INTRODUCTION

So much has already been discovered about life between tide-marks that it has become difficult to see the wood for the trees. Yet despite the host of publications dealing with intertidal life, the field untouched is so vast that our knowledge of the natural laws which control intertidal affairs is still elementary. For these reasons we must examine intertidal arrangements, where possible, on a broad scale as well as intensively.

Until recently there has been a stronger tendency to study the problems of tidal biology in great detail on a small scale than in less detail on a large one. This has resulted in many accounts of the natural history of individual plant and animal species, and in numerous descriptions of the occurrence of plants, animals (or both) in small areas varying in size from square yards, individual rock-pools or narrow traverses to short stretches of coastline, estuaries and similar areas. The general examination of long stretches of coast, or of the coastlines of whole countries, has lagged far behind the more detailed studies, and there have been few examples of it. We have, it is true, such surveys as those of Fischer-Piette on the European coasts, of Ricketts on the Pacific coast of North America, and of the present authors and their collaborators in South Africa; but the list is not a long one. Recent progress in intertidal studies has been ably summarized by Fischer-Piette (1940), and the volume in which his paper appears represents, as a whole, an important contribution to the subject.

At the present time there is evidence of a tendency to undertake the examination of long coastlines more readily than before, and this is of course facilitated by car and plane travel, and by the construction of roads in many places which were previously inaccessible. An example of such work is the survey, by Dakin and his assistants, of 1000 miles of coastline in New South Wales, the results of which were published in 1948. A series by R. G. Evans on parts of the British coast is at present appearing, and while this deals with much shorter stretches, its point of view is a broad one, looking towards an eventual general account of the British coasts. There is similar work now progressing in several parts of the
world. Another welcome development has been an increasing willingness to include both the plants and the animals in marine ecological studies, which have suffered too often in the past from the omission of one or other of these elements which are, in nature, so inextricably interrelated that no balanced account can be achieved without both.

During the preparation of a book on the intertidal fauna and flora of the world, we have come to certain tentative conclusions about intertidal zonation which we think it advisable to put forward without further delay. As it may well be 5 or 10 years before we can present these in full detail with all the supporting evidence, we venture to state them in outline now, in the hope that they will be of assistance to those following similar lines of work during the coming decade.

This paper, though short, is based on first-hand experience of coastal areas in several parts of the world, extending over more than 30 years. The regions studied are situated in the following areas:

(1) England, Scotland and Wales.
(2) South Africa between the mouth of the Orange River in the west and the border of Portuguese East Africa in the east.
(3) The Indian Ocean and Red Sea—Mauritius, Mombasa, Mozambique, Port Sudan.
(4) The Great Barrier Reef of Australia.
(5) The coasts of North America between Prince Edward Island and Key West on the Atlantic side, and between Vancouver Island and San Diego on the Pacific side.

Zonation between tide-marks

I. The standard zonation (Figs. 1–3)

Authors describing the distribution of plants and animals between tide-marks, in different parts of the world, have usually found that the tidal belt is subdivided into strips or zones, one above the other, each of them characterized by distinctive features of its own. The number of these zones varies from shore to shore, and each author has adopted for them whatever system of nomenclature seemed to be appropriate to the particular place which he studied. The result is that various local names exist, but none has so far been invented which is of universal application; nor has there been any serious attempt to compare the parts of the world with one another. It is our purpose in the following paragraphs to introduce a system which we believe may prove to be of universal application.

It may well be asked, is there any reason to suppose that any universal type of zonation exists? Should we not rather suppose that, in view of the numerous known variations of tidal behaviour, there must be a corresponding diversity of zonations showing little in common? Let it be stated at once that nobody can give a final answer to these questions at the present time. There is information available upon which answers in both senses could be devised, and an affirmative to the second one might be developed, for instance, from an important recent paper by Doty (1946) or from unpublished observations of our own in North America. We believe, however, that it is at least true that zonation has certain features which are very widespread, frequently recurrent, and perhaps even universal in occurrence. It is our object to indicate these features and to suggest a terminology suited to them, because we feel that it will probably contribute towards clarity of thinking, in the future development of intertidal studies, if a general system is introduced, even if it is experimental at the present stage. If the same system could be adopted by
everyone, it would make the accounts published in one part of the world much more intelligible to workers in other parts; and if the features which tend to be universal are pointed out, they can be looked for as new coasts are described, until we have a body of information extensive enough for a final decision. Even should the final decision be against the applicability of a general system, it cannot be reached until the possible system has been identified, defined and tested.

