

# The Zonation of Marine Algae at Piha, New Zealand, in Relation to the Tidal Factor<sup>1</sup> (Studies in Inter-tidal Zonation 2)<sup>2</sup>

W. A. BEVERIDGE AND V. J. CHAPMAN<sup>3</sup>

## INTRODUCTION

THIS PAPER forms part of an inquiry into the operation of tidal factors in determining littoral zonation, and provides a comparison with work performed on the east coast of the Auckland Province (unpublished). There is still considerable confusion concerning the terminology that should be used in these ecological investigations. One of us (Chapman, 1947) has suggested that the time is now ripe for the application of ecological terms in the sense used by land workers. This viewpoint has been contested recently by Womersley (1947) but on grounds that scarcely seem adequate. In view of this confusion, however, it is still desirable to define the terms used, and in the present investigation they are as follows:

The *littoral* region is regarded as all that part of the shore between highest wash and the lowest level of spring tides. This definition is also adopted by Oliver (1923) and by Cranwell and Moore (1938).

*Formation* is a unit of vegetation formed by the habitat and expressed by distinctive life forms (Tansley, 1944), e.g., the Laminarian formation of Europe and the giant kelp formation of the north Pacific. (Owing to the small area studied formations have not been considered in this paper.)

<sup>1</sup>This paper is a résumé of work carried out by the first author for a Master of Science degree at Auckland University College, Auckland, and has been prepared for publication by the second author.

<sup>2</sup>For Studies in Inter-tidal Zonation 1, see *Pacific Science* 4(1): 63-68, 1950.

<sup>3</sup>Forest Officer in the Malayan Forest Service and Professor of Botany, Auckland University College, respectively. Manuscript received March 29, 1949.

*Association* is the largest unit of the plant formation dominated by more than one species and with at least some subordinate species, the dominants having the same ecological requirements.

*Consociation* is a community characterised by a single major dominant.

*Society* is a subordinate community *within* an association or consociation and characterised by a locally dominant subsidiary species.

*Belt* (*zone* of some authors) is a horizontally extended association which may be continuous round the coast, or which may be interrupted by another community, the presence of which depends on slightly different local conditions.

*Aspect society* is a seasonal community locally dominant.

*Clan* is a small aggregation of subordinate species.

*Fasciation* is a modification of the association in which a secondary species becomes a dominant or co-dominant.

*Exposure* can mean one of two things—exposure to the air during low tide periods or exposure to strong wave action. These two different types of exposure will be designated in the text by the terms *air* and *wave* exposure, respectively.

In this paper the viewpoint is adopted that the biome of the rocky sea shore represents a *physiographic climax*, since it is dependent upon the tide rather than upon the climate.

## LOCALITY

Piha is situated about 7 miles north of the Manukau Heads on the west coast of New Zealand, where there is exposure to the waves

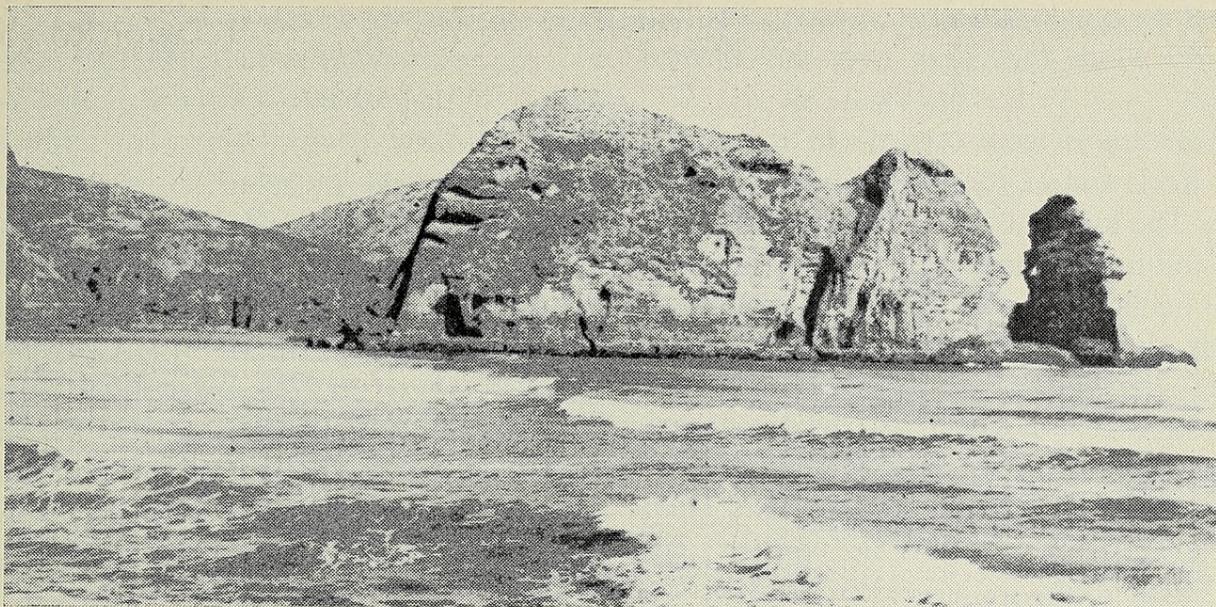


FIG. 1. View of Camel Rock, Piha, from the north. The gap is behind and to the left. The wave-cut platform at the base of the rock is clearly visible.

