# THE LITTORAL ENVIRONMENT OF ROCKY SHORES AS A BORDER BETWEEN THE SEA AND THE LAND AND BETWEEN THE SEA AND THE FRESH WATER

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## SUMMARY

Many ecologists have occupied themselves with the problem of the littoral zonation and they still disagree among themselves about the delimitation of the zones and the factors which cause the zonation. In this paper the problem has been approached in two different ways. In the first place the littoral zone *sensu lato* has been regarded as the border area between the sea and the land. This approach does not result in an explanation of the 'submergence' of many eulittoral organisms in the Arctic waters and the Baltic. Secondly the littoral zone *sensu lato* has been considered as the border zone between the sea and the fresh water, in other words as a brackish environment. This approach gives a reasonable explanation for the 'submergence' of littoral organisms in low-salinity waters. It appears that both tidal movements and wave action (wash, splash, and spray) cause salinity fluctuations and that salinity is one of the major factors acting in the littoral zonation. Most of the organisms which do not show 'submergence' in low-salinity waters are restricted to the supralittoral and the upper part of the intertidal zone, where they are beyond the influence of the daily tidal rhythm. The vital factor for these organisms is contact with the air. The third active factor, light, is of some importance in the lower part of the eulittoral. These three abiotic factors, together with biological stress (competition), effectuate the littoral zonation pattern. Both the supralittoral and the eulittoral are well-defined ecological units, characterized by their own physical features and their own species composition. In fact they have almost no common species. Strong wave action allows some eulittoral species to survive in the supralittoral; this has to be regarded merely as an interference phenomenon.

The littoral border environment is in comparison with other brackish habitats extremely rich in species peculiar to it. In this environment the influence of the salt extends far above the tidal influence. In the estuarine environment, which has very few species exclusively bound to it, the reverse is the case. This could indicate that marine salt beyond the reach of the regular tidal rhythm creates conditions favourable for speciation.

## 1. INTRODUCTORY REMARKS

One of the most outstanding features of the shore is the arrangement of the plants and animals in a number of often very sharply demarcated zones. Three main zones have been distinguished:

1. The *sublittoral* is always submerged except for its extreme upper margin which may sometimes be exposed under exceptional circumstances. The occurrence of belts within the sublittoral is generally ascribed to decreasing light intensity and to a gradual change in the light quality with increasing depth.
2. The *eulittoral* or intertidal zone is the zone subjected to the tidal oscillations and where emersion and submersion alternate. It is usually defined as the zone between the levels of mean low-water springs (MLWS) and mean high-water mark (MHW); sometimes mean high-water springs (MHWS) is chosen as its upper limit. The zonation pattern within the intertidal belt is regarded as the product of the vertical tidal movements and the various ecological side-effects coupled with the tidal factor.

3. The *supralittoral* is the zone under the influence of the spray. Its lower margin is sometimes reached by the waves for a short time. The various degrees of exposure to spray are considered to be responsible for a further zonation within this zone. The upper limit of the supralittoral is generally indistinct.

Light and spray have generally been accepted as the major causal factors for the zonation patterns of the sublittoral and the supralittoral respectively. There is, however, no general agreement with respect to the major factors governing the eulittoral zonation pattern. In my opinion the tidal factor is too complex for one to be satisfied with the statement that the littoral zonation is a result of the tidal movements. In a number of cases the borders of the various belts in the intertidal zone have been found to coincide with hydrographic lines, such as the average levels of high- and low-water mark during spring and neap tides (Colman, 1933; Doty, 1946), but in many other cases such a correlation could not be found. Numerous modifying factors play their part in determining the position of the various belts in the intertidal zone, e.g. wave action, the nature of the substratum, the quantity of suspended matter in the flood water, the slope and the aspect of the shore, the time of the day when the lowest tides occur, etc.

The exposure factor in particular is very important. On exposed shores several algal belts occur at levels far above the upper limit of the intertidal zone, while the corresponding belts on sheltered coasts are obviously intertidal. Børgesen (1905) recorded the existence of a community of *Porphyra umbilicalis* from the Faeroes reaching up to 40—50 feet above mean sea-level. He also observed a marked 'raising' of various *Fucaceae* communities on exposed shores and recorded the occurrence of *Pelvetia canaliculata* at *c.* 5 m above mean sea-level. Burrows, Conway, Lodge & Powell (1954) and Conway (1954) also recorded the 'raising' of the various *Fucaceae* belts under the influence of increasing exposure on Fair Isle and some other places along the coasts of the British Isles.

The nature of the substratum can also play an important role, especially in the higher parts of the intertidal zone. In the south-western part of the Netherlands it was observed that the *Pelvetia*-belt is situated higher on the shore on Vilvordian limestone than on basalt, while on granite it occurs at a level between these two (den Hartog, 1959).

Another feature which certainly complicates the correlation of the biotic communities with tidal levels is the seasonal shift of various algal belts. Børgesen (1905) reported that the supralittoral extension of *Porphyra umbilicalis* is much greater in winter than in summer. In the Netherlands I observed that the *Bangia-Urospora-*, the *Blidingia minima-*, and the *Enteromorpha-Porphyra* associations show an upward shift in the winter half-year, while they move downwards in summer. These shifts are shown not only by the upper limits of these vegetations but also by their lower limits (den Hartog, 1959). These observations have been confirmed by Nienhuis (unpubl.) and Lewis (1964). In general it can be concluded that by the action and counteraction of the various modifying factors the borders of the plant and animal belts in the eulittoral zone will rarely show any direct correlation with the tidal levels. Further the eulittoral, here meaning the intertidal zone, will rarely coincide exactly with a biological unit. This was a difficulty already recognized by Kylin (1918), who defined the 'physiological high-water line' in order to account for the effect of the modifying factors. Nevertheless, workers continued trying to correlate the borders of some conspicuous species with tidal levels in order to find an easily detectable border between the eulittoral on the one side and the supra- and sublittoral on the other side (Sjøstedt, 1928; Levring, 1937, 1940). Lewis (1961, 1962), therefore, was quite right when he objected against the procedure of trying to fit the various biotic belts into the physically defined eulittoral zone. In place of this he proposed the definition of the various belts according to their dominant organisms. An important objection to this scheme is that dissimilar environments may have the same dominant organism, as an example of this the *Fucus vesiculosus* belt may be mentioned. The floristic composition of this belt in the non-tidal Oslo Fjord (Sundene, 1953) and along the also non-tidal Swedish west coast (Kylin, 1918) differs in many respects from its composition along the tidal coasts of the Atlantic (Børgesen, 1905; Jonsson, 1912; den Hartog, 1959); in the first mentioned areas it contains numerous sublittoral species which on tidal coasts are usually only found near low-water mark.

