A BIOLOGICALLY-DEFINED EXPOSURE SCALE FOR THE COMPARATIVE DESCRIPTION OF ROCKY SHORES

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WAVE action on the shore varies greatly even over quite small distances. Some shores are almost landlocked, so sheltered that no waves larger than ripples ever reach them, while others are buffeted on most days by great rollers or the breaking swell from storms far out to sea. Every kind of intermediate condition exists between these extremes.

A scale which could measure the relative exposure of shores to wave action would be very useful. The biologist constantly finds himself saying that one shore must be considered more exposed than another, but he may find it difficult to justify his statement. A physical scale, derived from measurements of the amount of wave-action on different shores, would be one way of solving this problem.

A different and more biological approach is another possibility. This approach would define the problem in slightly different terms. The shore ecologist needs a frame of reference, preferably a simple scale, in which different shores can be directly compared. It is not necessary that the scale should be an exact or direct measure of wave action provided it allows biological data to be related in an orderly and understandable way.

Biological measurements made of the abundance and levels of growth of the common animals and plants could be used as the basis of the scale. This scale would be closely related to the amount of wave action, although not a precise measure of it. Different species growing on rocky shores require different degrees of protection from certain aspects of the physical environment, of which wave action is often the most important. They can survive and flourish in different degrees of exposure to these forces. Thus the scale is an exposure scale in the broad everyday sense of that word.

PROBLEMS IN THE USE OF PHYSICAL MEASUREMENTS

Few attempts have been made to measure wave action or to compare its strength at different points. Moore (1935) determined the "number of days per hundred days in which any wind blew into the area over more than three miles of sea", but in doing so he ignored wind speed, fetch and any swell. Southward (1953) measured the height of swash above predicted tide-levels under known wind conditions. Some account was taken of wind speed but not of fetch or swell. Most workers have relied upon subjective estimates. These may be useful in purely local studies but, in the absence of any measurements, comparisons with other areas or the results of other workers are unrewarding.

"Very exposed" shores in the Isle of Man (Burrows and Lodge, 1951) and the Plymouth area (Evans, 1947) are very different from one another and the same phrase applied to an open Atlantic shore might imply yet another set of conditions.

The dimensions and energy of free water waves depend on the speed of the wind, its duration and the distance of open water over which it can blow (fetch), and these factors have to be known if the dimensions of the waves are to be calculated. This information is often not available even for local winds and rarely if ever for distant storms which give rise to swell.

Continuously recording instruments, placed below low water, can measure the height of the waves passing over them. Such instruments are, however, expensive, difficult to install and maintain, and must be run for long periods to provide useful information.

Waves are often refracted and their form altered as they approach a shore, and the distribution of their energy on the shore itself is governed largely by the slope and detailed configuration of the rocks.

Finally, it is by no means obvious how even perfect data for different shores should be compared. For example, what amount of continuous moderate wave action on one shore is equivalent to the infrequent heavy storms which attack another.

Thus, although considerable progress is being made in the measurement of waves and wave action (see King, 1959, for review), the present state of knowledge is not very helpful to ecologists engaged in shore surveys.

PROBLEMS IN THE USE OF BIOLOGICAL MEASUREMENTS

It has long been recognized that wave-beaten shores have a characteristic pattern of communities and that sheltered shores have a very different pattern. The argument for a biological scale of exposure requires that between these two extremes the community patterns fall on to a roughly linear sequence or trend. Intermediate linking patterns do exist, but it can be objected that some shores do not fall neatly into this trend.

This is the first limitation of the biological scale. The shores considered must be moderately uniform slopes of bedrock. Very uneven shores with large stacks and jagged reefs cannot be considered as a whole, although one slope of a very large stack or reef could be considered on its own. Furthermore, gullies, pools, caves, boulders (unless very large and never moved by the waves) and shingle beaches must be excluded. Since these features would produce anomalies on almost any scale this limitation should probably be accepted with patience. When more information is available, modifications might be derived to cover some of these situations.

The second major difficulty arises when a physical factor other than wave-action and topography begins to have an over-riding influence. For example, what happens when decreased salinity becomes more important than freedom from wave action. No one seems to know exactly where, or under what conditions this takes place, although the situation must occur in the estuary of every river. I would suggest that the exposure scale, or some modification of it, can be used to investigate such problems. The exposure scale represents a standard trend of community patterns correlated with a continuous decrease of the major limiting physical factor (wave action). Where this situation does not obtain, the application of the scale will produce anomalies. However, because the scale is biological and quantitative, these anomalies will be quickly apparent, interesting in an ecological sense, and definable in trend and amount. This should make it easier to discover where the salinity drop (for example) begins to have its effects and what kind of effects, in community terms, they are. The discussion provides examples of such anomalies and shows how information can be gained from them.

Other major criticisms of the exposure scale aim at the basic theory. They may be summarized as follows:

(*a*) It is not clear what, if anything, is being measured by the scale.

(*b*) The scale is based on a circular argument: a shore is exposed because it has a certain community pattern and it has this pattern because it is exposed.

