tubicolous polychaetes, amphipods (*Corophium*) and isopods (*Tanais cavolinii*); or, indeed, to all animals with slow powers of movement. The latter, it is true, might find shelter in the denser parts of the algae they inhabit, or in minute crevices of the substratum filled with sediments inaccessible to bigger animals, and so possess the ability of counterbalancing the challenge of the environment if this becomes too unfavourable, but the movements are too small to effect the average vertical distribution on the shore. A great deal of the microfauna belongs to this class, e.g. nematodes, ostracods, small molluscs like *Rissoa* and *Lasaea*, halacarids, etc. There are other animals which would be able to swim or to crawl quickly and to change place during, say, the rise and fall of the tide, but which do not in fact do so, since they are hardy enough to stand any change in the environmental conditions. In this respect they behave like hemi-sessiles. Among them may be included several amphipods, especially *Hyale* spp., which are well-adapted inhabitants of the littoral seaweeds on all rocky coasts.

Finally, there is a group of animals not only able to move relatively far and fast, but also using this ability, i.e. compensating for changes in the environmental conditions by active motion over comparatively great distances. Many of the harpacticids and some amphipods like *Stenothoë monoculoides* seem to belong to this group. The study of their average vertical distribution does not give a true picture of their actual distributions, which might be quite different under different conditions, for example during high and low tide.

Results of the Survey at Tinside

The Population Counts from Different Algae

Gelidium corneum

For investigating the vertical distribution of the microfauna inhabiting a single species of alga in the Tinside area no better prototype could be chosen than *G. corneum*. Not only does it extend over a sufficiently large vertical range of about 1·65 m., but also, due to its dense, tuft-like shape, it contains an almost incredibly large fauna, whereby the numerical comparison of different samples is facilitated.

The results are given in Table I. The numbers of specimens are referred to 1 g. of living alga weighed in dry condition after pressing between pieces of cloth. The samples are arranged from left to right in descending sequence of tidal level. As was to be expected, the number of specimens in the different samples varies very much, from 343 in G-14 to 2818 in G-4. This variation is due in a very slight degree only to differences in the vertical position of the sample. In my opinion the most important factor is the silt content. An attempt was made to estimate the amount of silt by recognizing five arbitrary classes, ranging from 0 to 4. Plotting number of specimens against these classes brought out an evident correlation, at least for nematodes, sabellids and oligochaetes. This agrees with Dahl (1948). This interesting subject is, however, beyond the scope of the present paper. It is treated, at least as far as the nematodes are concerned, in my previous papers (Wieser, 1951, 1952).

In spite of fluctuating values, the distribution of several species throughout the range of the zone shows an obvious vertical gradient. For that purpose it

TABLE I. ANIMALS INHABITING SEVENTEEN SAMPLES OF *GELIDIUM CORNEUM* PER G. DRY WEED

(Note. It has not been possible to determine the oligochaetes. Possibly more than one related species is involved.)

No. of sample ...	G-1	G-2	G-3	G-4	G-5	G-6	G-7	G-8	G-9	G-10	G-11	G-12	G-13	G-14	G-15	G-16	G-17
Height (m.) ...	+2·75	2·75	2·50	2·50	2·00	2·00	2·00	1·90	1·80	1·75	1·60	1·55	1·50	1·50	1·50	1·40	1·10
Sediment-classes ...	3	0	2	2	3	3	1	3	1	3	3	1	1	1	3	2	4
Weight (g.) ...	1·3	2·2	1·2	1·0	0·8	1·4	1·3	1·2	1·4	1·3	1·6	2·0	0·6	0·6	1·6	1·2	0·8
Nematoda	1270	215	665	600	964	657	470	638	286	658	700	172	373	103	487	370	835
Copepoda	140	48	23	26	180	19	55	65	30	140	113	72	171	51	185	12	14
Ostracoda	130	25	17	32	280	21	41	30	88	119	87	23	40	45	103	7	19
Amphipoda:																	
Hyale nilssoni	5	25	6	18	10	2	10	.	1	.	1	1	.	.	.	2	26
Corophium spp.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	12	9
Stenothoë monoculoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	35	18
Polychaeta:																	
Fabricia sabella	38	.	29	26	614	311	217	483	4	548	420	142	375	40	270	150	44
Amphiglena mediterranea	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	5	.
Oridia armandi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Grubea pusilla	.	.	.	.	125	8	2	3	.	4	3	1	.	.	3	6	.
Syllis armillaris	.	.	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.
Polydora hoplura	.	.	.	.	.	.	.	2	.	.	.	.	.	.	3	3	.
Exogone gemmifera	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	.	.
Cirratulus cirratus	.	.	.	.	.	.	.	1	.	.	.	.	.	.	6	.	.
Aonides oxycephala	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.
Odontosyllis ctenosoma	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
Capitellides giardi	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Oligochaeta	225	130	.	12	230	258	77	64	70	292	172	32	139	2	50	89	90
Halacarida	14	7	13	28	14	6	5	20	6	21	43	4	21	12	3	62	227
Hyadesia sp.	.	1	.	3	3	.	10	2	.	.	1	.	.	.	.	.	.
Chironomidae (larvae)	58	51	70	114	129	24	48	60	23	100	54	40	75	50	45	10	9
Gastropoda:																	
Littorina obtusata	.	.	2	1	.	.	4	.	4	.	.	.	.	.	.	1	3
Skeneopsis planorbis	3	.	14	83	14	5	7	10	3	.	30	5	21	.	1	50	83
Cingulus cingillus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Rissoa parva	.	.	.	4	.	.	2	.	.	.	.	.	.	.	.	.	.
Indet.	2	.	1	3	.	.	.	.	.	36	.	.	6	25	.	.	.
Pelecypoda:																	
Lasaea rubra	685	265	348	1864	164	371	120	20	78	3	2	.	5	9	6	50	431
Mytilus edulis	16	3	10	4	5	10	2	5	3	1	2	3	5	2	3	8	12
Isopoda + Anisopoda:																	
Idothea neglecta ? + granulosa	.	.	.	.	.	.	.	.	.	.	.	.	11	.	.	5	10
Jaera marina	.	3	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.
Naesa bidentata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Munna sp.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Tanais cavolinii	32	2	.	.	4	3	1	.	.	.	23	.	.	3	.	7	23
Pantopoda:																	
Phoxichilidium femoratum	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.
Total	2618	775	1208	2818	2737	1697	1079	1409	597	1925	1651	497	1243	343	1173	885	1853

is convenient to combine several samples and to consider their average number of specimens.

The most interesting change is the decline in number of *Fabricia sabella* between +2·0 and +2·5 m. Up to +2·0 m. the average number of specimens is 263 per g. dried weed, while it drops to 25 in the four uppermost samples at +2·50 and +2·75 m. It appears, therefore, that a 'critical level' for the species may exist between +2·00 and +2·50 m. This level may be taken and tested with respect to other species or groups. In Table II are given the average values for stations G-1 to G-4 compared with those for G-5 to G-17. Three of the more numerous types are selected—*F. sabella*, Oligochaeta and *Lasaea rubra*. Each deserves comment.

(i) *Fabricia sabella*. I do not hesitate to call the level between +2·0 and +2·5 m. a true 'critical level' (in the sense of Colman and Evans) in the Tinside area for this species. The bulk of the population does not extend beyond this level (which does not preclude the penetration of some specimens into higher zones). It is difficult to compare my figures with those of Colman (1940) from Wembury Bay, since that area shows some important ecological

TABLE II. AVERAGE POPULATION DENSITY PER G. OF DRIED WEED

Height (m.)	... +2·75 to +2·50 m.	+2·00 to +1·10
Fabricia sabella	25	263
Oligochaeta	94	117
Lasaea rubra	790	97

differences from Tinside. Colman reports a few *F. sabella* (which also at Wembury penetrates farther upshore than any other polychaete) from *Fucus spiralis* about 1 m. higher up than the upper level of my *Gelidium corneum*, and a great number of specimens from a single sample of *Ascophyllum nodosum*+*Polysiphonia lanosa*, about +3·30 m. Then it is not until the *Laminaria* holdfasts that *Fabricia sabella* makes its appearance again in great numbers (this habitat being the lowest and most sheltered in Colman's samples).

(ii) *Oligochaeta*. The vertical gradient has apparently no significant influence on the distribution of this (or possibly two) species. These animals show a strong affinity to rich silt-content, and vertical differences could not be detected with certainty in the seventeen *Gelidium* samples. In Colman's tables, also, the oligochaetes (*Lumbricillus pumilus* and *L. scoticus*) show a somewhat irregular distribution with no apparent correlation with tidal exposure.