According to Lewis the supralittoral and eulittoral cannot be regarded as separate units, because the supralittoral zone of exposed shores contains quite a number of species which are intertidal on sheltered coasts. In fact he, like Børgesen (1905), regarded the supralittoral zone merely as an upward extension of the eulittoral ('midlittoral' in his terminology). For the united eulittoral and supralittoral Lewis proposed the term 'littoral' and he defined it 'biologically' as the zone extending from the upper limit of the sublittoral organisms to the upper limit of all marine organisms. I have various objections to a littoral belt defined in this way. In the first place this definition needs to be accompanied by a definition of the concepts 'littoral organism' and 'sublittoral organism'. It is not enough just to refer to species of *Fucus* and *Laminaria* as Lewis did. Along the Atlantic coasts *Fucus vesiculosus* is confined to the eulittoral belt but in the tideless Baltic Sea it is a permanently submerged species. In the second place I think that the supralittoral and the eulittoral have to be regarded as separate biological units (see also p. 000). Along the tideless Baltic coast wave action is strong enough to produce a well-developed supralittoral zone (Du Rietz, 1925, 1932; Levring, 1940; Waern, 1952). In very sheltered localities along a tidal coast wave action is negligible and here the supralittoral is very reduced. The fact that the zonation pattern of a number of species is essentially the same on an exposed coast and on a sheltered coast indicates that in the supralittoral zone of an exposed coast wave action can produce a habitat with more or less the same gradients as produced by the tidal factor in the upper part of the eulittoral of a sheltered coast. This feature may be the key to an explanation of littoral zonation. Moreover, in all his diagrams Lewis (1961, 1964) distinguished between a 'littoral fringe' (containing the communities usually regarded as supralittoral) and a 'mid-littoral zone' (comprising the eulittoral communities). This means that he noticed himself that biological differences exist between the two zones. Although in my opinion the two zones have sufficient individuality to be kept separate, it may be useful to consider them together. In such cases I will refer to them as the 'littoral complex'.

In this paper I will approach the problem of the littoral zonation in two ways, first the littoral complex will be regarded as the transition between sea and land (see also Gerlach, 1963) and secondly, it will be regarded as the transition between sea and fresh water.

## 2. THE LITTORAL ZONE SENSU LATO AS A BORDER ZONE BETWEEN SEA AND LAND

If the intertidal belt is considered as representing the border between the sea and the land then the most important ecological factor is obviously the tidal factor, as during the periods of high water the intertidal zone is completely submerged and subjected to the marine regime, while during low tides the same zone can be regarded as a terrestrial habitat because it is then subjected to the influences governing the adjacent land habitats. In the transition zone between these two conflicting regimes one can expect the occurrence of a population composed of a mixture of very tolerant and very resistant species, penetrating the zone from the sea on the one side and from the land on the other side.

Usually when a transition zone is sufficiently stable it contains an element of its own, composed of a number of specialised forms, well adapted to the transitional environment. This is not true, however, of the rocky-shore population of the intertidal zone. It is quite obvious that here the marine element is absolutely dominant. The terrestrial element is extremely poorly represented in every respect. Among the algae there is not one terrestrial species. The littoral element is well-developed but mainly derived from marine forms. This is true for a number of *Rhodophyceae*, *Phaeophyceae*, and *Chlorophyceae*, and for most animal groups. The origin of the few intertidal *Cyanophyceae* is uncertain — they might be derived from terrestrials. The intertidal lichens, e.g. *Verrucaria mucosa* and *Lichina pygmaea*, are certainly of terrestrial origin, but are now strictly confined to the eulittoral. Most of the littoral forms of terrestrial origin are Arthropods.

Almost all the intertidal forms of the *Araneae*, *Acarina*, *Pseudoscorpionidea*, *Chilopoda*, *Collembola*, *Orthoptera-Gryllidae*, *Coleoptera-Staphylinidae*, and *Diptera-Chironomidae* belong to genera and species which are completely restricted to the intertidal environment. Only the two last-mentioned groups have species which occur in the eulittoral as well as on non-marine saline soils. None of these Arthropods penetrate the sublittoral. Although these organisms show a distinct zonation in their pattern of occurrence Schuster (1962) could not find any correlation between the zonation of these organisms with tidal levels or algal vegetations. He found, however, that they were obviously dependent on the structure of the substratum. Their penetration to lower levels is governed by the number of cavities in the substratum. These cavities are essential for the air supply needed for respiration during the period of submersion. Schuster found that they tolerate submersion in sea water much better than in fresh water.

In the supralittoral, even above the highest flood level, there are still quite a number of species of marine origin which are tolerant to long periods of desiccation and obviously obtain the salt and moisture necessary for their existence from spray. Several of these species are eulittoral on sheltered coasts but 'rise' to levels high in the supralittoral on exposed shores. In fact all species of marine origin in the supralittoral are more or less faithful to the communities of the littoral complex. The supralittoral is also the home of a number of terrestrial species which are completely absent in all other terrestrial environments. They are mainly lichens, e.g. *Lichina confinis*, *Verrucaria maura*, *Caloplaca marina*, *Lecanora actophila*, *L. helicopis*, *Rhizocarpon constrictum*, and *Ramalina siliquosa*, but bryophytes, e.g. *Schistidium maritimum*, and the small fern *Asplenium marinum* also belong to the faithful species of the supralittoral. A few of these true supralittoral species invade the upper part of the eulittoral on sheltered coasts. Further the supralittoral contains a number of resistant and salt-tolerant terrestrial species, some of which can even tolerate a short-lasting submersion in sea water, e.g. species of the lichen genera *Parmelia*, *Lecidea*, *Xanthoria*, *Rhizocarpon*, *Ramalina*, and *Lecanora*. The last four genera have also developed true supralittoral species (Davy de Virville, 1930, 1932, 1938, 1940; Davy de Virville & Fischer-Piette, 1931; Du Rietz, 1925, 1932; von Hübschmann, 1957; Degelius, 1939). It is striking, however, that the marine influence in this terrestrial domain is still so important that the majority of the species, no matter whether they are of marine or terrestrial origin, are restricted in their distribution to this zone. The conclusion to be drawn here is that the intertidal zone cannot be regarded as the transition zone between sea and land; this transition zone consists of the intertidal belt and the supralittoral together.