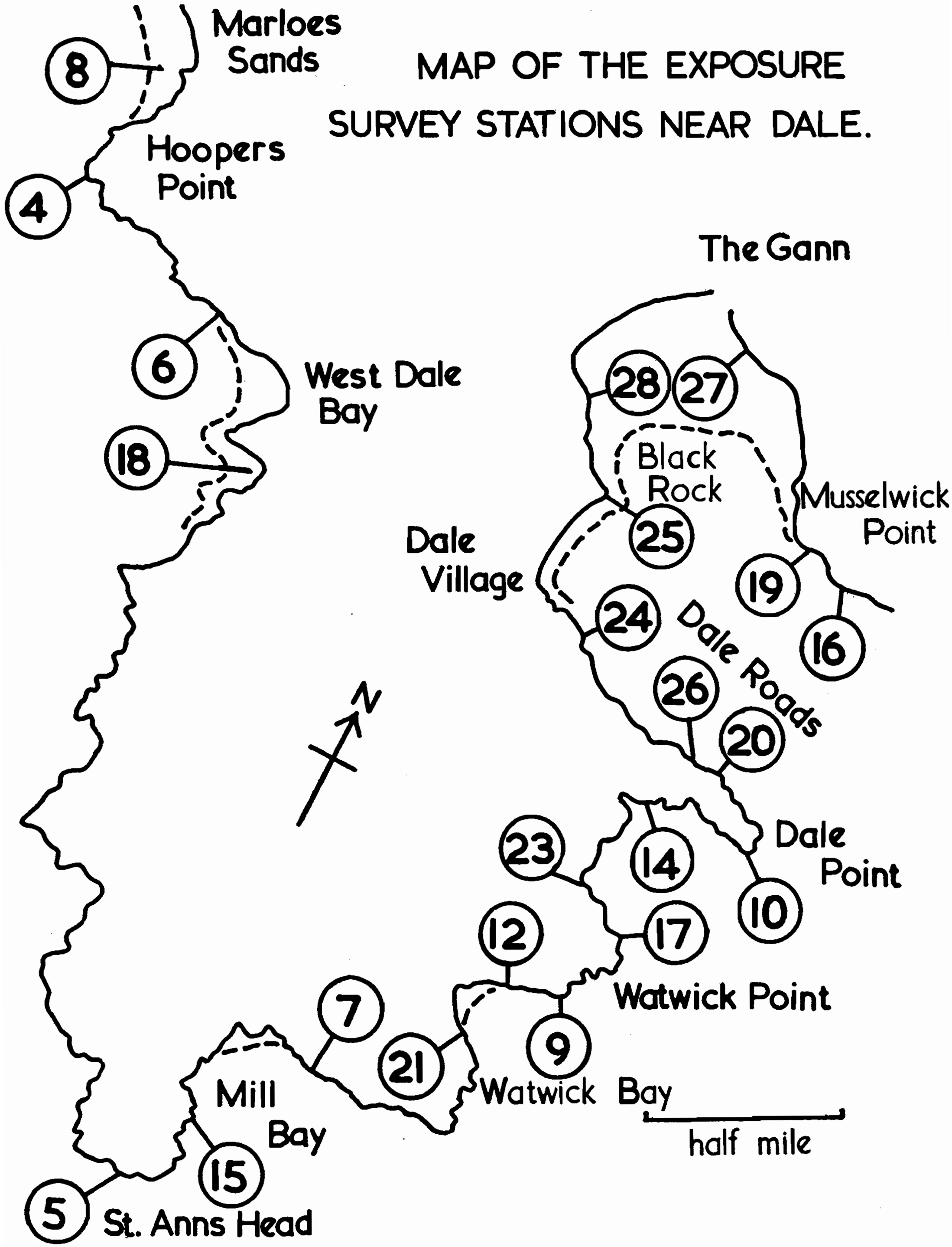
(*c*) The scale is a tautology. It merely states that a shore with a certain pattern of communities is equivalent to one with the same pattern.

Since the exposure scale is intended as a tool for research it should help to uncover new information and order it in an understandable fashion. If it does this, the objections listed above lose most of their force and become relatively unimportant. The latitudinal trend discussed later was discovered by the use of the scale and is, I believe, of some interest. Moreover, there is already in existence an accepted system of comparison about which the same criticisms could be (and were) made. No one is quite certain what the position of the barnacle line measures in terms of physical conditions, or even that they are the same conditions in every case. To say that the barnacle line in one place is equivalent to the barnacle line in another may seem to be a circular argument or tautological according to certain points of view. Nevertheless, the barnacle line (the upper limit of the barnacles in quantity) is used as one of the major reference points in the Stephensons' scheme for the comparison of vertical zonation (Stephenson and Stephenson, 1949). This scheme is widely accepted and has proved more useful in comparisons than physical measurements of tide-levels.

The exposure scale for horizontal comparisons is at a much lower stage of development than the Stephensons' scheme for zonation, and it is not likely to have such a wide application. The comparison between the two is made simply to suggest that the theoretical criticisms stated above may not be so devastating as they appear at first sight.

Methods

Some species occurring on rocky shores are abundant only in wave-beaten places—positive correlation with exposure; others are commonest in shelter—negative correlation. The vertical ranges of the various species may alter with the degree of wave action (Lewis, 1955), also the absolute levels (Evans, 1947); however, with a few exceptions, the judging of range limits is a difficult and subjective process. For comparable results between shores the abundance of each species provides an easier, quicker and more reliable guide to exposure than does their range.



MAP OF THE EXPOSURE SURVEY STATIONS NEAR DALE.

I have included notes on zonation where this provides extra information. The terminology of zonation used was devised by the Stephensons (1949).

The following indicator species were selected (the correlation with exposure is given beside each species, positive or negative):

Algae		Fauna	
Pelvetia canaliculata	−	Chthamalus stellatus	+
Fucus spiralis	−	Balanus balanoides	−
Ascophyllum nodosum	−	Patella vulgata	"intermediate"
Fucus vesiculosus	two forms*	Patella aspera	+
Fucus serratus	−	Patella depressa	+
Laminaria digitata	"intermediate"	Littorina littorea	−
Alaria esculenta	+	Littorina obtusata	−
Laminaria saccharina	−	Littorina saxatilis	two forms*
Porphyra, high level form	+	Littorina neritoides	+
"Lithothamnia"	two forms*	Gibbula umbilicalis	−
Lichen		Monodonta lineata	−
Lichina pygmaea	+	Nucella lapillus	"intermediate"

* One form positive, the other negative.

A transect line was established at each of 28 stations in the Dale area (see Map and Table 2 for positions) and the abundance of each indicator species was recorded using the notation developed by Crisp and Southward (1958), see Table 1.

The stations were arranged in order by the abundance of each species separately at first. These orders were checked for consistency using rank correlation methods. The final order of stations (Table 2) was the average of the single species orders. The final order was divided up into convenient sections to provide the data for the exposure scale.

Table 1. *The notation used to describe abundance*

Balanus balanoides and *Chthamalus stellatus*:

- A More than 1 per sq. cm., rocks well covered.
- C 0·1 to 1 per sq. cm., up to one-third of the rock covered.
- F 0·01 to 0·1 per sq. cm., individuals never more than 10 cm. apart.
- O 10 to 1,000 per sq. metre, few within 10 cm. of each other.
- R Only a few found in 30 minutes' search.

Limpets:

- A Over 50 per sq. metre or more than 50% of limpets at certain levels.
- C 10 to 50 per sq. metre, or 10-50% at certain levels.
- F 1 to 10 per sq. metre, or 1-10% at certain levels.
- O Less than 1 per sq. metre, or less than 1% of the population.
- R Only a few found in 30 minutes' search.