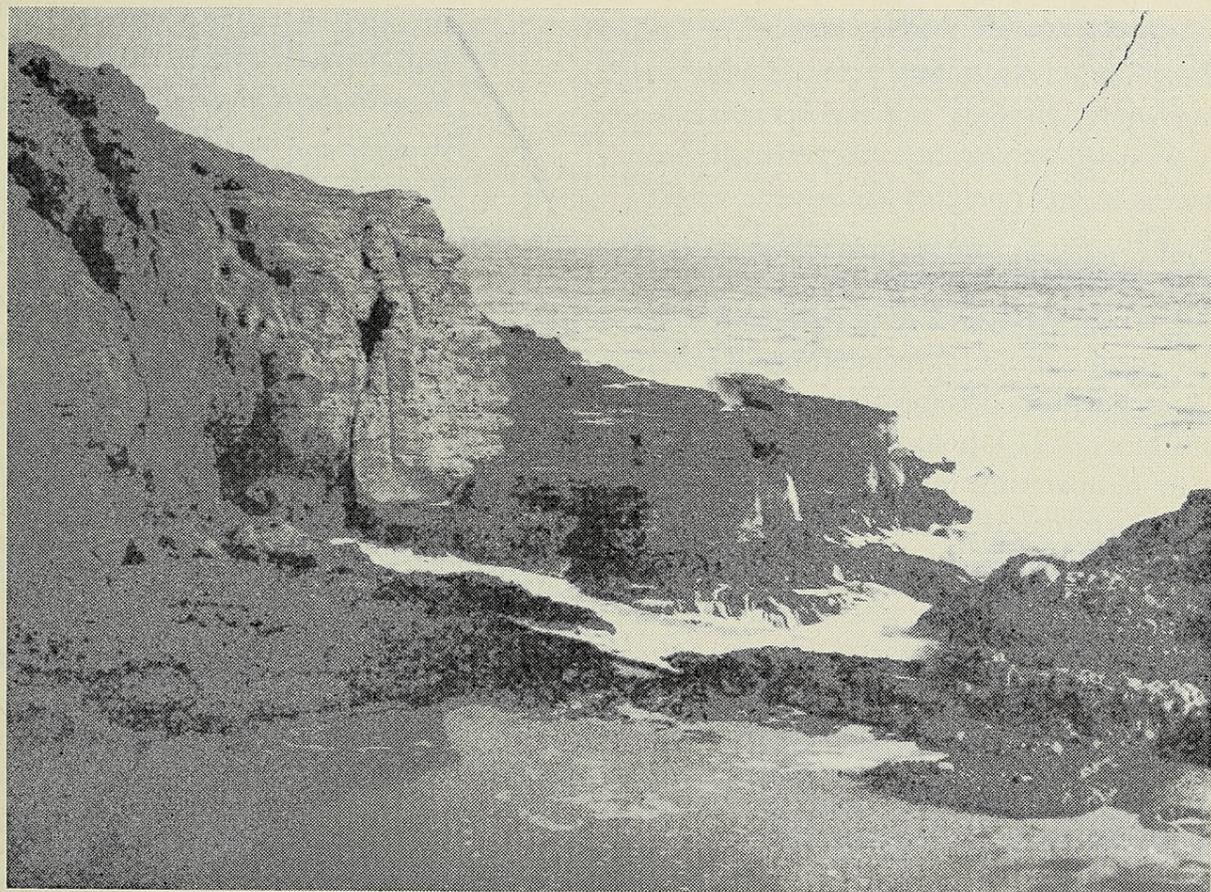


FIG. 2. Mouth of the gap, south of Camel Rock. Note the sharp upper limit to the algal zonation, most of which is *Durvillea*.

created by the full force of the prevailing westerly winds that blow over the Tasman Sea.

Observations were carried out mainly on Lion Rock and at the "Gap" behind Camel Rock. The former is an isolated rock 330 feet high and has a broad wave platform at about storm height. The sides of this platform slope steeply down to low water mark at most points. The second area is formed by a large off-shore rock (Camel Rock) with a narrow channel between it and the mainland; through this the sea surges with great force. There is also a tunnel through the northern end of Camel Rock in an east-west direction. (Fig. 1.)

Geologically the rocks belong to the Manukau Breccia series and consist of andesitic fragmental beds with numerous intrusive dykes and minor interbedded flows. There is no variation in the area studied.

#### CLIMATE

The climate is mild and equable with prevailing westerly winds, but the open coast is often exposed to strong gales which send the waves to great heights against the vertical cliffs. The sea is seldom calm and there is normally a strong surf, and even on the quietest day a considerable swell is present.

The mean annual precipitation is about 44.73 inches and the mean annual amount of sunshine, 1,914 hours. The average annual air temperature range is 26° C. with a daily shade range of about 7.0° C. The maximum shade temperature is 32.8° C. and the minimum — 0.5° C.

#### LITTORAL COMMUNITIES

These are described more or less from high water mark downwards.

##### 1. *Lichina pygmaea*-*Melaraphe* association

Range: upper limit of spray to M.H.W.S.<sup>4</sup>

*Lichina pygmaea* (d)<sup>4</sup>  
*Melaraphe oliveri* (d)  
*Melaraphe cincta* (d)  
*Entophysalis deusta* (l)  
 various limpets

In positions of maximum wave exposure this association may reach great heights. It is usually absent from crevices and other strongly shaded places. Of the two gastropods *M. oliveri* has the wider range since it may descend to M.H.W.N. whereas *M. cincta* occurs in the lower part of this association and in the narrow band formed by the next community.

##### 2. *Bostrychia arbuscula* consociation

Range: wash of M.H.W.S. to M.H.W.N.

*Bostrychia arbuscula* (d)  
*Rhizoclonium riparium* (lf)  
*Lophosiphonia macra* (lf)  
*Caloglossa leprieurii* (lf)  
*Melaraphe oliveri* (f)  
*Melaraphe cincta* (f)  
*Entophysalis deusta* (seasonal)  
*Enteromorpha ramulosa* (seasonal)

The dominant species occurs on shady exposed rock faces in a permanently juvenile and sterile prostrate form; the adult, dark red, fertile form is to be found in moist and dark crevices.

<sup>4</sup>The following abbreviations are used throughout this discussion:

E.H.W.S. = Extreme high water spring tides.  
 M.H.W.S. = Mean high water spring tides.  
 M.H.W.N. = Mean high water neap tides.  
 E.(L).H.W.N. = Extreme (lowest) high water mark neap tides.  
 M.S.L. = Mean sea level.  
 E.(H).L.W.N. = Extreme (highest) low water mark neap tides.  
 M.L.W.N. = Mean low water neap tides.  
 M.L.W.S. = Mean low water spring tides.  
 E.L.W.S. = Extreme low water spring tides.  
 d = dominant  
 a = abundant  
 f = frequent  
 o = occasional  
 r = rare  
 l = local

The consociation attains its best development amidst boulders at the back of the rock platform or in more sheltered places. *Bostrychia* does not appear able to withstand direct strong wave action. In general this belt occurs below the *Lichina* but above the main development of the barnacle zone.

Under conditions of extreme shade *Bostrychia* is replaced by *Rhizoclonium riparium* above and *Lophosiphonia macra* below. Where the shade is rather less intense *Caloglossa leprieurii* is a common associate. *Entophysalis deusta* occurs on sunny faces in summer and *Enteromorpha ramulosa* in winter.

### 3. *Chamaesipho* association

Range: M.H.W.S. to M.S.L.

*Chamaesipho columna* (d)  
*Chamaesipho brunnea* (d)  
*Porphyra columbina* (f-ld)  
*Modiolus neozelanicus* (f)  
*Elminius plicatus* (f)  
*Centroceras clavulatum*

The configuration of the rock is important in relation to the upward extension of this association. Where the wave platform is bounded by vertical walls the association occurs up to the edge, but where the rock is sloping the surge of the waves elevates the upper limit considerably. *Chamaesipho columna* is most abundant from M.H.W.N. upwards; below it enters into competition with *Modiolus* and *Elminius*. *Porphyra columbina* apparently exists in two forms in this association. The first, which is usually small, tufted, and light green, occupies a belt from H.W.N. to H.W.S., being most abundant in sheltered and sunny areas. From H.W.N. to L.W.N. there is a larger, more flaccid, olive-red form, which, however, grades into the other form where shading occurs. The two forms may therefore represent sun and shade types.

### 4. *Modiolus-Chamaesipho columna* association

Range: M.H.W.N. to M.L.W.N.

*Chamaesipho columna* (d)  
*Modiolus neozelanicus* (d)  
*Elminius plicatus* (f-la)  
*Centroceras clavulatum*  
 (spring and summer)  
*Gelidium pusillum* (o)  
*Apophloea sinclairii* (o)  
*Chaetangium corneum* (o)  
*Lophosiphonia macra* (r)

The composition of this association varies, depending on wave action. One may therefore recognise two fasciations. The principal difference is in the greater abundance of *Elminius plicatus* under conditions of moderate wave action, whereas where there is strong wave action this species is restricted to crevices and sheltered areas. In places the *Modiolus* forms a close cover; under these circumstances it appears to be antagonistic to other animals and to plants. Only a few algae appear capable of attaching themselves to the mollusk.