Fig. 1. A diagram illustrating three of the possible types of zonation met with on the British coasts (e.g. on steep rock-faces in Argyllshire). In column A the three widespread zones described in the text (Littorina zone, Balanoid zone and sublittoral fringe, represented here by a Laminarian zone) are alone developed. In column B the Balanoid zone is colonized by patches of brown algae at different levels (the lower ones surrounded by areas of bare rock more or less free from barnacles). In column C, a full series of Fucoid zones is superimposed on the Balanoid zone, overshadowing the barnacles. (In this diagram only part of the width of the Littorina and Laminarian zones is included. The relative widths of the other zones are accurate for the places chosen. For column C a locality without Fucus vesiculosus or Porphyra was selected.) Reproduced by courtesy of the Linnean Society.

We first developed the idea that zonation may have features of widespread occurrence during our survey work in South Africa (1931-40). This conception was referred to in the Journal of the Linnean Society (Zoology, vol. 40, 1939, pp. 506–10), where a short and
preliminary comparison was made between the zones recognizable in South Africa and those of coral reefs on the one hand, and of British coasts on the other. It was concluded that, so far as the available evidence permitted us to judge, there are three zones on the shore which are likely to be of widespread occurrence, though undergoing numerous local modifications. Our more recent work in America (1947–8) has strengthened this impression. These zones are, from above downwards:

(1) The Littorina zone. This is an arid zone subject to transitional conditions between land and sea, affected by spray in suspension, but wetted by the waves only in heavy weather or at the higher spring tides, when at least its lower parts become washed or submerged. The number of species inhabiting the zone is small, and includes snails adapted to arid conditions and belonging to the genus Littorina and to related genera, or to genera including similarly adapted species. The surface of the rock in the Littorina zone or its lower part is commonly blackened by encrusting Myxophyceae and/or lichens of the Verrucaria maura type, and this blackening may exist as patches or may form a distinct blackish belt, often overlapping into the zone below.

(2) The Balanoid zone. This is the middle part of the shore, the most fully intertidal region, at least part of which is covered and uncovered every day. The inhabitants are more numerous than in the Littorina zone, and typically include numerous balanoid (acorn) barnacles belonging to genera such as Balanus, Chthamalus and Tetractita. The upper limit of the zone is marked by the cessation of barnacles (in quantity). There is a strong tendency for the zone to become differentiated into two or more subzones. In the upper of these the barnacles tend to be maximal in number and are either the dominant forms or among these; in the lower, they are usually in competition with other sedentary forms, which may overshadow or obliterate them.

(3) The sublittoral fringe. This is the lowest part of the shore, uncovered at spring tides and not at neaps, and sometimes, where wave-action is persistently strong, only at the lowest spring tides in calm weather. It supports the fringe of the sublittoral population (i.e. the population of the region which never uncovers at all), is exposed to the air for a relatively small proportion of the time, and in many places rarely if ever dries off. The population is very variable but usually rich. In many cold-temperate regions it consists of a forest of large brown algae (Laminariales, etc.) with an undergrowth of smaller plants and animals among their holdfasts. On coral reefs it commonly contains the upper edge of the rich growth of coral which extends down the reef face below low-water level. In warm-temperate regions it may support (a) a dense covering of simple ascidians (Pyura); (b) a dense growth of rather small mixed algae, primarily Rhodophyceae; or (c) other communities. Large brown algae may or may not occur, but if they do, tend to be less strongly developed than in cold-temperate regions. In the sublittoral fringe the encrusting non-jointed calcareous algae of the family Corallinaceae (referred to broadly as ‘lithothamnia’) tend to encrust all surfaces suited to them, and this encrustation extends above the fringe where it can do so, though usually not forming a continuous growth above the lower Balanoid zone, except in pools, caverns or other special places.

In the foregoing paragraphs, the features of the zones have been indicated very broadly and as they appear when they exist in their most typical form. When dealing with anything as complex and variable as zonation there must be some arbitrary standard regarded as ‘typical’ with which variations can be compared. We have found, as have many others before us, that this standard is often best displayed on fairly smooth, con-
tinuous rocky slopes, whether steep or gradual, and that on the whole it is best seen where wave-action is neither absolutely maximal nor yet minimal. At the same time there are many intermediate degrees and types of wave-action, and the several zones vary independently, to some extent, in relation to these, so that it does not follow that all the features mentioned as typical are at their best under exactly the same amount of wave-action.