Top-shells and *Nucella lapillus*:

- A Exceeding 10 per sq. metre generally.
- C 1 to 10 per sq. metre, locally sometimes more.
- F Less than 1 per sq. metre, locally more.
- O Always less than 1 per sq. metre.
- R Only one or two found in 30 minutes' search.

Littorina neritoides and the small form of *L. saxatilis*:
- A Over 1 per sq. cm. at H.W.M., extending down the mid-littoral zone.
- C 0·1 to 1 per sq. cm., mainly in the supra-littoral fringe.
- F Less than 0·1 per sq. cm., mainly in crevices.
- O A few individuals in most deep crevices.
- R Only one or two found in 30 minutes' search.

Other *Littorina*:
- A More than 50 per sq. metre.
- C 10 to 50 per sq. metre.
- F 1 to 10 per sq. metre.
- O Less than 1 per sq. metre.
- R Only one or two found in 30 minutes' search.

Mytilus edulis:
- A More than 20% cover at certain levels.
- C Large patches at some levels.
- F Many scattered individuals and small patches.
- O Scattered individuals, no patches.
- R A few seen in 30 minutes' search.

Lichens:
- A More than 20% cover at some levels.
- C 1 to 20% cover, zone well-defined.
- F Large scattered patches, zone ill-defined.
- O Widely scattered patches, all small.
- R A few small patches seen in 30 minutes' search.

Fucoids, *Laminaria* spp. and *Alaria*:
- A More than 30% cover.
- C 5 to 30% cover.
- F Less than 5% cover, but zone still apparent.
- O Scattered individuals, zone indistinct.
- R A few plants found in 30 minutes' search.

A = abundant, C = common, F = frequent, O = occasional, and R = rare; N is used for absent.

N.B. The notation of abundance for each species should be applied only to the levels at which the species is normally found, e.g. for *Ascophyllum* abundant is more than 30% cover near mid-tide level, not over the whole shore.

THE EXPOSURE SCALE

For each unit of the scale, the criteria by which it is defined and may be recognized are given in the following order:

- (i) General comments
- (ii) Laminaria and Alaria
- (iii) The fucoids
- (iv) Other algae
- (v) Lichens
- (vi) Barnacles
- (vii) Limpets
- (viii) Littorinids
- (ix) Top-shells
- (x) Other animals

Dominant in this scale means the most abundant species in the group (e.g. barnacles or fucoids) at the specified level.

(1) *Extremely exposed* (based on stations 1, 2 and 3)

(i) Heavy surf occurs more or less continuously. Many abundance trends may be reversed because the isolation of the localities prevents or reduces

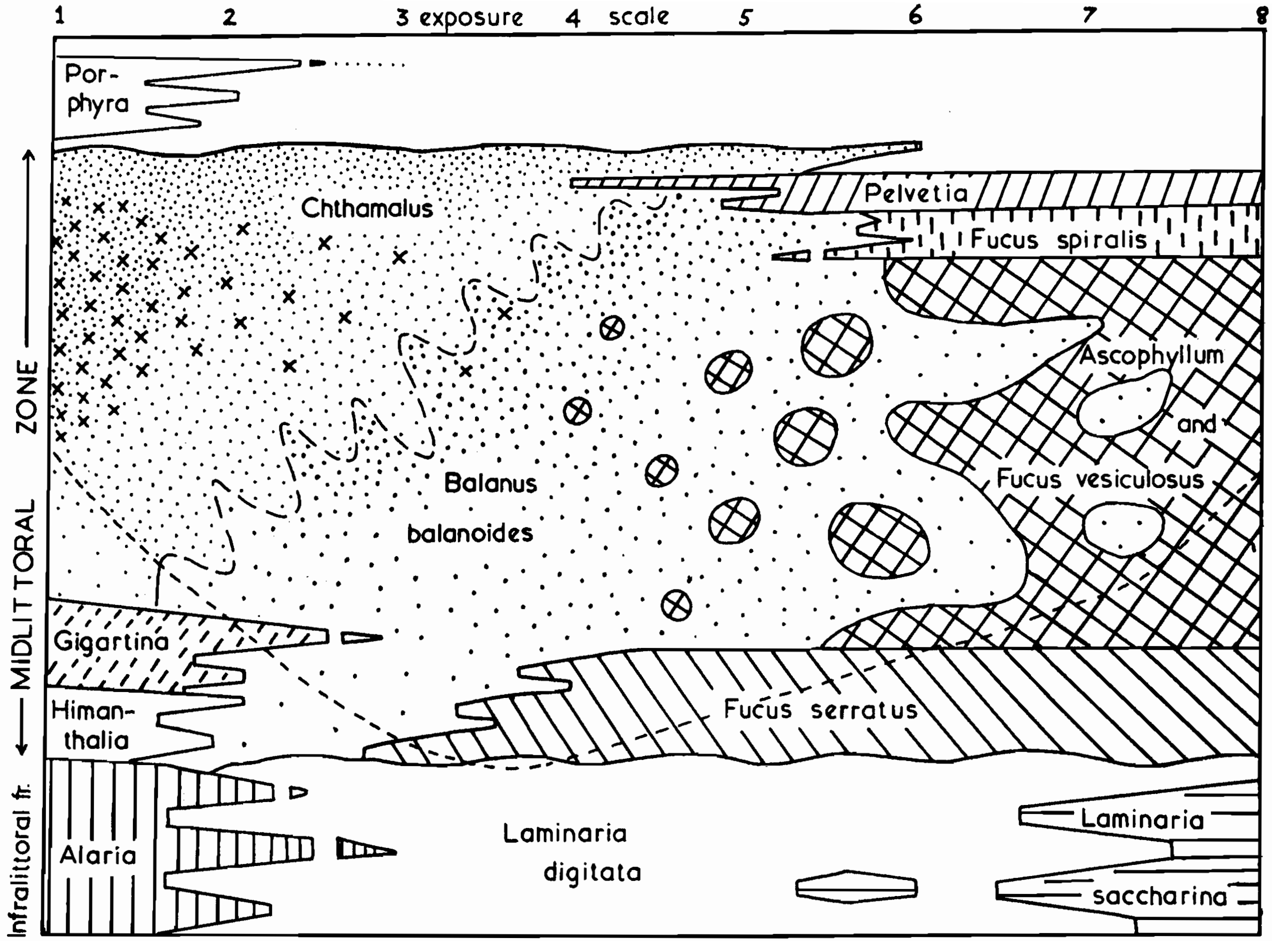


FIG. 1

The changes in distribution and zonation of the barnacles and algae with exposure. Based on shores in the Dale area, Pembrokeshire, except the extremely sheltered shore. Vertical scale according to Stephenson's universal scheme. Horizontal scale of exposure (sheltered to the right) with the approximate positions of the exposure scale given.