The conclusion reached by Southward (1958) that the variation in water-level is the primary factor causing the littoral zonation pattern has to be reconsidered. Wave action, regarded by Southward merely as a modifying factor, is just as important. It is probably even more important when looked upon from the point of view expressed by T. A. & A. Stephenson (1949). 'In a marine area with no tide and no wave action there would thus be zones corresponding to our supralittoral and infralittoral zones at once, each with its subzones. If we add considerable and steady wave action but no tide, we produce a third zone, the littoral, related to the average amplitude of the waves. We therefore have all essentials of intertidal zonation without any tide at all; but naturally if tidal action is added to the effects of wave action and of an interface between air and water, the zonation is strengthened and made more marked.' The importance of the wave action factor is also supported by the observation made by Lewis (1961) and other investigators that the belt of *Verrucaria maura* which is supralittoral on exposed shores occurs within the tidal limits on very sheltered shores without spray. In such places one sometimes can find that salt-tolerant terrestrial lichens are submerged during spring tides. Given an ideal coast without wave action then the vertical tidal oscillations will cause the littoral zonation. As soon as wave action becomes involved the plant and animal communities will move up the shore. When the degree of exposure to wave action increases these communities become more and more independent of the fluctuations in the water-level. Generally one can state that on sheltered shores wave action modifies the effect of the tidal movements, while on exposed shores the tidal movements modify only the effect of the wave action. Thus the transition zone between sea and land is generally governed by two cooperating factors, the tidal movements and the wave action ('spray').

It is known, however, that there are some areas where the pattern of the zonation is in general lines similar to that of a tidal coast but does not seem to be coupled to factors as vertical water movements and spray. In the Skagerrak, the Oslo Fjord, and the Kattegat, where the differences between high and low tides are very small, the general zonation pattern is the same as that on the west coast of Europe but is not correlated to level fluctuations. At irregular intervals strong off-shore winds cause changes in the water level, which can considerably exceed the fluctuations due to the tides; during such wind-induced low-water periods a part of the *Fucus vesiculosus*-belt may become uncovered. In these areas the *Fucus serratus*-belt remains permanently submerged. This phenomenon can be ascribed to the periodic influence of surface water of low salinity. The gradually decreasing light intensity in this sublittoral environment may also be of importance (den Hartog, 1959). In the southern Kattegat and in the Baltic the influence of low-salinity surface water becomes more and more evident. Parallel with the decrease in salinity the *Fucaceae* and *Laminariaceae* move deeper and deeper and the number of littoral species dwindles out. *Fucus serratus* does not reach the Baltic, but *Laminaria saccharina* (L.) Lamour. still occurs as far as Kiel Bay, and *Fucus vesiculosus* reaches the treshold of the Bothnian Gulf, where it occurs down to 10 m depth (Waern, 1952). In the northern Atlantic also the occurrence of usually littoral species in the sublittoral has been recorded. T. A. & A. Stephenson (1954) found that on the northern coast of Prince Edward Island (Nova Scotia) the *Fucus vesiculosus*-belt extended to below low-water mark, and that *Fucus serratus* occurred exclusively in the sublittoral. Similar records of 'submergence' of littoral species have been found along the Murmansk coast (Guryanova, Sachs & Uschakov, 1930), Greenland (Lund, 1954, 1959) and Novaya Zemlya (Zinova, 1929). This can be explained by the presence of low-salinity surface water, especially in the periods of melting ice. The phenomenon that in low-salinity waters many littoral species move into deeper water is not restricted to the algae; it has been observed in many animal groups as well. Remane (1955) refers to it as 'brackish-water submergence'. It has been observed for both littoral and sublittoral species.

This feature, however, is extremely important with respect to a possible explanation of the littoral zonation. Spray and fluctuations of the water-level are compound factors having a common salinity component. The degree of submergence of littoral organisms in a stratified brackish water such as the Baltic shows an obvious correlation with salinity and submergence itself rules out the possibility of desiccation being a causal factor in the zonation pattern of the littoral species which exhibit this. The fact that the salinity factor seems to be involved in the littoral zonation opens the possibility for considering the littoral complex as a transition zone between the sea and the fresh-water regime.

## 3. THE LITTORAL ZONE SENSU LATO AS A BORDER ZONE BETWEEN SEA AND FRESH WATER

Dahl (1959) has pointed out that the eulittoral zone must certainly have been one of the habitats where brackish-water species have evolved from marine organisms. The first step in becoming a poikilohaline brackish-water species is in fact already taken by every sublittoral species that penetrates into the intertidal zone. During the period of emersion the upper part of the population of such species is exposed to the various influences of the weather; they have to adapt to these influences in order to be more than ephemerous inhabitants. The extent to which they colonize the eulittoral zone can be taken as a measure of their ecological tolerance. Dahl supposed that the next step is the development of a special taxon completely confined to the intertidal zone. This is often accompanied by the loss of the pelagic phase in the life cycle, a factor of particular importance for many marine animals. Dahl wrote that 'at this stage we cannot any longer say definitely whether a species should be called marine or not, even if it lives on an oceanic coast.'

I have taken up this line of thought again (den Hartog, 1964, 1967) by regarding the intertidal zone as an area of conflict between the sea and fresh water. I have classified it as one of the main brackish habitats. The 'brackish' character of the intertidal zone is brought about by the alternation of submersion and emersion.

During the submersion period the intertidal population is subjected to the marine surface water which generally has a more or less constant salinity. During the period of emersion the same population is subjected to the direct influence of the weather. This means that in wet weather the species in the intertidal belt must be able to withstand rain for several hours, and at the higher levels possibly for several days. Further they must equally be able to withstand similar periods in which dry off-shore winds or strong insolation can cause desiccation. As a result of desiccation the salinity concentration increases. Finally they must be able to withstand the sudden shock of becoming submerged again and to re-adjust their metabolism to the marine concentration. There is thus every reason to regard the intertidal zone as an environment with unstable salinity conditions.

The level of mean high-water springs, however, is not the upper limit of the marine influence. Therefore, in my former paper on this subject (den Hartog, 1967) the matter was treated too simply. The supralittoral zone is also a part of the border environment between the conflicting marine and fresh-water regimes (Fig. 1).

The marine influence is exercised by the tidal movements and by wave action, in the form of wash, splash, and spray. The aerial transport of sea salt in the wind has been left out of consideration as the influence of this factor can be felt so far inland that it cannot be taken into account in a discussion of the littoral border environment. The availability of aerial salt certainly is responsible for the distribution of several maritime organisms for which the supralittoral is too saline, or for the unexpected occurrence of characteristic