II. Deviations from the standard (Figs. 1, 2 and 4)

To what extent are these zones recurrent, and how much do they vary? Their existence can at least be demonstrated on many parts of the coasts of Britain, the Mediterranean, North America (both Atlantic and Pacific sides), South Africa, Australia and Mauritius, and probably in many other areas. The range of variation is very great, but it seems to concern rather the number of subzones present than the broad general features of the primary zones. It must always be remembered that zonation, like everything else on the shore, responds in the most sensitive and immediate manner to the slightest changes in the amount, type and strength of the wave-action to which rocky faces may be exposed; and that a little more shade or a little more sun, a variation in the slope of the rock, and other changes of this kind, will produce their own effects. We must, therefore, expect one zonation where there is shade and quiet, another where there is shade and turmoil, a third in rock-pools, a fourth on open sunny rock-faces exposed to moderate waves, and many others. These variants do not as a rule, however, depart so far from the standard we have chosen to regard as typical, that they cannot readily be related to it. While it cannot be expected that the variations should be fully covered in a paper of this length, the following notes will indicate the type of change to be expected.

(1) Littorina zone. This is very often populated by myriads of small snails (species of Littorina, Tectarius, etc.) and by Lígias, and may have no vegetation beyond encrusting microphytes. It varies from this mean in both directions. It may become highly developed and organized, as it does on the Florida keys, where the snails include several species showing a zonation of their own, there is an invasion of flowering plants from above and of small moss-like marine algae from below, and the zone is divided into three well-marked subzones, in which the rock is differently coloured and supports different selections of species. At the other extreme the snails either become very few (at Marineland in northern Florida we found fourteen Littorina in 8 days) or disappear. This does not make it impossible to identify the limits of the zone, as these can be recognized either from the distribution of some other animals, or from that of plants. The blackening which has been mentioned above, as occurring in this zone, is a very widespread feature, but it has been noticed more often by botanists than by zoologists or by general workers. There seems to be no constancy about its cause, except that this commonly consists of a blackening film or crust of more or less microphytic Myxophyceae or lichens adapted for life at a particular level. There are Myxophyceae in all the intertidal zones, and also below tide-marks; and there are lichens throughout the tidal belt and above it; but the particular species of these groups which cause the blackening flourish at the levels which we are considering. The lichens are of the kind exemplified by Verrucaria maura, V. symbalana and V. striatula. The Myxophyceae belong to various genera and species, and during our American work about twenty were collected in this zone. The blackening, when present, may be vague and patchy, or it may form a sharply marked and conspicuous band (Pl. 8; Fig. 4). This band may occupy the Littorina zone almost exactly, extend somewhat above it or (probably
most commonly) occupy its lower part only, often overlapping into the upper Balanoid zone. The discoloration is not necessarily due to Myxophyceae and lichens, but can also be caused by small Chlorophyceae and by encrusting Rhodophyceae such as Hildenbrandia; and in special places such as the English chalk-cliffs other variations occur. Moreover, while the discoloration has been referred to broadly as a 'blackening', which it commonly is, the tint may vary from blackish towards grey, green, brown and other shades. Some accounts dealing with this vegetation are those of Anand (1937), Berner (1931), Chapman (1946), Cranwell & Moore (1938), du Rietz (1925), Feldmann (1938), Fritsch (1931, 1945), Geitler (1930–2), Ginzberger (1925), Grubb (1936), Johnson & Skutch (1928), Kylin (1937), and Smith (1921).

(2) Balanoid zone. Where this is most obviously developed, the barnacles form a dense continuous sheet on the rock, and the majority shows a rather sharp upper limit which forms one of the best landmarks on the shore; individuals usually straggle above this. Sometimes the barnacles continue downwards uninterrupted (though it need not be the same species all the way down) almost to the sublittoral fringe, either fading off gradually or ceasing with a distinct lower limit. Exceptionally they continue below low-water level of springs. More often something interferes with or suppresses them in the lower parts of the zone, and such interference may extend to quite high levels. The competing organisms may be turf-like growths of short algae, a mass of limy polychaet tubes, a sheet of zoanthids or various other sedentary forms; but there are influences other than competition which also tend to reduce the number of barnacles at the lower levels. Quite often there is a sharp line between an upper Balanoid zone, dominated by barnacles and (perhaps) limpets, and a lower one, which may support a patchwork of algal turf, polychaets and other forms competing with the barnacles. In other places no sharp line can be seen, and in yet others there are more subzones than two. There are also regions where the barnacles are reduced in number or even absent over the entire zone, and here the extent of the zone is indicated by other organisms of similar distribution. It should not be supposed that barnacles are necessarily absent from the zones below the Balanoid—this is not so; for instance, the large Balanus tintinnabulum often occurs near or even below low water. But the barnacles characteristic of the Balanoid zone are typically intertidal mid-level species, not the same as those lower down; and the population of the sublittoral fringe is not typically dominated by barnacles even where they occur.