× = *Fucus vesiculosus* f. *evesiculosus*.

— — — = upper limit of "Lithothamnia".

colonization (e.g. the total absence of *Lichina pygmaea* on Grassholm). However, extremely exposed shores are rare, often inaccessible and quite distinctive.

(ii) *Alaria* is abundant and dominant in the infralittoral fringe, *Laminaria* spp. are rare or absent.

(iii) The only fucoid present is *Fucus vesiculosus* form *evesiculosus* which is frequent to abundant as very short erect tough bladderless plants with complete barnacle cover underneath.

(iv) The thick form of "lithothamnia" and *Corallina* are abundant under the *Alaria* and *Himanthalia* and *Gigartina* communities. *Porphyra* persists as a dense band above the barnacle line throughout the summer.

(v) *Lichina pygmaea* usually common, but see note (i). The lichens of the supralittoral fringe, which may extend up to 100 feet above sea-level, are all abundant and have very wide zones.

(vi) *Chthamalus* is abundant and dominant over the whole barnacle zone (the upper two-thirds of the midlittoral); *Balanus balanoides* is only frequent or less.

(vii) *Patella aspera* is abundant and dominant from amongst the *Alaria* to at least half way up the midlittoral; *P. vulgata* is common to abundant near the barnacle line, but all very small, 25 mm. max. shell-length except in crevices; *P. depressa* is usually common (always less common than *P. vulgata*).

(viii) *Littorina neritoides* and *L. saxatilis* common or abundant. *L. saxatilis* very small (max. shell-length 6-8 mm.) and *L. neritoides* nearly as large (max. 5-6·5 mm.). Other littorinids absent.

(ix) Top-shells absent.

(x) *Nucella* is confined to crevices and the individuals are all small (18-22 mm. max. shell-length) with thick shells, short spires and large apertures. *Mytilus edulis* is common in the lower midlittoral as tiny crowded individuals.

(2) *Very exposed* (based on stations 4, 5 and 6)

(i) The most exposed kind of shore to be found on the mainland, still very impressive physically and workable only on calm days.

(ii) *Laminaria digitata* common to abundant and always dominant; *Alaria* less, frequent to common.

(iii) *Fucus vesiculosus* f. *evesiculosus* rare to common, no other fucoids except possibly some *Pelvetia* on landward-facing slopes and scattered *Fucus serratus* just above the *Laminaria*.

(iv) A "lithothamnia": *Corallina*: *Gigartina* zone occurs at the base of the midlittoral zone. *Porphyra* persists in summer on *Fucus* and as scattered tufts above the barnacle line.

(v) *Lichina pygmaea* common at the top of the midlittoral; the supralittoral fringe lichens are normally abundant and have wide zones.

(vi) *Chthamalus* is abundant and dominant over the upper half of the midlittoral; *Balanus balanoides* frequent to common in the lower half and often dominant there.

(vii) *Patella aspera* is abundant and dominant in the infralittoral fringe and lower midlittoral zone; *P. vulgata* abundant and dominant over the rest of the midlittoral; *P. depressa* common amongst the *P. vulgata*.

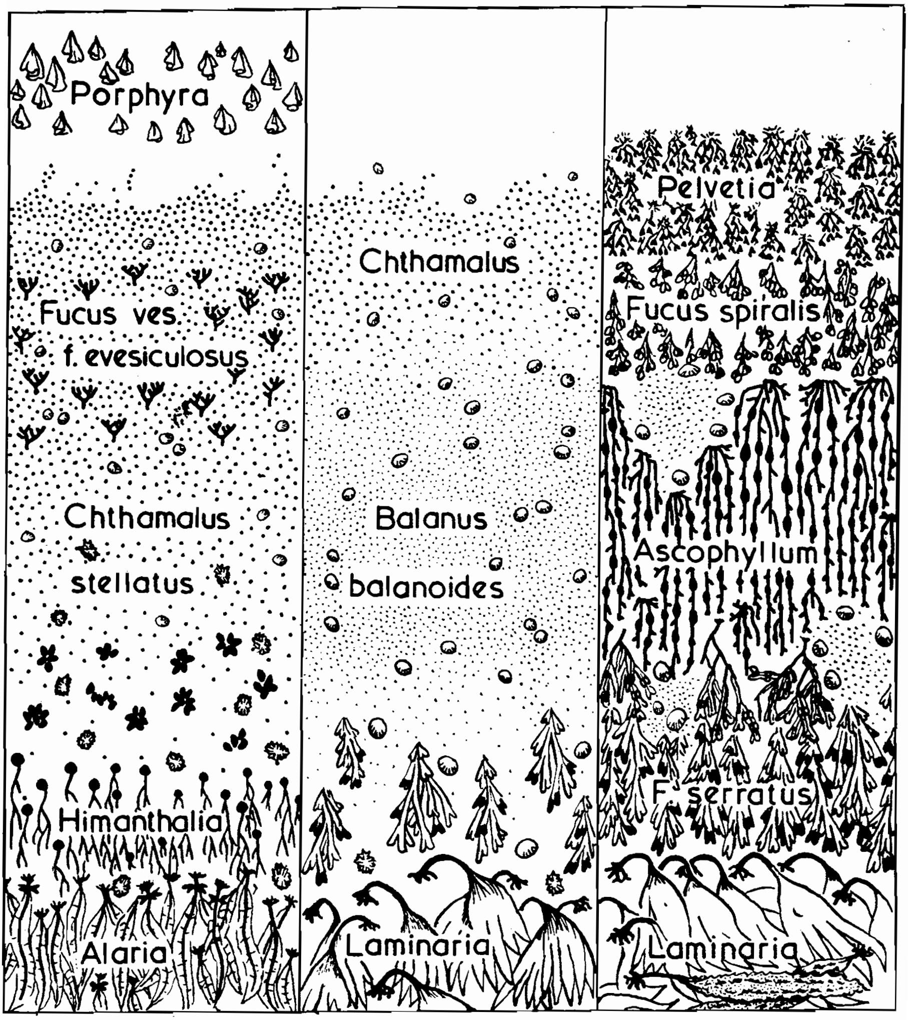


FIG. 2
An extremely exposed shore

FIG. 3
A semi-exposed shore

FIG. 4
A very sheltered shore

= *Mytilus* patches

= *Fucus vesiculosus*

= *Patella aspera*

= *Fucus vesiculosus* f. *evesiculosus*

= *Balanus balanoides*

= *Patella vulgata*

= *Chthamalus stellatus*

Diagrams of the main zonation on three shores of the exposure scale in the Dale Area, Pembrokeshire (midlittoral reduced to same vertical scale in each case).