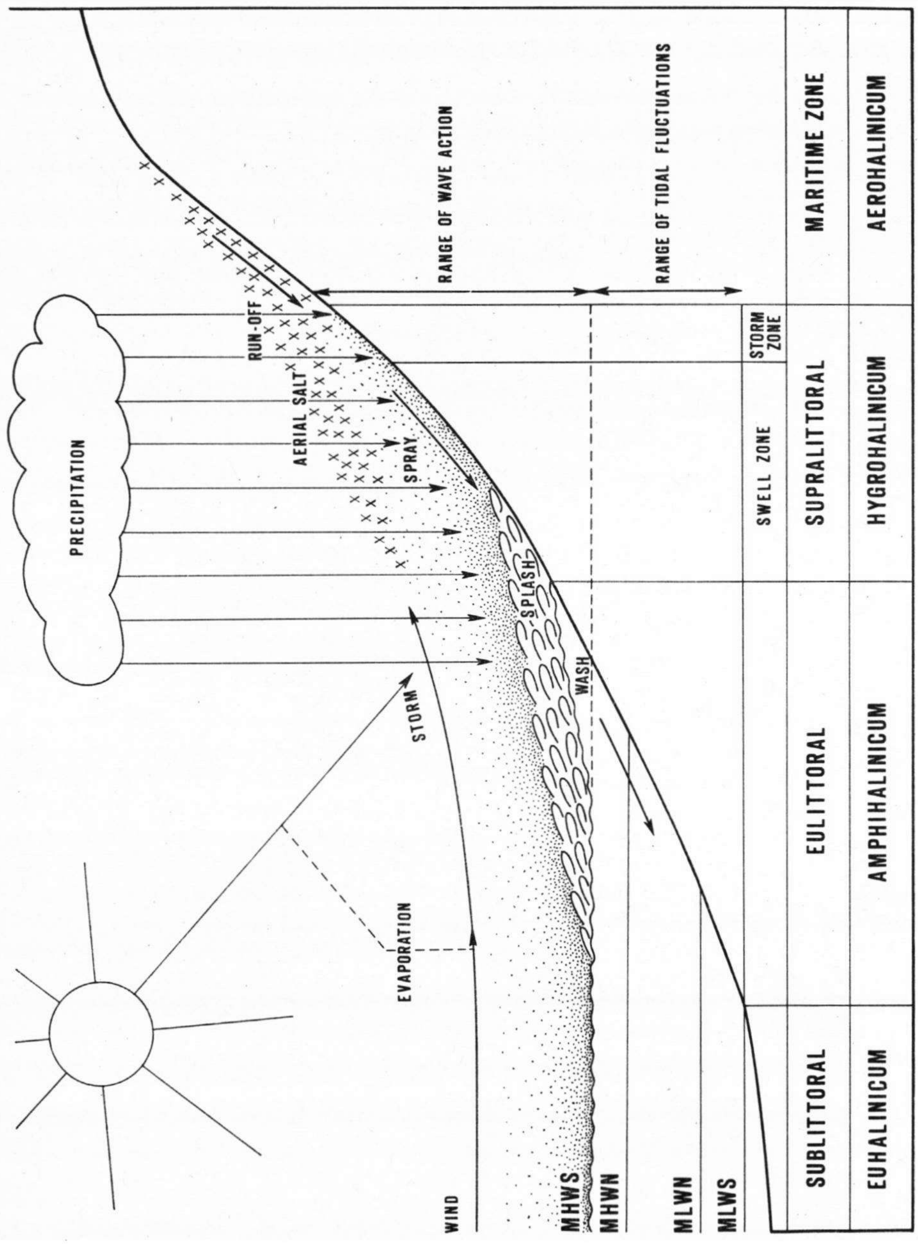

Fig. 1. Diagram of the conflict situation between the sea and the fresh water on a rocky shore.

littoral species at some distance from the sea, e.g. *Rhodochorton purpureum* in the streets of Flushing.

The fresh-water influence is exercised mainly by the various forms of precipitation, such as rain, snow, dew, etc. Further there is the surface run-off, which is usually considerably enriched by dissolved materials from the ground over which it has flown. Besides mineral compounds this run-off water also contains organic substances originating from bird droppings and rotting seaweeds. It can have a marked effect on the composition of the vegetation, as it favours the growth of *Prasiolaceae*. According to Du Rietz (1925, 1932) and Degelius (1939) the lichen vegetations on supralittoral rocks frequently visited by birds are quite different in composition to those not frequented by birds.

Further, phreatic fresh water may trickle along the rocks. This usually follows the small gullies cut through the littoral zone, giving rise to a very special eulittoral biotope, the 'shock biotope', where during every tidal cycle two sudden salinity 'shocks' take place, one from a minimum to a maximum and the other vice versa. This biotope is inhabited by a very characteristic fauna of amphipods, isopods, archiannellids, and turbellarians, some of which are faithful indicator species. The vegetation is limited to *Blidingia minima* and a few *Enteromorpha* species, if there is any vegetation at all.

On a coast with a semidiurnal tidal cycle the littoral border environment can be subdivided into a number of belts, according to the discontinuously increasing fresh-water influence. Although I am well aware that the relation with the tidal levels is only indirect, as it is the modifying factors which finally determine the actual position of the belts, nevertheless I will use the tidal levels to indicate the various belts, as this seems the clearest way to demonstrate the discontinuity in the gradient of the fresh-water influence.

1. The belt between the levels of mean low-water springs and mean low-water neap is exposed only for very short periods and the effect of weather conditions is small. As a result the fluctuations in salinity are usually small. However, when low water and pouring rain coincide they can have a very destructive effect on the algal growth, since stenohaline forms die under such conditions.
2. The belt between the levels of mean low-water neap and mean high-water neap is covered and uncovered during every tidal cycle. As a consequence of the relatively short periods of exposure the salinity fluctuations are not very extreme. Most of the algae occurring in this belt are rather euryhaline and penetrate into the polyhaline section of estuaries.
3. The belt between the levels of mean high-water neap and mean high-water springs is submerged only for very short periods and most of the time is fully exposed to the various weather conditions. The fluctuations in the salinity are very large. The algae of this belt must be euryhaline and several of them are widely distributed in other brackish waters.
4. Above the level of mean high-water springs there follows a belt which is more or less continually under the influence of splash, spray, and aerial salt transport. The lower part of this belt is reached by the sea now and then. This belt is the 'swell zone' or lower supralittoral as defined by Sjøstedt (1928). The salinity in this belt fluctuates greatly, extremes being due to excessive evaporation or excessive rain fall. The average salinity here is completely dependent on climatic circumstances.
5. Finally there is a belt where the spray exercises its influence only seasonally and during storms. This belt is the 'storm zone' or upper supralittoral in the sense of Sjøstedt (1928). The salinity in this belt is on an average very low, but may increase considerably during periods of bad weather.

This exposition of the littoral zonation between the fully marine sublittoral and the maritime zone beyond the reach of the sea water would not be complete without reference to the occurrence of a disturbance belt between the levels of extreme low low-water springs and of mean low-water springs. This strip is either partly or completely uncovered only a few times each year and then for very short periods. The chance that its vegetation and fauna will be damaged during such an emersion period is small, but this does happen now and then.

Although one would expect a similar disturbance belt at the border between the storm zone and the maritime zone, as the force of storms is also a very variable factor and the influence of the spray will vary with it, this is not the case as the effects of exceptional conditions are neutralized by the fact that the maritime zone is normally under the influence of aerial salt.

