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MARINE COASTAL ZONATION IN SOUTHERN AUSTRALIA IN RELATION TO A GENERAL SCHEME OF CLASSIFICATION

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(*With one Figure in the Text*)

Introduction

Marine ecological studies on coastal regions have been greatly advanced in recent years by the publications of T. A. Stephenson and his co-workers on the South African intertidal zone. In three papers Stephenson (1939, 1944 and 1947) described the zonation and distribution of marine animals and algae over nearly 2000 miles of South African coast. In a later paper T. A. & A. Stephenson (1949) have proposed a general scheme for the zonation of organisms between tide-marks (including the zones above and below the actual intertidal zone), which they believe will apply to rocky coasts generally. This scheme was founded on studies of coasts in England, parts of the Indian Ocean, on both Atlantic and Pacific coasts of North America and on the Great Barrier Reef, as well as on their South African survey. Stephenson has examined more coastal regions than any other worker in marine ecology, and consequently is in an excellent position to put forward a generalized scheme.

However, while aware that we have seen a comparatively small range of coasts, it appears to us that the Stephensons' scheme does not apply satisfactorily to Southern Australian coasts, and also that certain objections can be raised to their terminology.

This paper aims at setting out our criticisms of their scheme, and proposing a modified scheme which we have found satisfactory for Southern Australian coasts. Our proposed scheme appears, from published descriptions of coasts elsewhere in the world, to be of general application.

The scheme does not involve any fundamentally new terms. It is, rather, an integration of terms and zones, used by other marine ecologists, which seem most suitable to Australian conditions.

With much of the Stephensons' paper, however, we are in full agreement. Their discussion of 'standard' zonation, and variations from this, hold for Southern Australian rocky coasts, and while balanoid and littorinid zones are features of most of our coasts, we agree that these terms cannot be used in a general scheme.

The Stephensons' scheme, from the title of their 1949 paper, is intended to apply to rocky coasts. A general scheme of coastal zonation should be applicable to any type of coast (whether it be a gently shelving mud flat with a sandy beach or mangroves at the rear, the many variations of rocky coasts, or any other kind). Whilst schemes developed for rocky coasts will probably be applicable to other types of coast, this may not always be so. In particular, different species may need to be used as indicator species.

In a later paper we propose to give a more detailed description of the generalized algal and animal zonation on Southern Australian coasts, in which further supporting evidence for the scheme set out below will be given. Papers by Womersley (1947, 1948) and Edmonds (1948) have previously described the basic zonation on parts of the coast of Kangaroo Island, South Australia.

THE SUBLITTORAL ZONE

The littoral-sublittoral boundary

The evidence of many observers suggests that on most coasts there exists an important critical level in the vertical distribution of organisms at some distance above extreme low water mark of spring tides (E.L.W.S.).

On the Pacific coast of the United States of America, Doty (1946) found that this level corresponded with the mean of lowest low water, which was about 18 in. above the lowest low of low water* (E.L.W.S.). His figures show strikingly that this level is by far the most important tidal level for limitation of algal species.

Colman (1933), in his detailed survey of zonation in Wembury Bay, England, found critical levels between M.L.W.S. and E.L.W.S. and also between M.L.W. of neap and spring tides.

Evans (1947), working near Plymouth, found that the position of critical levels changes in relation to local variations in surf action, rock configuration, and illumination, but was convinced of the real existence of critical levels. He found the region between M.L.W.S. and M.L.W.N. critical as the majority of intertidal organisms reached their lower limits here, and certain sublittoral species (including *Laminaria*) extended up to a level just below M.L.W.N.

Feldmann (1937), in his monograph on the algal vegetation of the Mediterranean, limits the littoral at zero low water, but in this sea tides are almost absent and barometric pressure and winds play an important part. Feldmann shows clearly in his Table 1 that the zero water mark is a limiting level for most species, and the number of species limited to his 0–5 m. upper infralittoral zone is most striking.