(3) Sublittoral fringe. Some indication of the variations to be found in this zone has already been given (p. 292). It is usually recognizable, though there are abnormal regions where it departs in many ways from the standard, usually in the direction of

Fig. 2. A diagram comparing the widespread features of zonation with an example which complicates them.

A coast is shown on which smooth granite spurs are exposed to considerable wave-action. On the middle spur some of the widespread features are summarized, and the following succession is shown: A, supralittoral fringe (= Littorina zone), blackened below by Myxophyceae; B, midlittoral (=Balanoid) zone, occupied by barnacles above and lithothamnion below; C, infralittoral (=sublittoral) fringe, dominated in this case by Laminarians, growing over lithothamnion. On the other spurs (foreground and background) an actual zonation from the Atlantic coast of Nova Scotia is shown. Here the simplicity of the basic plan is complicated by (a) map-like black patches in the supralittoral fringe, consisting of Codium, Calothrix and Plectonema; (b) the existence of a strongly developed belt of Fucus (mostly F. vesiculosus and F. edentatus in this example) occupying a large part of the midlittoral zone and overgrowing all but the uppermost barnacles; and (c) a distinct belt of Chondrus crispus, overgrowing the lower part of the midlittoral zone, and largely obliterating the belt of lithothamnion which, on the middle spur, extends above the Laminarians.
Zonation between tide-marks on rocky coasts

a reduction of the population (including a reduction or suppression of the lithothamnium) connected with some special local feature such as, for instance, the wide flats laden with calcareous sediment which occur at this level along the Florida keys. Where well developed, on the other hand, the fringe may include subzones, as in New South Wales, where a Pyura belt occurs above a kelp zone (Dakin, Bennett & Pope, 1948).

(4) Other zones. The complexities of intertidal zonation are due, not only to variations in the three basic zones, but also to the introduction into the simple basic pattern of additional zones, both in particular parts of the world and under certain combinations of conditions. In Britain, for instance, zonation was long described in terms of the series of seaweeds which frequently form bands along the shore, including the conspicuous brown Pelvetia canaliculata, Fucus spiralis, F. vesiculosus, F. serratus and Ascophyllum nodosum. It has now been realized (Stephenson, 1939, p. 509; Evans, 1947a, p. 283, etc.; 1947b, p. 190) that these Fucoïd zones are subzones which, given sufficient shelter from wave-action, become superimposed upon the Balanoid zone and interfere with the barnacles. They are local in two senses: (a) they occur on British rocky coasts only under certain conditions; and (b) they occur only over a certain region of the northern hemisphere, and are not even universal in Europe. Another example of a special zone is the Patella cochlear belt of South Africa. This again occurs, in South Africa, only under certain conditions; and, although covering more than a thousand miles of coast, is limited to South Africa. From the account given by Cranwell & Moore (1938) of the Poor Knights Islands, New Zealand, it seems probable that there again additional zones must be recognized. But all these special zones are in one sense or another local, whereas the three basic zones approach much more nearly to universality. Furthermore, in view of the enormous numbers of variations in tidal range and behaviour, and in degrees of wave-action which occur in the world, it cannot be expected that everywhere the existence of the three primary zones will be realized in a simple form so that they are superficially obvious to the eye on a first inspection of the shore. They may be obvious, as on some of the western coasts of Scotland; but elsewhere the zonation may at first sight seem to have little relation to them, and it is only on detailed study that their reality appears.