When the littoral zone *sensu lato* is considered as a conflict area between the sea and fresh water it appears that the marine element is preponderant among its flora and fauna. Further, there are a number of species, mostly of marine origin, characteristic for such conflict areas, and undoubtedly these are brackish-water species. Examples are *Blidingia minima*, *Monostroma oxyspermum*, and various *Enteromorpha* species. Generally there is no fresh-water element. This is in fact not surprising as the fresh water involved originates directly or indirectly from precipitation, and thus has a very ephemerous character. True fresh-water species occur in the supralittoral, where phreatic water flows off, e.g. *Cladophora glomerata* (L.) Kütz. The weak representation or total absence of a fresh-water element is a regular feature of the various conflict areas between sea and fresh water. In the estuary of the rivers Rhine, Meuse, and Scheldt, where there is open communication between the sea and fresh water, the fresh-water element in the benthos is only represented by a few animals which occur in the section with an average salinity between 0.3 and 1.8 $^0/_{00}$ Cl′ (den Hartog, 1967, 1968, unpubl.).

Further, there are species which seem to be confined to the eulittoral and the supralittoral, and which seem to be faithful indicator species for the littoral border environment. If the reaction of these various littoral species to salinity is considered it becomes obvious that this group is very heterogeneous with several of the species showing the feature of submergence in brackish water, descending into the sublittoral to a considerable depth. In his study on submergence in brackish water Remane (1955) distinguished three different types of submergence.

a. In the case of 'upper-limit submergence' only the upper limit of a species is involved. It can be caused by several factors. Decreased salinity of the surface water drives the species to greater depths where the salinity conditions are more in agreement with their physiological requirements. In transition areas, such as the Skagerrak and the Kattegat the change from the regular tidal movements to irregular wind-induced fluctuations of the water-level excludes several sublittoral species from the lower levels of the eulittoral. Unfavourable temperatures may also cause a downward shift of the upper limit of a species, especially along the border of its area of distribution.

b. 'Basal submergence' involves the lower limit of a species descending to greater depths when it penetrates into the brackish-water environment. The species involved are usually eurybiontic species and in brackish waters, therefore, they have less competition from stenohaline species. This appears to be the deciding factor for the downward extension of their distribution. Examples are given in table 1.

Table 1

LITTORAL SPECIES WHICH EXHIBIT BASAL BRACKISH-WATER SUBMERGENCE

- Chlorophyceae:
  - Enteromorpha intestinalis (L.) Link
  - Enteromorpha prolifera (O. F. Müll.) J. Ag.
  - Rhizoclonium riparium (Roth) Harv.
  - Ulothrix flacca (Dillw.) Thur. in LeJol.
  - Ulothrix pseudoflacca Wille
  - Ulothrix subflaccida Wille
- Rhodophyceae:
  - Hildenbrandia prototypus Nardo
  - Rhodochorton purpureum (Lightf.) Rosenv.

c. 'Complete submergence' involves the descent of both the upper and lower limits of a species. This feature is shown by many littoral species in the Kattegat and the Baltic. These algae usually follow the layer of water with the same salinity conditions and dwindle out where this layer reaches a depth where light becomes the limiting factor. Examples are given in table 2.

Table 2

LITTORAL SPECIES WHICH EXHIBIT TOTAL BRACKISH-WATER SUBMERGENCE

- Chlorophyceae:
  - Monostroma grevillei (Thur.) Wittr.
  - Tellamia contorta Batt.
- Phaeophyceae:
  - Ascophyllum nodosum (L.) LeJol.
  - Elachista fucicola (Vell.) Aresch.
  - Fucus distichus L.
  - Fucus serratus L.
  - Fucus vesiculosus L.
  - Pilayella littoralis (L.) Kjellm.
  - Ralfsia verrucosa (Aresch.) J. Ag.
  - Spongonema tomentosa (Huds.) Kütz.
- Rhodophyceae:
  - Callithamnion scopulorum C. Ag.
  - Dumontia incrassata (O. F. Müll.) Lamour.
  - Gigartina stellata (Stackh.) Batt.
  - Plumaria elegans (Bonnem.) Schm.

'Submergence' has not been recorded for algae in estuaries. This is easily explained by the fact that in the estuarine environment the daily salinity fluctuations are generally too large and the salinity stratification too unstable for most algae. I have already shown earlier (den Hartog, 1964, 1967) that under the rather stable salinity conditions of the Baltic many algae and animals can live permanently in water with a much lower average salinity than they can withstand in an estuary. Further, as the waters of estuaries are usually loaded with suspended material light penetration is strongly reduced, preventing any considerable descent of the algae. Finally, because of sediments the substratum in estuaries is often unsuitable for epilithic algal growth. It has to be pointed out, however, that some animals from sand- and sediment bottoms do show submergence in the estuarine environment. The amphipod *Bathyporeia pilosa* Lindström offers an excellent example of 'complete submergence' (Vader, 1965), while the polychaete *Nereis diversicolor* O. F. Müll. shows only 'basal submergence'.

It is apparent that the tidal alternation of emersion and submersion is not at all essential to the species which submerge in brackish water. The latter are partly specialists adapted to a certain range of salinity fluctuations and partly extremely eurybiontic species with a reduced capacity for competing with stenobiontic forms in a stable environment.

Submergence in brackish water is not exhibited by supralittoral species, nor by a considerable number of eulittoral species. These all remain in the zone of the water fluctuations, in the wave-dashed zone, or in the spray zone. Remane (1955) had already observed that the forms which have invaded the littoral zone from the fresh-water and terrestrial domains do not exhibit submergence in brackish water. He gave as examples the oligochaetes, the rotifers, and the *Halacaridae*. To these I can add the lichens and the musci. It is in fact remarkable that almost all the species which are typically 'littoral' inhabit the higher belts on the shore, where they are not exposed to the daily tidal rhythm, but rather to the irregularities in the tidal rhythm and to the spray.

A list of species which are restricted to the littoral zone and do not exhibit submergence in brackish water is given in Table 3.

Table 3

SPECIES CONFINED TO THE LITTORAL COMPLEX

Chlorophyceae:
  Supralittoral:
    Blidingia marginata (J. Ag.) Dangeard
    Monostroma groenlandicum J. Ag.
    Prasiola stipitata Suhr in Jessen
    Rosenvingiella constricta (Setch. & Gardn.) Silva
    Rosenvingiella polyrhiza (Rosenv.) Silva
    Urospora hartzei Rosenv.
    Urospora penicilliformis (Roth) Aresch.
  Eulittoral:
    Blidingia minima (Näg. *ex* Kütz.) Kylin
    Capsosiphon fulvescens (C. Ag.) Setch. & Gardn.
    Monostroma oxyspermum (Kütz.) Doty
Phaeophyceae:
  Supralittoral:
    Waerniella lucifuga (Kuck.) Kylin
  Eulittoral:
    * Fucus spiralis L.
    * Fucus virsoides (Don) C. Ag.
    * Mesospora macrocarpa (Feldm.) den Hartog nov. comb. 1)
    * Nemoderma tingitanum Schousboe
    * Pelvetia canaliculata (L.) Dcne & Thur.
    * Petalonia zosterifolia (Reinke) Kuntze

* Species which need to be submerged now and then in undiluted sea water to survive.