(iii) *Lasaea rubra*. The difference in numbers between the four higher and the thirteen lower samples is more striking than in any of the species investigated. It should, however, be noted that the lowest samples (G-17), whose content of sediments was extremely high, also contained an unexpectedly high number of *Lasaea*. My figures agree fairly well with Colman's statement to the effect that his four samples of the lichen *Lichina pygmaea* (between +2·68 and +4·13 m.) contained almost incredible numbers of *Lasaea rubra*, while the species did not occur farther down. The relation between the shape of the weeds and their populations (Wieser, 1951) should also be kept in mind: *Gelidium corneum* and *Lichina pygmaea* are very alike in shape and structure, and both may harbour large populations of this lamellibranch for the same reason. (Colman has found an average of about 945 specimens per 1 g. damp *Lichina*, while I got about the same number in my four highest *Gelidium* samples but per 1 g. of dried weed: thus, Colman's figures are still higher; although, if we remember that in my *Gelidium* samples the numbers of nematodes, polychaetes, oligochaetes, copepods and ostracods were often higher and sometimes not very much lower than those of *Lasaea rubra*, while in Colman's samples *Lasaea* is absolutely dominant, the *Gelidium* of Tinside proves to be still richer in living organisms than the *Lichina* of Wembury Bay. As a matter of fact, the number of organisms in *Gelidium corneum* is comparable with those of rich soils which—according to Franz (1950) and not to the authors mentioned by Colman—often reach several million specimens per $m.^2$).

There are several other types which might illustrate the three possible relations to the factor of tidal exposure, viz. (i) the decline in number down-shore, (ii) the decline in number upshore, and (iii) the more or less even distribution. Thus to the first belong *Hyale nilssoni* (although low down at G-17 a fairly large number was found), *Hyadesia* sp., probably *Jaera marina* and the chironomid larvae (*Clunio marinus* + *Trichocladius* cfr. *vitripennis*, not separated). For the latter (average of seventy-eight specimens above, fifty-one below +2·0 m.) there may be a critical level at about the lower limit of *Gelidium corneum*, which also accords with Colman, who did not find any insect larvae below +1·20 m. It should be mentioned that on all seashores which I have had the opportunity to investigate I have always found chironomid larvae among those animals which could be regarded as typical inhabitants of the higher intertidal zones.

To the second group belong *Corophium* spp., *Stenothoë monoculoides*, and all Polychaeta errantia (none of which passes above the +2 m. level). To the third group belong *Mytilus edulis*, most of the common nematodes like *Anticoma limalis*, *Thoracostoma figuratum*, *Enoplus communis* (the dominant species in nearly all samples), *Dolicholaimus marioni*, *Halichoanolaimus robustus*, *Monoposthia costata*, *Chromadora nudicapitata*, etc. (see Wieser, 1951); and probably *Tanais cavolinii* and the two Halacarida (most probably *Rhombognathus pascens* and *R. seahami*).

The Leaf-Like Algae Porphyra laciniata *and* Nitophyllum punctatum

It might be permissible to study numerically the microfauna not only within one species of seaweed but also within a single morphological type.

If it is agreed that it is the shape and consistency of the weed that is of prime importance to the composition of its fauna, two different species of algae of similar shape can be treated as a single species. At any rate in the very simple case of two seaweeds with flattened, uniform thalli like *Porphyra laciniata* and *Nitophyllum punctatum* there can hardly be any objection to this method. In the Tinside area *Porphyra* extends to about +2·0 m., while *Nitophyllum* is a typical infralittoral species which I have collected down to −3·0 m. The vertical distribution of the microfauna can thus be examined over a range of about 5 m. on a more or less comparable substratum. What is

TABLE III. DOMINANCE-VALUES OF NEMATODES IN THREE SAMPLES OF *PORPHYRA LACINIATA* AND FOUR SAMPLES OF *NITOPHYLLUM PUNCTATUM*

(*P.* = *Porphyra*; *N.* = *Nitophyllum*.)

No. of sample ...	L-1 to 3	L-4	L-5	L-6	L-7
Height (m.) ...	+1·50–1·95	−0·70	−1·20	−1·20	−3·00
Alga ...	*P.*	*N.*	*N.*	*N.*	*N.*
Anticoma limalis	.	.	.	.	5
Enoplus communis	16	9	4	18	15
Dolicholaimus marioni	5	.	.	.	.
Oncholaimellus diodon	.	.	.	.	8
Oncholaimus dujardini	5	.	.	.	.
Total Enoplidae	26	9	4	18	28
Cyatholaimus demani	5	5·5	6	4	4
Desmodora serpentulus	.	.	.	4	.
Monoposthia costata	5	.	2	.	.
Parasabatiera similis	.	.	2	.	.
Total Cyatholaimidae + Desmodoridae	10	5·5	10	8	4
Spilophorella paradoxa	.	2	.	.	.
Euchromadora tridentata	5	3·5	2	4	4
Hypodontolaimus inaequalis	.	.	2	.	.
Prochromadorella paramucrodonta	.	7	2	22	.
P. neapolitana	.	2	4	.	.
Neochromadora poecilosomoides	.	16	26	22	33
Chromadora nudicapitata	32	18	2	7	8
C. brevipapillata	.	29	47	15	19
C. macrolaima	10	.	.	.	.
Heterochromadora germanica	16	.	.	.	.
Prochromadora longitubus	.	2	.	.	.
Total Chromadoridae	63	79·5	84	70	64
Theristus setosus	.	5·5	.	4	4
Total Monhysteridae	.	5·5	.	4	4
No. of specimens examined	19	55	47	27	27

still more important to this study is that the change in the fauna which takes place between the intertidal and infralittoral zones can now be investigated. Altogether, I obtained three samples of *Porphyra laciniata* between +1·50 and +1·95 m. and four samples of *Nitophyllum punctatum* between −0·70 and −3·00 m. The results are given in Tables III and IV. For the nematodes in Table III, I have to confine myself to dominance-values, since I was unable to study the whole collection. Therefore only a rough picture of the composition of the fauna is given. The three samples of *Porphyra* are pooled.

TABLE IV. NUMBER OF SPECIMENS PER 50 G. OF DRIED WEED IN THREE SAMPLES OF *PORPHYRA LACINIATA* AND FOUR SAMPLES OF *NITOPHYLLUM PUNCTATUM*

(+ = common; + + = very common. *P.* = *Porphyra*; *N.* = *Nitophyllum*.)

	Littoral			Infralittoral			
No. of sample ...	L-1	L-2	L-3	L-4	L-5	L-6	L-7
Height (m.) ...	+1·95	1·50	1·50	−0·70	−1·20	−1·20	−3·00
Alga ...	*P.*	*P.*	*P.*	*N.*	*N.*	*N.*	*N.*
Weight (g.)	35	22	16	3·4	9	5	2·9
Nematoda (see Table III)	23	22	10	2130	462	380	544
Copepoda	4	90	95	1605	885	490	1071
Ostracoda	.	.	.	60	38	50	34
Amphipoda:							
Hyale nilssoni	2	2	.	.	.		.
Jassa falcata	.	2	6	15	15		136
Stenothoë monoculoides	.	.	3	.	.		.
Aora typica	.	.	.	60	112		.
Nannonyx goesi	.	.	.	30	.		.
Leucothoë spinicarpa	.	.	.	15	.		.
Corophium spp.	.	.	.	1020	455		102
Apherusa bispinosa	.	.	.	.	28		.
Polychaeta:							
Amphiglena mediterranea	.	4	.	.	.		.
Oridia armandi	.	.	.	45	.		17
Platynereis dumerilii	.	4	3	840	70		34
Lagisca extenuata	.	.	.	75	.		17
Odontosyllis ctenosoma	.	.	.	330	21		.
Exogone gemmifera	.	.	.	60	7		34
Grubea clavata	.	.	.	75	7		.
Autolytus aurantiacus	.	.	.	.	21		.
Pterosyllis formosa	.	.	.	.	7		.
Sphaerosyllis hystrix	.	.	.	.	7		.
Halacarida	.	2	3	.	126	30	34
Chironomida (larvae)	7	2	3	.	.	.	.
Gastropoda:							
Littorina obtusata	.	4	3	.	5	.	.
Rissoa parva	.	2	6	180	38	80	51
Tricolia pullus	.	.	.	.	11	30	.
Pelecypoda:							
Lasaea rubra	2	.	.	.	.	.	.
Mytilus edulis	.	.	.	60	5	.	.
Isopoda:							
Idothea neglecta ? + *granulosa*	18	12	.	15	.	.	.
Munna sp.	.	.	.	15	.	.	.
Bryozoa:							
Membranipora membranata	.	.	.	++	.	.	.
Tunicata:							
Botryllus schlosseri	.	.	.	++	+	+	+
Total no. of specimens	56	146	132	6630	3400		2074

In Table IV the number of specimens is given per 50 g. *of dried weed.* Sample L-4 was completely overgrown with *Membranipora membranata* and *Botryllus schlosseri*, and was extremely rich in specimens. The amphipods and polychaetes in samples L-5 and L-6 had to be treated together.