Although this association is here regarded as distinct from the preceding association it must be recognised that some workers might prefer to regard it as a fasciation of the *Chamaesipho* association. It does differ however in the co-dominance of the *Modiolus*, the greater abundance of the *Elminius* under certain circumstances, and in the levels it occupies. It is for these reasons that it is here treated as a separate association.

### 5. *Vermilia-Hermella* association

Range: M.S.L. to M.L.W.N.

*Vermilia carinifera* (d)  
*Hermella spinulosa* (d)  
*Modiolus neozelanicus* (o)  
*Chamaesipho columna* (o)  
*Gigartina alveata* (o)  
*Gelidium caulacanthum* (o)  
*Centroceras clavulatum*  
 (spring and summer)  
*Pleonosporum hirtum* (o)  
*Caulacanthus spinellus* (f)

This is an association which occurs constantly in all areas except where there is very strong wave action, and which is characterised by a distinctly restricted vertical range (about 18 inches). Both the dominants are important because they eliminate larger algae that otherwise might be present.

6. *Gigartina alveata* consociation (Fig. 3)

Range: M.S.L. to M.L.W.N.

*Gigartina alveata* (d)  
*Modiolus neozelanicus* (lf)  
*Chamaesipho columna* (f)  
*Gelidium caulacanthum* (la)  
*Pleonosporum hirtum* (summer)  
*Scytothamnus australis* (o)

The consociation forms a compact belt in those places where there is neither strong wave action nor extreme shelter. It always occurs above *Pachymenia himantophora* when both are present. On boulders at the head of gullies the community tends to be closed so that there are very few, if any, associated algae. In wave-exposed situations bleached and stunted specimens of *Gigartina* are scattered sparsely over the rocks.

7. *Pachymenia himantophora* consociation (Fig. 4)

Range: E.(H).L.W.N. to about 12–18 inches below.

*Pachymenia himantophora* (d)  
*Lophurella caespitosa* (o)  
*Champia novae-zelandiae*  
*Gelidium caulacanthum* (o)

The consociation is absent in the more sheltered localities of the open coast, and appears to reach its maximum development in gullies where the plants are exposed to heavy surge as distinct from breaking waves. On the open coast it occurs on the shoreward side of rocks with *Durvillea* at the same level on the seaward side.

8. *Gigartina marginifera* consociation (Fig. 4)

Range: M.L.W.S. upwards for 6–9 inches.

*Gigartina marginifera* (d)  
*Stenogramme interrupta* (o)  
*Champia novae-zelandiae* (o)  
*Carpophyllum maschalocarpus* (l)

The consociation occurs below the *Pachy-*



FIG. 3. A view of *Gigartina alveata* consociation with *Modiolus neozelanicus*.

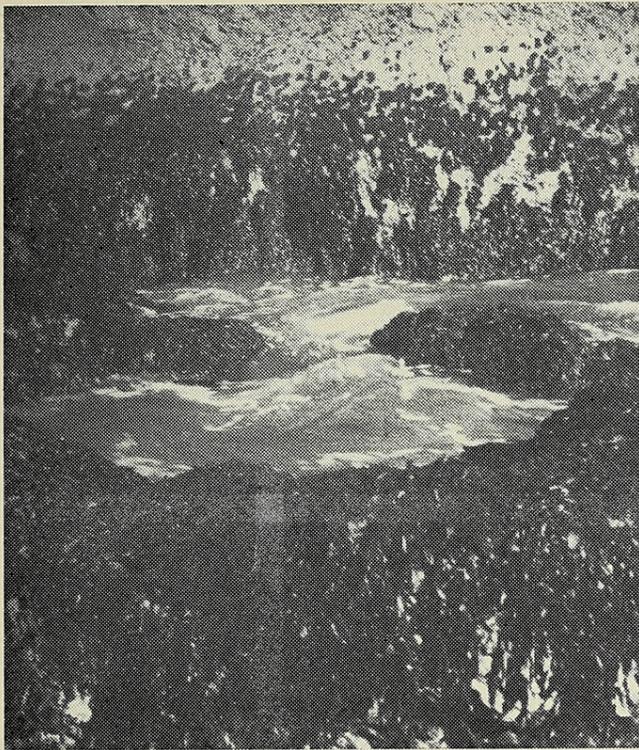


FIG. 4. Algal zonation in a gully to the west of Lion Rock. At the top there is a well-marked zone of *Gigartina alveata*, below a belt of *Pachymenia himantophora* and below that *Gigartina marginifera*.

*menia*, flourishing especially on the flat tops of boulders in strong surge.

#### 9. *Durvillea*-*Mytilus* association

Range: E.(H).L.W.N. to E.L.W.S.

*Durvillea antarctica* (d)

*Mytilus canaliculus* (d)

*Gigartina marginifera* (1)

The association occurs in the form of consociations dominated either by *Durvillea* or by *Mytilus*, because the two species appear to be antagonistic to each other. The upper limit of the *Durvillea* is clearly defined but the lower plants seem to thin out gradually with decreasing power of the surf. The species is essentially surf loving, and in this respect is like *Postelsia* of California. The *Mytilus* consociation is better developed in the more sheltered areas.

#### 10. *Mytilus*-attached algae association

Range: M.L.W.N. to M.L.W.S.

*Mytilus canaliculus* (d)

*Porphyra columbina* (d)

*Ulva rigida* (d)

*Ulva linza* (d)

*Scytothamnus australis* (d)

*Gigartina atropurpurea* (d)

*Gigartina alveata* (o)

*Splachnidium rugosum* (o)

*Laurencia* sp. (o)

*Corallina* sp. (o)

*Centroceras clavulatum* (o)

*Glossophora kunthii* (o)

The association is found on the shallowing floors of small caves, on flat shelves, and on boulders in moderately sheltered areas. The attached algae form colonies on the *Mytilus*, though both *Ulva* and *Porphyra* are capable of colonising the bare rock.

#### 11. *Gigartina* association

Range: M.L.W.N. to M.L.W.S.

*Gigartina atropurpurea* (d)

*Gigartina marginifera* (d)

*Mytilus canaliculus* (o)

*Ulva rigida* (1a)

*Laurencia gracilis* (f)

*Champia novae-zelandiae*

*Corallina* spp. (1)

*Plocamium* spp. (1)

The association occurs in moderately sheltered areas, *G. marginifera* tending to dominate seaward and *G. atropurpurea* shoreward. Shifting sand constantly buries parts of the association temporarily and removes the plants by scour. On re-exposure to air *Ulva* quickly recolonises the area but is replaced later by the dominants.

#### LOCAL COMMUNITIES OF THE MID-LITTORAL

#### 12. *Nemastoma oligarthra* society

Range: M.H.W.N. to M.S.L.

The *Nemastoma* society was noted but once in a large gully. It disappeared in winter.

13. *Splachnidium rugosum* society

Range: M.S.L. to L.W.N.

A seasonal community that disappears in winter.

14. *Cladhymenia oblongifolia*-*Schizymenia* sp. association

Range: M.L.W.S. to E.L.W.S.

The association occupies the sublittoral where there is a shallowing shore and a moderate surf. It is to be found from spring to autumn and it reaches its maximum development in summer. *Champia novae-zelandiae* and *Stenogramme interrupta* are common associates.