(viii) *Littorina neritoides* and *L. saxatilis* common in the supralittoral fringe and amongst barnacles; other littorinids absent.

(ix) Top-shells absent.

(x) *Nucella* common and occurs on the open rock in places. *Mytilus* usually only in crevices but on isolated stacks may cover much of the lower midlittoral zone.

(3) *Exposed* (based on stations 7, 8, 9 and 10)

(i) Shores of this unit are fairly common on the west coast. They occasionally receive almost the full force of Atlantic storm waves.

(ii) *Laminaria digitata* common or abundant, dominant; *Alaria* rare or absent.

(iii) *Pelvetia* rare on seaward slopes; *Fucus vesiculosus* f. *evesiculosus* rare or occasional; *F. serratus* occasional. Other fucoids absent.

(iv) "Lithothamnia" and *Corallina* common; no high-level *Porphyra* in summer.

(v) *Lichina pygmaea* common or abundant; supralittoral lichens common.

(vi) *Chthamalus* abundant and dominant in the upper midlittoral; *Balanus balanoides* abundant and dominant over rather more than half (lower half) of the midlittoral zone.

(vii) *Patella aspera* common in the upper part of the infralittoral fringe and in "lithothamnia"-lined pools; *P. vulgata* abundant and dominant over the whole of the midlittoral; *P. depressa* frequent or common.

(viii) *Littorina neritoides* and *L. saxatilis* common or abundant. Other littorinids absent.

(ix) Top-shells absent except perhaps for a few *Gibbula umbilicalis* in deep pools.

(x) *Nucella* common on the open rock. *Mytilus* confined to cracks except on small isolated stacks where it may be abundant.

(4) *Semi-exposed* (based on stations 11, 12, 13, 14 and 15)

(i) Shores in this unit occur commonly. The reduction in wave action from the full possible force is at once apparent to the critical observer.

(ii) *Laminaria digitata* common or abundant; *Alaria* absent.

(iii) *Pelvetia* occasional to common, but rarely forming a distinct zone; *Fucus vesiculosus* rare, plants without air-bladders, but larger than the typical f. *evesiculosus*; *F. serratus* occasional to common, usually forming a definite zone above the *Laminaria*; *F. spiralis* and *Ascophyllum* absent. No fucoid invasion of the main midlittoral zone, which is barnacle and limpet dominated.

(iv) "Lithothamnia" and *Corallina* common in pools and damp places beneath *Fucus serratus* and *Laminaria*.

(v) *Lichina pygmaea* common only on south-facing rock at the top of the midlittoral. Supralittoral lichens common, but zones now only a few feet in vertical extent.

(vi) *Chthamalus* common or abundant, dominant for a few feet at the top of the midlittoral; *Balanus balanoides* abundant and dominant over the remaining midlittoral zone (75% of the total population, 100% of the lower half).

(vii) *Patella aspera* occasional to common, largely confined to pools; *P. vulgata* abundant and dominant over the entire midlittoral zone; *P. depressa* frequent.

(viii) *Littorina neritoides* and *L. saxatilis* usually common; *L. littorea* absent or rare; *L. obtusata* absent.

(ix) *Monodonta* rare or absent; *Gibbula umbilicalis* occasional to common in pools or damp places.

(x) *Nucella* common or abundant on the open rock; *Mytilus* rare or absent.

(5) *Fairly sheltered* (based on stations 16, 17 and 19)

(i) Shores in this unit are common. Large stones present are rarely moved; by the waves and develop a semi-permanent flora and fauna.

(ii) *Laminaria digitata* abundant and dominant; *L. saccharina* rare or absent *Alaria* absent.

(iii) *Pelvetia* frequent to common, forming a definite zone; *F. spiralis* absent or at most a few scattered plants; *Ascophyllum* usually present as isolated short plants; *Fucus vesiculosus* often present on the smaller rocks, plants with some air-bladders; *F. serratus* frequent to common, forming a dense zone.

(iv) "Lithothamnia" and *Corallina* only under dense seaweed or in pools.

(v) *Lichina pygmaea* rare to frequent on rough rock in sunny places.

(vi) *Chthamalus* frequent to common, with a very narrow zone of dominance at the barnacle line; *Balanus balanoides* common to abundant, but although it dominates almost all the barnacle area, fucoids are regularly present as isolated plants in the midlittoral.

(vii) *Patella aspera* absent or confined to pools; *P. vulgata* abundant over most or all the midlittoral; *P. depressa* frequent only on sunny slopes.

(viii) *Littorina neritoides* occasional to common in supralittoral fringe only; *L. saxatilis* common (max. shell-length 8-12 mm.); *L. littorea* occasional in pools; *L. obtusata* rare to frequent on the fucoids.

(ix) *Monodonta* rare to common; *Gibbula umbilicalis* common to abundant.

(x) *Nucella* common; *Mytilus* rare or absent.

(6) *Sheltered* (based on stations 21, 22, 23 and 24)

(i) Shores in this unit are normally "good collecting shores". They are sheltered enough to have a considerable permanent fauna beneath stones, but not so sheltered that mud and silt are deposited in quantity.

(ii) The infralittoral fringe often consists of stone and shingle, but *Laminaria digitata* and *L. saccharina* may be common.

(iii) *Pelvetia* abundant, forming a dense zone of large plants; *Fucus spiralis* frequent to common forming a distinct zone; *Ascophyllum* occasional to common, forming dense patches on the more jagged bedrock; *Fucus vesiculosus* common, typical plants with paired air-bladders, on stable shingle and small rocks; *F. serratus* common or abundant on bedrock or stones.