These two tables seem to show some significant contrasts between the littoral (intertidal) and infralittoral zones. Foremost, the increase in total population, in the descent across the low-water level, is most striking. The average number of specimens in the three *Porphyra* samples is 111 per 50 g. as against 3026 in the four *Nitophyllum* samples. Likewise I found twenty species above as against forty species below C.D. (excluding copepods, ostracods and halacarids). Some of the species found in the *Nitophyllum* samples do not reach a maximum until the infralittoral zone is reached (although some of them might well extend farther upshore in denser weeds where they are better sheltered from desiccation—see p. 149 above). Amongst the nematodes are *Neochromadora poecilosomoides*, *Prochromadorella paramucrodonta* and *Chromadora brevipapillata*. Most of the polychaetes, as for example *Lagisca extenuata*, *Exogone gemmifera* and *Grubea clavata*, as well as the tunicate *Botryllus schlosseri*, and the snail *Tricolia pullus* appear to belong to this group. Colman's data agree with respect to polychaetes and tunicates, since it is only in his lowest and most sheltered samples of the *Laminaria* holdfasts that the Polychaeta errantia suddenly occur, being exceedingly rich here both in specimens and species (amongst them *Lagisca extenuata* and *Exogone gemmifera*). The tunicates similarly are strictly confined to the *Laminaria* holdfasts. Comparably, with regard to the true littoral species, viz. *Hyale nilssoni*, the chironomid larvae, and *Lasaea rubra*, the conclusions drawn from the *Gelidium corneum* samples find further support from those of the leaf-like algae (or, if the data seem too scanty to be confirmative, at least they do not contradict them). *Hyale nilssoni*, as well as *Lasaea rubra* and the insect larvae in Colman's samples, are confined to the upper part of the littoral region.

It is no doubt primarily due to the shape of the leaf-like weeds that the difference in the littoral and infralittoral populations, and analogously the difference in the littoral and infralittoral ecological conditions, can be so clearly demonstrated. The flattened thalli of these weeds offer almost no protection to their inhabitants. It is thus natural that they are deprived of animals in zones where the degree of tidal exposure is great, while as soon as the environmental conditions become more favourable (as in the infralittoral zone and especially beneath the protective canopy of tall algae like *Laminaria*) life reappears in the abundance typically associated with surfaces below the level of the sea.

The Tufted Algae: Ceramium *sp.*, Cladophora rupestris *and* Lomentaria articulata

These three weeds occupy much of the tidal zone. Altogether twenty samples were collected ranging from +0·8 to +3·25 m. The results are given in Table V. The three algae differ somewhat in their structure, but as a whole I think their populations can be compared numerically without

TABLE V. TUFTED ALGAE: *CERAMIUM* SP. (*CE.*), *CLADOPHORA RUPESTRIS* (*CL.*) AND *LOMENTARIA ARTICULATA* (*LOM.*), ANIMALS PER G. OF DRIED WEED

(N.B. Samples T-12, 13 and 14 held a particularly large quantity of sediment.)

No. of sample ...	T-1	T-2	T-3	T-4	T-5	T-6	T-7	T-8	T-9	T-10	T-11	T-12	T-13	T-14	T-15	T-16	T-17	T-18	T-19	T-20
Height (m.)	+3·25	3·25	2·75	2·60	2·50	2·50	2·50	2·50	2·50	2·50	2·25	2·00	2·00	1·90	1·75	1·60	1·60	1·40	1·40	0·80
Seaweed	*Cl.*	*Cl.*	*Ce.*	*Cl.*	*Ce.*	*Cl.*	*Ce., Cl.*	*Cl.*	*Cl.*	*Cl., Ce.*	*Ce.*	*Ce.*	*Ce.*	*Lom.*	*Lom.*	*Ce.*	*Ce.*	*Ce.*	*Ce.*	*Ce.*
Weight (g.)	0·9	0·9	0·5	1·8	1·0	2·0	0·8	0·15	1·2	0·4	2·0	0·5	0·5	2·0	3·6	2·0	1·7	3·5	2·6	1·7
Nematoda	91	84	20	17	120	53	172	28	4	55	93	1400	1096	31	249	450	40	71	116	70
Copepoda	27	10	34	34	16	9	29	7	21	42	3	86	48	4	4	27	4	105	3	20
Ostracoda	10	14	44	17	32	11	20	13	9	67	.	88	92	15	3	6	2	1	1	.
Amphipoda:																				
Hyale nilssoni	28	25	2	14	34	20	33	28	12	25	.	8	.	3	2	.	.	1	.	.
Stenothoë monoculoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Corophium spp.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	1	.	3
Jassa falcata	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Polychaeta:																				
Fabricia sabella	1	2	.	.	.	1	.	.	.	2	.	172	168	13	.	11	.	1	.	2
Oridia armandi	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.
Grubea pusilla	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.
Odontosyllis ctenosoma	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1	.	.	.	.	.
Amphiglena mediterranea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	5	.	.	.	.
Oligochaeta	15	25	.	.	3	.	.	.	.	.	1	116	18	3	2	.	.	.	1	.
Halacarida	14	17	.	2	3	2	7	7	2	7	.	68	10	4	15	2	.	2	.	2
Hyadesia sp.	.	.	.	.	1	.	.	.	.	.	1	.	.	3	9	2	5	1	.	.
Chironomida (larvae)	25	27	10	35	34	31	85	14	2	152	4	28	22	11	4	27	12	6	3	4
Gastropoda:																				
Skeneopsis planorbis	.	.	.	.	3	1	.	7	.	.	.	182	.	25	1	.	2	1	.	.
Rissoa parva	.	.	.	.	.	.	.	.	.	.	1	10	.	.	.	.	1	3	.	1
Littorina obtusata	.	.	.	2	1	1	.	6	.	.	.	6	.	3	.	.	.	3	.	.
Cingulus cingillus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Indet.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	23	.	1	.	.
Pelecypoda:																				
Lasaea rubra	261	239	42	8	4	83	325	56	2	20	.	234	.	1	14	62	.	1	.	.
Mytilus edulis	.	.	.	.	.	.	.	.	.	.	.	12	6	1	3	3	.	.	.	.
Isopoda+Anisopoda:																				
Idothea neglecta ?+*granulosa*	.	.	.	14	1	3	4	13	3	5	3	.	16	2	2	2	3	6	1	8
Jaera marina	2	.	2	.	1	1	.	.	.	.	.	8	.	.	.	.	.	.	.	.
Naesa bidentata	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	4
Tanais cavolinii	.	.	.	2	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.
Total	474	443	154	145	253	217	676	179	55	377	107	2428	1482	119	312	623	68	205	125	116

important adjustments for the differences between them. The results agree satisfactorily with those obtained from the other algae, and only brief comment is necessary.

Decline in number downshore. The distribution of *Hyale nilssoni* agrees particularly well with what has been said above. The average lower level seems to lie at about +2·0 to +2·5 m. with some allowance, of course, for individual irregularities and special ecological conditions. In the tufted algae there is an average of 22 specimens per 1 g. dried weed above, against 1·4 below +2·5 m. Again, the distribution of *Lasaea rubra* agrees fairly well. The bulk of the numbers is at any rate to be found above +2·0 m. The samples T-1 and T-2 (+3·25 m.) with their average number of about 250 per g. almost approach the centre of the area which according to Colman is occupied by *L. rubra* in Wembury Bay—i.e. between +2·68 and +4·13 m. For the chironomid larvae *Clunio marinus* and *Trichocladius* cfr. *vitripennis* the results derived from *Gelidium corneum* (p. 153) also apply here: the lower level seems to be situated at about +1·10 m., which accounts for the rather slow decline in numbers in the present samples. There is, nevertheless, a marked difference between the samples above and those below 2·5 m. (41·5 against 12 specimens per g.).

Decline in number upshore. The 2 m. level proves again to be critical for all polychaetes. From Table IV it is suggested that *Rissoa parva* has the centre of its distribution decidedly lower than the lower level of the tufted algae, probably in the infralittoral zone (where it has been found, too, by Kitching *et al.* 1934), although single specimens can go up to about +2·50 m.

Even distribution. This appears to be shown by *Idothea neglecta* and the halacarids, the numbers of other species being too scarce for any conclusions to be drawn. Referring to data, as yet unpublished, I can add here most of the common nematodes, especially *Enoplus communis*, *Chromadorella parapoecilosoma*, *Heterochromadora germanica* and *Chromadora nudicapitata*.