Dakin, Bennett & Pope (1948), in their study of the New South Wales coast in Australia, use the term 'littoral-sublittoral fringe'. This zone comprises the kelp zone (extending just above E.L.W.S.) and above it a zone of an ascidian *Pyura* which extends to 2 ft. above E.L.W.S. The *Pyura* zone here may perhaps be better placed in the littoral zone, and the top of the kelp considered as marking the sublittoral-littoral boundary.

Stephenson (1944, p. 335) regards the *Pyura* of South African coasts as forming part of his sublittoral fringe, as it occurs at the same level as the uppermost kelp. This appears to be different from the position in New South Wales. Stephenson & Stephenson (1949) in their generalized scheme draw their midlitorral-infralittoral fringe boundary at the top of the zone of laminarians (or other dominant algae).

Our experience on Southern Australian coasts is that there is a most important critical level a short distance above E.L.W.S. The small tidal rise along most of the coast (2–4 ft.) makes accurate fixing of this critical level difficult, but below it there exists a zone of brown

* There is need for standardization of terminology used in relation to tidal phenomena. The following levels seem to be of general importance, and are abbreviated as follows in this paper:

E.H.W.S. = Extreme high water of spring tides.
M.H.W.S. = Mean high water of spring tides.
E.H.W.N. = Extreme high water of neap tides.
M.H.W.N. = Mean high water of neap tides.
M.S.L. = Mean sea level.
M.L.W.N. = Mean low water of neap tides.
E.L.W.N. = Extreme low water of neap tides.
M.L.W.S. = Mean low water of spring tides.
E.L.W.S. = Extreme low water of spring tides.

algae (*Cystophora* spp., *Sarcophycus* and sometimes *Sargassum*) or occasionally of red algae in some calm localities (e.g. *Hypnea*, *Spyridia* (Womersley, 1947)).

All the above reports, as well as many others, on widely scattered areas of coasts, have recognized the existence of a critical level some distance above E.L.W.S. Where accurate studies have been made its position has been fixed at somewhere between or about M.L.W.S. and M.L.W.N., but the precise level probably varies slightly under different conditions of wave action, rock configuration, etc. In any case, it seems logical that this natural line of demarcation should be fixed as the littoral-sublittoral boundary.

Further, the work of Evans and Doty shows that below M.L.W.S. the amount of exposure to air is very small (less than 3 or 4 %), while it increases rapidly above M.L.W.S. This small degree of exposure is unlikely to affect the distribution of many organisms, especially where there is some wave action to wet this zone at extreme low tides.

On most coasts of cold-temperate regions the top of the zone of large brown algae (laminarians or fucoids) can safely be considered to mark the littoral-sublittoral boundary. On tropical coasts the upper boundary of corals and *Sargassum* could be used, though critical correlation of the organisms with tidal phenomena in the tropics is needed. Chapman (1946, p. 654) criticizes the use of organisms to delimit such critical levels, but sufficient detailed studies have been carried out to make this possible on extended coastal surveys such as those of Stephenson in South Africa, of Dakin, Bennett & Pope in New South Wales and of Womersley (1947, 1948) on Kangaroo Island in South Australia.

Gislen (1944) advocates referring the limits of all intertidal communities to mean sea level. This is no doubt very satisfactory where tidal records are available, but in coastal areas where there are no established tide gauges for hundreds of miles (such as much of southern Australia) it is extremely difficult. The irregular tidal and wave conditions on most of the southern Australian coast raise doubts as to whether the distinctive zones of organisms do not indicate the environmental conditions in the intertidal zone better than measurements of tidal and other phenomena. Further attempts to correlate zones with tidal levels in southern Australia are needed to clarify this problem.

The sublittoral fringe and upper sublittoral

Stephenson (1939) introduced the term 'sublittoral fringe' for the uppermost part of the sublittoral which is exposed only at extreme low tides. On most temperate and cold water coasts throughout the world this is essentially a zone of large brown algae, usually laminarians or fucoids. In their 1949 paper, the Stephensons regard the lower limit of the sublittoral fringe as being at E.L.W.S. In actual fact this restricted zone includes only the upper part of a uniform zone which extends down much below E.L.W.S. On English coasts the kelp zone extends down to 10 fathoms, and in Stephensons' scheme the uppermost plants of this zone, and often the upper parts of the plants only, would come within the sublittoral fringe. Many other algae and animals which occur just above E.L.W.S. also occur below this level.