(iv) "Lithothamnia" (thin form) and *Corallina* are present under thick fucoids.

(v) *Lichina pygmaea* is absent; the supralittoral fringe lichens are not more than frequent.

(vi) *Chthamalus* occurs only at or above the barnacle line; *Balanus balanoides* common or locally abundant in the central midlittoral, but even here fucoids predominate if the rock is not suitable for continuous limpet grazing.

(vii) *Patella aspera* absent; *P. vulgata* abundant throughout the midlittoral except in the densest fucoid patches; *P. depressa* occasional or absent.

(viii) *Littorina neritoides* rare to occasional; *L. saxatilis* common, small in the supralittoral fringe, but a large form (12-18 mm. shell-length) present in the *F. spiralis* zone; *L. littorea* occasional to frequent on fucoids and in gullies; *L. obtusata* common on the denser fucoids.

(ix) *Monodonta* and *Gibbula umbilicalis* common or abundant.

(x) *Nucella* occasional to common. *Mytilus* rare or absent.

(7) *Very sheltered* (based on stations 26, 27 and 28)

(i) Rocky shores of this unit are not common since where wave action is so reduced sand and mud are usually deposited in quantity.

(ii) The infralittoral fringe was sandy at all the stations visited in the Dale area. *Laminaria saccharina* occurred on the few small stones.

(iii) All the fucoids are common or abundant, and form a continuous cover over most of the shore. The zones of *Pelvetia* and *F. spiralis* are very narrow and consist of very large individual plants. *Ascophyllum* covers most of the midlittoral bedrock, and *Fucus vesiculosus* covers the stones and shingle down to the *F. serratus* zone.

(iv) The thin form of "lithothamnia" and some *Corallina* exist under the lower fucoids.

(v) *Lichina pygmaea* is absent. The supralittoral fringe is at most only a few feet in vertical extent and the lichens growing there are occasional or rare.

(vi) *Chthamalus* is rare or absent; *Balanus balanoides* is frequent to common, but only on the steepest pieces of bedrock.

(vii) *Patella aspera* and *P. depressa* are absent; *P. vulgata* grows very large (50 mm. or more shell-lengths are common), but it is confined to small areas of well-drained rock beneath the fucoids and the few barnacled slopes.

(viii) *Littorina neritoides* is absent; *L. saxatilis* (almost entirely the large form 16-22 mm. max. shell-length) is common amongst the upper fucoids; *L. obtusata* is abundant; *L. littorea* common amongst fucoids, locally abundant.

(ix) *Monodonta* and *Gibbula umbilicalis* are common or abundant.

(x) *Nucella* is occasional, the shells are long and thin and taper gradually to a fine point; *Mytilus* may be common as groups of large specimens in the shingle.

(8) *Extremely sheltered*

(i) No rocky shores of this unit exist in the Dale area, but they are common in south-west Ireland and some other regions. They occur at the heads of intricate rocky inlets which receive no silt and where fetch is reduced to a few yards. Wave action and tidal currents are absent.

(ii) The infralittoral fringe is not usually present, but if the rock at this level does occur it is dominated by *Laminaria saccharina*.

(iii) All the fucoids are present and develop 100% cover even on vertical faces. Unattached fucoids such as *Ascophyllum nodosum* f. *mackii* are very common.

(v) *Lichina pygmaea* absent; the supralittoral fringe scarcely exists and grass and other land plants grow within a foot of the *Pelvetia*.

(vi) *Chthamalus* and *Balanus balanoides* are absent or rare.

(vii) *Patella vulgata* is at most rare; other limpets absent.

(viii) *Littorina neritoides* absent; *L. saxatilis* (large form only) common in upper fucoids; *L. obtusata* and *L. littorea* abundant.

(ix) *Monodonta* rare; *Gibbula umbilicalis* common.

(x) *Nucella* absent or rare.

The use of the exposure scale

To find the position of a shore on the exposure scale, the following procedure is recommended:

(*a*) Fix the position of the transect line.

(*b*) Measure the slope along the line. If this varies considerably the exposure of each section may have to be measured separately.

(*c*) Measure the abundance of the indicator species in the transect area, using the notation given in Table 1.

(*d*) Note the general features of the zonation, the physical configuration of the shore, its aspect and exact geographical position.

(*e*) Determine the approximate position of the shore on the exposure scale by examining Figures 1 to 4.

(*f*) Make a detailed comparison between the notes taken on the shore (under *c* and *d*) and the units of the scale to decide the precise position of the shore.

A test of the biological scale of exposure against physical estimates of wave action

The shore survey work on which the exposure scale is based was carried out during June 1958 and June 1959. Most of the stations were visited in both years and no significant change was seen. All the mainland stations can be included within a circle of 1½ miles radius and even the island of Grassholm is only 14 miles from Dale. The rock at all the stations (except Grassholm and Skomer) is uniformly sandstone or mudstone. There is no evidence of any significant variation in tidal range, pattern or timing within the survey area. The aspect of the stations does vary, but south or south-west facing stations occur in all units of the scale. Most of the stations are of a uniform and moderate slope of bedrock. There was no noticeable pollution or other human interference at the time of the survey.

The action of such variables as season, year, geology, geographical region, tidal regime, aspect to the sun, slope and pollution was thus minimized or at least randomly distributed relative to exposure. This leaves wave action as the only remaining variable likely to influence large changes in the composition of the shore communities.

In the Dale area all fetches fall into three groups: (*a*) more than 2,000 miles; (*b*) between 50 and 150 miles; (*c*) less than 10 miles. Moreover, the majority of gales acting on the coast (70%+) blow from the same direction (SSW. to W.) as that of the greatest fetch. Because of this fortunate geographical accident, it is possible to divide shores in the area into three groups of greatly different wave action. When the open angle of the shore to its maximum fetch is considered and refraction taken into account, the shores can be graded into a series of relative wave action. Wind speeds and frequency may be ignored only because of the great differences between the three classes of fetch and the coincidence of the direction of high winds and long fetch in the Dale area.