'Average' Distribution

As already noted (p. 149), when data are presented of the fauna of seaweeds of very different structure, the numbers per unit weight tend to reflect the effect of the different substrata on the fauna rather than that of the vertical gradient. To overcome this difficulty it is usual to express the occurrence of the animals as a percentage of the total (giving so-called 'dominance values') and to compare as many samples as possible, aiming at an average picture of their vertical distribution. This procedure is followed in the present section, in which the vertical zoning is examined of amphipods, polychaetes and nematodes, in the littoral and upper infralittoral zones, regardless of the different algae from which they have been taken.[1]

[1] The data of this section are not only based on the samples dealt with in the previous chapter but of all those listed in the Appendix. It was, however, impossible to study every specimen; only a fraction of each sample has been examined taxonomically, the number of which is referred to in the tables of this section.

Amphipoda

The vertical distribution of the ten species found (excluding *Corophium* spp.) is given in Table VI. It is possible to compare these data with the distribution of the amphipods at Wembury combining Colman's and Kitching's results, from collections obtained between 1930 and 1932. Kitching obtained his samples by diving to about 10 ft. below C.D.

TABLE VI. DISTRIBUTION OF AMPHIPODS IN THE TINSIDE AREA. THE FIGURES GIVE PERCENTAGE OCCURRENCE AT EACH LEVEL ('DOMINANCE VALUES')

Height (m.)	+3·50 to +2·75	+2·75 to +2·00	+2·00 to +1·50	+1·50 to 0	0 to −3·00
Hyale nilssoni	100	87·3	46·7	7·0	.
Apherusa jurinei	.	11·1	10·3	16·2	15·7
Jassa falcata	.	0·3	31·7	18·4	33·2
Stenothoë monoculoides	.	.	10·0	51·0	9·3
Gammarus locusta	.	.	1·3	.	.
Pleonexes gammaroides	.	.	.	7·7	.
Apherusa bispinosa	.	.	.	.	4·0
Aora typica	.	.	.	.	29·0
Nannonyx goesi	.	.	.	.	6·2
Leucothoë spinicarpa	.	.	.	.	3·1
No. of samples containing amphipods	4	8	20	13	4
No. of specimens	108	199	166	276	49

TABLE VII. DISTRIBUTION OF AMPHIPODS IN WEMBURY BAY, COMPUTED FROM COLMAN (1940) AND KITCHING *et al.* (1934). FIGURES GIVE PERCENTAGES OF TOTAL AMPHIPODA (DOMINANCE VALUES)

	Colman			Kitching
Height (m.)	+4·63 to +3·50	+3·50 to +1·50	+1·50 to about 0	about 0 to −3·30
Hyale nilssoni	100	97·3	8·7	.
Melita sp.	.	0·2	.	.
(?) *Marinogammarus obtusatus*	.	0·2	.	.
Amphithoë rubricata	.	1·7	0·5	.
Microjassa cumbrensis	.	.	3·0	.
Pleonexes gammaroides	.	.	1·6	.
Hyale pontica	.	.	0·6	.
Stenothoë monoculoides	.	.	0·5	.
Tritaeta gibbosa	.	.	0·3	.
Leucothoë incisa	.	.	0·3	.
Biancolina cuniculus	.	.	0·17	.
Jassa falcata	.	.	50·3	22·6
Apherusa jurinei	.	0·5	9·4	6·4
Elasmopus rapax	.	.	7·1	4·5
Microdeutopus damnoniensis	.	.	5·0	} 1·8
M. chelifer	.	.	1·0	
Podocerus variegatus	.	.	5·3	0·17
Eurystheus maculatus	.	.	4·0	1·3
Lembos websteri	.	.	2·3	1·0
No. of samples	13	14	17	11
No. of specimens	466	618	621	593

To make this comparison I computed the dominance values of the amphipods from Colman's tables and from Kitching's *Distomus-Halichondria* association. The Caprellidae were omitted, and from Kitching's tables only those species were extracted which were also represented in Colman's samples. I am fully aware of the objections which might be made to this combining of samples taken at different times and by different methods but, nevertheless, the results, set out in Table VII, are not discordant.

Owing to differences in the ecological conditions and positions of samples (algae extending farther upshore, no samples taken between +2·00 and +1·50 m.) the zones of height applied to Colman's data differ from those used for Tinside. Furthermore, the number of specimens and of species found at Wembury is much higher than that found at Tinside, mainly due to the extremely rich *Laminaria* holdfasts and to the fact that the lower zone in Wembury has been more thoroughly investigated. Nevertheless, it appears as if the distribution of *Hyale nilssoni*, *Apherusa jurinei* and the few *Pleonexes gammaroides* agrees fairly well in the two areas, although *Apherusa jurinei* is distinctly more common at Tinside than at Wembury. Kitching's *Jassa 'dentex'* should be merged with *J. falcata* (see Sexton & Reid, 1951), so *J. falcata* is about as abundant in the infralittoral and lowest littoral zone in Wembury as at Tinside, though it reaches higher upshore in the latter area. The increase in number of species downshore seen in both areas is only to be expected for a marine group of animals.

TABLE VIII. DISTRIBUTION OF POLYCHAETES AT TINSIDE, AS IN TABLE VI

Height (m.)	+3·25 to +2·75	+2·75 to +2·00	+2·00 to +1·50	+1·50 to about 0	About 0 to −3·00
Fabricia sabella	100	100	61·2	32·4	.
Grubea pusilla	.	.	22·7	6·5	.
Amphiglena mediterranea	.	.	8·5	7·8	.
Syllis armillaris	.	.	1·9	0·5	.
Polydora hoplura	.	.	0·8	4·0	.
Cirratulus cirratus	.	.	0·3	1·8	.
Syllis krohni	.	.	0·5	.	.
Capitellides giardi	.	.	0·16	.	.
Odontosyllis ctenosoma	.	.	3·0	24·5	20·4
Platynereis dumerilii	.	.	0·8	13·2	56·1
Exogone gemmifera	.	.	0·8	0·7	6·0
Oridia armandi	.	.	0·3	5·6	2·0
Grubea clavata	.	.	.	1·8	5·1
Autolytus aurantiacus	.	.	.	1·3	2·6
A. prolifer	.	.	.	0·2	.
Spionidae sp.	.	.	.	0·5	.
Aonides oxycephala	.	.	.	0·2	.
Lagisca extenuata	.	.	.	.	5·1
Pterosyllis formosa	.	.	.	.	1·0
Sphaerosyllis hystrix	.	.	.	.	1·0
Phyllodocae maculata	.	.	.	.	1·0
No. of samples (only those with polychaetes)	1	5	26	19	4
No. of specimens	2	23	628	447	119

Species of the genus *Hyale* contribute to the fauna of the highest algal zones on most rocky seashores. For example, in the Mediterranean we find *Hyale prevosti* and *H. nilssoni* f. *stebbingi* to be the dominant amphipods for this 'biotope' and on the Chilean coast *H. hirtipalma*, *grandicornis* and one or two other species. (For this information I am indebted to Dr E. Dahl, who kindly permitted me to quote it from his yet unpublished material.)

TABLE IX. POLYCHAETA FROM WEMBURY. (SEE TABLE VII)

(+ = less than 0·1 %.)

	Colman			Kitching
Height (m.)	4·63 to 3·50	3·50 to 1·50	1·50 to about 0	about 0 to about 3·30
Fabricia sabella	100	98·3	54·2	4·4
Spirorbis borealis	.	1·5	7·0	2·8
Nereidae	.	0·2	See species	
Amphiglena mediterranea	.	.	10·6	.
Sphärosyllis erinaceus	.	.	6·1	.
Polydora giardi	.	.	6·0	.
Micromaldane ornithochaeta	.	.	5·8	.
Oridia armandi	.	.	4·3	.
Capitellides giardi	.	.	1·4	.
Polydora ciliata	.	.	0·6	.
P. caeca	.	.	0·4	.
Pholoë minuta	.	.	0·17	.
Exogone gemmifera	.	.	0·17	.
Odontosyllis ctenosoma	.	.	0·14	.
Dodecaria concharum	.	.	0·14	.
Sphaerosyllis ovigera	.	.	0·1	.
Eulalia bilineata	.	.	+	.
Eteone picta	.	.	+	.
Grubea limbata	.	.	+	.
Eusyllis lamelligera	.	.	+	.
Exogone brevipes	.	.	+	.
E. verrugera	.	.	+	.
Perinereis cultrifera	.	.	+	.
Polydora hoplura	.	.	+	.
Heterocirrus alatus	.	.	+	.
Polycirrus calientrum	.	.	+	.
Potamilla torelli	.	.	+	.
Jasmineira elegans	.	.	+	.
Hydroides norvegicus	.	.	+	.
Pomatoceros triqueter	.	.	0·5	22·0
Syllis gracilis	.	.	1·0	0·9
Trypanosyllis zebra	.	.	0·4	2·8
Platynereis dumerilii	.	.	0·17	12·5
Syllis variegata	.	.	0·17	1·4
S. armillaris	.	.	0·17	2·0
S. prolifera	.	.	0·1	0·6
Sabellaria spinulosa	.	.	+	4·4
Dasychone bombyx	.	.	+	1·2
Potamilla reniformis	.	.	+	0·6
Lagisca extenuata	.	.	+	0·3
Syllis ferruginea	.	.	+	0·3
No. of samples	2	6	13	11
No. of specimens	6	871	7975	358

TABLE X. NEMATODA FROM TINSIDE, FROM ALL SAMPLES EXAMINED (DOMINANCE VALUES)

(+ = less than 0·1 %.)