(5) The local absence of ecologically important species. This is a line of inquiry to which we should like to direct the attention of future workers, as it may in time lead to very interesting discoveries. It has a bearing on the zonation problem, as some at least of the species concerned are forms which commonly characterize zones. Before our recent visits to America we had supposed—and this supposition is certainly widely held among marine biologists—that on any rocky coast subject to average environmental conditions there would be a fairly standard set of plant and animal forms represented. In other words, if any locality were free from restricting influences such, for instance, as those which prevail in an estuary, one would expect to find on the shore species of periwinkles, acorn barnacles, crabs, limpets, anemones, whelks and other common forms of life. There are certain 'ecological niches' such as those tenanted on many shores by limpets, which one might always expect to find occupied by these animals, although it is well known that in different parts of the world they are filled by different species. These may belong to different genera or different groups, but are still 'limpets'. Thus many limpets are Prosobranchs, while others (Siphonaria, Gadinia) are Pulmonates; Patella is a leading genus in some parts of the world, Acmaea in others; but it is so general a feature of shores that limpets of some kind are common on open rock surfaces that it is difficult to believe that on some shores
there are none. Yet this seems to be the truth. On the south-east coast of the United States, for instance, the common limpets of Florida are Siphonarias; but during our stay in North and South Carolina we could not find a single open-rock limpet of any sort. There are under-stone limpets (Crepidula, Diadora) there, but these belong to quite a different ecological sphere, the cryptofauna. Farther north again, AcmAEA testudinalis becomes plentiful on open rock, but even within its range there are shores which lack it, and in any case it appears to be a less dominant limpet than the British and South African Patellas. We also found examples in other groups—there seem to be rocky shores lacking (or almost lacking) periwinkles, whelks, crabs, anemones and barnacles. In some cases the absence can be explained as, for instance, a reduction of barnacles in marine inlets separated by intricate channels from the open sea, or an absence of limpets on rocks which are scraped by ice during the winter. Some of the absences again may be seasonal. But when these explanations have been applied, there remain examples which at present seem inexplicable. We do not consider that the cases of absence which we have ourselves observed are as yet fully established, because it is not an easy matter to certify the complete absence of some species from a locality, especially during a short time. A fuller search over a longer period is needed. At the same time the apparent absences we have noted are certainly not to be put down to defective observation. After working on the shore over 25 years two experienced people cannot spend several weeks working in a district, keeping a watch for limpets all the time (and having found thousands the month before a few hundred miles away), and see not a single one, unless limpets, at that place and season, are at least very scarce. While, therefore, we feel that confirmation is needed, we shall be much surprised if the general position here outlined does not prove to be correct.

**Terminology**

On the assumption that the three basic zones are more or less world-wide in distribution, it would be desirable to find names for them which do not depend on the occurrence in each of some particular organism. This has been achieved in the case of the sublittoral fringe, a term introduced by us in 1937 (pp. 352, 360), which has worked well in practice. The names Littorina and Balanoid zone are satisfactory in the main, as the belts to which they refer do, on all the more typical shores, support a population of Littorinae and acorn-barnacles respectively; but it is quite possible to find shores on which, in the Balanoid zone, barnacles are few or even absent, and also shores with few if any Littorinae. In the absence of these animals, however, the zones themselves can still be recognized, they are real entities. We have discussed a possible improved terminology with many marine biologists, and have gradually worked out the system introduced below. Dr Wesley Coe of the Scripps Institution would like it to be simply ‘upper, middle and lower’ zones. As we are ourselves much in favour of simplicity, we are not averse to this, but it has practical disadvantages. For instance, the Balanoid zone is commonly divided into upper and lower subzones, and while it is satisfactory to refer to the ‘upper Balanoid zone’ it is less suitable to speak of the ‘upper middle zone’. Also, the terms proposed are not in the least descriptive, and bring nothing particular to one’s mind. After long consideration we propose the name supralittoral fringe as an alternative to ‘Littorina zone’. This is descriptive and accurate; and just as the sublittoral fringe is the fringe or boundary zone between the tidal and subtidal areas, so is the Littorina zone the upper fringe of the tidal area, the boundary

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belt between land and sea. 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. This is quite a serious drawback, and we therefore propose to substitute the word *infralittoral* for *sublittoral*; it means much the same thing and does not visually resemble supralittoral. The most difficult zone to re-name is the Balanoid. This is the middle zone on the shore, the most fully intertidal, and in view of the fact that at least part of it tends to uncover twice a day, could be referred to as the ‘semidiurnal zone’. This would not, however, cover it for regions where the tides are *not* semidiurnal, and on the whole we favour the name *midlittoral zone* as being in keeping with the other terms proposed. We therefore formally propose that the three main zones of the shore be called:

- Supralittoral Fringe
- Midlittoral Zone
- Infralittoral Fringe

and that these terms be applied in the same sense as the terms ‘Littorina zone’, ‘Balanoid zone’ and ‘Sublittoral fringe’, used on p. 292. The belts thus named are represented graphically in Fig. 3.