Table 2 lists the stations of the exposure survey in order of exposure as given by the biological data. The physical data for the estimation of wave

Table 2

No.	Station: Name	Aspect in ° from True North	Biological Exposure Scale Unit	Physical Data for the Estimation of Wave Action
1.	Grassholm	225	extremely exposed	Shores open over 67° to fetches of more than 2,000 miles; refraction concentrates waves on to these shores. Headlands on off-shore islands.
2.	Skokholm	235		
3.	Skomer	185		
4.	Hooper's Point	225	very exposed	Shores open over 40°-50° to fetches of more than 2,000 miles; refraction reduces this open angle slightly. Headlands on the mainland.
5.	St. Ann's Head	175		
6.	West Dale Bay	195		
7.	Mill Bay	180	exposed	Shores nearly open to fetches of more than 2,000 miles; refraction of about 10° required to bring waves from this direction to bear.
8.	Marloes Stacks	230		
9.	Watwick Point	160		
10.	Dale Point	160		
11.	Monk Haven a	165	semi-exposed	Shores open over more than 20° to fetches of 50-150 miles; refraction of 90° required to bring waves of 2,000 miles fetch to bear.
12.	Watwick Bay N.	155		
13.	Skokholm E.	125		
14.	Castlebeach	160		
15.	St. Ann's NE.	90		
16.	Musselwick E.	185	fairly sheltered	Shores with less than 10° open angle to fetches of 50 or more miles, and even this reduced by refraction.
17.	Gunkel E.	35		
18.	Gt. Castle Bay	260		
19.	Musselwick W.	200		
20.	Dale Ft. Pier	10	sheltered	Shores open to fetches of less than 10 miles over at least 60°; refraction of 90° required to bring waves of 50 or more miles fetch to bear.
21.	Watwick Bay S.	35		
22.	Monk Haven b	180		
23.	Gunkel W.	40		
24.	Point Wood a	30		
25.	Black Rock	100	very sheltered	Shores open to fetches of less than 10 miles over less than 60° and even this reduced by refraction; refraction of more than 90° required to bring waves of 50 miles fetch to bear.
26.	Point Wood b	345		
27.	Gann Quarry	205		
28.	Cliff Cottage	35		

action is also shown. These two things correlate well, and so the biological exposure scale does appear to give a good estimate of wave action.

It is important to note that this does not imply that there is a direct causal relationship between the existence of individual species on a shore and the size or frequency of the waves.

Discussion

(1) *The nature of the exposure scale and its implications*

The exposure scale given above is not a simple mathematical scale. The intercepts are not necessarily equal, they are merely at convenient intervals. It is not possible to say that one shore is twice as exposed as another.

Exposure as measured on the scale includes the effects of other factors besides incident waves. The same waves breaking on a gentle slope will produce less "exposure" than on a steep shore.

At present we know relatively little about the nature of waves which break on rocky shores, and still less about the way they affect individual organisms and communities. Thus, although some method of systematizing shore description and comparison is needed, it is important that this should not include assumptions which may prove misleading. Any physical method of describing and comparing shores assumes that it is known which physical factors are important; it must do this or become cumbersome by recording everything. The biological scale avoids this by starting at the other end of the problem. It states that the shores of an area, for all their variety and complexity do not have random collections of organisms on them. There is a pattern, a trend, in the communities. To take a simple example in the Dale area—if a shore has *Alaria* abundant and dominant in the infralittoral fringe and *Porphyra* exists as a dense band above the barnacles in midsummer, then, without seeing it, one can say that the majority of the barnacles will be *Chthamalus* and that *Patella aspera* will be abundant. No causal relationships are implied in this deduction. It is simply a correlation with a very high degree of probability. This idea is implicit in much of the literature. Most local shore survey reports describe a "typical exposed shore" and a "typical sheltered shore" as a short-hand for the whole area and then fill in the detail. However, I have not been able to find the implications of this discussed fully. The exposure scale merely describes the main trend or pattern of communities and divides it up into convenient but arbitrary sections. The scale is flexible and can easily be modified, improved and refined to suit particular regions or problems. At the same time, since it is based on quantitative measurements, it enables strictly accurate comparisons to be made from shore to shore.

The community trend described in the exposure scale is not by any means the whole story; innumerable other trends and effects occur which tend to confuse the main pattern. There are pools and crevices, the communities on boulders, the effects of sand abrasion and shade to mention only a few. The main pattern itself is likely to change with time and in different geographical regions. Nevertheless, if a pattern can be established for even one area and time these modifications can be dealt with separately. Attempts to deal with the whole complex web of communities at once are unlikely to succeed.

(2) *The use of the exposure scale in south-west Britain*

The exposure scale has been tested in south-west Ireland and in the Plymouth area. In both regions it worked well and the shores could be quickly classified and so were at once comparable to those at Dale. One or two anomalies were immediately apparent. *Patella depressa* was absent from Ireland, although many shores seemed identical in other respects with those at Dale where the species was common. At Plymouth the relative abundance of *Chthamalus stellatus* and *Balanus balanoides* was consistently out of phase with the other indicator species, *Chthamalus* penetrating much further into shelter than at Dale.

Several important points arise from this work. Firstly, the scale works well up to 100 miles or so from Dale where it was derived. Secondly, the anomalies that do occur are as nothing compared to geographical/geological anomalies which render a scale based on physical measurements so unsatisfactory. Thirdly, the biological anomalies are of considerable direct interest and significance to the shore biologist (see Crisp and Southward, 1953, and Southward and Crisp, 1956), and the use of the exposure scale enables them to be defined in a concise and accurate manner.

(3) *The fate of the exposure scale further afield*

During 1959 I made some observations on shores in Norway (Bergen to Hammerfest) and at Santander in north Spain. These span a difference of latitude of some 2,000 miles. The scale produced in the Dale area proved unworkable so far away, but the attempts to use it gave some interesting data which are summarized in Fig. 5. The principle conclusion to be drawn from this is the existence of a latitudinal trend down the coast of western Europe similar to the local trend at Dale from sheltered to exposed shores. Thus, if the Dale exposure scale is applied rigorously, one would be led to believe that there are no exposed shores in Norway and no sheltered shores in Spain. In fact it seems that many species show a progressive change in their exposure tolerances from north to south.