Eulittoral, but also in pools:
- * Bifurcaria bifurcata Ross
- * Cystoseira myriophylloides Sauv.
- * Elachista scutulata (Sm.) Aresch.
- * Herponema velutinum (Grev.) J. Ag.
- * Himanthalia elongata (L.) S. F. Gray

Rhodophyceae:
- Supralittoral:
  - Bangia fuscopurpurea (Dillw.) Lyngb.
  - * Porphyra linearis Grev.
- Eulittoral:
  - Bostrychia scorpioides (Huds.) Mont.
  - * Callithamnion arbuscula (Dillw.) Lyngb.
  - * Callithamnion tetricum (Dillw.) S. F. Gray
  - Catenella repens (Lightf.) Batt.
  - * Caulacanthus ustulatus (Mert.) Kütz.
  - * Ceramium deslongchampsii Chauv. in Duby
  - * Ceramium shuttleworthianum (Kütz.) Silva
  - * Erythrotrichia welwitschii (Rupr.) Batt.
  - * Gelidium spinulosum (C. Ag.) J. Ag.
  - * Lithophyllum tortuosum (Esper) Foslie
  - * Nemalion helminthoides (Vell. in With.) Batt.
  - * Polysiphonia lanosa (L.) Tandy
  - Porphyra elongata (Aresch.) Kylin
  - * Porphyra leucosticta Thur. in LeJol.
  - * Porphyra purpurea (Roth) C. Ag.
  - * Porphyra umbilicalis (L.) J. Ag.
  - * Rissoella verruculosa (Bertoloni) J. Ag.

Cyanophyceae:
- Supralittoral:
  - Calothrix scopulorum [(Web. & Mohr) C. Ag.] Born. & Flah.
  - Entophysalis deusta (Menegh.) Dr. & D.
  - Lyngbya confervoides [C. Ag.] Gom.
  - Lyngbya majuscula [(Dillw.) Harv.] Gom.
  - Lyngbya semiplena [(C. Ag.) J. Ag.] Gom.
  - Microcoleus tenerrimus Gom.
  - Plectonema battersii Gom.
  - Schizothrix calcicola [C. Ag.] Gom.
  - Symploca atlantica Gom.
- Eulittoral:
  - * Rivularia mesenterica (Thur.) Born. & Flah.
  - * Rivularia bullata [(Poir.) Berk.] Born. & Flah.

Lichens:
- Supralittoral:
  - Anaptychia fusca (Huds.) Vain.
  - Bacidia umbrina (Ach.) Bausch var. marina Degelius
  - Caloplaca aractina (Fr.) Häyrén
  - Caloplaca granulosa (Müll. Arg.) Jatta
  - Caloplaca marina (Weddell) Zahlbr.
  - Caloplaca scopularis (Nyl.) Lettau
  - Caloplaca thallincola (Weddell) DR.
  - Catillaria chalybeia (Borr.) Mass.
  - Lecanora actophila Weddell
  - Lecanora helicopis (Wahlenb.) Ach.
  - Lecanora leprosescens Sandst.
  - Lecanora poliophaea (Wahlenb.) Ach.
  - Lecanora rimicola H. Magn.
  - Lecanora salina H. Magn.
  - Lichina confinis (Müll.) C. Ag.
  - Physcia subobscura Nyl.
  - Ramalina siliquosa (Huds.) A. L. Sm.

- Rhizocarpon constrictum Malme
- Rinodina salina Degelius
- Roccella fuciformis (L.) DC.
- Verrucaria ceuthocarpa Wahlenb.
- Verrucaria maura Wahlenb.
- Verrucaria symbalana Nyl.

Eulittoral:

- Arthopyrenia orustensis Erichs.
- * Lichina pygmaea (Lightf.) C. Ag.
- Verrucaria erichsenii Zschacke
- Verrucaria microspora Nyl.
- Verrucaria mucosa Wahlenb.

Ascomycetes:
  Eulittoral:
    * Didymella balani (Winter) Feldm.
Bryophyta:
  Supralittoral:
    Schistidium maritimum (Turn.) B.S.G.
Ferns:
  Supralittoral:
    Asplenium marinum L.
Angiospermae:
  Supralittoral:
    Crithmum maritimum L.
    Inula crithmoides L.
    Spergularia rupicola Lebel *ex* LeJol.

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[1]) **Mesospora macrocarpa** (Feldm.) den Hartog, *nov. comb.* — *Ralfsia macrocarpa* Feldm., Bull. Soc. Hist. Nat. Afr. Nord 22 (1931) 211—213, Pl. 10, *pro parte.* — *Mesospora mediterranea* Feldm., ibid. 26 (1935) 364—365; Rev. Algol. 9 (1937) 263—267, f. 40—41.

In his paper on 'Les algues marines de la Côte des Albères' Feldmann (1937) recorded that his earlier described species *Ralfsia macrocarpa* in fact had been based on a mixtum, viz. a sample of *Ralfsia verrucosa* (Aresch.) J. Ag. overgrown by *Mesospora mediterranea.* In his original description of *R. macrocarpa* he had indeed reported that the structure of the thallus of this 'species' was very similar to that of *R. verrucosa,* but that it differed in the sizes of the unilocular sporangia and the paraphyses, and by the presence of small pedicellar cells at the base of the sporangia. The insertion of the pedicellate sporangia, not only at the base but also on the middle part of the paraphyses, was regarded as 'absolument caractéristique du *Ralfsia macrocarpa*'. All these differentiating features appeared to be characteristic of *Mesospora mediterranea.*

Although the mode of growth of these crustaceous brown algae does not permit a separation of the material it is possible by means of cross-sections to observe the line of demarcation between the *Ralfsia* and the *Mesospora* elements (see Feldmann, 1937, p. 267). The preparation of cross-sections is indispensable for the identification of crustaceous *Phaeophyceae.* Therefore, the name *Ralfsia macrocarpa* does not have to be rejected as it is possible to select one of these elements as a satisfactory type (Article 70 of the Intern. Code of Bot. Nomencl.). The transfer of the epithet *macrocarpa* from *Ralfsia* to *Mesospora* is the nomenclatural consequence of this.

Of these species only a few seem to be confined to the lower levels of the intertidal belt, e.g. *Himanthalia elongata* and *Bifurcaria bifurcata.* As these species inhabit both places where they become fully exposed to the air and littoral pools it is improbable that they are ecological specialists. They are probably restricted to the eulittoral as a result of competition with the sublittoral dominants. A similar explanation can perhaps be given for the occurrence in the eulittoral of some *Rhodophyceae,* such as *Callithamnion arbuscula, C. tetricum,* and *Ceramium shuttleworthianum. Elachista scutulata* and *Herponema velutinum* are specific epiphytes of *Himanthalia elongata,* and are for that reason limited to the eulittoral. *Cystoseira myriophylloides* is only known from pools in the upper part of the eulittoral; in this case competition with the sublittoral *Cystoseira* species is probably the reason for restricting its distribution to such an unusual biotope.