How far is this system in keeping with the terminologies introduced locally by previous workers? Needless to say there has been no general agreement and no general practice, otherwise it would not be necessary to introduce a new scheme. It would probably be true to say that many workers have recognized the reality of the three zones, but their reactions to them have been very various. The term *supralittoral* has often been used, though not always as a synonym for our Littorina zone. Some authors have substituted *subterrestrial*, but this sounds too much like *subterranean* and has therefore no advantage over supralittoral. The word *midlittoral* is less common, though it has been used by Dakin *et al.* (1948) in their recent account of the New South Wales coast, even if not as an exact equivalent of our Balanoid zone. The word *sublittoral* is common enough in the literature, though as usual it is used in several senses; but Feldmann (1938) introduced the term *infralittoral* as being more analogous with supralittoral, and for the reasons given above we prefer this. Dakin *et al.* (1948) have introduced another term, ‘littoral-sublittoral fringe’, but this is not only cumbersome but unnecessary, as it is the same thing as our sublittoral (= infralittoral) fringe. Moreover, it directly uses the word *littoral* itself (as distinct from its combinations), and that introduces difficulties to which reference will be made below. From all this it will be seen that the system we propose does not depart very fundamentally from previous usage, but it seeks to standardize this and to choose those words which will be most generally suitable and most widely applicable. We would, however, draw attention to our use of the word *fringe*, in connexion with the adjectives supralittoral and infralittoral. This is our personal contribution, and it has the advantage of indicating that both the zones designated are boundary-belts, literally the upper and lower fringes of the tidal area; and it avoids linking them up too closely with any specific tidal levels with which, as will be explained below, they do not necessarily coincide.

There is one fence left to climb. If we use combinations such as supra- and infralittoral, what is their relation to the word ‘littoral’ itself? We have avoided using the latter word as far as possible in our own papers, because it is given such widely different meanings by different authors: hence our use of the terms *intertidal zone* or *tidal belt* for the whole region between extreme high and low water of spring tides. The term ‘littoral zone’ has
three main usages in the literature: (i) as the equivalent of our intertidal zone; (ii) as the equivalent of our midlittoral zone (i.e. something narrower than the whole intertidal zone); and (iii) as covering not only the intertidal zone (and sometimes including higher levels)

but also the whole submerged surface of the continental shelf. If we ourselves have to choose between these meanings we would prefer to make littoral the equivalent of intertidal (probably the classic usage), as this makes the term ‘infralittoral zone’ available for

Fig. 3. Diagram illustrating the terminology introduced in the text; see pp. 297-302.
the zone extending from extreme low water to the edge of the continental shelf (with our infralittoral fringe as its upper border), and the term 'supralittoral zone' available for the maritime region above high water, of which our supralittoral fringe includes the marginal part.

Lastly we cannot altogether pass over the terminology to be applied to plant and animal communities within the several primary zones of the shore. It is well known that, although a single zone or subzone may be occupied throughout a long stretch of coast by one and the same community, in many cases a given zone will be occupied by a complex patchwork of different communities. So many of these patches and subzones are of local occurrence that it is difficult to see how any universal terminology can be devised for them, and it seems to us unobjectionable to speak of a 'Pyura subzone' or a 'Pyura community' as occurring in the broader zone known as the infralittoral fringe. This usage has been employed very intelligibly by a number of authors as, for instance, by Feldmann in his excellent account of the algae of the western Mediterranean. But we are very doubtful whether it

Fig. 4. A diagram illustrating the impossibility of attempting to define zones in terms of tidal levels, in view of the marked differences in level of some of the zones and zone-boundaries on the two sides of a small island.

The first column shows the zonation on the sloping, sunny, southward-facing slope of Brandon Island (in Departure Bay, British Columbia); the second column the zonation on the shady, cliffed, northward-facing side (see also Pl. 8). The two sides are less than 100 yards apart, are subject to similar degrees of (relatively slight) wave-action and are differentiated only by the features already mentioned. It will be noted that the Fucus zone (EF, LM), the upper limit of the majority of barnacles (D, K) and the black zone (CD, JK) are at quite different levels on the two sides. The details are as follows:

- **A** Lower limit of macroscopic maritime land-lichens.
- **B** Upper limit of the majority of Littorinae.
- **C** Upper limit of the densest blackening (due here at least partly to impoverished Hildenbrandia).
- **D** Upper limit of main barnacles.
- **E** Upper limit of main growth of Fucus.
- **F** Lower limit of main growth of Fucus (chiefly F. furcatus).
- **G** Lower limit of main barnacles.
- **H** Upper limit of infralittoral fringe, which is here dominated by a dense brown beard-like growth consisting of diatoms and small Rhodophyceae, and by very large violet starfish (Pisaster ochraceus).
- **I** Level of extreme lower low water of spring tides in July 1947.
- **J** Lower limit of macroscopic maritime land-lichens. This is also approximately the upper limit of Littorina and the level of extreme higher high water of spring tides in July 1947.
- **K** Upper limit of main barnacles.
- **L** Upper limit of main Fucus.
- **M** Lower limit of main Fucus.
- **N** Approximate upper limit of most Serpula.
- **O** Upper limit of infralittoral fringe, dominated on these shaded slopes by a community of violet starfish (Pisaster ochraceus) with anemones (Meditium) and Serpula.
- **P** Level of extreme lower low water of spring tides in July 1947.
- **AD, JK** Supralittoral fringe. In the first column this has only a slight blackening, maximal in its lower part (CD); in the second, it is blackened throughout by Verrucaria striatula and other forms, and also inhabited by Littorina.
- **DH, KO** Midlittoral zone. In the first column this is occupied almost throughout by barnacles, although it has a belt of Fucus (hiding the barnacles) in the middle, and a narrow bare zone (GH) at the bottom, where the barnacles are reduced. In the second column the Fucus belt is higher up, the barnacles fade away gradually below, and the lower part of the zone is invaded by Serpula.
- **HI, OP** Infralittoral fringe.

(The scale is shown in feet between the two columns. The figure deals only with the distribution of the main populations of selected species—outlying patches of barnacles, Fucus, etc., follow different rules from the main populations, and will be dealt with in detail elsewhere.)
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is usefully possible to go much further than this, at any rate unless it can be done along new lines rather than along any as yet laid down. There is a school of ecologists who seem to feel that it is more scientific to say ‘The undersigned executed autotrophic reactions in relation to the Graminetum’ than to say ‘We had tea on the lawn’. This is doubtless a delusion; but it has led to a positively terrifying outburst of terminology referring to communities. We have read many papers which use these terms: but we can never convince ourselves either that they have substantial advantages or that they do much to advance our knowledge. For our own part, therefore, we propose to continue to refer to a mussel-bed as a mussel-bed, and not as either a ‘Mytiletum’ or as ‘an example of the Mytilus-Balanus Biome without the Balanus’. One cannot help recalling Charles Singer’s characterization of this ecological terminology, in his book A Short History of Biology (1931, p. 279), where he says: ‘From the beginning, however, it [ecology] has been cursed, more than most sciences, by a horde of technical terms equally hideous, unnecessary and obfuscating.’

Relation of zones to tidal levels

In the short definitions of the three zones given above (p. 292) they are related only very approximately to tidal levels. This is intentional because, although we believe the zones themselves to be persistently recurrent, their relation to tide-levels is not necessarily a matter of exact coincidence, and varies according to the nature of the shore. One cannot, having determined a given level (e.g. mean low water of neaps), expect to find that this coincides exactly with a boundary between two zones. Sometimes it does; but in other cases the boundary is related to a tidal level rather than coincident with it. Moreover, the relation between zones and levels may be different, on the same shore, at points only a few yards apart (Fig. 4). The levels of high and low water vary progressively from day to day, and while it is not yet clear whether we must attach most importance to mean levels or extreme ones (more likely both are effective), it is clear that the relation of levels to zones is complex. The zones are therefore best defined in terms of organisms. In the usage here advocated, the upper limit of the infralittoral fringe is that of the bulk of the population, on open rock, of some dominant organism (e.g. Laminaria, Pyura) which inhabits it: this is also the lower limit of the midlittoral zone. The upper limit of the midlittoral zone (=lower limit of supralittoral fringe) is the upper limit of barnacles in quantity (or of some equivalent organism if the barnacles are missing). The upper limit of the supralittoral fringe may be fixed as is locally convenient—e.g. by the upper limit of Littorina or the lower limit of maritime land-lichens. This usage fixes the boundaries by means of the organisms; and the tidal levels are then found to be related to them in a definite way even though not necessarily coincident with them.

Zones between tide-marks have no constant depths whatever. Tidal behaviour and tidal ranges vary so much in different parts of the world that no such constancy is to be expected; and the depths of zones are controlled not only by tidal phenomena, but also by variations in amount of wave-action, distribution of sun and shade, and other features. This means that even on a single stretch of coast with the same tidal range, the zones may vary in depth from one rocky face to another. It is possible that if enough measurements were made, and if a sufficient number of corrections were applied to them (for differences in tidal range, exposure to wave-action, sunshine, etc.), a constant proportion between the depths of the main zones could be demonstrated; but this has not been ascertained. The widths of zones naturally vary in relation to the slope of the rock, apart from the factors
which control their vertical depth. Thus a zone which, on a vertical wall, is a foot deep, may also occur on a nearly horizontal rocky platform where, although its vertical extent may still be only a foot, its width may be many yards.