Height (m.)	+4·50 to 3·25	+3·25 to 1·50	+1·50 to 0	0 to −3·00
Leptosomatidae:				
Anticoma limalis	.	6·5	5·5	2·0
A. pellucida	.	0·5	+	.
Leptosomatum bacillatum	.	.	+	.
Thoracostoma figuratum	.	2·4	1·0	.
Th. (Pseudocella) trichodes	.	0·2	+	.
Oxystomatidae:				
Trefusia longicauda	.	0·3	.	.
Thalassoalaimus tardus	.	+	.	.
Halalaimus gracilis	.	+	.	.
Phanodermatidae:				
Phanoderma albidum	.	+	0·3	.
Enoplidae:				
Enoplus communis	62·0	30·0	36·4	13·0
Dorylaimidae:				
Dolicholaimus marioni	.	3·8	0·4	.
Syringolaimus striaticaudatus	.	+	+	.
Oncholaimidae:				
Krampia acropora	.	0·1	0·3	.
Cavilaimus macramphis	.	.	0·1	.
Pontonema vulgaris	.	+	.	.
P. donsi	.	+	0·15	.
Metoncholaimus demani	.	+	0·1	.
Oncholaimus dujardini	.	+	0·75	.
Oncholaimellus diodon	.	+	.	2·0
Oncholaimide juv.	.	.	+	.
Enchelidiidae:				
Eurystomatina filiformis	.	.	+	.
Symplocostoma longicollis	.	+	.	.
Catalaimus maxweberi	.	0·5	0·8	.
Cyatholaimidae:				
Cyatholaimus demani	1·4	0·5	1·5	6·0
Paracanthonchus coecus	.	4·0	0·3	.
P. kreisi	.	+	.	.
Choanolaimidae:				
Halichoanolaimus robustus	.	1·7	0·4	.
Desmodoridae:				
Desmodora serpentulus	.	4·8	1·0	1·0
D. scaldensis	.	1·0	+	.
Xenodesmodora porifera	.	+	.	.
Monoposthia costata	.	1·0	0·5	0·5
Microlaimidae:				
Crassolaimus bipapillatus	.	+	.	.
Comesomidae:				
Parasabatiera similis	.	.	.	0·5
Chromadoridae:				
Spilophorella paradoxa	.	1·8	2·8	0·5
Spilophora gracilicauda	.	0·3	0·7	.
Chromadorina parva	.	1·0	0·3	.
Euchromadora vulgaris	3·0	1·0	0·1	.
E. tridentata	.	0·3	+	3·5
Hypodontolaimus inaequalis	.	0·4	0·4	0·5
Prochromadorella neapolitana	.	.	.	1·5

TABLE X (*continued*)

Height (m.)	+4·50 to 3·25	+3·25 to 1·50	+1·50 to 0	0 to −3·00
Chromadoridae (*cont.*):				
Prochromadorella mediterranea	.	+	.	.
P. paramucrodonta	.	+	0·8	0·8
P. macro-ocellata	.	0·8	.	.
P. obtusidens	.	1·3	.	.
Chromadorella parapoecilosoma	.	2·6	1·0	.
C. microlaima	.	0·3	0·6	.
Neochromadora poecilosomoides	.	+	0·5	17·0
Chromadora nudicapitata	32·0	13·5	34·0	10·0
C. brevipapillata	.	.	0·2	29·5
C. macrolaima	.	0·6	0·1	.
Heterochromadora germanica	.	10·1	4·0	.
H. granulo-pigmentatus	.	0·8	0·2	.
H. cervix	.	0·3	.	.
Prochromadora longitubus	.	+	0·2	0·5
Axonolaimidae:				
Odontophora setosa	.	0·1	.	.
Araeolaimidae:				
Araeolaimoides paucisetosa	.	+	.	.
Camacolaimidae:				
Camacolaimus tardus	.	2·1	1·1	.
C. conicaudatus	.	+	+	.
Halaphanolaimidae:				
Dermatolaimus membranatus	.	0·6	.	.
Linhomoeidae:				
Linhomoeus elongatus	.	0·2	0·3	.
Paralinhomoeus lepturus	.	+	.	.
Metalinhomoeus typicus	.	+	.	.
Monhysteridae:				
Theristus acer	.	2·0	1·0	.
T. normandicus	.	+	.	.
T. setosus	.	.	.	4·0
Theristus sp.	.	+	.	.
Monhystera parva	.	+	0·2	.
M. luisae	1·1	.	.	.
M. refringens var. *britannica*	0·5	+	0·2	.
M. disjuncta	.	+	0·8	.
No. of samples	3	33	11	4
No. of specimens	262	4160	1327	156

Polychaeta

In Table VIII is summarized the distribution of the polychaetes at Tinside (the serpulids were not counted and are, therefore, omitted). It must be stressed that the absence of species in the lowest zone is not at all conclusive since only relatively few specimens and only from one single biotope, viz. *Nitophyllum punctatum*, were studied.

By the same method as above the data from Colman's tables and Kitching's *Distomus-Halichondria* association have been extracted (Table IX). Still more striking than in Amphipoda is the abundance of species and individuals in the *Laminaria* holdfasts which makes this habitat almost incomparable with any other. Despite the differences between Tinside and Wembury Bay, in number of specimens studied and in the habitats sampled, two facts seem to be fairly well established. First, *Fabricia sabella* is the polychaete with by far the highest power of resistance to exposure, and it dominates the higher zones. Secondly, the level at about +2 m. is critical for nearly all other species, indicating that most polychaetes are fairly susceptible to exposure.

Nematoda

The distribution of the nematode fauna in the Tinside area has been dealt with in a previous paper (Wieser, 1951). It has been shown that nematodes are more dependent on the shape of the algae on which they live and on the silt content than any of the groups examined. The study of the vertical distribution is somewhat hampered by these facts since we are even less sure about the 'causae efficientes' of the presence or absence of a given species than in other animals.

All the available data, however, are summarized in Table X, giving the vertical distribution of the seventy species found at Tinside amongst 5945 specimens picked out from fifty-one samples. The uppermost and the lowermost zones were not so well studied as the two middle zones, and their data are thus less reliable. These deficiencies remembered, attention may be called to a few points.

(i) The most evenly distributed species are *Enoplus communis*, *Cyatholaimus demani* and *Chromadora nudicapitata*. (ii) In my opinion there are several species which can be called true infralittoral forms, viz. *Neochromadora poecilosomoides*, *Chromadora brevipapillata*, possibly *Theristus setosus* and *Prochromadorella neapolitana*. (iii) In two genera very closely related species seem to replace each other in the upper and lower part of the shore respectively, viz. *Euchromadora vulgaris* (high) and *E. tridentata* (low) and *Chromadora nudicapitata* (high) and *C. brevipapillata* (low).

Critical Zones

Colman (1933) and Evans (1947*a*, *b*) introduced and applied the term 'critical level' which accounts for the observation that 'certain levels (of the intertidal region) have been shown to be more critical than others in connexion with the distribution of intertidal plants and animals' (Evans, 1947*b*). Colman and Evans studied critical levels only in macro-organisms. In micro-organisms inhabiting seaweeds the problem becomes more complicated since the effect of the substratum, i.e. the seaweeds, on the vertical distribution of the fauna has to be taken into account. Where certain algae reach their upper limit most of the animals living among them will also find there the limit for their penetration into the intertidal zone. It is, however, not established whether this is due to the same change in the degree of tidal exposure which causes the disappearance of the algae or to the fact that they are dependent on the presence of the latter from a purely mechanical point of view. I therefore want to apply the term 'critical level', as far as the microfauna is concerned, only to those limits which do not correspond with the disappearance of algae. It can, however, be concluded from the data presented above that changes in the algal fauna may reflect the influence of the substratum to a greater degree than found in organisms attached to rocks. Differences in shape of the seaweeds cause the 'critical level' to oscillate somewhat in different habitats of the same area so that one could rather speak of a critical 'zone'. Or, in other words, the range of variation of the upper and (or) lower limits of certain animals seems to be greater in species inhabiting seaweeds than in those living as hemi-sessile or slowly moving animals on the surface of the rocks.