Feldmann (1937) used the term 'upper infralittoral' for the zone of 5 m. deep below the littoral. This zone is very similar to Womersley's (1947) 'upper sublittoral' on Kangaroo Island, and is a much more natural zone than Stephenson's sublittoral fringe. The lower limit of the upper sublittoral will vary from place to place, and it is best regarded as a useful distinction for the upper part of the sublittoral which is dominated by large brown algae in colder waters, or by other forms in the tropics. The sublittoral may be regarded as extending down to the lower limit of plant life.

In some restricted areas, however, sublittoral fringe is a distinctly useful term. On rough coasts on Kangaroo Island the uppermost zone of the sublittoral is dominated by the brown alga *Cystophora intermedia*, which extends down for only 2 or 3 ft. This zone is often completely exposed—though momentarily—between heavy waves at low tides, and it does constitute a distinct fringing zone to the sublittoral.

On calmer coasts of Kangaroo Island other species of *Cystophora* extend from just above E.L.W.S. to 10 or 15 ft. or more below. Here the term 'upper sublittoral' is more appropriate than 'sublittoral fringe'.

The affinities of organisms occurring in the sublittoral fringe are largely with those of the sublittoral, and the uppermost zone is logically regarded as being a fringe of the sublittoral and not of the littoral.

We propose therefore that the upper zone of the sublittoral be known as the 'upper sublittoral' in a general scheme, and that 'sublittoral fringe' be used only for localities where there is a true fringing zone of algae or animals, not extending much below E.L.W.S.

'Sub'- or 'infra'-littoral

The Stephensons, after using the term *sublittoral* in all previous papers, in the 1949 paper change this to *infralittoral*, on the grounds that 'the only objection to supralittoral which we have encountered lies in the fact that on a printed page it looks very like sublittoral, and in reading over our own notes we find that the eye often confuses the two, with unfortunate results'. They therefore propose to substitute the word infralittoral for sublittoral.

We have never found this difficulty in distinguishing sub- and supra-, either in printed papers or in our own field notes (where sublittoral is abbreviated to S.L. and supralittoral to supra-L.). If terms are to be changed for such slight reasons as 'looking alike', only confusion can result.

Probably the majority of marine biological workers have used the term sublittoral, while Feldmann introduced the term infralittoral in 1937. The two words are almost identical in their meaning of 'under the littoral', and we prefer to use the older and better established term sublittoral, especially as there seems no real reason to change it.

THE LITTORAL ZONE

The littoral zone comprises the intertidal region proper, above the sublittoral. The upper limit of the littoral is difficult to fix with any certainty, being complicated by factors other than the tidal range—e.g. the amount of splash and spray, and the presence of shade.

It is not our purpose here to review the different interpretations placed on the littoral, and we agree with the Stephensons in defining the upper limit of the littoral (Stephensons' midlittoral) as the region where littorinids become dominant. This does constitute a line of demarcation on most rocky shores, and corresponds to a level at or above M.H.W.S., depending on the degree of wave splash. Where wave splash is heavy the littoral may be elevated several feet above actual high water mark. While littorinids are useful indicator species for the littoral-supralittoral boundary, on some sheltered coasts other species will probably have to be used as indicators.

In their earlier papers, Stephenson and his co-workers considered that so many different interpretations had been placed on the term littoral that they discarded it, using instead 'intertidal' for that zone of the shore. However, they did use sublittoral and supralittoral, and as long as these terms are used the region between them must logically be the littoral. In their most recent paper, the Stephensons rename this zone the *midlittoral*, classing the sublittoral fringe and the lower half of their supralittoral fringe as parts of the littoral. As already pointed out, the sublittoral fringe is related to the sublittoral rather than the littoral in its affinities, and should therefore not be placed within the littoral. The supralittoral fringe will be referred to later.