15. *Vidalia*-*Melanthalia*-*Pterocladia lucida* association

Range: M.L.W.S. to sublittoral.

An association that occurs in long gullies below the *Pachymenia* belt. *Vidalia colensoi* is the dominant near the mouth but it is replaced by *Melanthalia abscissa* and *Pterocladia* near the head.

## 16. Brackish water community

*Enteromorpha ramulosa*  
*Enteromorpha bulbosa*  
*Enteromorpha flexuosa*  
*Enteromorpha nana*  
*Bangia fusco-purpurea*  
*Calothrix* sp.  
*Rhizoclonium riparium*

The composition of this community varies from place to place.

## 17. Seasonal communities

*Scytosiphon lomentarius* forms an aspect society at L.W.N. during spring but the plants are very small. *Colpomenia sinuosa*, together with *Myriogloia lindaueri*, is also abundant in spring and early summer. *Ilea (Phyllitis) fascia* is another casual occurring around L.W.N. during winter and spring.

Stephenson (1939) in his work on the zonation of South African shores distinguished three principal zones in the inter-

tidal region: (a) *Littorina* zone; (b) balanoid zone; (c) sublittoral fringe.

It seems that this concept can be well applied to the zonation at Piha. *Melaraphe* is closely allied to *Littorina* and the balanoid zone is well represented by the species of *Chamaesipho* and *Elminius*. The sublittoral fringe can be regarded as extending from M.L.W.S. to E.L.W.S. and is occupied by the *Vidalia*-*Melanthalia*-*Pterocladia*, *Cladhymenia*-*Schizymenia*, *Durvillea*-*Mytilus*, and *Gigartina* associations according to the nature and degree of wave action.

## TIDAL MEASUREMENTS AND PROCEDURE

As no tidal data were available for Piha it was necessary to erect a tide pole and to take a series of readings at high and low water. The tide pole was erected near Camel Rock in a sheltered area with its foundation at approximately E.L.W.S.T. Owing to the surf and swell, readings were restricted to calm days. When the Piha scale had been correlated with the data of the Auckland Harbour Board (A.H.B.) charts, the complete records of the Auckland tides could be used to calculate the tidal phenomena at different levels, especially those that appeared to be highly significant in respect of zonation.

The correlation data showed that on an average both high and low water records at Piha on the arbitrary tide pole scale were 0.98 (= 1 foot) foot below the corresponding levels at Auckland (A.H.B. datum). This indicates also that the tidal range at Piha is approximately the same as that at Auckland (10 feet at average spring tides).

The various fundamental tide levels were calculated using the actual Auckland marigrams for 1945. M.H.S.W., M.L.W.S., M.H.W.N., and M.L.W.N. were obtained by averaging the highest and lowest tides, respectively. The means of the equinoctial high and low spring tides gave E.H.W.S.T. and E.L.W.S.T., respectively. Similarly the figures

for E.(L).H.W.N.T. and E.(H).L.W.N.T. are obtained by calculating the means of the extreme neap tides, i.e., those with the smallest range.

	A.H.B. datum (feet)
E.H.W.S.T. . . . .	11.94
M.H.W.S.T. . . . .	11.34
M.H.W. . . . .	10.30
M.H.W.N. . . . .	9.26
E.(L).H.W.N. . . . .	8.79
M.S.L. . . . .	6.22
E.(H).L.W.N. . . . .	3.82
M.L.W.N. . . . .	3.24
M.L.W. . . . .	2.14
M.L.W.S. . . . .	1.03
E.L.W.S. . . . .	0.44

ANALYSIS OF THE TIDAL FACTOR

The tidal factor may be considered under three heads:

1. Hours of submergence and air exposure.
2. Periods of continuous air exposure or submergence.
3. Number of submergences and air exposures.

In most cases it is probable that it is a combination of factors that renders a certain level critical insofar as zonation is concerned. In respect to air exposure, the principal effect is the degree of desiccation (in its widest sense) to which the species are subjected. In the case of submergence the amount of incident light becomes important. Also to be considered is the operation of these factors at different periods in the life of the individual plants.

*Level and percentage of annual air exposure (Fig. 5)*

In most cases where tidal factors limit the distribution of a species, the limitation will be due not so much to a gradual change in conditions but to a more or less sudden variation in some factor. In Fig. 5 such changes

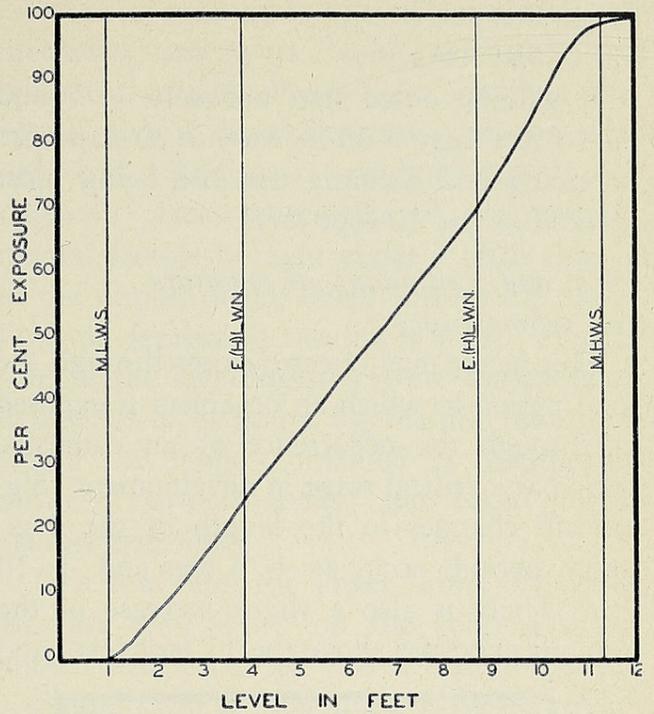


FIG. 5. Graph showing relationship between the level and percentage annual exposure. The major tide levels are also included.

occur at the 1-, 2-, 4-, 10-, and 11-foot levels. A gradual change may, however, be equally important; thus the amount of exposure is trebled between + 2 and + 3 feet. The increase at this level may be far more important than a similar increase at + 9 to 10 feet.

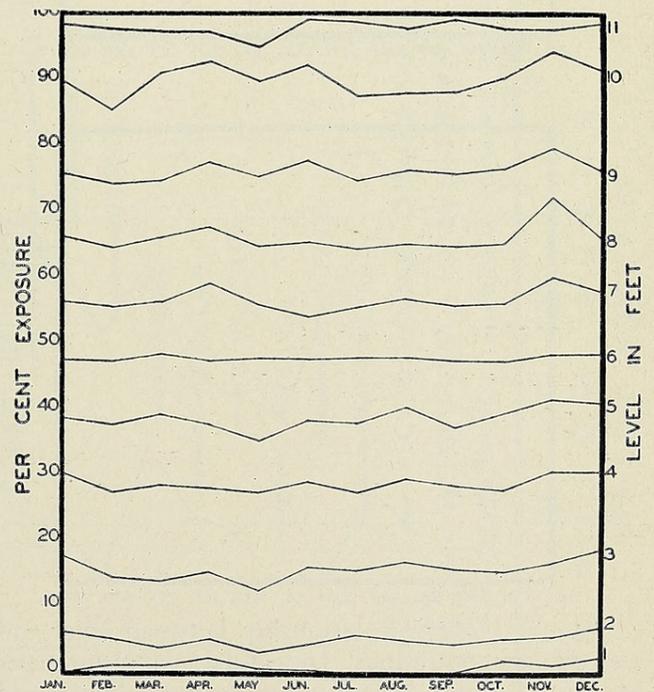


FIG. 6. The relationship between level and percentage monthly exposure.