The five critical levels distinguished by Evans (1947*a*, p. 211 *et seq.*) are as follows: (1) between M.L.W.S. and E.L.W.S., where the majority of intertidal species achieve their lower limits; (2) between M.L.W.S. and M.L.W.N., which marks the lower limits of certain other intertidal species; (3) just above M.L.W.N., where several sublittoral species reach their upper limits of penetration into the intertidal zone; (4) just below M.H.W.N., marking the upper limit of one set of intertidal species; (5) between M.H.W.S. and E.H.W.S., where a further set of intertidal plants and animals achieve their upper limits. According to what has been said above I must leave out levels nos. 4 and 5, since they would only concern species which disappear together with their seaweeds. Furthermore, levels (1) and (2) which overlap even in Evans's figure (his p. 213) must be regarded as one as far as the microfauna is concerned. This I call 'Zone A', which is situated between M.L.W.S. and M.L.W.N. in the area under consideration. In this zone the true intertidal species which were found reach their lower limits.

I recognize an analogue of Evans's level no. 3, which I call 'zone B' and which is situated between E.L.W.N. and M.T.L. This is slightly higher upshore than Evans's level, for which the reason is believed to be the dense tufts of *Gelidium corneum* which allow several species to penetrate farther into the intertidal region than they do in any other weeds examined. In this 'zone B' a set of infralittoral animals reaches its upper limit.

A third 'zone C' deserves mention which either has no counterpart in Evans's survey or must be regarded as the lower part of his level 3 (though in my samples well distinct from 'zone B'). It marks the upper limit of another set of infralittoral species. It happens here to coincide with my 'zone A', but it should not be assumed that it necessarily does everywhere.

Summing up, the following 'critical zones' may be distinguished in the Tinside area:

(A) Between M.L.W.S. and M.L.W.N., where several intertidal species reach their lower limits.

(B) Between E.L.W.N. and mean tide level, marking the upper limit of a set of infralittoral species.

(C) Between M.L.W.S. and M.L.W.N., where another set of infralittoral species achieves its upper limit.

The results are given in Fig. 1. It is only meant to show the one (upper or lower) limit of the species concerned that falls within the critical zone. This limit is indicated by broken lines marking somewhat deliberately the oscillations of the zone. The line 'bulk of *Fabricia sabella*' indicates the sudden

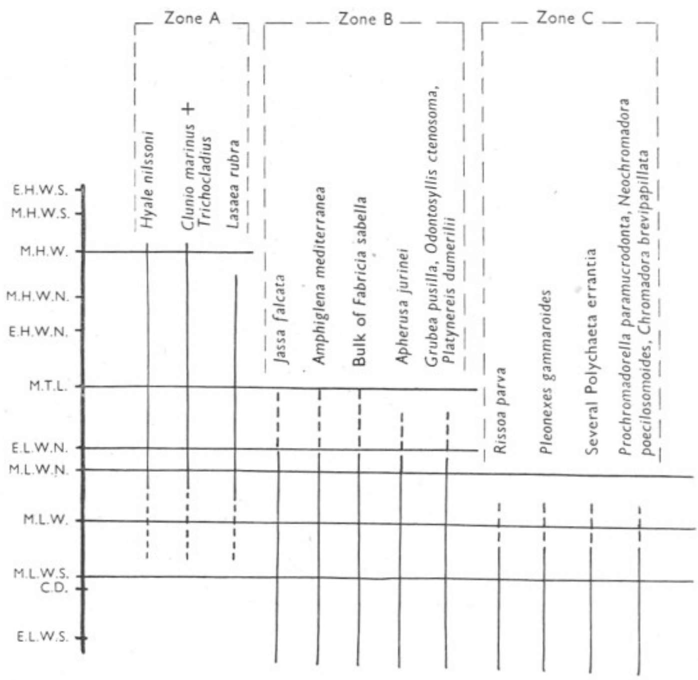

Fig. 1. Distribution of certain faunal types in relation to critical levels (see text for further explanation).

decline in number of individuals of this species at about the +2·0 m. level (Table II), though single specimens might reach farther upshore.

The following comparisons can be made with the data on the macrofauna published by Colman (1933), Evans (1947*b*) and Yonge (1949).

The species of zone A (*Hyale nilssoni*, *Clunio marinus*, *Trichocladius* cfr. *vitripennis* and *Lasaea rubra*) are the counterpart of *Littorina littorea*, *L. obtusata*, *Patella vulgata*, *Osilinus lineatus*, *Chthamalus stellatus*, *Ascophyllum nodosum*, and *Fucus vesiculosus*; the species of zone B (*Jassa falcata*, *Apherusa jurinei*, *Amphiglena mediterranea*, *Grubea pusilla*, *Odontosyllis* *ctenosoma*, *Platynereis dumerilii*) approximately coincide in their distribution with *Gibbula cineraria*, *Rhodymenia palmata*, *Gigartina stellata* and *Chondrus crispus*.

The most interesting species, however, are those which achieve their upper limit in zone C (*Pleonexes gammaroides*, *Rissoa parva*, *Oridia armandi*, several Polychaeta errantia, and nematodes like *Prochromadorella paramucrodonta*, *Neochromadora poecilosomoides* and *Chromadora brevipapillata*), since they correspond with the organisms of the 'infralittoral fringe' (Stephenson, T.A. & A., 1949), i.e. species which are typically infralittoral but nevertheless occupy a small fringe in the lower part of the intertidal region. To them belong *Laminaria digitata*, *Himanthalia lorea*, *Pyura stolonifera* and most probably *Verruca stroemia* and *Calliostoma ziziphinum*, quoted by Colman (1933). Furthermore, Yonge's 'average low tide level' (1949) coincides with the upper level of the infralittoral fringe and therefore, also, with my zone C (as upper limit of a set of infralittoral species) and zone A (as lower limit of some intertidal species). Briefly, this level between M.L.W.N. and M.L.W.S. appears to be the most critical throughout the intertidal area: it is a true 'turning-point' of the highest ecological significance.

'Dynamics' of Vertical Distribution

In the previous sections the distribution of the microfauna was dealt with from a purely 'static' point of view, i.e. the upper or lower limits of certain species or their level of maximum abundance was given by using the average values of several samples disregarding the state of changes (rhythmical or sporadic) which might occur in the environment. The result is an *average distribution* of the species in question which fully corresponds with the *actual distribution-area* in sessile organisms, to a very great extent also in hemi-sessiles, slowly moving and highly euryoecous species. But with active and (relatively) stenoecous species care should be taken not to mix together samples which have been taken under quite different environmental conditions (as, for example, height of tide), since by this method it is impossible to detect movements which may counterbalance environmental changes if they become too unfavourable. In this case a more discriminating method should be applied and samples taken under different conditions should be kept separate. The term 'actual distribution-area' therefore is meant to comprise all changes in the distribution of a given species correlated with fluctuations in the environment. Naturally, certain restrictions have to be made, since over sufficiently long periods even sessile organisms extend or restrict their area of distribution for the special requirements of reproduction. Therefore only short-period fluctuations and their effect on some species will be discussed. Similar behaviour has been thoroughly investigated in movements of marine and limno-plankton in connexion with changes of light intensity, etc.

As is well known, tidal movements are of great importance in the littoral region. In areas with a big tidal range, in particular, extensive movements of the more mobile animals may occur with the rise and fall of the tide, but these are almost unknown in the microfauna. Watkin (1941) has shown the changes occurring in the arthropod fauna of a sandy intertidal area during high water. Two sorts of movements were found: the passive (and active?) upward transport by the rising tide of animals living in deeper water, and the (active) migration of true sand-dwelling species of the intertidal area into the waters above. With qualifications this can be compared with Remane's division into 'horizontal' and 'vertical migrants' (1940, p. 107).