Further difficulties arise when the littoral zone shows several subzones, as it does in many localities. On Southern Australian coasts two or three zones often occur within the littoral, and these can conveniently be called the upper and lower, or the upper, mid- and lower littoral zones. An example of three littoral zones is found on moderately sheltered Southern Australian coasts where the zonation is:

Upper littoral—barnacles.
Midlittoral—limpets, *Galeolaria* and blue-green algae.
Lower littoral—*Jania-Corallina* mats.

On coasts with greater tidal ranges the littoral could be further subdivided as found necessary. In some cases it has been possible to give the exact tidal range of the different zones (Doty, Evans), but where the tidal range is small and tidal data are inadequate this is not possible.

However, if *midlittoral* is used as suggested by the Stephensons for the main intertidal region, these subzones would then become the upper midlittoral, mid-midlittoral, and lower midlittoral. Such terms are far too cumbersome for standard usage.

The supralittoral zone

The supralittoral has usually been regarded as the region above the littoral (above direct tide or wave action) comprising organisms of marine affinities, and extending up to the limit of influential spray or to the land vegetation. The lower limit can often be drawn at the bottom of the littorinid zone, which seems to be a feature of most, though not all, coasts (for some very calm coasts have few littorinids). Few algae occur in this zone, and these are usually small and inconspicuous. On Southern Australian coasts *Melaraphe unifasciata* is the dominant littorinid of the supralittoral.

The Stephensons place the littorinid zone in their *supralittoral fringe*. This zone in their scheme comprises part of the littoral and part of the supralittoral. They do not indicate how far the remaining supralittoral zone extends upwards, nor in any detail the organisms which occur in it, though the lichens common on most rocky coasts occur here.

We question, however, whether their separation of the supralittoral fringe and supralittoral zone is distinct enough for general recognition of these two zones. The littorinids extend for varying distances upwards, depending on spray, and on Southern Australian coasts often occur among the lichens and almost up to the land plants. Dakin, Bennett & Pope, referring to the N.S.W. coasts, state, 'of our three common littorinids, *Bembicium*, *Melaraphe* and *Nodilittorina*, the first is restricted to the upper parts of the barnacle zone (upper intertidal); *Melaraphe* occurs at the same levels, but also higher; and *Nodilittorina* is best adapted to the conditions of dry land'. Other migratory animals such as *Ligia* and crabs may extend above the littorinids but also occur within the littorinid zone where there is shelter in cracks and hollows.

As far as South Australian coasts are concerned, we feel that the littorinids (excluding *Bembicium* which is a mid- and upper littoral inhabitant) should not be separated as a distinct zone, but regarded as simply the lower part of the supralittoral.