*Level and percentage of air exposure per month (Fig. 6)*

It will be noted that between + 7 and + 10 feet there is an increase in air exposure in spring and autumn, this rise being most marked at the 10-foot level.

*Level and continuous air exposure and submergence*

This factor may operate either through the total period to which an organism is exposed or through the occurrence of an extensive period at a critical stage in development. Significant changes in the length of the maximum periods occur at + 3 feet and + 10 feet. There is also a slight increase in the total air exposure above the 11-foot level and

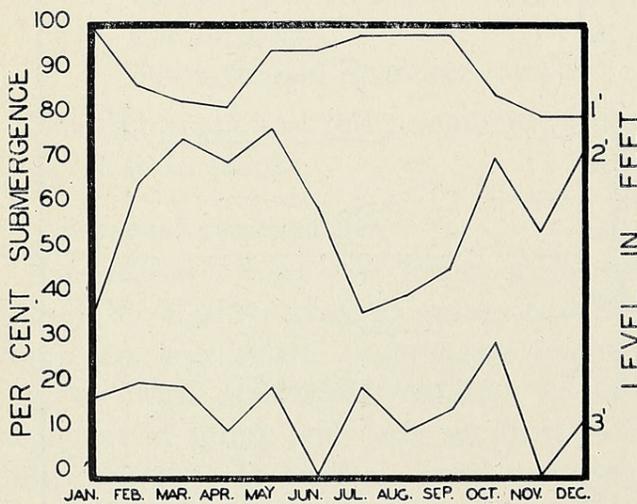
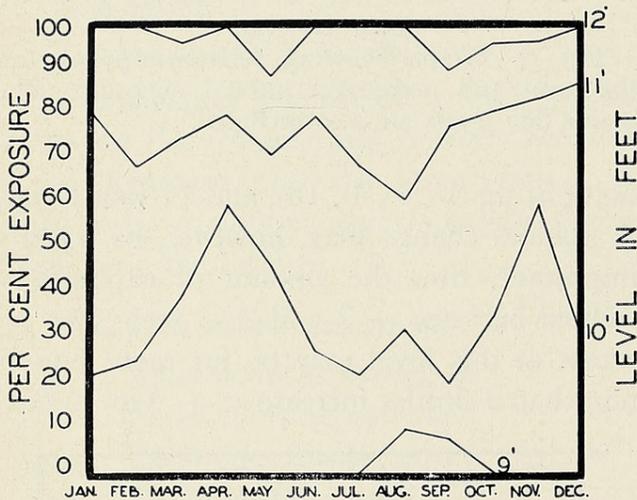


FIG. 7. Upper. Relationship between level and percentage continuous (non-tidal) exposure per month. Lower. Relationship between level and percentage continuous (non-tidal) submergence per month.

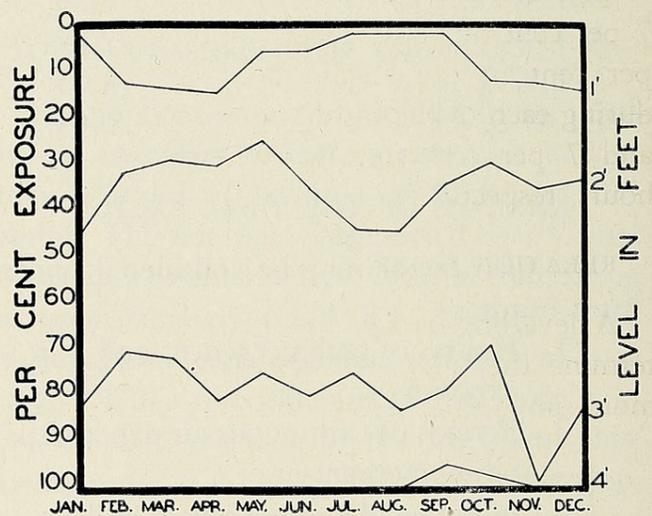
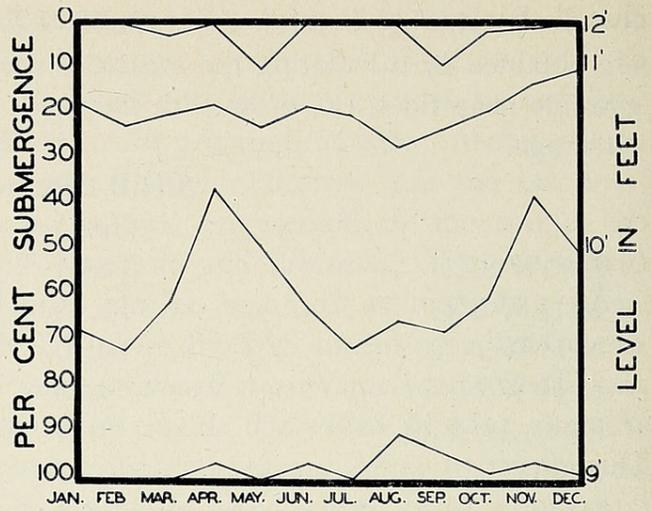


FIG. 8. Upper. Percentage monthly submergence at high tides. Lower. Percentage monthly exposure at low tides.

an increase in total submergence at + 3 feet. *Level and percentage of continuous air exposure and submergence per month (Fig. 7)*

There are significant changes in continuous air exposure at both the 9- and 10- foot levels. The short periods of continuous air exposure occurring in August and September at the 9-foot level may also be important in determining the upper limits of some of the more sensitive species. At the 2-foot level long submergences occur from February to May but toward winter there is a rapid decrease in length of submergence which may be of significance.

*Percentage of monthly submergences and exposures (Fig. 8)*

From the data given here it may be con-

cluded that species requiring a wetting each day will not grow above the 9-foot level. It will be seen too that the percentage of air exposure increases rapidly between + 2 and + 3 feet. Further, there is a significant decrease in the percentage of submergence between 9 and 11 feet.

An additional factor, that of tidal flow, which has been studied by Elmhirst (1933) and David (ms.), may exert a certain effect around E.(L).H.W.N. and E.(H).L.W.N. This effect is related to regular variations in rate of tidal flow during ebb and flood. Thus from either high or low water the tide runs 7 per cent of its height in the first hour, 18 per cent in the second hour, 25 per cent during each of the third and fourth hours, 18 and 7 per cent during the fifth and sixth hours, respectively.

RELATION OF SPECIES TO TIDE LEVELS

A levelling survey was carried out to determine the upper and lower limits of the more important algal and animal species.

Only the optimum range of a species was measured, stragglers being excluded, and wherever possible levels were obtained that would give a direct expression of the tidal influence. Additional readings were also taken in places where one of the environmental factors brought about a local change in the normal level, either raising the upper limit or depressing the lower limit. The results of the levelling survey are incorporated in a series of diagrams for the different areas where the range (obtained by taking the mean of several levels) has been plotted against tide level.