A mistaken idea, which is commonly held, is that intertidal zonation is a result of tidal action. This is not so. Zonation occurs, both above and below the water-level, round static waters such as ponds and lakes, where there is no tidal change.* The primary cause of it is the existence of an interface between air and water. Below the surface of the water there is a gradient in light-penetration, and this can be accompanied by other gradients such, for instance, as a change in sedimentation with increasing depth. Zonation results from these gradients. Above the water-surface there is further zonation, controlled by the degrees to which the surrounding rock-surfaces are exposed to influences emanating from the body of water or connected with its presence—such as spray, or moisture formed during evaporation. 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 the 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. We cannot, however, make any general statement to the effect that zonation is more marked where the tidal range is great than where it is small, because it is now well known that very marked zonations can occur with small tidal ranges; and the zonation in the Bay of Fundy, where the tidal range is maximal, is no more elaborate than anywhere else, in fact it is less marked (in the places we have visited) than on the Atlantic coast of Nova Scotia where the range is much less. It is also a feature of zonation which has struck a number of observers that the zones are often very sharply marked in places where the oceanic surge is so constant that much of the rock is wet in almost any weather and at almost any state of the tide, so that the existence of sharp zonal boundaries becomes peculiarly difficult to explain. That the argument of this paragraph is not fanciful is well illustrated by the state of affairs in the Mediterranean. While that sea is not, as generally imagined, literally tideless, there are many parts of it where the tidal amplitude is small (e.g. rarely exceeding a foot), and where the sea-level varies a good deal more in accordance with irregular changes in barometric pressure and in force and direction of wind, than it does as a result of tidal action. (This is illustrated graphically by, for instance, Feldmann, 1938, p. 31). As Feldmann has shown, for the stretch of the Mediterranean coast of France nearest to Spain, the three usual zones exist, but the midlittoral is apparently very narrow in sheltered places, achieving a much more distinct existence where there is considerable wave-action.

Summary

On the basis of 30 years' first-hand experience of rocky coasts in Britain, North America, South Africa, the Indian Ocean and Australia, it is suggested that certain features of zonation between tide-marks are of such widespread occurrence in the world that they may even be universal. The terminology applicable to the widespread zones is discussed, and a scheme is proposed which defines them and attempts to name them appropriately.

* It is true that the water-level in ponds and lakes can change owing to rain or evaporation, and that this variation can affect the zonation; but this is an irregular variation unlike that of the tides and hardly affects the present argument.
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The zonation of open rock-surfaces exposed to degrees of wave-action intermediate between maximal and minimal is regarded as the standard from which deviations may most conveniently be recognized. From above downwards shores tend to show the following belts:

(1) *Supralittoral zone.* The maritime belt lying near the sea, above tide-marks, but subject to some maritime influence (e.g. to finely divided spray in rough weather). The lower limit of this zone is the same as the upper limit of the one below. Its upper limit is not within the scope of this paper.

(2) *Supralittoral fringe.* From the upper limit of barnacles (in quantity) to the nearest convenient landmark above this (e.g. the upper limit of Littorinae or the lower limit of maritime land-lichens or flowering plants). High water of spring tides invades at least the lower part of this zone.

(3) *Midlittoral zone.* From the upper limit of barnacles (in quantity) down to the upper limit of the zone below. This belt tends to be covered and uncovered every day, at least in part.

(4) *Infralittoral fringe.* From the upper limit of any convenient dominant organism (e.g. *Laminaria, Pyura*) to extreme low-water level of spring tides, or to the lowest level ever visible between waves. This zone uncovers only at the major tides, and sometimes only in calm weather.

(5) *Infralittoral zone.* From extreme low water of springs to a depth which has yet to be settled—it may be to the edge of the continental shelf or to the lower limit of seaweed vegetation.

An account is given of (a) the standard populations of these zones (p. 292); (b) of some of the principal variations in these populations (p. 293); (c) of the existence of additional local zones (p. 296); and (d) of the local absence of ecologically important species (p. 296). The terms littoral, supralittoral and infralittoral are discussed, in relation to others, and ‘littoral’ is defined as the equivalent of ‘intertidal’. It is maintained that within the framework of the principal zones, subzones and patch-forming communities, which are much more local in occurrence, can suitably be named, as heretofore, from the organisms which dominate them. The relationship between the zones and tide-levels is discussed (p. 302), especially to emphasize that the zones cannot be defined in terms of tidal levels although related to these, but must be defined in terms of the distribution of organisms.

REFERENCES

The following list includes only those publications to which direct reference is made in the text, and makes no attempt to cover the whole subject of intertidal zonation.