Among the high-littoral and supralittoral species two groups can be recognized, one of species which seem to be quite insensitive to a lowering of the salinity of the flood water or the spray, and the other of species confined to the fully marine coast. The first group contains some species which occur along every coast and which penetrate even into freshwater, e.g. *Bangia fuscopurpurea* and *Blidingia minima*. Many species in this group depend on contact with the air for their metabolism, e.g. the lichens and the nitrogen-fixing *Cyanophyceae*. The other group contains species such as *Pelvetia canaliculata*, *Fucus spiralis*, *Porphyra umbilicalis*, and *Nemalion helminthoides*, which can tolerate enormous fluctuations in the salinity but for some reason seem to need undiluted sea water to survive. Among the animals of this group some can be considered to be stenohaline, e.g. the barnacles *Balanus balanoides* (L.) and *Chthamalus stellatus* (Poli). During the periods of emersion they keep their valves closed, avoiding every contact with the surroundings, opening them during the short period of submersion when they feed. Their pelagic larvae are strictly marine. Similar mechanisms to escape unfavourable effects during the emersion period occur among molluscs. The gelatinous structure of the thalli of *Nemalion* and *Rivularia* probably has a protective function also. All representatives of this group of 'stenohaline' eulittoral species are adapted to water metabolism.

The group of species which do not submerge in brackish water are the true littoral species, and as they show a great tolerance with regard to salinity they could be regarded as brackish-water species. However, when the various mechanisms developed by some stenohaline marine species to escape the effects of the instability of the habitat are taken into account, then it seems more correct to regard them as indicator species of the littoral border environment.

The fact that the great majority of the true littoral species are restricted to the supralittoral and the uppermost part of the eulittoral accentuates the importance of wave action on the process of speciation.

As both the factors wave action and fluctuation of the water level have a salinity component in common, one may wonder whether salinity alone is the cause of littoral zonation. For the supralittoral this factor has been accepted as such, but just the bare fact that the supralittoral species do not show submergence in brackish water indicates that contact with the air is just as important for them. In the eulittoral the salinity factor is certainly of preponderant importance and the factor aerial contact seems to be of less significance. As light is the causal factor for the zonation in the sublittoral this factor must exercise also some influence in the eulittoral during the period of submersion. The influence of the light on the intertidal zonation depends on the tidal difference and on the clarity of the flood water. Thus salinity, air ('the terrestrial influence'), and light are the three major abiotic factors which dominate the littoral border environment (Fig. 2).

## 4. BIOLOGICAL STRESS AS AN ACTIVE FACTOR IN THE LITTORAL BORDER ENVIRONMENT

The joint action of the three abiotic factors salinity, air, and light is insufficient to explain the often very sharp demarcations between the belts in the littoral border environment. Without the action of a fourth factor, biological stress or competition, the various species would have much wider ranges on the shore and instead of clear-cut belts one would find a series of intensely mixed populations which gradually merge into each other. This factor is not always fully appreciated and is usually omitted in studies on littoral zonation. It is not mentioned in the work of T. A. & A. Stephenson (1949), nor in the

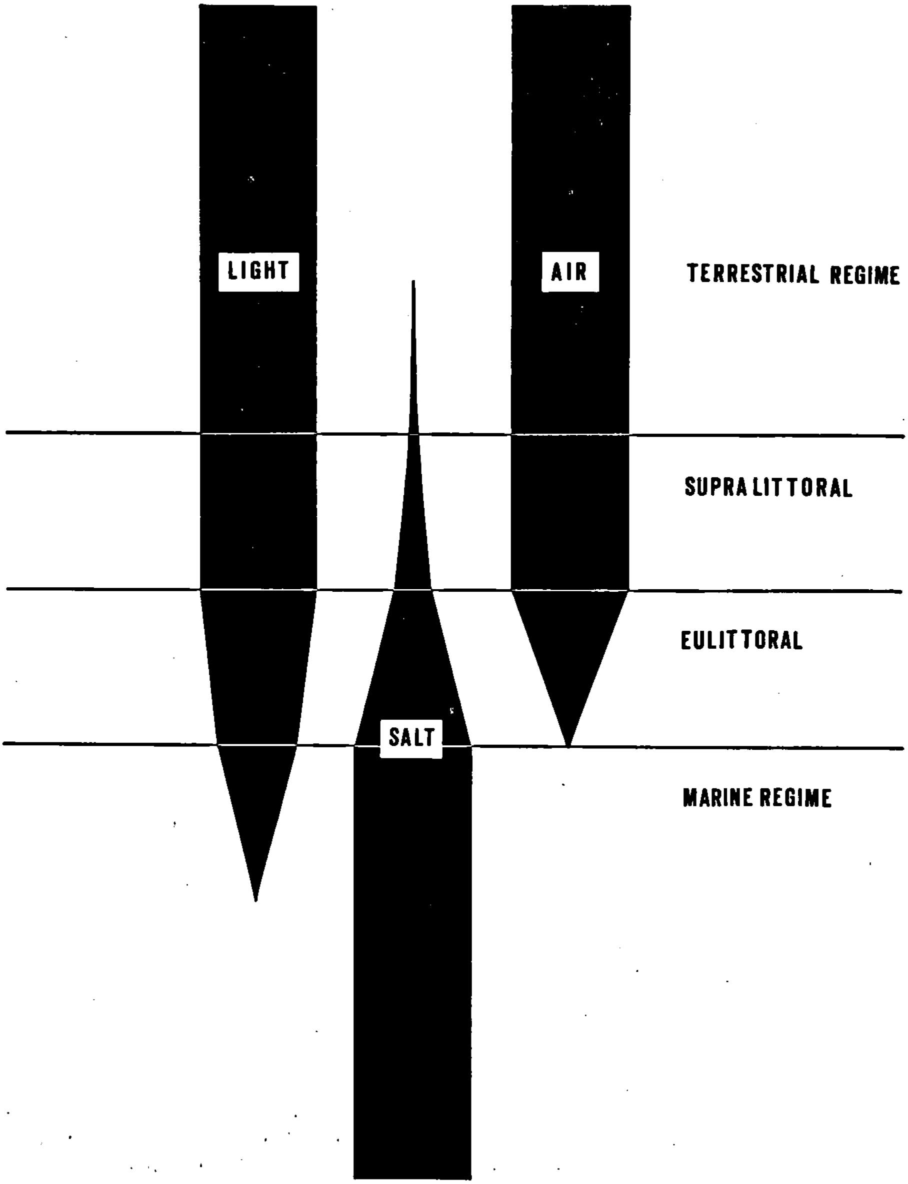

Fig. 2. Diagram showing the influence of the three abiotic major factors in the littoral complex.

works of Doty (1957), Southward (1958), Lewis (1961), and Davy de Virville (1964).