In a few cases the lower limits of species growing well down on the shore are not known with certainty; this is because the sea is seldom calm at Piha and it is therefore difficult to obtain levels at low water. In these cases observation has had to supplement actual readings. Thus the levels of species growing in the vicinity of the tide pole were compiled from observations made while watching the tide pole. One may also say that up-

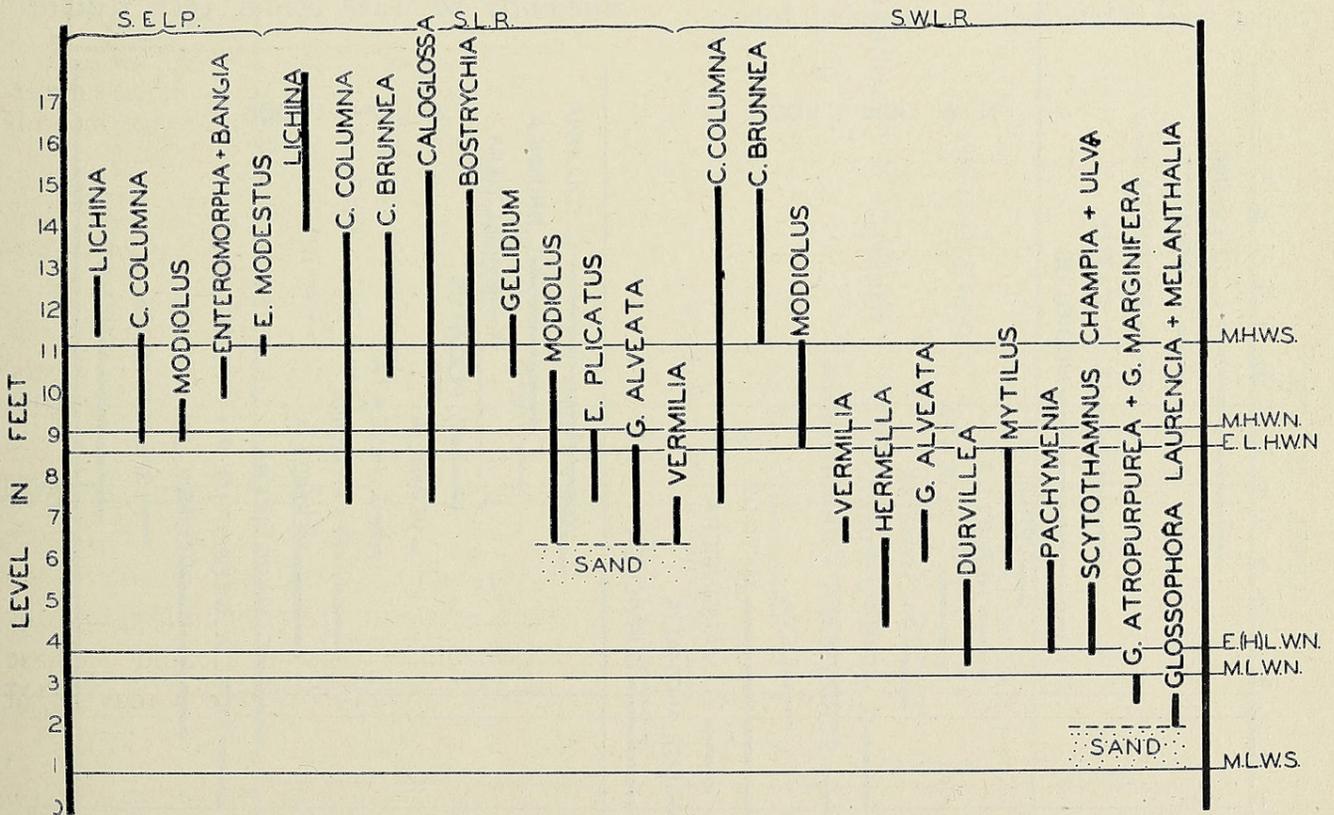


FIG. 9. Vertical distribution of the species southeast of Lion Rock (S.E.L.R.), south of Lion Rock (S.L.R.), southwest of Lion Rock (S.W.L.R.).

per limits of higher species are fairly definite but the lower limits are less pronounced unless there is severe competition.

There is also the problem of thallus length. Thus the long thalli of *Pachymenia* hang down well below the holdfast. Since, however, the sporeling phase is probably the most critical period in the life history of an alga, it is the levels delimited by the holdfasts which should be significant.

If the diagrams (Figs. 9-12) for the various areas are examined it will be seen that two major points are emphasized:

1. The zonation changes with degree and manner of wave action.
2. With increasing exposure to wave action the levels of some species are raised, those higher on the shore being more affected than those lower down.<sup>5</sup> At high levels the upper limit of a species is often elevated more than the lower. Thus in Figure 13 the lower

<sup>5</sup>The height to which breaking waves raise the uppermost tide mark above its predicted or recorded level is referred to as the splash zone.

limit of *Lichina* is raised by some 4 feet. In areas with maximum wave action *Lichina* and *Melaraphe* may rise at least 40 feet higher than normal.

In other species, e.g., *Chamaesipho* spp., the lower limit may remain unaffected whereas the upper limit is raised many feet by wave exposure. By contrast, *Vermilia* and *Hermella*, found in more sheltered areas, are apparently independent of wave action.

In the diagrams it will be noted that Lion Rock provides a series of habitats characterized by increasing exposure to wave action and depth of water. The diagrams show that in the different areas most species retain the same relative positions wherever they occur. *Vermilia* and *Hermella* are exceptions because they retain their positions relative to the absolute levels.

Finally, using these diagrams as a basis, an attempt was made to summarize the levelling data after making an allowance for the influence of wave action. The result is depicted in Figure 14. Since each species is affected differently by wave action, each requires a