Like the exposure trend, this latitudinal trend is mainly concerned with the fucoid : limpet : barnacle balance. Limpets graze fucoid sporelings; fucoids tend to smother barnacles and barnacles compete with limpets for space and reduce their feeding efficiency (Lodge, 1948; Southward, 1956). Although barnacles and fucoids are directly affected by wave action, the competition between the three groups of organisms may be just as effective a control on the distribution and abundance of any of them. The relative efficiency of all the species changes with latitude, but at different rates. *Balanus balanoides* holds the barnacle field alone in Norway, shares it with *Chthamalus* at Dale, and is completely eliminated by the latter in Spain. Fucoids are dominant on most shores in Norway, but at Santander they are confined to sheltered places and common only in considerable shelter. *Patella vulgata* is an animal which thrives best on the edge of the fucoid : barnacle boundary and follows this in its movement from exposure towards shelter as one goes south. As the number of *Chthamalus* dominated shores increases *Patella depressa* becomes the commonest limpet. It should be observed that all the species behave in the same way, occupying increasingly sheltered shores towards the southern end of their range.

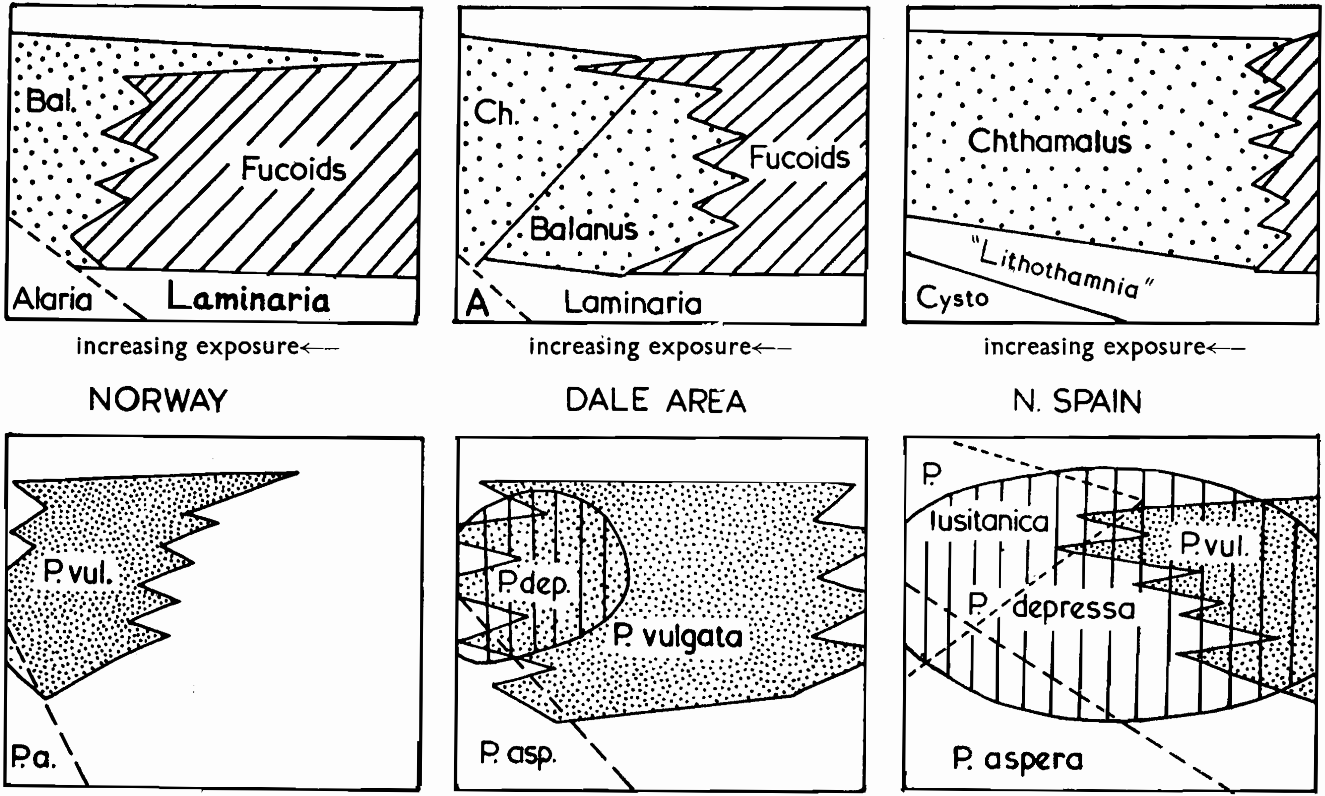


FIG. 5

Diagrams showing the changes in the barnacle: fucoid balance from north to south (top row); and the associated changes in distribution of *Patella* spp. (bottom row). Each diagram represents a series of shores in the area stated, exposed to the left and sheltered at the right. The top of each diagram represents the top of the midlittoral zone and the bottom passes into the infralittoral fringe. Cysto. =*Cystoseira* zone.

Alternative explanations for this phenomenon might be:

(*a*) That there is a trend in gradually increasing complexity of coastal configuration from south to north and that the resulting wave refraction reduces exposed shores in the north to theoretical points, i.e. that only submerged off-shore reefs and tiny islets receive the full wave action.

(*b*) That the far greater proportion of sheltered shores in the north may produce a recruitment advantage to sheltered shore organisms and push the exposure-loving species further towards exposure or even eliminate them altogether.

(*c*) That there may be a relationship between exposure and latitude (of a climatic nature) which produces similarities between northern exposed and southern sheltered shores. At any latitude exposed shores are not so warm in summer and not so cold in winter as are sheltered shores; and this may imply a higher mean annual temperature in exposure. South-west Ireland with its cool summers and relatively warm winters is a more favourable place for sub-tropical land plants than the south-east of England which has much higher summer temperatures but much lower winter ones. Exposed shores may be more temperate in a similar way.

I believe that there is some truth in each of these explanations, but that (*c*) is probably the most important. It may be possible eventually to produce a latitudinal correction for the exposure scale, but as I have described it here its use should be restricted to south-west Britain.

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Summary

(i) Wave action on rocky shores and the concept of exposure are discussed. The advantages of using a purely biological exposure scale rather than physical estimates of wave action for comparing shores are assessed.

(ii) Exposure is considered as a trend in the composition of the shore fauna and flora. The abundance of the common species is used to produce a scale of exposure in the Dale area, Pembrokeshire.

(iii) The scale enables rocky shores consisting of moderate slopes of bedrock in south-west Britain to be directly compared with one another. Further away from Dale, and in certain conditions, modifications of the scale will be required.

(iv) Using experience on shores in Norway and north Spain, the nature of some of these modifications is discussed. A change in the exposure tolerances of many species from north to south is postulated.

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