It was possible to detect similar differences in the distribution of certain animals between low and high water on a rocky coast, such as at Tinside. This could be proved by collecting samples in several localities during low tide, and, by diving, during high tide. If the same differences of distribution occurred in all samples they could be regarded as significant. Naturally, not all the algae examined gave the same results. For example, in the small tufts of *Gelidium corneum* it was not possible to detect any differences in the composition of the fauna between high and low water. The most obvious differences were seen in the tall and shrub-like seaweeds *Gigartina stellata* and *Fucus serratus*. These weeds are most liable to desiccation when the tide is out and it is quite understandable that a set of mobile animals should leave them in this state and occupy them again on the succeeding flood. Those animals which cannot counteract the challenge of the environment in this active manner will mostly—as has been suggested in the general remarks at the beginning of this paper—find shelter in minute crevices, between the tiny roots and branches of epiphytes and epizoids.

I think it possible to distinguish two modes of migration within the fauna of seaweeds according to whether the animals are able to swim or merely able to crawl about. To illustrate the second condition I would refer to *Littorina obtusata*, the 'average' distribution of which is confined to the lower two-thirds of the intertidal area. The numbers of this species in twelve samples of *Gigartina stellata*, six of them taken during high tide, the other six during low tide, is shown in Fig. 2. Each column represents a different station within the area investigated. The whole column shows the number of specimens (per 20 g. dried weed) of the high-water sample, the black part that of the low-water sample at the same location. Thus the white part of each column represents the surplus of the flood samples over the ebb samples, and this appears to be quite significant.

These data strongly suggest that the snail carries out movements synchronous with the rise and fall of the tide. During high water it is more numerous on the fronds than during low water, when it seeks shelter within the denser and lower part of the seaweeds and in crevices of the rocky substratum nearby, escaping therefore detection if the seaweed is collected.

These movements are explicable if we keep in mind that *Littorina obtusata* feeds directly on algae and therefore the submerged and slowly floating fronds provide a much better opportunity than the dry and shrunken shrub to which tall algae like *Gigartina* are reduced during low water.

That it is the degree of humidity of the substratum and of the snail itself which causes these migrations is supported by the results of Haseman (1911), who found the same oscillatory movements corresponding to those of the tides in *Littorina littorea* at Woods Hole, Mass. This species feeds on small algae growing on rocks. It never crawls on dry surfaces and it has been shown by various experiments that 'the primary directive force for rhythmical

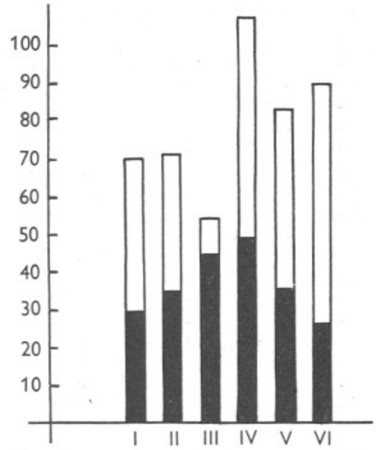

Fig. 2. Numbers of *Littorina obtusata* in six low-water and six high-water samples. Each column represents a different station. On the ordinate the number of specimens per 20 g. of dried weed. (For further explanation see text.)

movements is the surface film of water' (Haseman, 1911, p. 120). These vertical movements shown by *Littorina* make them comparable with Remane's 'vertical migrants', i.e. the species inhabiting an intertidal sandy area, which, when the tide recedes, crawl downwards into the interstitial spaces of the sand-grains, thus remaining in a zone of optimal humidity.

A similar mode of distribution, at least in appearance, is found in several copepods. But, since we know that copepods can swim ('bivagil' according to Remane, 1940, p. 191), in addition to probable movements within the seaweed itself, there are possibly more extensive migrations from one level to another, following the falling tide downshore and rising again with the flood. I am inclined to regard this type of migration as prevailing in the copepods in view of the abundance in plankton catches made by night of the species which are known to inhabit seaweeds (observation of Dr E. Dahl on the Swedish west coast, unpublished).

The present material was not adequate for studying several species separately, mainly because of the patchiness of their distribution (see also

Colman, 1940, p. 147). The distribution of the individual species is given in Table XI, while in Fig. 3 all the species are treated together. Again the high-water samples are represented by the whole columns and the low-water samples by the black part of them. (Owing to accidental loss of the tubes, a full examination of no. III and no. I from low water was not made.)

TABLE XI. OCCURRENCE OF COPEPODS IN TWELVE SAMPLES OF *GIGARTINA STELLATA*, DIVIDED INTO HIGH-WATER AND LOW-WATER SAMPLES

(+ = present; + + = very common.)

	High water						Low water					
No. of sample ...	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Dactylopodia vulgaris	.	++	.	.	+	.	.	.	.	+	++	++
Idya minor	++	.	.	.	.	.	.	.	.	.	.	.
I. graciloides	.	.	.	+	.	.	.	.	.	.	.	.
Zaus spinatus	.	.	.	+	+	+	.	.	.	.	.	.
Saccodiscus littoralis	.	.	.	.	.	.	.	.	.	.	+	.
Rhynchothalestris rufocincta	.	.	.	.	.	.	.	+	.	.	.	+
Parathalestris clausi	.	.	.	.	+	++	.	+	.	.	++	.
P. harpacticoides	.	.	.	+	+	.	.	.	.	.	.	.
Laophonte similis	.	.	.	.	.	.	.	.	.	+	.	.
L. inopinata	.	.	.	.	.	.	.	.	.	.	.	+
Heterolaophonte sp.	.	.	.	.	.	.	.	+	.	.	.	.
Amphiascus sp.	.	.	.	.	.	.	.	.	.	.	.	+
Pseudonychocamptus koreni	.	.	.	.	.	.	.	.	.	.	+	+
Parastenhelia spinosa	.	.	.	.	.	.	.	+	.	.	.	.
Ameira longipes	.	.	.	.	.	.	.	++	.	.	.	.
Harpacticidae juv.	.	.	.	.	+	.	.	.	.	.	+	.
Oithona helgolandica	.	.	.	+	.	.	.	.	.	.	+	.
Acartia clausi	.	.	.	+	.	.	.	.	.	.	.	.
Total no. of specimens per 20 g.	31	53	32	65	50	31	12	14	30	14	25	18

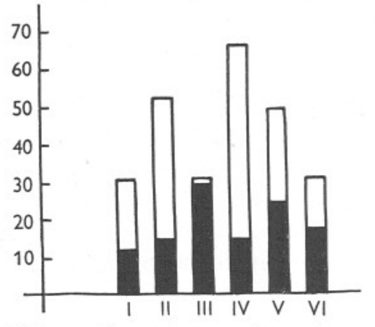

Fig. 3. Total Copepoda numbers at six stations, as in Fig. 2.

Since the copepods leave their seaweed cover with the receding tide and occupy it again on the flood we should reckon them (at least those species mentioned in Table XI) amongst Remane's 'horizontal migrants', though, with the exception of *Oithona helgolandica*, they do not come in from off-shore but only from lower levels of the algal zone. Nevertheless, a 'horizontal gradient' takes part in the movement and makes the analogy suggestive.

Finally, the vertical distribution of the amphipod *Stenothoë monoculoides* has been studied in twenty-four samples, ten of which were taken during high water, from *Fucus serratus* and *Gigartina stellata*. The results are given in Fig. 4 and Table XII. Since the collecting was carried out more thoroughly than in the former examples, I can give the exact height above C.D. of the samples taken. Within a limited vertical range 2 to 5 samples were collected, the average value of which is represented by the columns in Fig. 4.

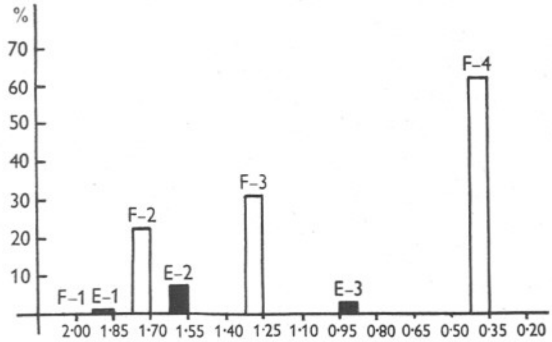

Fig. 4. Distribution of *Stenothoë monoculoides*. Every column represents the average 'dominance value' of two to five samples within a limited vertical range. The mean vertical position of the samples above C.D. is shown by the position of the columns on the abscissa (metres above C.D.). Black columns represent low-water, white columns high-water samples.

TABLE XII. DISTRIBUTION OF *STENOTHOË MONOCULOIDES*. SPECIFICATION OF ALL TWENTY-FOUR SAMPLES EXAMINED (FOR FURTHER EXPLANATION SEE TEXT)

	Low water			High water				
Station no. ...	E-1	E-2	E-3	F-1	F-2	F-3	F-4	Total
No. of *Gigartina* samples	3	3	2	1	2	2	0	13
No. of *Fucus* samples	2	2	2	1	1	1	2	11
Range of height above C.D. (m.)	2·0	1·9–1·4	1·3–0·7	2·0	1·8	1·6–1·0	0·7–0·2	2·0–0·2
No. of specimens in each sample	1, 0, 0, 0, 0	14, 2, 0, 0, 0	1, 1, 0, 0	0, 0	39, 2, 0	5, 72, 0	5, 20	162
Average dominance value of all samples	1	8	3	0	23	31	62	.