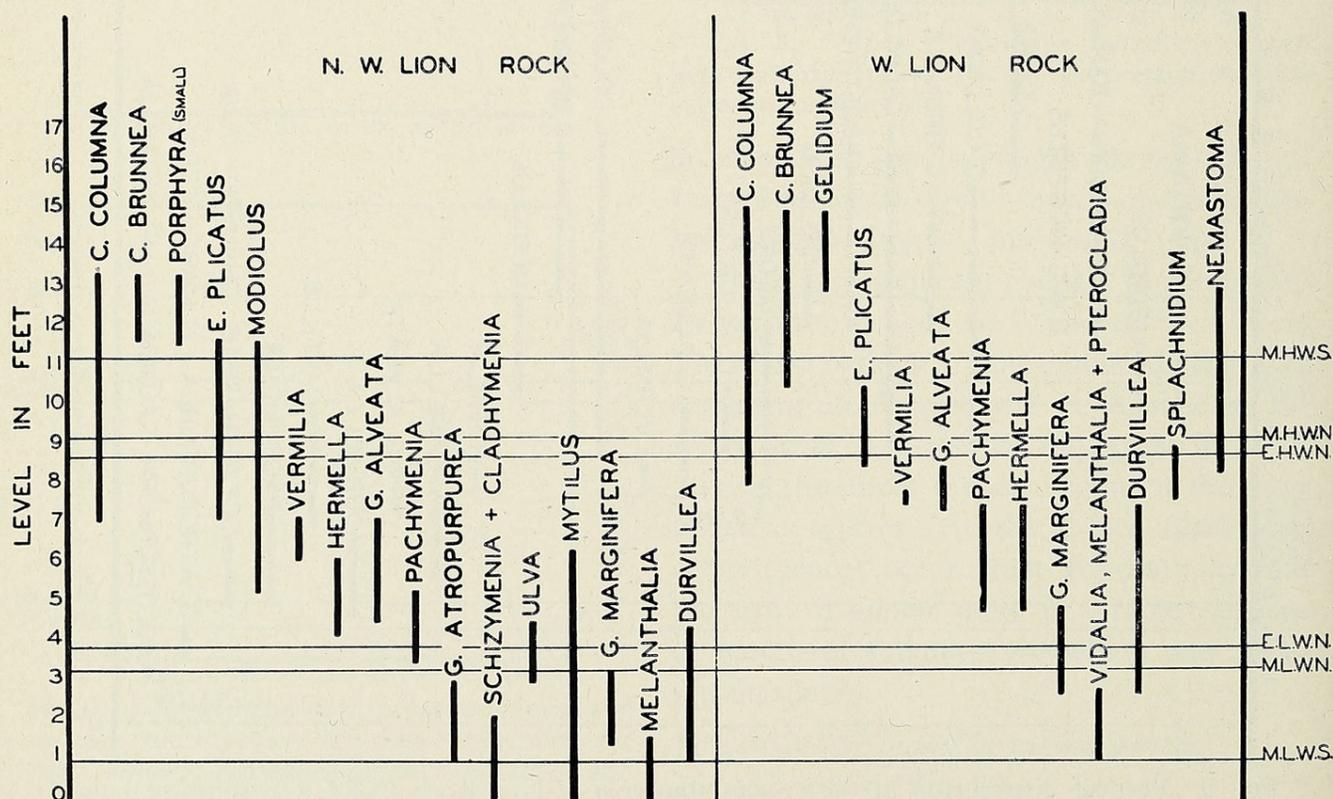


FIG. 10. Vertical distribution of species on the northwest and west of Lion Rock.

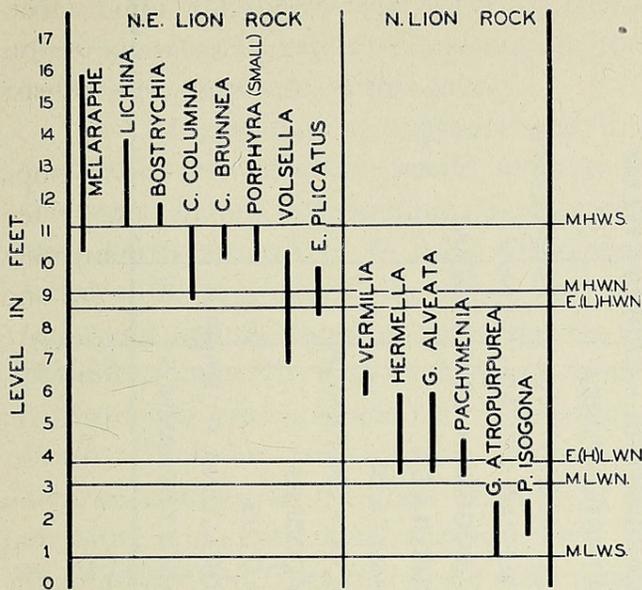


FIG. 11. Vertical distribution of species of the northeast and north of Lion Rock.

different adjustment. The chief guide used in making this adjustment was the level of the species in the most sheltered habitats. It

must, however, be emphasised that owing to the great difficulties involved this attempt at allowing for wave action can only be a first approximation. From a study of this diagram it may be concluded that the most marked critical levels (i.e., levels where a number of species reach their upper or lower limit) are as follows:

	Upper limits	Lower limits	Total
11 feet—M.H.W.S.	6	3	9
Between 8.5 and 9.5 feet	3	3	6
4 feet—E.(H).L.W.N.	5	2	7
3 feet—M.L.W.N.	5	1	6
2.3 feet	4	3	7
1.4 feet—M.L.W.S.	5	4	9

It will be seen that there are nine upper or lower limits between 11 feet and M.H.W.S. so that this, together with 1.4 feet, is one of the more distinctive levels. Reference to Fig-

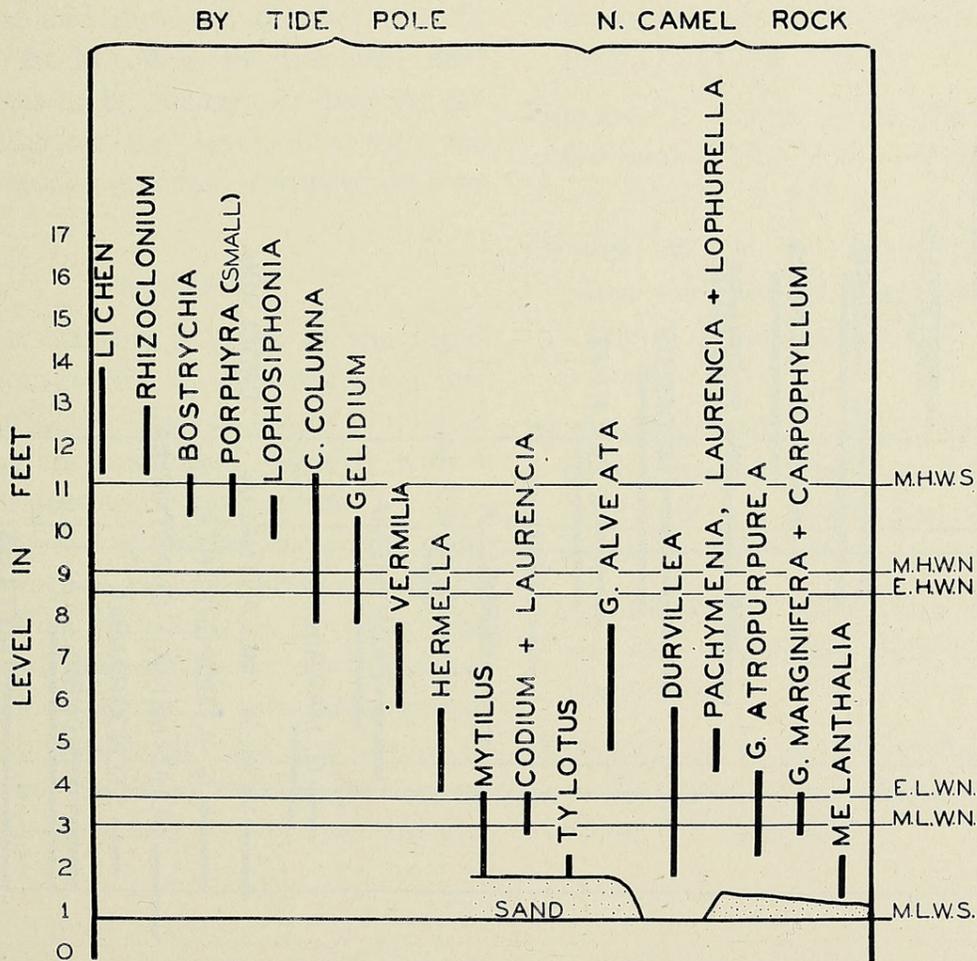


FIG. 12. Vertical distribution of species by the tide pole and on the north of Camel Rock.