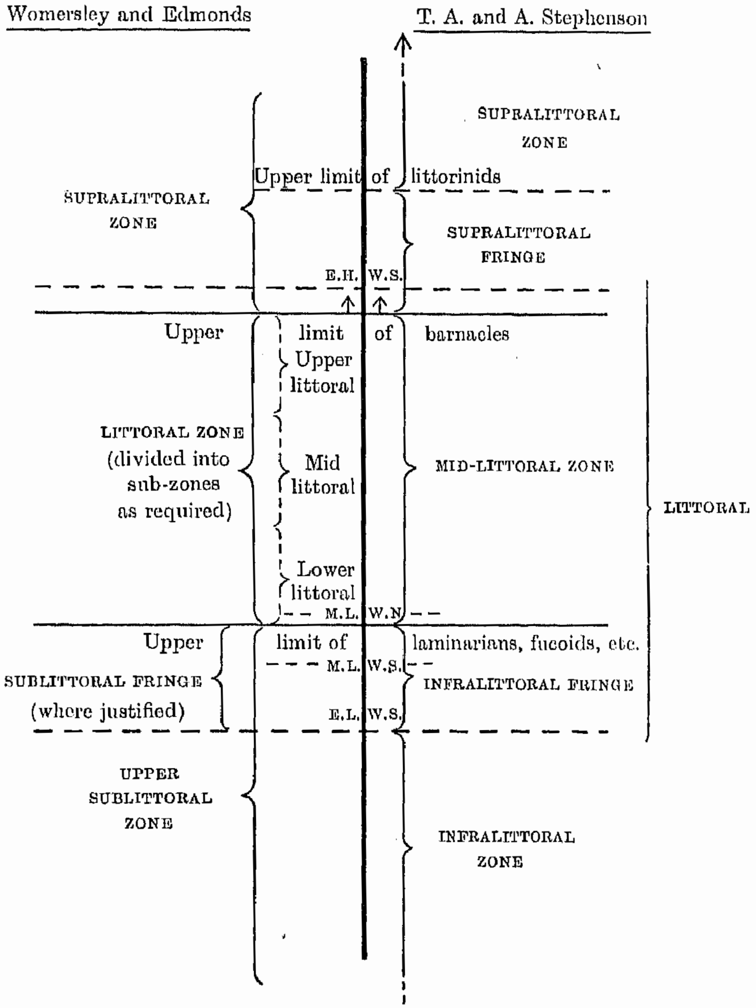

Fig. 1. Comparison of zonation schemes.

A further difficulty about the supralittoral fringe is that the organisms present in the littorinid zone are more closely related to those in the upper part of the littoral, and this region should therefore be called the 'littoral fringe' if it is to be regarded as a fringe zone.

It appears to us difficult, and probably unnecessary, to recognize a supralittoral fringe zone in a general scheme. A supralittoral zone has been found adequate by most workers in the past. If zones within the supralittoral occur in particular localities, these can perhaps be referred to as upper and lower supralittoral zones, etc.

We have found the above scheme (Fig. 1) suitable for Southern Australian coasts, and it seems to us to be of general application. Whether it will prove to be so must rest on its critical examination and application to coasts elsewhere, especially coasts varying in topography and habitat conditions from typical rocky coasts.

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REFERENCES

Chapman, V. J. (1946). Marine algal ecology. *Bot. Rev.* **12**, 628–72.

Colman, J. (1933). The nature of the intertidal zonation of plants and animals. *J. Mar. Biol. Ass. U.K.* **18**, 435–76.

Dakin, W. J., Bennett, I. & Pope, E. C. (1948). A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast. *Aust. J. Sci. Res.* B, **1**, 176–230.

Doty, M. S. (1946). Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. *Ecology*, **27**, 315–28.

Edmonds, S. J. (1948). The commoner species of animals and their distribution on an intertidal platform at Pennington Bay, Kangaroo Island, South Australia. *Trans. Roy. Soc. S. Aust.* **72**, 167–77.

Evans, R. G. (1947). The intertidal ecology of selected localities in the Plymouth neighbourhood. *J. Mar. Biol. Ass. U.K.* **27**, 173–218.

Feldmann, J. (1937). Recherches sur la végétation marine de la Méditerranée. La Côte des Albères. *Rev. algol.* **10**, 1–339.

Gislen, T. (1944). Physiographical and ecological investigations concerning the littoral of the northern Pacific. *Lund Univ. Arssk.* N.F. Avd. 2, Bd. 40, Nr. 8.

Stephenson, T. A. (1939). The constitution of the intertidal fauna and flora of South Africa. Part I. *J. Linn. Soc.* (*Zool.*), **40**, 487–536.

Stephenson, T. A. (1944). Ibid. Part II. *Ann. Natal Mus.* **10**, 261–358.

Stephenson T. A. (1947). Ibid. Part III. *Ann. Natal Mus.* **11**, 207–324.

Stephenson, T. A. & Stephenson, A. (1949). The universal features of zonation between tide-marks on rocky coasts. *J. Ecol.* **37**, 289–305.

Womersley, H. B. S. (1947). The marine algae of Kangaroo Island. I. A general account of the algal ecology. *Trans. Roy. Soc. S. Aust.* **71**, 228–52.

Womersley, H. B. S. (1948). Ibid. II. The Pennington Bay Region. *Trans. Roy. Soc. S. Aust.* **72**, 143–66.