This time the dominance value of *Stenothoë monoculoides* in the whole amphipod population is given along the ordinate, since the algae were overgrown by epiphytes (*Elachistea fucicola*) and epizoids (*Membranipora membranacea*, *Dynamena pumila*) to very different degrees, making it impossible to compare the numbers per weight-unit. (The numbers as well as 'dominance values' are given in Table XII.) The data clearly show that the occurrence of the amphipod in the two algae considered, and between +2·0 and +0·2 m., is much more abundant during high than during low water. Furthermore, there might also be decrease in the density of the population upshore during high water, pointing to the same susceptibility to desiccation which causes emigration from the intertidal area with the fall of the tide. For these reasons *Stenothoë monoculoides*, too, should be regarded as a 'horizontal migrant'.

SUMMARY

The vertical distribution of the microfauna inhabiting seaweeds in the Tinside area of Plymouth Sound has been discussed from various points of view. Samples were collected by diving below water-level (infralittoral and intertidal during high water) to ensure uniformity in the method of collecting.

A very strong influence of the substratum on the distribution of the fauna was observed. The extent to which different powers of locomotion of the animals concerned might help to counteract environmental changes is discussed.

The fauna of *Gelidium corneum* was studied in seventeen samples between +2·75 and +1·10 m. (above C.D.). Examples of the three possible relations to the factor of tidal exposure shown by littoral animals—(i) decline in number downshore, (ii) decline in number upshore, and (iii) more or less even distribution—are given.

The fauna of the two leaf-like algae *Porphyra laciniata* and *Nitophyllum punctatum* was studied in seven samples extending from +1·95 to −3·00 m. A most striking increase in population density was observed passing below low-water mark. Some species are indicated which are confined to the infralittoral or the littoral samples respectively.

The three tufted algae: *Ceramium* sp., *Cladophora rupestris* and *Lomentaria articulata* were studied between +3·25 and +0·8 m. in a total of twenty samples. Further support for the results gained from the *Gelidium* samples was obtained. The 'average' distribution of amphipods, polychaetes and nematodes in all samples studied is given. A comparison with published data on the fauna of Wembury Bay (Colman, Kitching, etc.) shows interesting agreement in some points.

It is pointed out that 'critical zones' for the distribution of the microfauna might occur in the area studied. Three zones are suggested, viz. zone A, between M.L.W.S. and M.L.W.N., where several intertidal species reach their lower limits; zone B, between E.L.W.N. and M.T.L., marking the upper limit of a set of infralittoral species; zone C, between M.L.W.S. and M.L.W.N., where another set of infralittoral species achieves its upper limit.

For each zone examples are given and comparisons drawn with the results obtained by Colman, Evans and Yonge.

The term 'dynamics of vertical distribution' is introduced, taking into account that various species might have a very different distribution in the intertidal area according to the state of the tide. The differences in the distribution between low and high water are suggested for *Littorina obtusata*, several copepods and the amphipod *Stenothoë monoculoides*. The agreement with the results obtained by Haseman, Watkin and Remane is discussed.

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Appendix. List of all Samples Examined. Specification, Position, Numbers of Amphipods, Polychaetes, Nematodes and Total of Specimens.

Alga	Sample no.	Height relative to C.D. (m.)	Weight (g.)	Degree of silting (0–4)	Epi-growth (0–4)	Covered with water (+) or not (–)	Amphi-pods	Poly-chaetes	Nema-todes	Total of specimens
Gelidium corneum	G-1	+2·75	1·3	3	0	–	6	49	1650	3400
	G-2	2·75	2·2	0	0	–	54	.	472	1697
	G-3	2·50	1·2	2	0	–	8	34	798	1427
	G-4	2·50	1·0	2	0	–	18	26	600	2816
	G-5	2·00	0·8	3	0	–	8	591	771	2186
	G-6	2·00	1·4	3	0	–	2	445	920	2364
	G-7	2·00	1·3	1	0	–	14	288	511	1307
	G-8	1·90	1·2	3	0	–	4	587	765	1685
	G-9	1·80	1·4	1	0	–	2	8	400	829
	G-10	1·75	1·3	3	0	–	.	723	856	2505
	G-11	1·60	1·6	3	0	–	1	675	1200	2714
	G-12	1·55	2·0	1	0	–	2	289	344	997
	G-13	1·50	0·6	1	0	–	.	227	224	749
	G-14	1·50	0·6	1	0	–	.	24	62	203
	G-15	1·50	1·6	3	0	–	1	458	779	1870
	G-16	1·40	1·2	2	0	–	60	196	450	1106
	G-17	1·10	0·8	4	0	–	42	35	668	1480
Cladophora rupestris	T-1	+3·25	0·9	0	0	+	25	1	82	427
	T-2	3·25	0·9	0	0	+	22	2	76	398
	T-4	2·60	1·8	0	0	–	25	.	32	240
	T-6	2·50	2·0	0	0	–	40	1	107	426
	T-8	2·50	0·15	0	0	+	4	.	4	24
	T-9	2·50	1·2	0	0	+	14	.	5	67
	T-10	2·50	0·4	0	0	+	10	1	22	152
Ceramium sp.	T-3	+2·75	0·5	0	0	–	1	.	10	77
	T-5	2·50	1·0	0	0	–	34	.	120	253
	T-7	2·50	0·8	0	0	+	27	.	138	542
	T-11	2·25	2·0	0	0	–	.	.	187	210
	T-12	2·00	0·5	2	0	–	4	93	700	1216
	T-13	2·00	0·5	2	0	–	3	84	548	741
	T-16	1·60	2·0	0	0	–	.	36	900	1246
	T-17	1·60	1·7	0	0	–	.	.	66	111
	T-18	1·40	3·5	0	0	–	3	2	247	690
	T-19	1·40	2·6	0	0	–	.	.	302	322
	T-20	0·80	1·7	0	0	–	8	2	118	190
Lomentaria articulata	T-14	+1·90	2·0	1	0	–	6	32	62	233
	T-15	1·75	3·6	1	0	–	6	7	708	930
Porphyra laciniata	L-1	+1·95	35·0	0	0	–	1	.	13	32
	L-2	1·50	22·0	0	0	–	2	4	10	66
	L-3	1·50	16·0	0	0	–	3	1	3	44
Nitophyllum punctatum	L-4	–0·70	3·4	0	4	+	76	95	142	444
	L-5	–1·20	9·0	0	1	+	90	205	84	376
	L-6	–1·20	5·0	0	1	+			38	131
	L-7	–3·00	2·9	0	1	+	14	6	32	121
Gigartina stellata	S-1	+2·00	18	0	0	+	2	10	25	212
	S-2	2·00	35	0	1	+	23	61	95	719
	S-3	2·00	45	0	1	–	19	95	52	493
	S-4	2·00	40	0	?	–	1	19	7	114
	S-5	1·80	15	0	1	+	5	37	48	245
	S-6	1·80	22	0	2	+	66	20	36	445
	S-7	1·80	40	0	2	–	57	143	196	992
	S-8	1·80	55	0	3	–	16	154	273	881
	S-9	1·50	17	0	?	+	4	9	18	211
	S-10	1·50	3	0	2	–	1	17	5	28
	S-11	1·40	32	0	2	+	67	39	51	528
	S-12	1·40	40	0	4	–	30	52	119	580
	S-13	1·30	20	0	3	+	128	12	24	420
	S-14	1·25	60	0	4	–	85	213	588	1629
	S-15	1·00	40	0	2	–	20	159	259	650
Fucus serratus	F-1	2·00	135	0	1	–	.	23	205	347
	F-2	2·00	24	0	1	–	2	3	18	67
	F-3	1·90	8	0	3	+	1	25	127	191
	F-4	1·90	25	0	0	+	1	2	52	100
	F-5	1·60	13	0	0	+	.	3	1	12
	F-6	1·50	20	0	0	–	.	1	16	23
	F-7	1·50	16	0	0	–	4	13	11	77
	F-8	1·40	65	0	1	–	1	19	56	128
	F-9	1·00	165	0	1	–	26	8	123	307
	F-10	1·00	21	0	0	+	.	.	1	10
	F-11	0·70	75	0	2	–	32	34	135	464
	F-12	0·70	28	0	3	+	27	16	200	423
	F-13	0·20	25	0	3	+	19	26	228	437