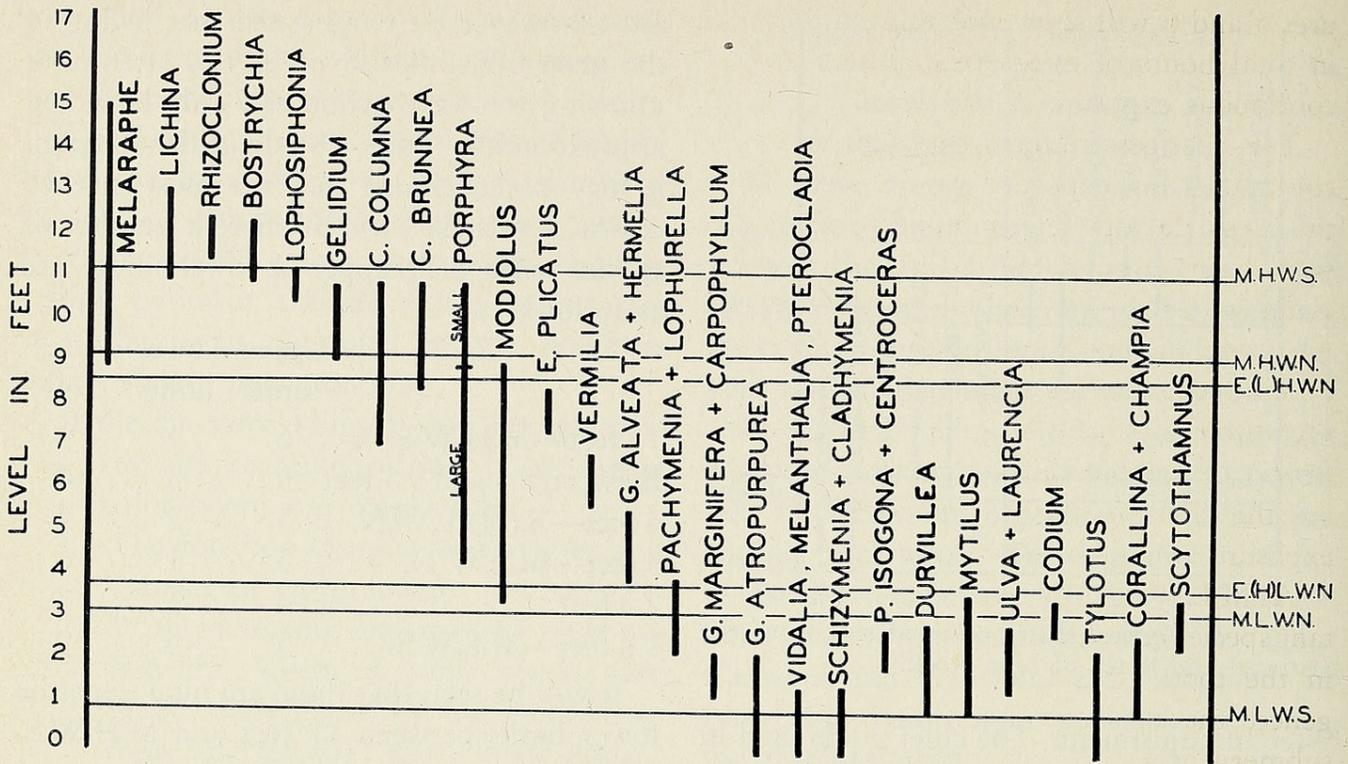


FIG. 13. Generalized vertical range of upper species at Piha after allowance has been made for the effect of wave action.

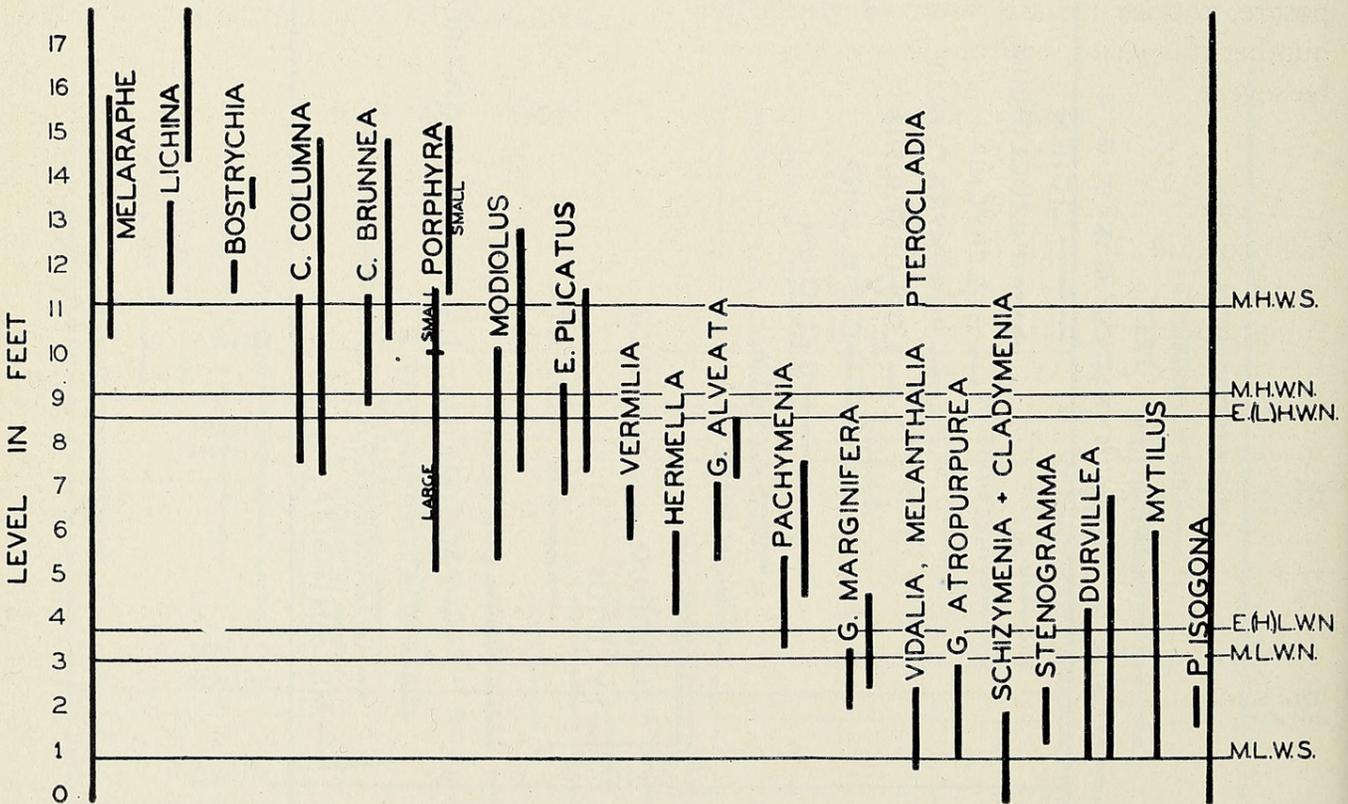


FIG. 14. Vertical distribution of dominant species at Piha generalized in positions of moderate shelter and exposure.



Beveridge, W. A. and Chapman, V. J. 1950. "The Zonation of Marine Algae at Piha, New Zealand, in Relation to the Tidal Factor (Studies in Inter-tidal Zonation 2)." *Pacific science* 4(3), 188–201.

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