Lewis (1964), in his book 'The ecology of rocky shores', mentions the influence of biotic factors on the zonation pattern and rather reluctantly refers to the possibility of competition delimitating the lower borders of some algal belts. I must agree that one does not notice the action of competition in well-balanced communities, as there it is 100 % effective. However, from recolonization experiments it is apparent that competition must play an extremely important role in belt-forming.

Along the coast of the Netherlands, where the zonation pattern often becomes disturbed as a result of dike maintenance, I obtained some fine data which support this view. On a newly laid dike slope the following succession usually takes place in the eulittoral. At first diatoms appear, forming a brownish slime on the stones. They are soon followed by patches of *Blidingia minima, Ulothrix flacca, Enteromorpha compressa* (L.) Grev., *Ulva lactuca* L., *Pilayella littoralis, Porphyra umbilicalis*, and *P. purpurea*. Although these species at first seem to be randomly distributed the vegetation soon becomes differentiated into two belts, an upper belt dominated by *Blidingia minima* and a lower belt where *Enteromorpha compressa* is the most numerous. After a time germlings of *Fucaceae* and small *Rhodophyceae* appear in this pioneer vegetation. The various species grow at random without any trace of zonation, for example I even found *Pelvetia canaliculata* low on the shore, together with *Fucus vesiculosus, F. serratus*, and *Ascophyllum nodosum*. (Plate 1). Within a few years, however, the normal zonation pattern was reinstated.

In early spring settlement of the barnacle *Balanus balanoides* may sometimes prevent the establishment of *Chlorophyceae*.

The influence of browsing by patelloid snails on the vegetation pattern of the intertidal belt is well-known from the studies by Conway (1946), Jones (1948), Lodge (1948), Burrows & Lodge (1950), Southward (1956), and Koumans-Goedbloed (1965). In the Netherlands where *Patella vulgata* L. is too rare to have any influence on the zonation pattern its place is taken by littorinid snails (den Hartog, 1959).

I am well aware of the fact that much experimental work is needed before the role of biological stress in littoral zonation can be evaluated in its real proportions. It is, however, quite obvious that its significance for belt-forming is greatly underestimated.

## 5. THE INDIVIDUALITY OF THE SUPRALITTORAL AND EULITTORAL

Although I have discussed the supralittoral and eulittoral together the differences between them are sufficiently essential to warrant maintaining them as separate units.

The typical supralittoral is a product of wind and wave action, particularly of spray. It does not contain species whose occurrence is correlated with fluctuations of the water-level. Neither does it contain species which show 'complete submergence' in brackish water. Only a few of the species occurring in the supralittoral show 'basal submergence' in brackish water. There are no species which are confined to undiluted sea water, with perhaps a single exception. A number of salt-tolerant terrestrial species penetrate the zone from its upper side, but marine invaders from the sublittoral are absent. Many of the species occurring in the supralittoral are peculiar to this zone.

The eulittoral is essentially the zone of the fluctuations of the water-level and the wash, one of the components of the wave-action factor. It contains a well-developed marine element in the form of sublittoral species which are able to tolerate emersion to some degree. Several species are confined to the eulittoral because they cannot compete with corresponding forms in the sublittoral. A number of species show 'complete submergence' in brackish water. Further a considerable number of species, not exhibiting brackish-water submergence, are strictly confined to coasts with undiluted sea water. Although several species of terrestrial origin occur, salt-tolerant terrestrial species are generally absent. A considerable number of species occurring in the eulittoral are restricted to this zone.

The upper part of the eulittoral has a transitional character.

The number of species which are common to the supralittoral and the eulittoral is extremely small. They are all ubiquists, e.g. *Rhizoclonium riparium*, *Hildenbrandia prototypus*, and *Rhodochorton purpureum*.

The facts that increasing exposure to wave action permits eulittoral species to move into the supralittoral — often in the form of reduced specimens — and that mixed populations of eulittoral and supralittoral species occur under such conditions, seem to me insufficient reasons for regarding the supralittoral as merely an impoverished fringe of the eulittoral. These features have to be ascribed to the interference by the effects of wave action and fluctuations of the water-level.

## 6. COMPARISON WITH THE ESTUARINE ENVIRONMENT

When the littoral border environment is compared with other brackish habitats its richness in species peculiar to it is striking. In an estuary, which is also a characteristic border environment, the number of species exclusive to it is surprisingly small, and includes only one algal species, *Fucus ceranoidos L.* (den Hartog, unpubl.). Most of the species which occur only in estuaries are confined to its intertidal zone or its supralittoral. In fact they belong not to the estuary but to the estuarine extension of the littoral border environment.

In the discussion of the littoral zone in its widest sense it became obvious that wave action must have exercised a much greater influence on the speciation than the tidal movements. In the estuarine environment tidal action is the most important factor, and its influence extends much further than that of the salt. In the littoral border environment just the reverse is true. This could indicate that the influence of marine salt out of the reach of the regular tidal rhythm creates conditions favourable for speciation. In this respect it is interesting that the littoral border environment of fresh-water tidal areas seems to be devoid of species exclusive to it (Caspers, 1955; den Hartog, 1967).

## 7. A NOTE ON TERMINOLOGY

It has been shown that the littoral border environment is a brackish environment, and one may wonder whether this should be expressed in the names given to the various belts. Such a terminology has already been applied by Du Rietz (1925, 1932) in his work on the zonation along the Baltic coast, and by Degelius (1939) in his work on the lichens of the Swedish west coast. Du Rietz distinguished an 'hydrohaline zone', more or less coinciding with the joint eulittoral and sublittoral. Degelius applied the term hydrohaline in the sense of eulittoral. For this reason the term 'hydrohaline' can better be avoided. The term 'amphihaline', now proposed, expresses in fact better the character of the eulittoral zone. The 'hygrohaline zone' of Du Rietz and Degelius coincides with the supralittoral, and their 'aerohaline zone' is exactly the same as the maritime zone, i.e. the part of the terrestrial area that is under the influence of wind-transported marine salt.

The terminology used by Du Rietz and Degelius may please those who object to the use of the term littoral, as this has been used in several senses and thus may sometimes cause confusion. It may also be useful to those who reject the use of the term supralittoral and prefer a dubious term like 'littoral fringe'. The new terms are not charged with any other interpretation. Although I myself prefer the current 'littoral terminology' I consider the terms presented here to be fully equivalent alternatives, as long as they are applied to marine coasts. Another set of terms has been proposed by Du Rietz in 1940 in an attempt to unify the terminology for the zonation of the sea shore and that of the shores of lakes and other inland waters ('limnological-thalassological zonation system'), but these were too complicate to meat any approval.

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